Do Monkeys and Chimpanzees Climb the Same Way? A Kinematic Analysis of the Upper Limb During Vertical Climbing in a Wild Monkey (*Cercocebus atys*) and Ape (*Pan troglodytes*)

Mary Joy
Department: Anthropology
Faculty Advisor: Jeremy M. DeSilva
Graduate Advisor: Luke D. Fannin

Abstract

Vertical climbing has been posited as the primary driver of upper limb (elbow and shoulder) evolution in apes. However, a quantitative kinematic comparison of the upper limb has never been performed on vertical-climbing primate species in the wild. Here, I provide these data and put the vertical climbing hypothesis to the test by comparing the maximal excursions of the elbow and shoulder during vertical climbing bouts of wild *Cercocebus atys* in the Taï forest, Ivory Coast and *Pan troglodytes schweinfurthii* (Kibale Forest, Uganda). There was no statistically significant difference in joint excursion angles at the elbow or the shoulder between apes vertically climbing in an upward direction and monkeys climbing in either an upward or downward direction. However, maximal excursions differed significantly on downward climbs between the two species and between downward and upward climbs in chimpanzees. These results indicate that previous work focusing on how primates get into a tree have overlooked the potentially important challenges facing a large ape descending to the ground. Downclimbing may have been a primary driver of increased flexibility in the upper limb. The vertical climbing hypothesis should be revisited to include downclimbing strategies. These data are consistent with the important role of suspension in driving upper limb evolution in apes.

Keywords: cercopithecoid, ape, upper limb, climbing

INTRODUCTION

Background

Bones tell the story of a vertebrate's life. Markings of pressure, bony lipping around the perimeter of a joint, the occasional remodeling, are the skeleton's memories of happenings in the life of an individual. These are unique, individual -- the stamp of a life lived.

This same story plays out, on an evolutionary scale, in the skeletal anatomy of species. Many bony features characteristic of the anatomy of a particular species reflect the typical movements that that species takes, or needs to take, during life. For example, species that walk bipedally need robust weight-bearing limb bones, with features at the joint that allow them to move in that way. Evolutionary studies provide a roadmap for tracing the formation of these features across species and through time, to give scientists an understanding of when these features formed and how they evolved among different species. Of particular note to anthropologists are how these bony features change throughout human history, both early and modern.

But *why* did these features evolve? There are many branches of anatomy and evolutionary biology that attempt to explain where traits originated and why they appear the way they do. One such concept is functional morphology.

Functional Morphology

Functional morphology is a science predicated on the notion that all organisms have evolved physiological attributes adapted for specific functions—a concept also referred to as symmorphosis (Weibel et al., 1991). In particular, functional morphology holds that musculoskeletal form is suited to its function in the organism, and that given one, the other can be reasonably inferred and understood. This is a foundational idea that forms the basis of many fossil reconstructions, including in primate paleontology. Acceptance of form-to-function explanations allows biological anthropologists to map skeletal differences in related species onto changes in their environments, giving them a basis by which to trace the selective regimes behind evolutionary change. The validation of form-to-function hypotheses has implications for human evolution as well, particularly in understanding why humans possess or lack certain skeletal traits present in our ancestors and extinct relatives.

Despite the satisfying nature of these explanations, however, it is important not to assume that any particular form-to-function hypothesis is automatically correct simply because it provides an elegant explanation. Any such hypothesis should be tested with intraspecific data from living populations or interspecific data across different species. This need for multiple sources of information to support or refute such a hypothesis requires biological anthropologists to study more than just the anatomy of the species. Form-to-function hypotheses based purely on osteology can be misleading, resulting in conclusions about evolution that do not correctly correspond to the behaviors that supposedly caused such osteological changes. This is why it is essential to use the behavior of living organisms in their wild habitats along with osteology of these species to test and justify form-to-function hypotheses.

One such example is the morphology of the upper limb in monkeys and apes. The differences between the skeletal anatomy of arboreal cercopithecoids (tree-dwelling monkeys from Africa and Asia) and hominoids (apes) are extensive; in particular, the anatomies of the arm and shoulder exhibit well-documented differences in the bony constitution of the joints (Arias-Martorell, 2019; Hunt, 2016; Isler, 2005; Fleagle et al., 1981). Primatologists and functional morphologists are particularly interested in why this is the case -- in particular, what behavioral differences, if any, drove these physical changes. One reason for this interest is the proposed form-function relationship between arboreal activity and upper limb anatomy, a relationship with implications for the role of tree climbing in human evolution (Venkataraman et al., 2013).

Skeletal Anatomy

Arboreal cercopithecoids have evolved upper limbs -- specifically, arms and shoulders -- with less mobility than those of apes. The main differences in anatomical features are concentrated at the two joints, the *glenohumeral* -- articulation of the scapula and head of the humerus -- and *ulnohumeral* -- articulation of the distal humerus and the trochlear process of the ulna. Hunt (2016) notes that in African monkeys, the bony composition of the shoulder is “crowded”; the humeral tubercles compress the space available for the glenoid, severely limiting not only shoulder extension, but also abduction (movement away from the midline, along the coronal plane). The narrow glenoid fossa permits only limited articulation of the humerus and the scapula, further lowering mobility (Hunt, 2016). This crowding prevents free rotational motion of the shoulder and allows only limited anterior-posterior movement (Fleagle, 1981), creating a compact and stable articulation that prevents collapse of the shoulder during quadrupedal motion. Most notably, there is an extreme craniocaudal curvature of the glenoid fossa, bookended by a large lip on the inferior surface of the fossa and a projection on the superior surface. The superior projection is present to different degrees of prominence in different species of cercopithecoids, but is present nonetheless, and the inferior lip is always present. These two features, particularly the glenoid lip, severely limit the ability of the humeral head to rotate and consequently limit the superior extension of the cercopithecoid shoulder joint.

In arboreal and terrestrial cercopithecoids, the elbow joint is similarly limited in its mobility compared to that of apes. The olecranon process of cercopithecoid monkeys is robust and elongated, extending along the ulnar plane past the olecranon fossa and creating an obstruction that potentially prevents it from fully inserting into the olecranon fossa. The shallow olecranon fossa further limits the space available for extension (Fleagle, 1981).

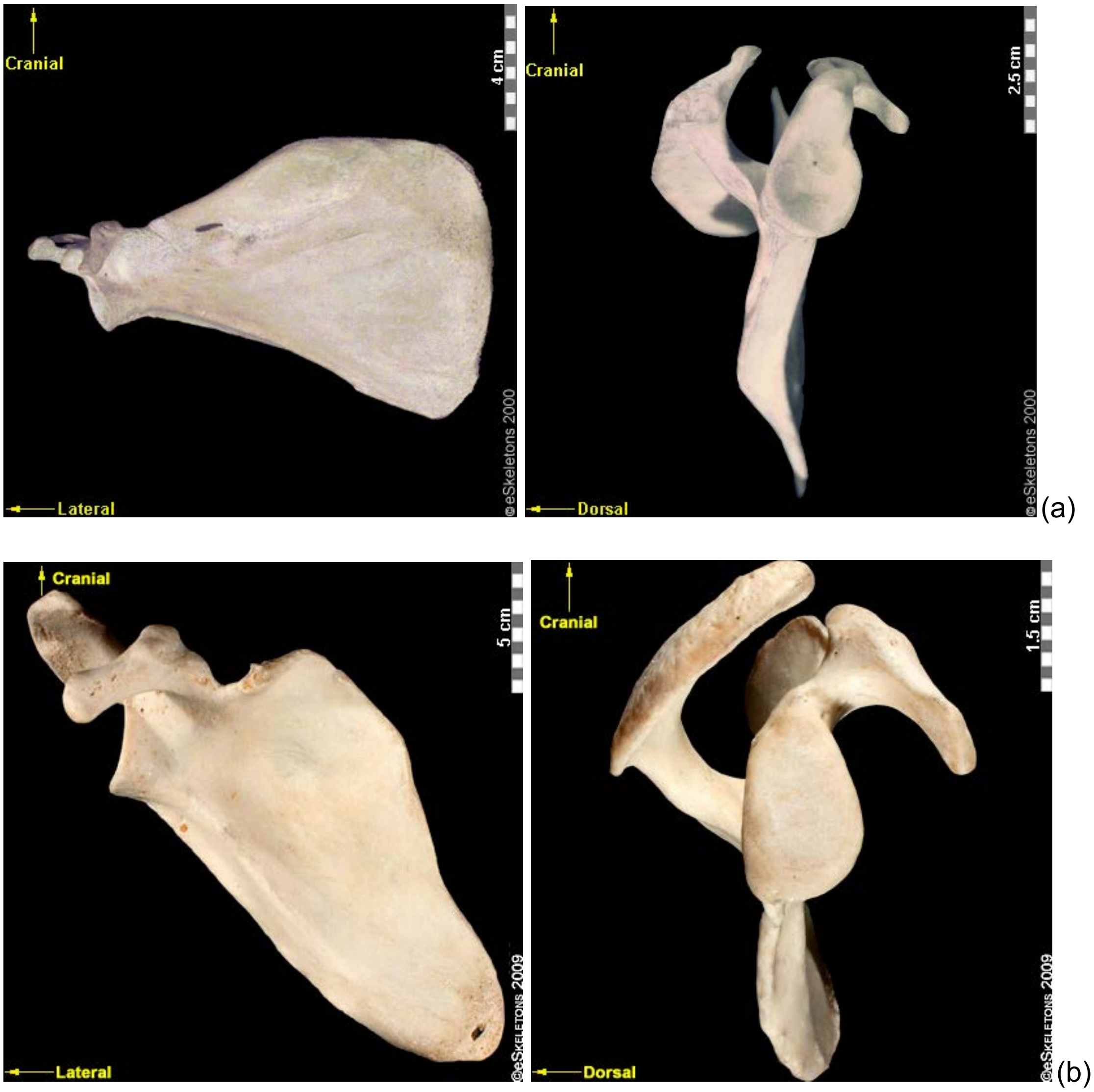


Figure 1.1: **a) Scapula of an adult male baboon in ventral and lateral view -- note the significant lipping on the inferior and superior surfaces of the glenoid fossa, the strong craniocaudal curvature, and narrowing of the superior glenoid. b) Scapula of an adult male chimpanzee in ventral and lateral view -- note the significantly flatter and wider glenoid fossa, with no evidence of lipping.** Images reproduced with permission from eSkeletons.org.

In contrast, brachial anatomy in the apes promotes more complex rotational and extensional motion (Hunt et al., 1996). As opposed to cercopithecoids, apes' broader thoraxes create greater distance between the glenohumeral joint and the neck (Hunt, 1996), resulting in less joint crowding. In addition, within the joint itself, the glenoid fossa is wider (MacLatchy et al., 2000) and tilted superiorly, allowing not only for complex rotational motion but also complete shoulder extension and abduction (Hunt, 2016). Importantly, the lipping found in cercopithecoids on the inferior surface of the glenoid is completely absent in hominoids, allowing for full upward extension of the shoulder joint.

The ape elbow possesses a reduced olecranon process of the ulna and a deeper olecranon fossa of the humerus. Since the olecranon process is comparatively much smaller in apes, full insertion of the process into the fossa is possible, making apes capable of increased excursion of this joint and consequently increased extension of the forearm.

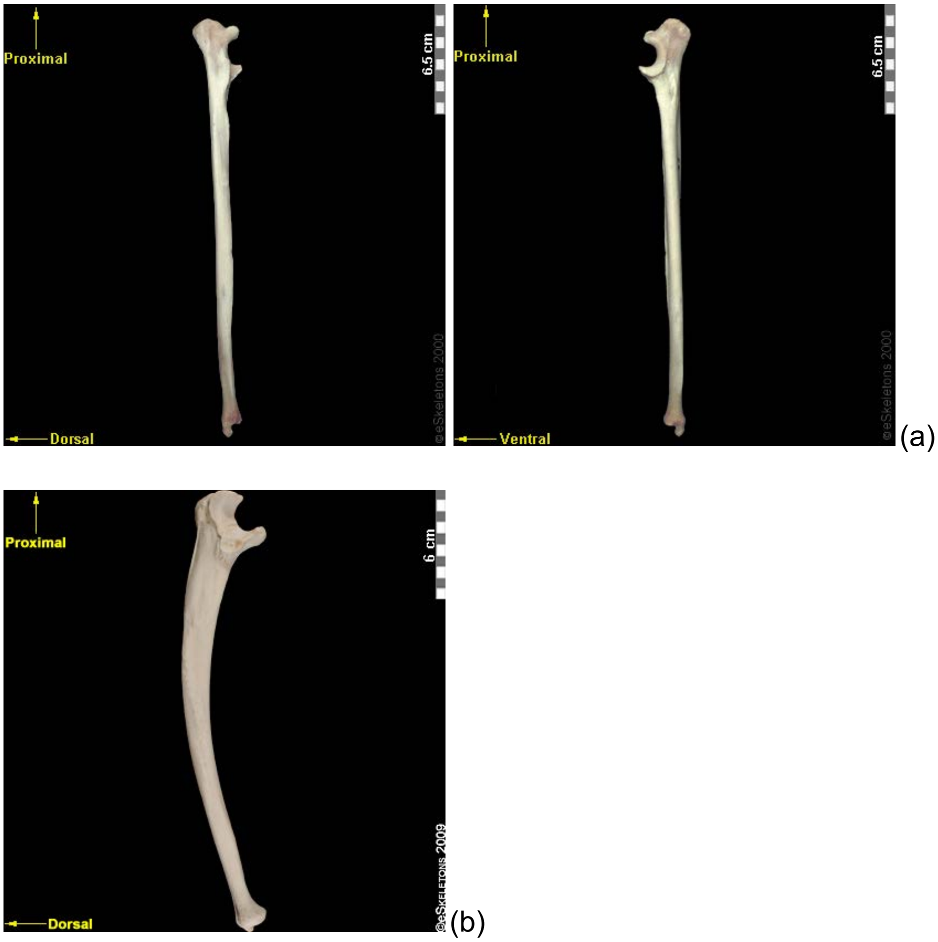


Figure 1.2: **a) Ulna of an adult male baboon in lateral and medial view -- note the robust olecranon process that extends beyond the trochlear notch along the plane of the ulna. b) Chimpanzee ulna in lateral view -- note the reduced olecranon process in comparison to that of the cercopithecoid above.** Images reproduced with permission from eSkeletons.org.

Overall, cercopithecoids have brachial anatomy that reflects a limited range of motion in comparison to apes. The specific presence of the aforementioned bony features -- the glenoid lip and the larger olecranon process -- in cercopithecoids is telling: it allows them to move in the trees while simultaneously preventing collapse of the anterior limb during pronograde, quadrupedal motion. Put simply, the osteology of the upper limb joints in arboreal cercopithecoids allows them to use two methods of locomotion -- including efficient quadrupedal travel -- but the trade-off of these features has been argued to be a significantly smaller range of motion in vertical climbing. It is important to note, additionally, that very few cercopithecoids actually do vertically climb -- mangabeys and mandrills being notable exceptions -- and a limited range of motion in vertical climbing may indicate a comparatively greater adaptation to terrestrial locomotion, the more-used form of movement.

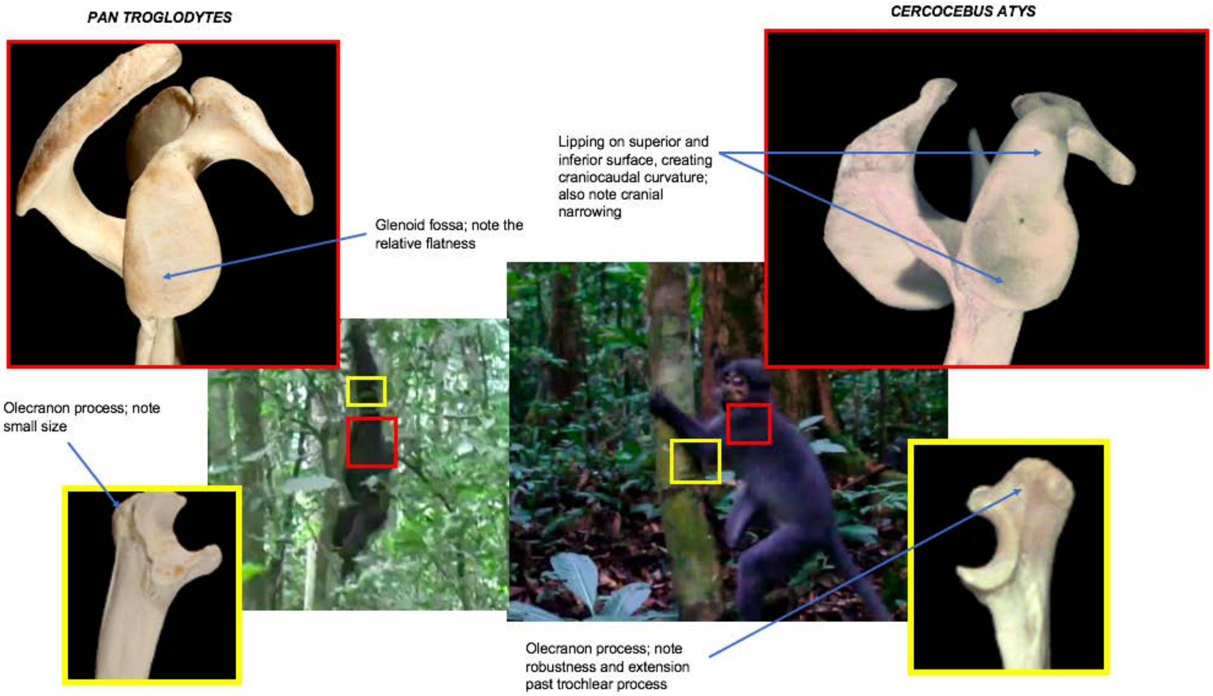


Figure 1.3: **Comparison of the ulnohumeral and glenohumeral bony features in *Pan troglodytes* (left), an ape, and *Cercocebus atys* (right), an arboreal cercopithecoid.** Images reproduced with permission from eSkeletons.org.

The absence of these traits in the apes, and the associated increase in range of motion, raises the question of whether this absence is derived or ancestral -- a concept called “trait polarity.” In other words, did modern apes evolve their limbs, lacking the above-described skeletal features, from an ancestor with monkey-like limbs -- possessing these features -- or vice versa?

Fossil evidence suggests that *Proconsul* and other early Miocene hominoids, with the exception of *Morotopithecus*, also possessed shoulders with relatively limited range of motion (Walker, 1997). Since modern apes, as previously discussed, have a full range of motion in the shoulder, this suggests an evolutionary gradient, where the glenoid lipping and curvature slowly reduced and eventually completely disappeared. The same is posited for the elbow (Ward, 1998). This interpretation of the data is supported by behavior -- while apes do move quadrupedally, the primary use of the full weight-bearing capacity of their flexible upper limbs is in arboreal contexts. The evolution of these features in apes seems to indicate that the cercopithecoid shoulder is ancestral and the ape shoulder is derived. Modern humans have retained an ape-like shoulder in essence, further lending credence to the notion that the absence of cercopithecoid-like features is an adaptation to some new behavior, increased frequency of an existing behavior, or environmental pressure.

Overall, the presence of joint features that limit the range of motion in arboreal cercopithecoids, and their absence in apes, is established. The question that remains is what specifically necessitated their modification over evolutionary time.

Hypotheses in the Field

So why do apes and tree-dwelling monkeys differ in their shoulder and elbow morphology? Two form-to-function hypotheses have been proposed to explain the differences in arm and shoulder anatomy in monkeys and apes:

1. The vertical climbing hypothesis posits that apes' brachial skeletal anatomy evolved to suit their distinct specific vertical climbing style, and thus apes have evolved anatomies suitable for these distinct styles of climbing (Fleagle et al, 1981; Gebo, 1996; DeSilva, 2009).

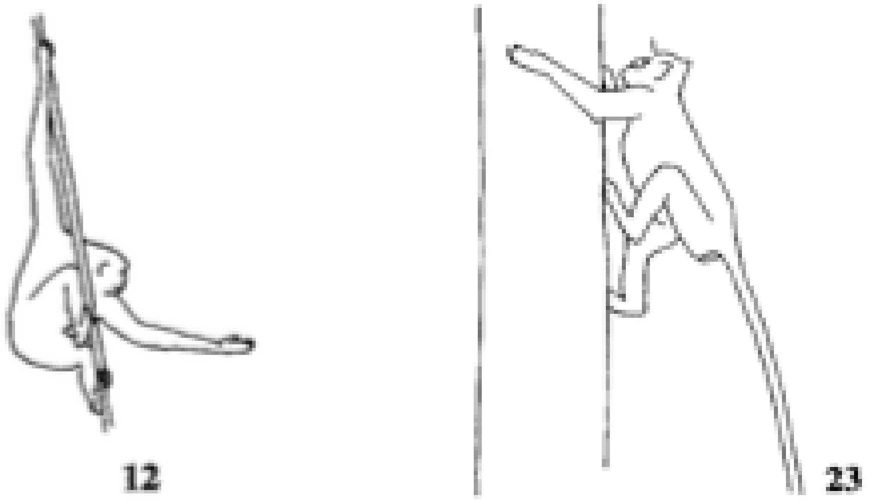


Figure 1.4**: Hypothetical side-by-side comparison of the above-noted two modes of vertical climbing.** Note the full extension of the glenohumeral and ulnohumeral joints on the left, and the very limited extension on the right. Reproduced from Hunt et al. (1996), redrawn from Fleagle (1976) Figure 10 and Ripley (1967) Figure 11.

2. The suspensory hypothesis posits that differences in arm-hanging (suspension), not vertical climbing per se, are sufficient to explain greater mobility in the arm and shoulder in apes (Hunt, 1992; Hunt, 2016). If this were the case, we would expect to see apes climbing with limited excursion of the elbow and shoulder -- kinematically equivalent to vertically climbing cercopithecoids -- with full excursion relatively exclusive to suspensory behaviors.

As previously mentioned, form-to-function hypotheses cannot be accepted without data. In the following study, I tested the vertical climbing hypothesis and the null hypothesis that monkeys and apes use their shoulders and elbows to climb trees in the same kinematic manner.

Climbing

Vertical climbing strategies in many species have been observed (McGraw, 1996; McGraw, 1998; Doran, 1993; Doran, 1994; Hunt, 1992). But why would apes need distinct skeletal adaptations to climb? The advantages of an increased range of motion are numerous. In terms of simple vertical movement, the ability to reach better hand and foot holds may lend itself to safer climbing. Additionally, it may allow for increased mobility in the trees; more flexible arms allows for shifts between substrates with relatively little energy expenditure, which is important for large animals for whom energy from food is a premium. Finally, a flexible shoulder and elbow may allow apes to climb with their bodies closer to the substrate. This decreases the distance between the center of mass and the substrate, lowering rotational torque and thus decreasing the likelihood of falls (DeSilva, 2009). Thus, a flexible shoulder may biomechanically facilitate efficient vertical climbing for apes.

An equally important, if not more important, driver is differential risk. Isler (2005) argues that lighter animals, like gibbons, have less risk associated with climbing and consequently have skeletal anatomy adapted for speedy climbing with more variable limb motion. On the other hand, heavier primates, like lowland gorillas, incur much higher risks when they climb, and have adapted their anatomy to vertically climb more slowly and deliberately, with greater joint excursion. Pontzer and Wrangham (2004) lend tentative support to this idea with energetic models demonstrating that chimpanzees spend less than 2% of their daily energy expenditure on climbing. They conclude from these data that chimpanzees are optimized to climb because of the danger climbing presents—falls can be fatal (Jurmain, 1997; Goodall, 1986).

Consequently, Pontzer and Wrangham (2004) postulate that morphological optimization for climbing might be a protective measure.

How so? Because of apes' size and weight, morbidity and mortality associated with falls are much higher than for smaller primates. This follows from the square-cube law, a relationship that states that when an object undergoes a change in size, its surface area increases as the square of the associated change, but the volume increases as the cube of that change (Haldane, 1927). Extrapolating this relationship to animal allometry, this means that a larger animal will have a much lower surface area-to-volume ratio than a smaller animal, making it less susceptible to air drag that would slow its downward acceleration during falls. Factoring in the mass increase -- increased bone and muscle mass, larger organs, etc -- associated with this exponential increase in volume and understanding that power = force/time, the contact between a larger animal and the ground generates significantly more power than this same collision in a smaller animal. Additionally, because muscular and bone strength is a function of cross-sectional area, which is a squared function, a larger animal's muscles and bones are weaker relative to its weight than are a small animal's, giving it less internal strength and structural integrity to resist the larger force of contact. These factors lead to a much higher likelihood of bone breaks, organ damage, and rupture of blood vessels in falls involving larger animals, increasing the likelihood of mortality and morbidity. Even if a larger animal survives such a fall, the morbidity resulting from the near-inevitable internal injuries is unlikely to permit successful hunting, food gathering, mating, or even locomotive behavior, and this inability to engage in normal survival strategies will most likely decrease fitness.

Chimpanzees are large primates, several times the size of the average arboreal cercopithecoid (Smith and Jungers, 1997). Thus, there is high selection pressure to avoid falls from the canopy during arboreal motion (Pontzer and Wrangham, 2004). Additionally, the necessity of vertical climbing as a locomotor strategy to reach food in many apes, including chimpanzees, might require the evolution of protective measures while so doing. Per Pontzer and Wrangham (2004), the optimization of climbing in chimpanzees lends strong support to the idea that vertical climbing drove the evolution of some aspects of chimpanzee skeletal anatomy.

On the other hand, the risk of morbidity or mortality from falls in the canopy for smaller arboreal quadrupeds like mangabeys is much lower. However, there are certainly other selective pressures to consider. One of these, per Pontzer and Wrangham (2004), is predation. In forests with high predation, mangabeys and other small cercopithecoids that have large, dense populations and are relatively small-bodied are especially vulnerable to attack (Zuberbühler and Jenny, 2002). Given that cercopithecoids tend to be small and predators like leopards are quick on the ground, this may have necessitated the ability to escape quickly to the trees in closed forests. While a quantitative association between decreased limb extension and increased speed during vertical climbing has not been shown, there is some evidence that decreased angles of extension in primates correlate with increased speed during quadrupedal walking (Isler, 2005). Thus, speed of movement is at least qualitatively associated with decreased angular extension, particularly of the elbow (Isler, 2005). While quantitative data is necessary to make any definitive conclusions, if arboreal cercopithecoids do indeed demonstrate decreased angular extension of the elbow during vertical climbing, it could be in response to an increased need for speed in the trees.

Behavioral Evolutionary Ties: What About Humans?

Functional morphology helps us understand how anatomy evolved to suit function(s) through evolutionary time. While tying chimpanzee and monkey behavior to their anatomy is an important pursuit in its own right, another reason for doing so is to give scientists a window into understanding hominin functional anatomy.

The degree to which fossil hominins similarly engaged in arboreal behaviors – including vertical climbing – is contested (Stern and Susman, 1983; Latimer and Lovejoy, 1989; DeSilva et al., 2009; Venkataraman et al., 2013; Wallace et al., 2020). Specifically, spirited debates have consumed paleoanthropology regarding vertical climbing in *Australopithecus afarensis*, the relevance of the role of arboreality in early hominins, and the traits that may have facilitated this arboreality. Did early hominins also vertically climb, and, if so, how frequently did they do so? The answer to these questions can be found by understanding the anatomy of known climbing primate relatives -- namely, chimpanzees -- and mapping it onto behavior.

Some scientists have argued that the flexible shoulders of early hominins evolved for facilitating vertical climbing from the ground, and then was put to different use in hominins that climbed less frequently but retained in hominins that did, like *A. sediba* (Churchill et al., 2018). Others posit that flexible shoulders allowed for the ability to reach terminal branch foods without drastically increasing the torque on the branch and breaking it, resulting in a catastrophic fall (Grand, 1972). However, we currently lack data testing how the joint kinematics of the behaviors associated with flexible shoulders relate to similar behaviors in modern apes. If scientists can understand how changes in terrestrial locomotion, upward movement, and climbing in our primate ancestors translated to specific skeletal anatomies, they can begin to understand the paleobiology of our ancestors and what past behaviors have influenced human anatomy as we know it today.

How does this relate to the upper limb? The even wider thorax, increased space in the shoulder complex, and nearly horizontal rather than vertical acromion in modern humans reflect changes from general ape anatomy, changes that potentially reflect a decreased frequency of arboreal movement in daily life or even competing functional demands on the shoulder, like throwing (Roach et al., 2013; Roach and Richmond, 2015). Understanding the functional reasons for chimpanzee elbow and shoulder anatomy will provide important clues for reconstructing behavior in early hominins like *Australopithecus afarensis*. These clues will further illuminate when the transition between primarily arboreal movement and bipedalism occurred in hominins, and what environmental factors (safety, food availability, etc) required this transition.

Current Work

Of the literature that does exist on vertical climbing kinematics in monkeys and apes, much of it looks at contrived climbing scenarios in captivity. This distinction is important. As Cartmill (1985) notes, substrate diameter as well as composition potentially require different climbing behaviors. For example, climbing a thin liana (or, in the contrived scenarios like Isler's 2005 study, a rope) would require different finger exertion, and consequently might transfer different forces to the wrist and the elbow, than would climbing a wider tree (Lewis, 1969). Substrate differences also extend to composition: a softer or less stable substrate, per Cartmill (1985), places variable loading forces on brachial joints that differ from those incurred while climbing harder, less yielding substrates. Currently, the most provocative piece about vertical climbing's effect on upper limb mobility is Hunt's 1991 study comparing previous studies on chimpanzee and bonobo brachiation. Hunt (1991) posited that vertical climbing behaviors in apes and cercopithecoids are too kinematically similar to be the primary drivers of these observed morphological differences; per Hunt (1991), brachiation behaviors (i.e. arm-hanging) were more likely to be the cause, with vertical climbing as a relatively small contributor.

However, to fully answer the question of what drove the shape differences in the elbow and shoulder in monkeys and apes, it is essential to examine representatives of these primate families in the wild, on the substrates that they typically climb. There are three components to such a test: 1.) a direct comparison between cercopithecoids and hominoids; 2.) this comparison taking place in the wild; and 3.) this comparison looking at the upper limb. All of the existing literature, even the kinematic studies, performs only qualitative comparisons or fails to address at least one of these components. Isler's 2005 comparison of hominoids and atelines was done in captivity, using a rope as a substrate. While giving us a view into climbing patterns, this is not enough to help the scientific community understand the evolutionary pressure on the bones of the upper limb. Hirasaki et al. (1993), while having performed an insightful kinematic study, did so on monkeys and atelines in captivity. DeSilva (2009) collected kinematic data on chimpanzees in the wild, but there were limited cercopithecoid comparisons and the focus was entirely on the ankle joint.

It is important to note, as mentioned before, that few cercopithecoids have been observed to vertically climb extensively in the wild; this presented an obstacle to such a test. *Cercocebus atys*, the sooty mangabey, is a notable exception. Their division of locomotion -- roughly 20% arboreal and 80% terrestrial -- makes them an appropriate comparative cercopithecoid to chimpanzees (McGraw, 1998); additionally, they do most of this climbing in closed forests like chimpanzees do (McGraw, 1998; Fleagle et al., 1981; Fleagle, 2013). In order to provide an accurate comparison, it was essential to choose an arboreal cercopithecoid that employed vertical climbing as a locomotive strategy with at least some frequency.

Overall, the existing literature acknowledges the large differences between cercopithecoid and chimpanzee brachial anatomy; however, there is a lack of data-driven explanation for why these differences evolved, because a direct comparison of two such species in the wild has never been undertaken. The best way to address this lack of understanding is to quantitatively compare arboreal cercopithecoid and ape climbing behaviors in the wild.

To do so, I designed a quantitative test. I hypothesized that the major osteological modifications in the shoulder and elbow morphology between monkeys and apes evolved largely as adaptations to vertical climbing. To test this, I compared video footage of *Cercocebus atys* (the sooty mangabey) climbing trees in the Taï Forest National Park (Ivory Coast) to footage of *Pan troglodytes* (the chimpanzee) climbing trees in Kibale National Forest (Uganda). Specifically, I obtained the highest angle of extension of both the elbow and the shoulder on each observed climb, separating downclimbs from vertical climbs to acknowledge the difference (if one exists) in these strategies. I tested the following hypotheses:

H_0 (null): There are no differences in elbow and shoulder extension between *C. atys* and *P. troglodytes* during vertical climbs (following Hunt, 2016).

H_1: There are kinematic differences in the elbow and shoulder extension of *C. atys* and *P. troglodytes* during vertical climbing, and these differences are driven by distinct vertical climbing strategies.

Because of the multifaceted nature of animal behavior, it was important to consider confounding variables. I considered the most important confounder to be substrate diameter -- kinematic differences could potentially be explained by behavioral response to different widths of trees being climbed.

These results are the first quantitative kinematic analysis of arboreal cercopithecoid versus ape climbing behaviors in the wild. As the first such quantitative examination of African monkeys' vs chimpanzees' climbing strategies in the wild, this study builds on the existing knowledge of primate anatomy and connects it to climbing strategies, providing data that could potentially be combined with similar data on modern human populations to understand the functional morphology of vertical climbing in modern humans (Venkataraman et al., 2013) and ancient hominins.

METHODS

Two major sources of kinematic data were collected for this study. *Cercocebus atys* data were obtained from 85 videos of mangabey climbs collected by LDF in the Taï forest in 2019. Chimpanzee data were obtained from 114 videos of chimpanzee climbs collected by JMD in 2006 in the Ngogo community of the Kibale National Park in Uganda. For this test, it was important that the two species be measured exhibiting climbing behaviors typical to the species -- that is to say, not unique to one group or environment. The Taï forest, a lowland rainforest, is one of the few locations where *Cercocebus atys*, the sooty mangabey, can be observed vertically climbing and simultaneously is one of the most well-studied sites for primatology research (Doran, 1993); this makes it an appropriate location to assess the sooty mangabey's natural vertical climbing behavior. In comparison, the Ngogo community of *Pan troglodytes schweinfurthii*, the common chimpanzee, is very large -- approximately 150 individuals -- making it a large enough sample of the species to observe ubiquitous behaviors (DeSilva, 2009) and draw appropriate inferences about the species.

Videos of the chimpanzees were filmed with a Canon GL2 hand-held digital video recorder (DeSilva, 2009). The distance between the observer and the subject varied with each climb, but all video recordings were taken in the lateral view (Fig. 2.1) and limited to the first 2-5m of ascent/descent to minimize angle-induced error (DeSilva, 2009). Videos were imported into Windows Movie Maker, QuickTime, and Elmedia Video Player to assess resolution and consequent usability for measurement. Videos of sooty mangabeys were filmed with a Canon EOS 7D digital camera with methods analogous to DeSilva (2009); these were also filmed opportunistically. Mangabey videos were also assessed in Windows Media Player for resolution and quality.

The videos were separated by vertical climbs (identified as "upclimbs") and downward climbs (identified as "downclimbs"), and then imported into Kinovea 0.8.15, a two-dimensional sports imaging and analysis software. In these videos, the angles of excursion, always defined as the maximal visible angle of excursion of the elbow (ulnohumeral) and shoulder (glenohumeral) in each video, were identified and marked. These points that defined these angles were as follows:

- For the elbow: the most distal point of the forelimb, the intersection of the lower and upper forelimb, and the most proximal point of the upper forelimb.
- For the shoulder: the intersection of the lower and upper forelimb, the most proximal point of the upper forelimb, and the hip joint.

These points, and the connection thereof, are depicted visually in the figure below.

Figure 2.1: **Video still of the ulnohumeral (blue) and glenohumeral (red) angles on the sooty mangabey.** The three points used to measure the ulnohumeral angle and the additional point for the shoulder angle, along with the plane of the hip used to demarcate the third point (dotted red line), are depicted.

Care was taken to ensure that the video subject was in lateral view or as close to such a view as possible; lateral view was defined as the view in which all three above-named points in each angle were clearly identifiable. For the chimpanzee videos, care was taken to be sure that the lines connecting these points were all in the same plane (since the observer in these videos did not correct for perspective). While ideally the research subject would be very close to the frame of the camera, angles were still measured on subjects at a significant distance, provided that the resolution was sufficient to make out the points of measurement. Of the 85 mangabey videos, 44 were considered usable for measurement of the ulnohumeral joint and 36 for the glenohumeral joint. Of the 114 chimpanzee videos, 55 were deemed usable for measurement of the ulnohumeral joint and 62 for the glenohumeral joint.

After all points were marked, angles were calculated for each mangabey video using the manual angle feature in Kinovea 0.8.15. A few elbow angles were calculated using the semi-automatic Track Path feature, which exported vector coordinates of each point whose intersecting angle could be calculated in MATLAB. However, the resolution of all of the chimpanzee videos and a number of the mangabey videos was not sufficient to continue reliably employing this feature, so the Manual Angle method was adopted for all videos for the purpose of consistency and the Track Path-computed angles used to assess intraobserver error. Angles for the chimpanzee videos were marked and measured using the same method, but in direct sequence.

It is difficult to obtain video footage of sooty mangabeys vertically climbing because they are notoriously fickle and their upward climbing behavior often occurs with little to no warning. While waiting for further data from the Taï field station, the nine climbs that featured exclusively upward climbing were considered. Of these, only four were usable (in appropriate lateral view and with the resolution necessary to identify the three points of measurement) for measurement on the ulnohumeral joint and only three for the glenohumeral joint. Qualitative and quantitative (a two-sample t-test) comparison of the climbing strategies displayed by the monkeys on upward climbing and downward climbing revealed few differences with regard to angle excursion and general approach. For this reason, the downclimb angles in mangabeys were used as a proxy for upclimbs for this group in statistical comparisons throughout this study.

The average excursion for each limb was computed in Microsoft Excel and JMP 14.0, along with an associated standard deviation and 95% confidence interval for each average. Two-sample t-tests were conducted in JMP 14.0 between the following groups:

- Mangabey upclimbs (downclimbs as proxy) vs chimpanzee upclimbs
- Mangabey downclimbs vs chimpanzee upclimbs
- Mangabey downclimbs vs chimpanzee downclimbs
- Chimpanzee upclimbs vs chimpanzee downclimbs

Additionally, regression analysis was performed to determine if tree diameter at breast height was a good predictor for angle excursion of either joint. Data for these analyses were obtained from the recorded field notes of LDF and JMD. This analysis was also performed in JMP 14.0.

RESULTS

Wild mangabeys vertically climb with a stilted motion, with elbows partially to fully extended and humerii barely extending superiorly along the sagittal plane. When downclimbing, they extend the elbow 132.6° ± 9.8° (n = 40) and the shoulder 120.2° ± 13.3° (n = 33). Maximum extension of the shoulder during upclimbs occurs approximately halfway through the climb stance, when weight is fully placed on the other arm and the shoulder in question is at its furthest point from the substrate; during downclimbs it occurs when full weight is placed on the shoulder itself.

In contrast, the data show that chimpanzees vertically climb employing two very distinct methods. Their ulnohumeral extension on upward climbing bouts is very similar to that of mangabeys, extending 126.1° ± 6.8° (n = 32), with shoulder extension 125.9° ± 7.5° (n = 39). In contrast, their downclimbs are much more erratic, with full extension of the shoulder and elbow frequently occurring simultaneously as they swing quickly from tree to tree during the descent.

Assumptions for inference were all met (see Supplemental Analysis A). Normality was considered liberally, given the observational nature of the study, and the Central Limit Theorem was invoked whenever the sample size was large enough. Outliers were retained in the analysis if they were not considered influential observations (i.e. did not bias the results toward H_1).

Unequal variances two-sample t-tests confirmed significant differences between chimpanzee downclimbs and mangabey downclimbs at both joints (Fig 3.2, 3.5). Additionally, t-tests showed significant differences between chimpanzee upclimbs and downclimbs on both joints (Fig 3.3, 3.6). Given the high potential for error in these measurements due to video resolution, all statistical analysis was performed conservatively -- unequal variances t-tests were performed on all comparisons regardless of whether or not Levene's test confirmed equal variances, and the univariate outlier of a 0° glenohumeral extension in a video where the mangabey was primarily feeding and sliding downward was excluded from the analysis in Figure 3.5 in order to avoid biasing the results toward $H_{1.}$ Unequal variances two-sample t-tests did not reveal significant differences between chimpanzee upclimbs and mangabey extension at either joint (Fig 3.1, 3.4).

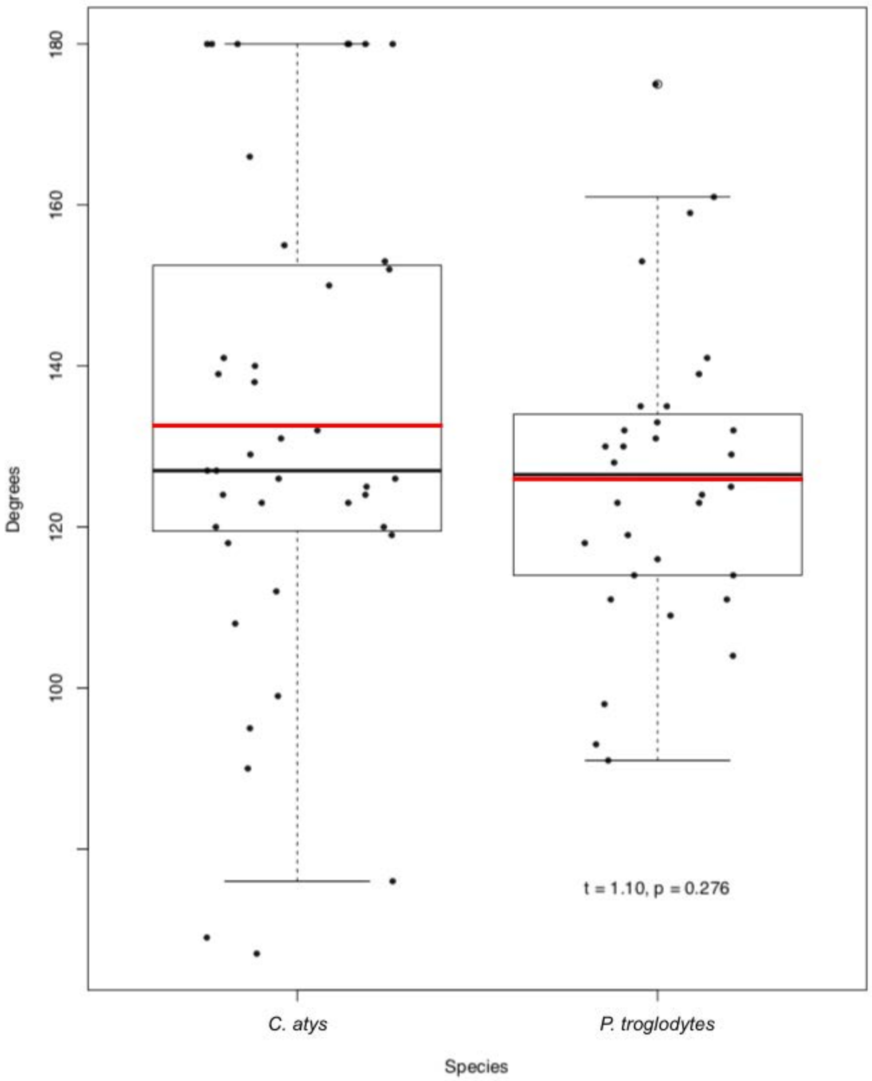


Figure 3.1: *Comparison of elbow excursion in chimpanzees and mangabeys during upward vertical climbs.* **There was no significant difference between the average chimpanzee ulnohumeral extension on upward climbs (n = 32; hereafter "upclimbs") and the average mangabey extension of the same joint (n = 40).** The means of the two groups (see red lines) differed by 6.5 degrees. The 95% confidence interval for mangabey ulnohumeral excursion was [122.8, 142.4], and the 95% confidence interval for chimpanzee ulnohumeral excursion on upclimbs was [119.3, 132.9]. There were two outliers in the mangabey data and one outlier in the chimpanzee data, which were retained in this analysis since they were not influential observations.

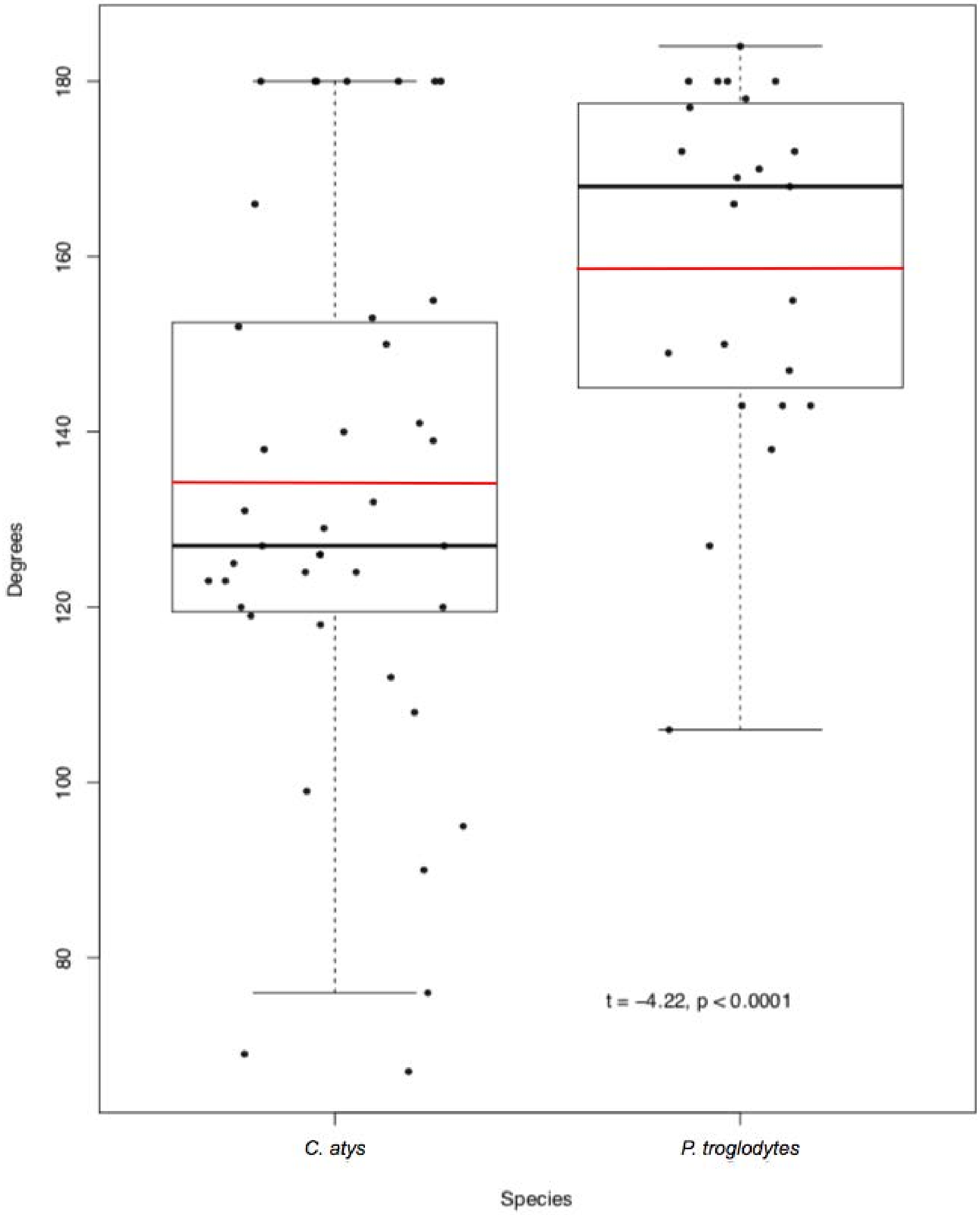
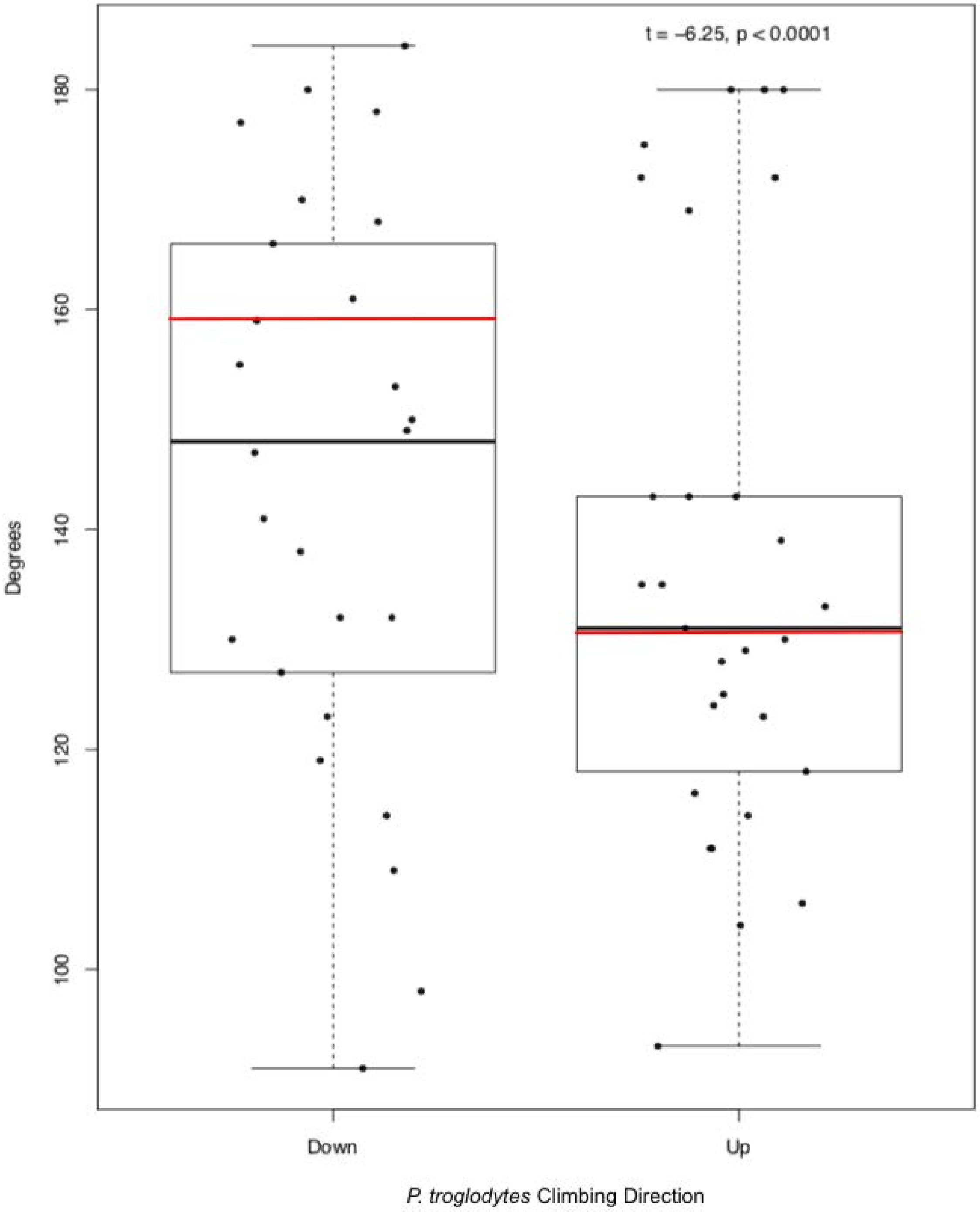


Figure 3.2: *Comparison of elbow excursion in mangabeys vs chimpanzees in downward climbs.* **There was a significant difference between the average chimpanzee ulnohumeral excursion on downward climbs (n = 23; hereafter "downclimbs") and the average mangabey ulnohumeral extension (n = 40).** The means of the two groups (see red lines) differed by 27.2 cm. The 95% confidence interval for mangabey ulnohumeral excursion was [122.8, 142.4], and the 95% confidence interval for chimpanzee ulnohumeral excursion on downclimbs was [151.1, 168.7].



<u>Figure 3.3</u>: *Comparison of maximum elbow excursion in chimpanzee upclimbs vs downclimbs.* **There was a significant difference between ulnohumeral extension on chimpanzee downclimbs (n = 23) and chimpanzee upclimbs (n = 32).** The means of the two datasets differed by 33.7 degrees. There were no univariate outliers.

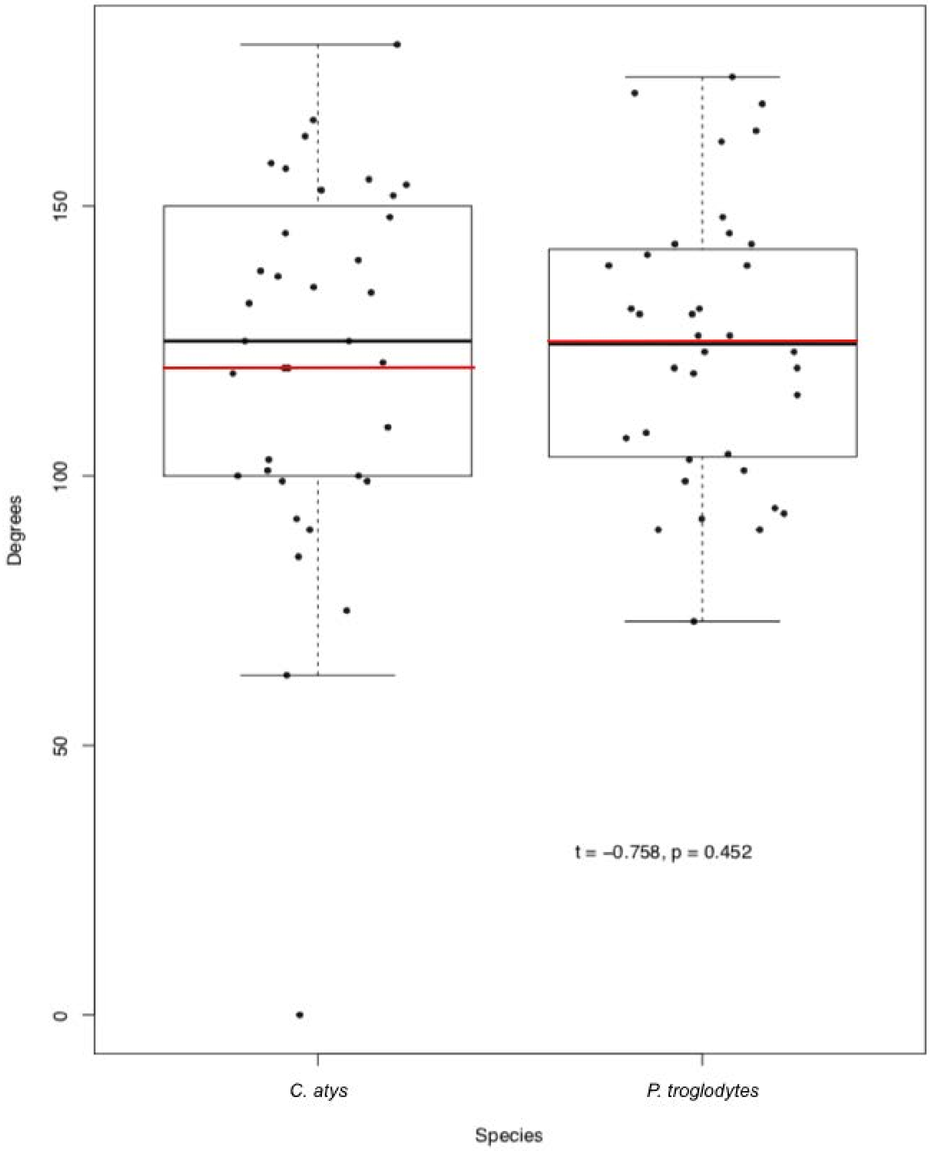


Figure 3.4: *Comparison of maximum shoulder excursion in mangabeys vs upward-climbing chimpanzees.* **There was no significant difference between the average glenohumeral excursion in chimpanzees on upclimbs (n = 39) and mangabeys (n = 33).** The means of the two groups differed by 5.68 degrees. The 95% confidence interval of the mangabey shoulder excursion was [106.8, 133.5], and the 95% confidence interval of the chimpanzee shoulder excursion on upclimbs was [118.4, 133.4]. There was one univariate outlier among the mangabeys, which was not considered an influential observation and therefore was retained in this analysis.

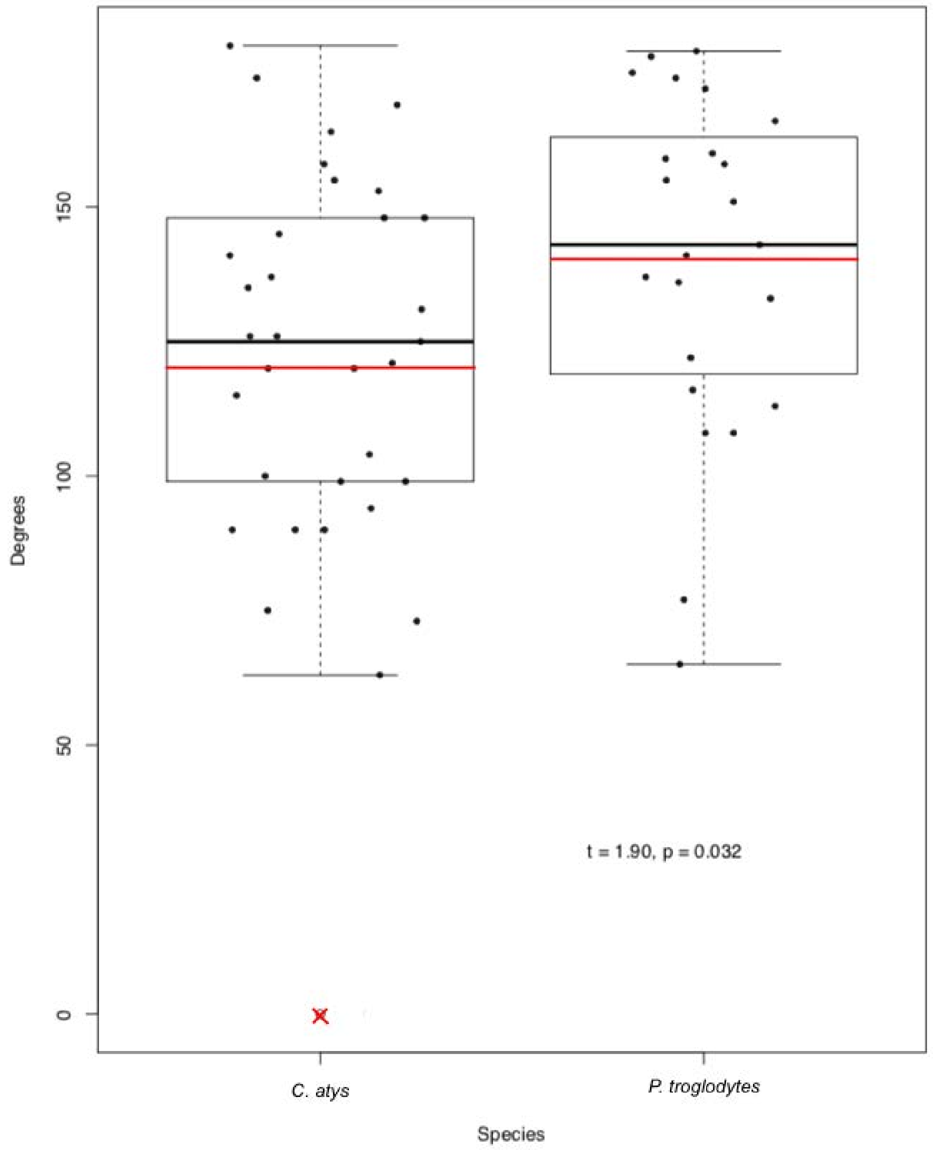


Figure 3.5: *Comparison of maximum shoulder excursion in mangabeys vs downward-climbing chimpanzees.* **There was a significant difference between the average glenohumeral extension of chimpanzees on downclimbs (n = 23) and mangabeys (n = 32).** The means of the two groups differed by 16.3 degrees. There was one univariate outlier among the mangabey data, and inclusion of it in the analysis yielded a p-value of 0.018, indicating an even more significant relationship. The outlier was excluded in this two-sample t-test for the purpose of a conservative analysis; associated outlier management can be found in the supplemental figures section.

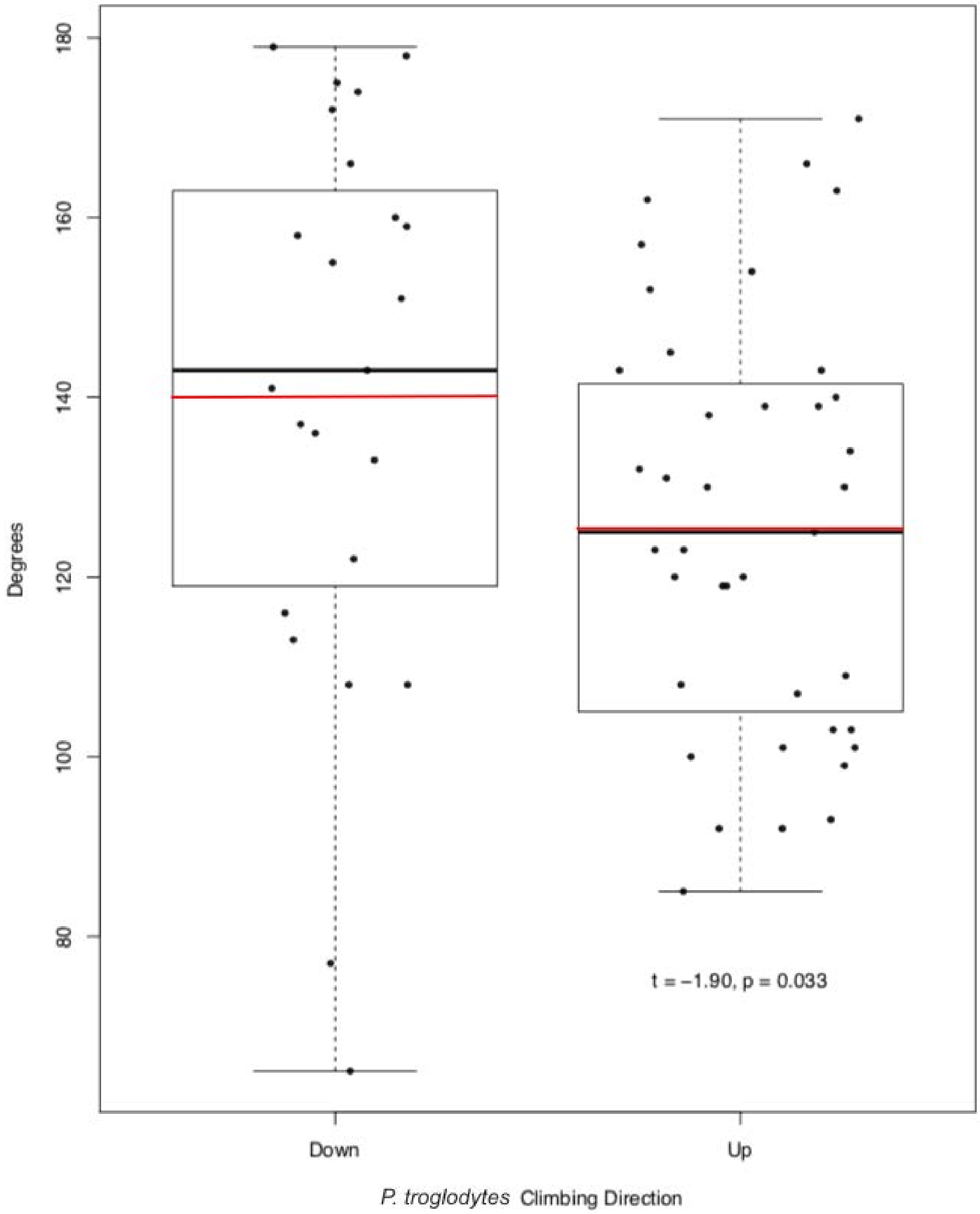


Figure 3.6: *Comparison of maximum shoulder excursion in upward-climbing chimpanzees vs downward-climbing chimpanzees.* **There was a significant difference between the average glenohumeral excursion in chimpanzees on downclimbs (n = 23) and upclimbs (n = 39).** The means differed by 14.3 cm, and there were no univariate outliers. The 95% confidence interval of the mean excursion on upclimbs was [118.4, 133.4], and the 95% confidence interval of the mean excursion on downclimbs was [126.6, 153.9].

The main identified confounder was tree diameter. As the two observed groups were not in the same forest, it was necessary to eliminate the possibility that the diameter of the trees they chose to climb in their respective habitats influenced the pattern of their joint excursion. For this reason, regression analysis was performed on tree diameter at breast height ("DBH") versus the maximum excursion of the individual climbing that tree.

Assumptions for inference from regression were all met (see Supplemental Analysis B). As there were generally fewer observations in these analyses, normality was still considered liberally. No bivariate outliers were identified.

This regression analysis revealed that tree diameter at breast height was an incredibly weak predictor of maximum excursion for all angles tested (see figure captions). For this reason, tree diameter in the different habitats could be eliminated as a potential confounder.

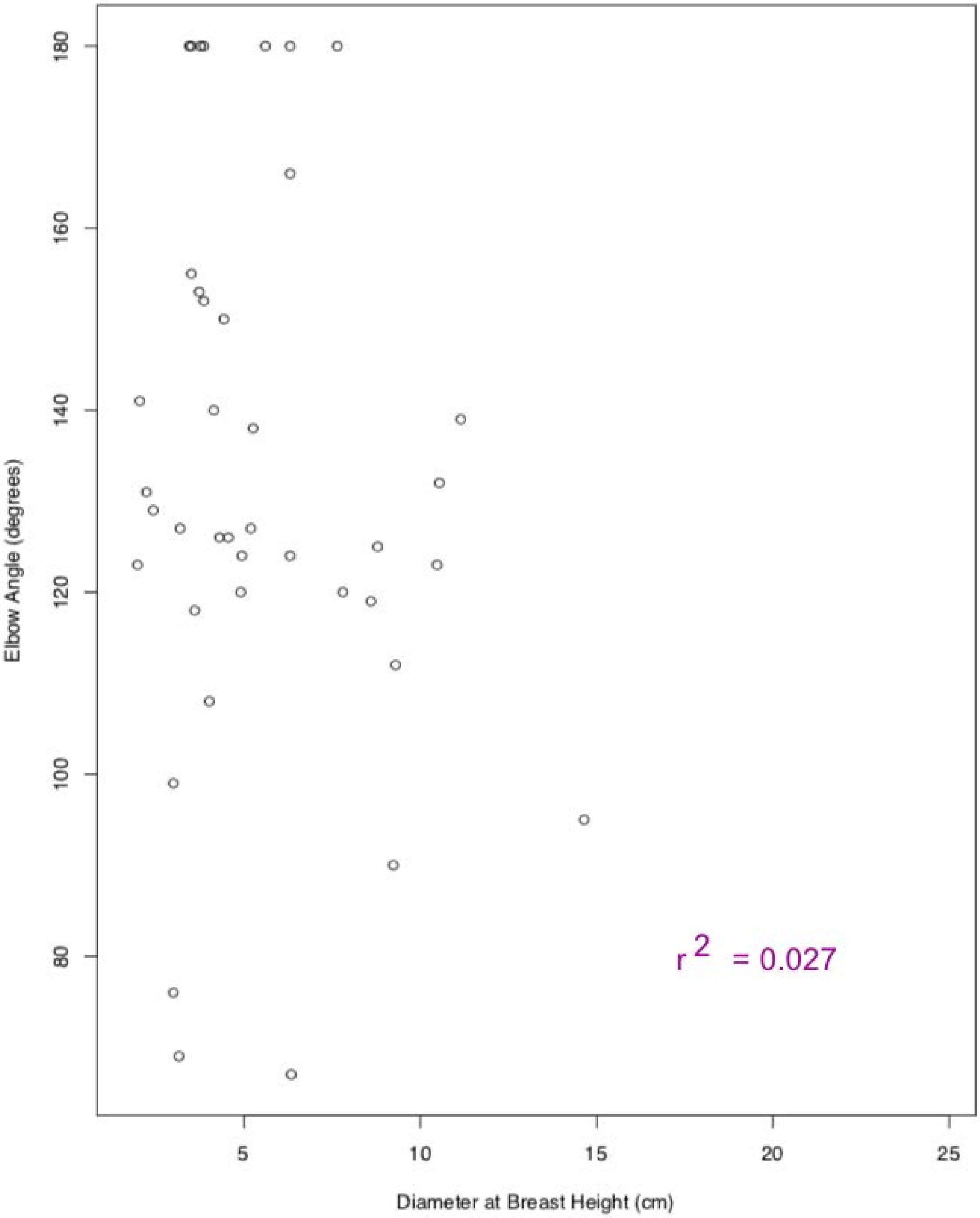


Figure 3.7: *Regression analysis of tree diameter at breast height vs maximum elbow excursion of the individual climbing it.* **Diameter of the climbed tree at breast height was an incredibly weak predictor of ulnohumeral extension in cercopithecoids (t_{39} = -1.03, p = 0.309, n = 40).**

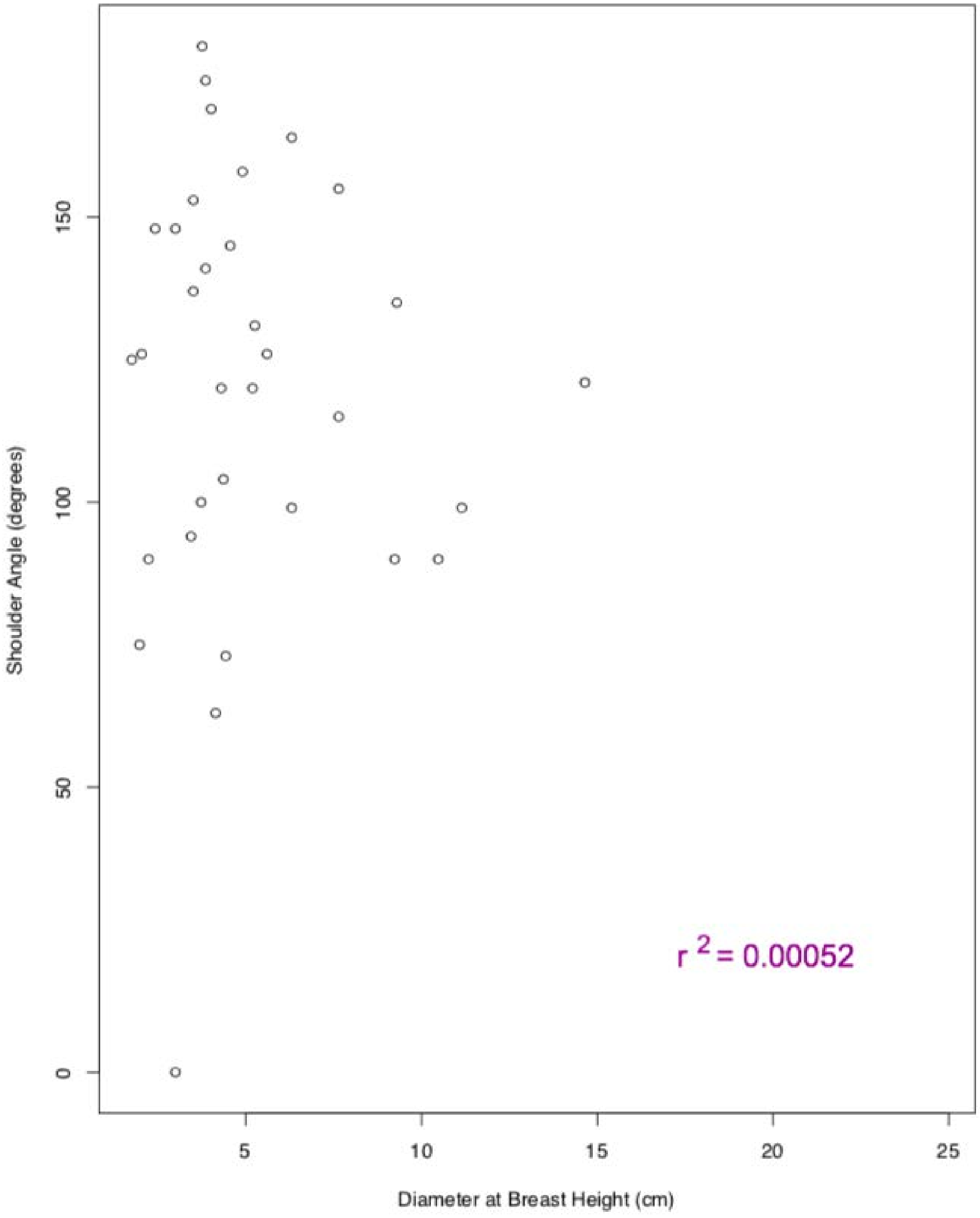


Figure 3.8: *Regression analysis of tree diameter at breast height vs maximum shoulder excursion of the individual climbing it.* **Diameter at breast height of the tree climbed was an incredibly weak predictor of glenohumeral angle excursion in cercopithecoids (t_{32} = 9.00, p = 0.900, n = 33).**

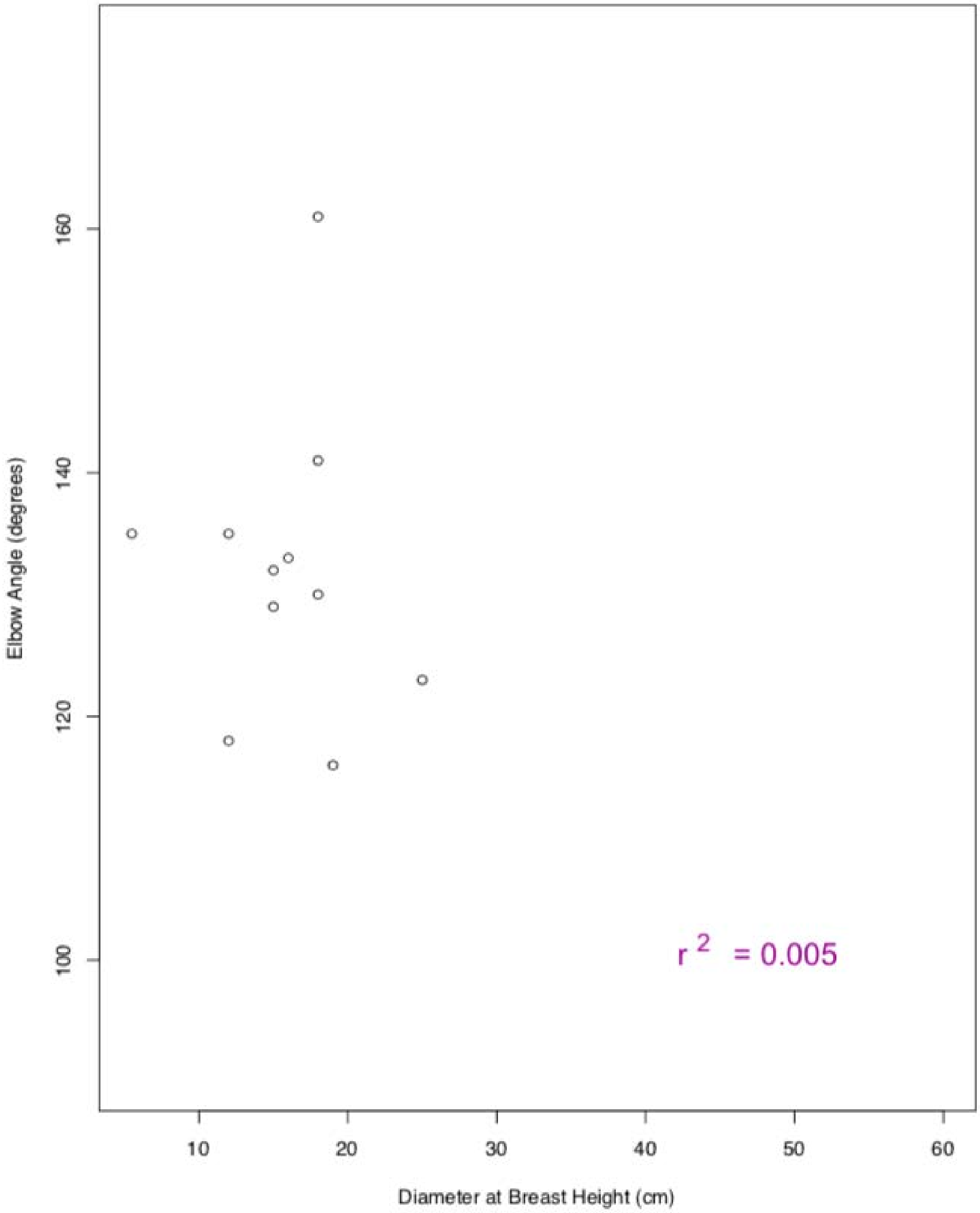


Figure 3.9: *Regression analysis of tree diameter at breast height vs maximum elbow excursion of the individual climbing it.* **Diameter at breast height of the tree climbed was an incredibly weak predictor of ulnohumeral angle excursion in chimpanzees (t_{10} = 10.0, p = 0.842, n = 11).**

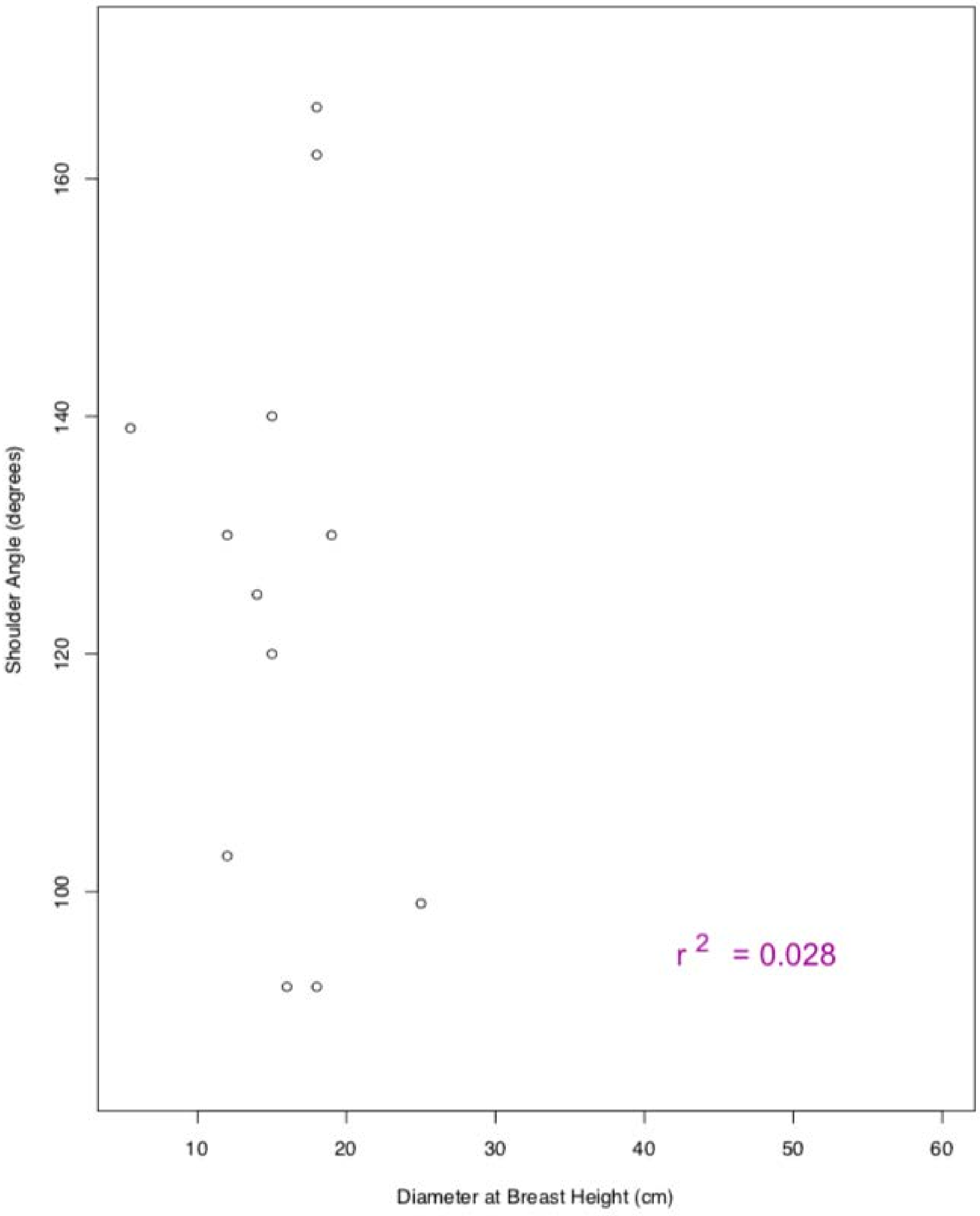


Figure 3.10: *Regression analysis of tree diameter at breast height vs maximum shoulder excursion of the individual climbing it.* **Diameter at breast height of the tree climbed was an incredibly weak predictor of glenohumeral excursion in chimpanzees (t_{11} = 5.19, p = 0.603, n = 12).**

These results collectively suggest that chimpanzees and mangabeys, and based on inference apes and arboreal cercopithecoids, adopt a kinematically similar vertical climbing strategy when climbing upward, but very different strategies when climbing downward. These results identify a difference (namely, in downclimbing strategies) that previous quantitative studies did not note, and is worthy of additional exploration.

DISCUSSION

In this observational study, I found that mangabeys and chimpanzees, and by extension arboreal cercopithecoids and apes, exhibit significant differences in maximum excursion in both the ulnohumeral and glenohumeral joints on downward climbs, but not on upward climbs. Additionally, chimpanzees themselves exhibit significant differences in excursion of both joints based on the direction of the climb. Finally, tree diameter was not a significant driver of maximum excursion in any joint for both species.

The results of his study corroborate Hunt's (1991) observations that there are no significant differences in the upper limb kinematics of vertical climbing in monkeys and apes when they are moving in an upward direction. However, there is a strong difference between climbing strategies on downclimbs. How these results are interpreted depends on how the field defines vertical climbing. Much of the literature in the field has treated vertical climbing as the action of moving from the ground upward into a tree, and consequently has only considered this upward movement to be evolutionarily consequential. The results of this study suggest that while upward climbing may not be a primary driver of anatomical evolution in the upper limb, movement out of the tree has been an understudied aspect of primate locomotion and may even be a selective driver of anatomical evolution in the upper limb. What this means is that while apes have more extension capability in their elbow and shoulder joints than do cercopithecoids, they do not necessarily deploy them in their upward climbing behavior, opting instead for a more limited, stiffer motion similar to the behavior of arboreal cercopithecoids. This finding is independent of the diameter of the tree at breast height, contrary to some predictions (Hunt, 1996).

What, specifically, is this motion? While mangabeys descend with virtually the same strategy they adopt on upward climbs, with controlled joint angles and similar speeds, chimpanzees' motion on downclimbs is markedly different from that of their upclimbs. Chimpanzees crash downward at significantly higher speeds, jumping from branch to branch and extending their limbs to grasp anything to stabilize their bodies on such a speedy descent. This markedly different strategy is evident in the data -- there are significant differences in both ulnohumeral and glenohumeral extension of mangabeys and chimpanzees on downward climbs, differences that are not significant during upward climbs.

Why is this the case? While upward climbing has been proposed as an explanatory factor for the mobile upper limb of hominoids (Fleagle et al., 1981; Gebo, 1996; DeSilva, 2009; Isler, 2005), few studies have considered the act of downclimbing itself as another potential selective factor on ape arm morphology. Downward climbing is an extremely dangerous activity for all primates; since downward motion is accelerated by the pull of gravity, the likelihood of missteps resulting in falls is very high. This is compounded by weight: larger animals have a higher risk of fatality than smaller ones because they possess a lower surface area-to-volume ratio, per the square-cube law (Haldane, 1927).

Unlike upward climbing, downclimbing also requires a balance between energetics and safety (Pontzer and Wrangham, 2004). Move too quickly, and a large individual runs the risk of a fall due to a misstep. But move too slowly, and that same individual must expend a significant amount of energy holding a large body against the force of gravity; a significant expenditure of energy may tire the muscles of the upper limb, increasing the risk of fatigue and possibly a fall from the tree. In larger animals, falls are more likely to be catastrophic (Carter et al., 2008). As a consequence, any downclimbing strategy must allow for movement that is quick to avoid energy loss and controllable to prevent missteps, as was observed here with the kinematics of chimpanzee downclimbs. The speedy, full-extension strategy exhibited by the chimpanzees in this study may be an adaptive solution to the challenges faced by large-bodied apes to avoid falls as they descend from the trees.

Large bodied apes would not be able to extend their elbows and shoulders if they possessed the bony structure of an arboreal cercopithecoid. Because of the enormous threat to fitness unsafe downclimbing presented in larger tree-climbing primate species, natural selection may have modified the bony geometry of the shoulder and elbow joints to allow for increased extension. This includes the elimination of the lipping on the superior and inferior surfaces of the glenoid fossa and the consequent flattening of the articulating surface itself, giving the humerus greater room to move and increasing the ability to extend the arm above the head. Additionally, selection on downclimbing in large-bodied apes may have prompted a reduction in the olecranon process to permit larger elbow extension. Coupled with other mobility-increasing changes, like the broadening of the shoulder space, natural selection adapted the upper limb to respond to the new safety challenges posed by downclimbing at a larger weight.

Contrary to Hunt's (1996) prediction, I did not find that the diameter of tree climbed influenced the divergent patterns of humeral extension observed in the two species. Regression analysis showed that diameter at breast height was not a good predictor of climbing behavior at the shoulder and elbow. This removes an alternative explanation for the aforementioned differences: that trees in their respective habitats force monkeys and apes to climb with different strategies. Therefore, these results collectively indicate that the higher average maximal excursion in chimpanzees is not due to the larger trees they climb. While measurement error is higher with a single-observer method in two-dimensional software (at least compared to a more technologically equipped study, such as XROMM), it is important to realize that the magnitude of intraobserver error does not significantly affect the conclusions associated with these data. The data were analyzed for comparative trends, not for the specific measurements themselves, and as a consequence the error in the numerical results is not a detractor from the scientific soundness of the conclusions. The trend of increased extension in chimpanzee vertical climbs compared to mangabey vertical climbs, coupled with the anatomical limitations on extension found in mangabeys and arboreal cercopithecoids in general and the inference capability of this data, are evidence that downward climbs are a selectively important, overlooked, aspect of primate locomotion.

CONCLUSION

The results of this observational study prompt revisiting of the vertical climbing hypothesis. While they lend support to the idea that vertical climbing, when defined as all behaviors associated with entry and exit from a tree, is at least partially responsible for the change in the osteology of the upper limb, they necessitate further studies focused specifically on downclimbing behavior in primates to understand the full range of pressures that downclimbing places on upper limb bones.

Perhaps more importantly, however, these findings may help contextualize the frequency of climbing in early hominins like *Australopithecus afarensis*. This study clarifies that a flexible shoulder would be vastly important, if not essential, to an early hominin climbing out of a tree. Additionally, if downclimbing presents such a safety concern to heavy primates, it would have benefited large-bodied hominins to reduce the frequency of such a motion to only what was strictly necessary -- for example, only climbing into the trees at night for shelter, when the danger posed by nocturnal predators was greater than the risk of death from an arboreal fall.

While other anatomical differences indicate that modern chimpanzees and early hominins both climbed in kinematically distinct manners (DeSilva, 2009), these results help us understand how safety in vertical climbing is a universal driver for heavier animals and required changes in osteology to address it. Nevertheless, although humans no longer climb with the frequency that chimpanzees do, the mutual absence of glenoid lipping, craniocaudal curvature of the fossa, and a robust olecranon process, among others, are the signature of a shared history, one that remains written in our bones.

SUPPLEMENTAL FIGURES

Analysis A: T-test Comparisons of Angle Extension

Table AS.1: Assumption table noting that all assumptions necessary for inference from an unequal variances two-sample t-test were met.

Assumption	**Do the data meet this assumption?**	**Associated Figure(s)**
Meaningful mean	Yes, when considered liberally.	AS1, AS2, AS3
Good study design	Yes; both data sets were collected over several months and the same measurement methods were applied to both datasets. Based on this, both samples can be considered simple random samples of their respective species and also as proxies for the families that fall into the inference space of this study.	N/A
Normal distribution or large n	Yes for all; the n values of mangabey climbs, chimpanzee downclimbs, and chimpanzee upclimbs were 40, 23, and 32, all large enough to invoke the CLT.	N/A
Independent groups	Yes; there was no overlap or violation of randomization associated with these two groups, which were observed in different forests over a decade apart.	N/A

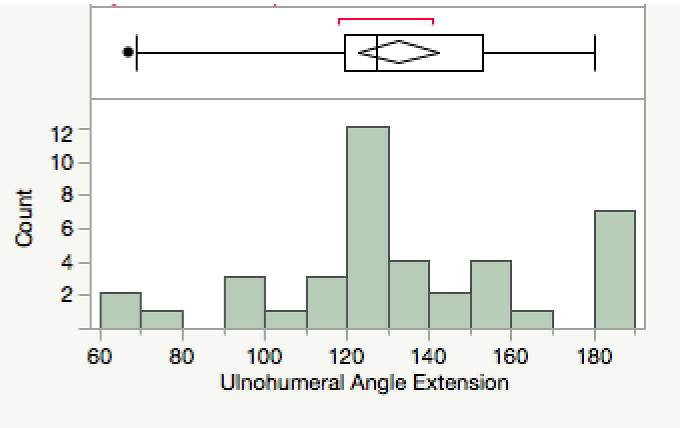


Figure AS1: **The distribution of ulnohumeral extension in mangabey climbs was unimodal and symmetric, with no skew, meeting the assumption of meaningful mean.** There was one univariate outlier.

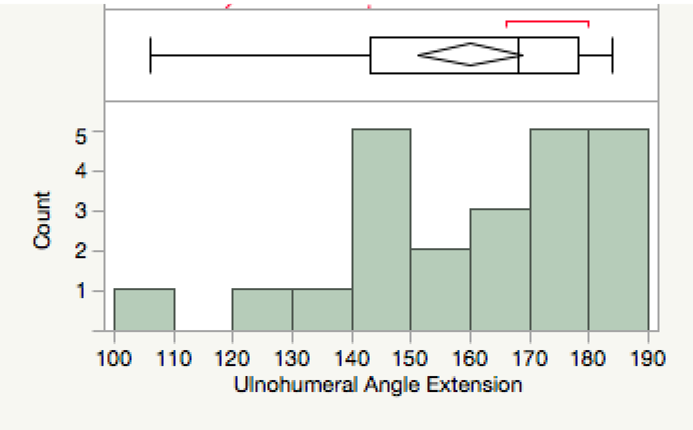


Figure AS2: **While the distribution of ulnohumeral extension in chimpanzee downclimbs was mildly left-skewed, there were few enough individuals in each bin to justify describing the mean as meaningful.** This could be described as a potential caveat to inference.

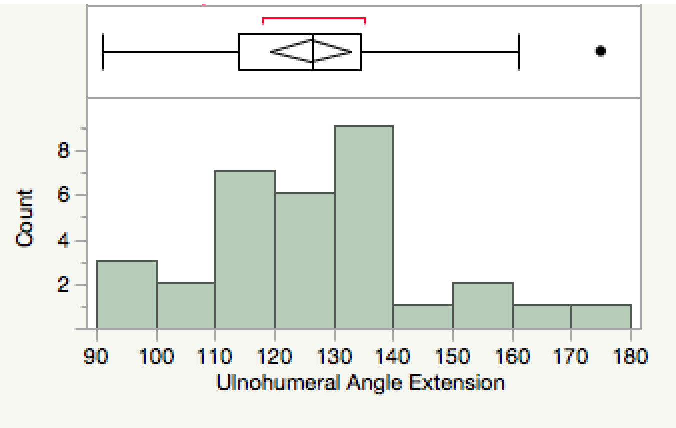
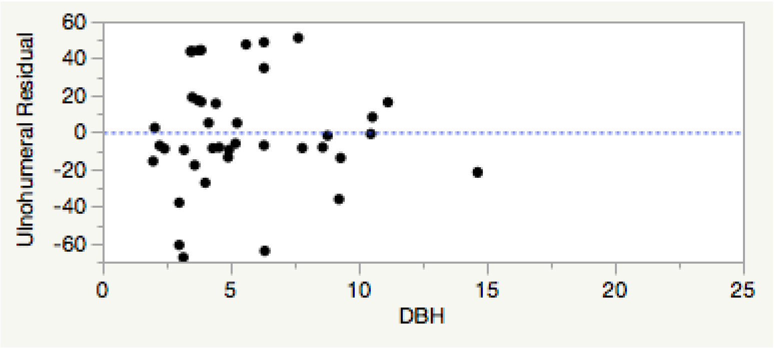


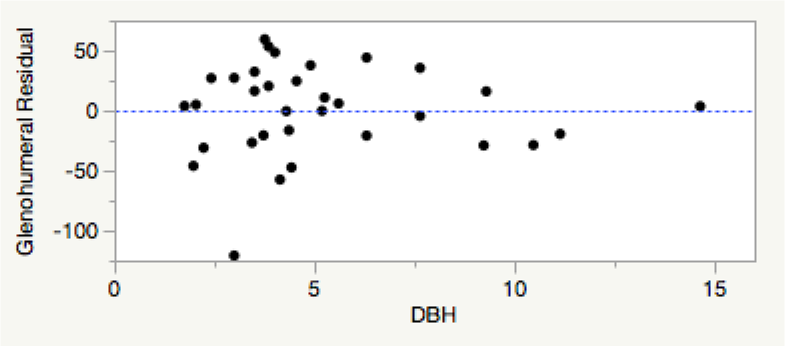
Figure AS3: **The distribution of ulnohumeral extension in chimpanzee upclimbs was unimodal and symmetric, with no skew, meeting the assumption of meaningful mean.** There was one univariate outlier.

Analysis B: Regression of Tree Diameter and Joint Extension

Assumption required for fit or inference?	**Assumption**	**Met?**	**Associated Figure(s)**
Fit	Linear	Yes; the residual plots of all four relationships indicated flat bands around x, with no obvious	BS1, BS2
Inference	Independent x,y pairs	Yes; the rows (individuals) were randomly chosen and were considered independent of one another.	N/A
Inference	Normal Residuals or large enough n to invoke CLT	Yes; for the mangabey climbs, n = 40, large enough to invoke the CLT for both relationships. For the chimpanzee climbs, both the ulnohumeral and the glenohumeral normal quantile plots show the points lying along the normal line for the most part, indicating relative normality.	BS3
Inference	Equal Variance	Yes; no funneling in residual vs x plot.	BS1, BS2

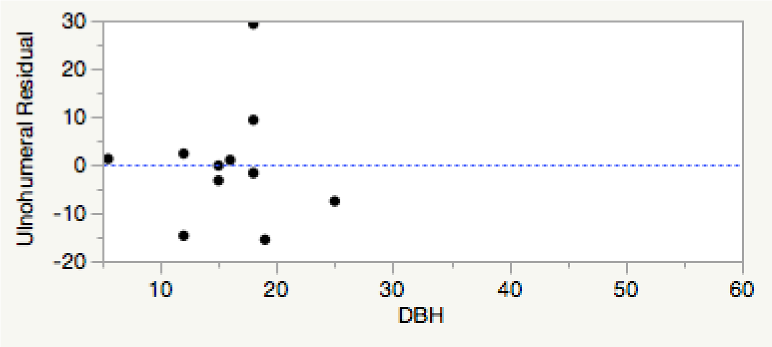


(a)

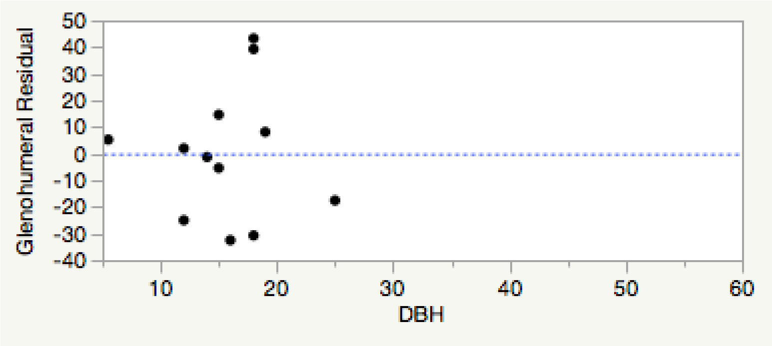


(b)

Figure BS1: **(a) Mangabey ulnohumeral and (b) mangabey glenohumeral residual plots displayed flat, random bands around x, meeting the assumptions of linearity and equal variances necessary to perform inference from regression.**

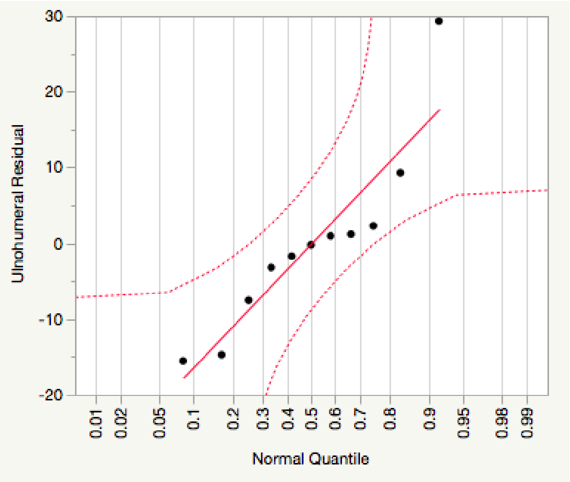


(a)

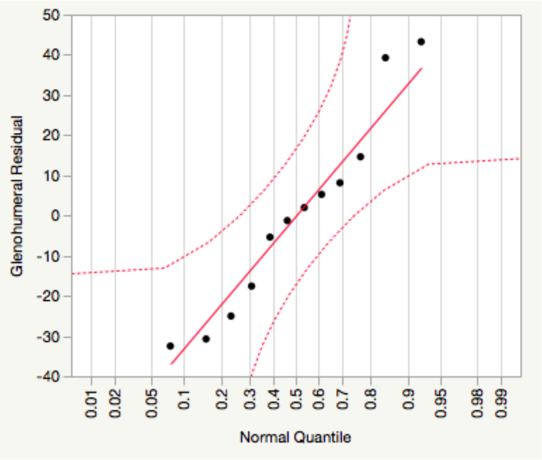


(b)

Figure BS2: **(a) Chimpanzee ulnohumeral and (b) chimpanzee glenohumeral excursion residual plots displayed flat, random bands around x, meeting the assumptions of linearity of relationship and equal variances necessary to perform inference from regression.**



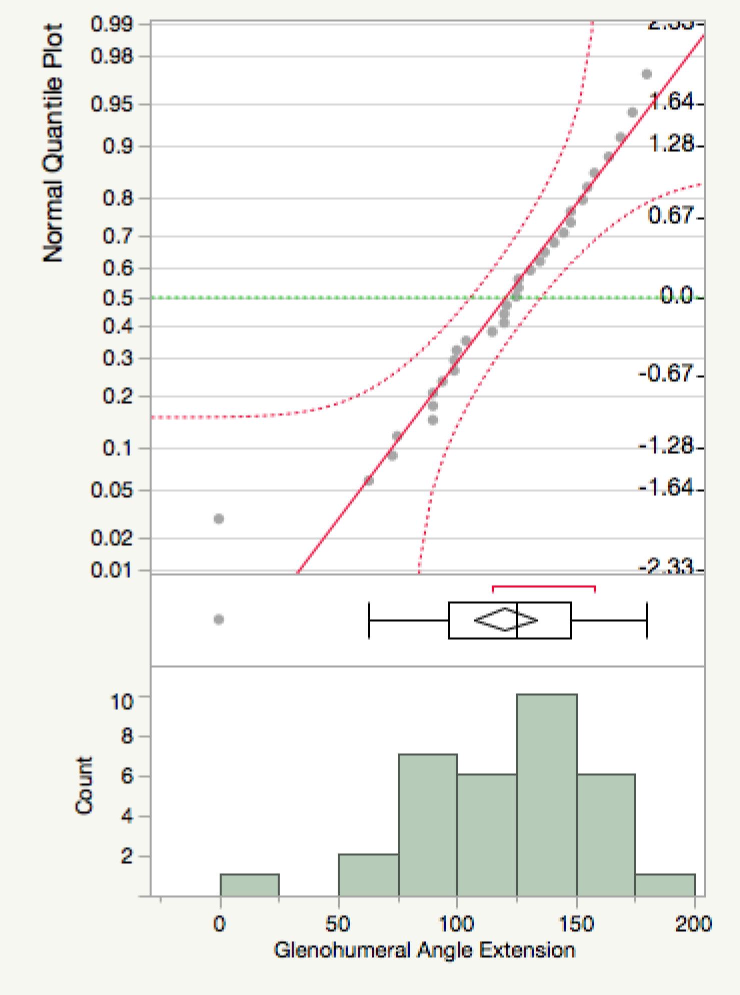
(a)



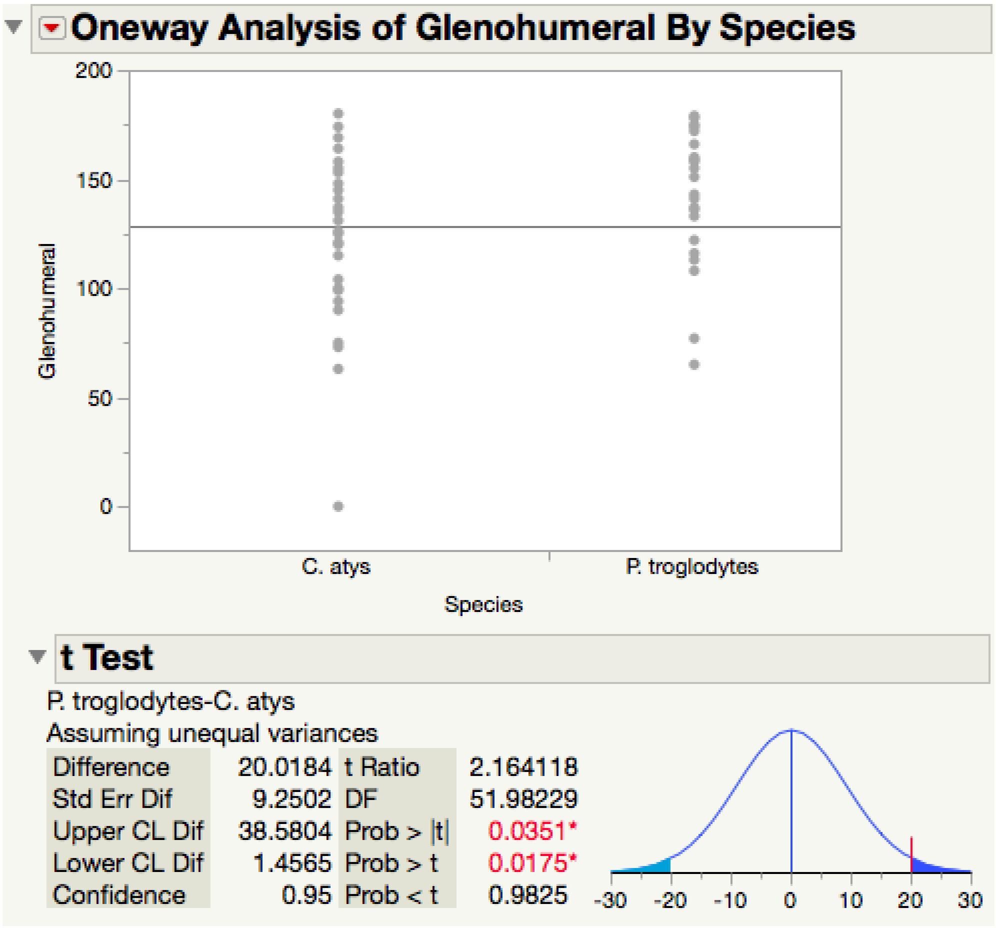
(b)

Figure BS3: **The normal quantile plots for the residuals of the excursion of chimpanzees' (a) ulnohumeral joints and (b) glenohumeral joints indicate relative normality, meeting the assumption of normality necessary for inference from regression.** While the outliers are present in these plots, the relatively low number of observations (n = 11) requires assertion of normality.

Analysis C: Outlier Management on Glenohumeral Extension of C. atys vs P. troglodytes (down)


Normal Quantile Plot
0.99
0.98
0.95
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.05
0.02
0.01
2.33
1.64
1.28
0.67
0.0
-0.67
-1.28
-1.64
-2.33
Count
10
8
6
4
2
0
50
100
150
200
Glenohumeral Angle Extension

(a)



Oneway Analysis of Glenohumeral By Species

t Test

P. troglodytes-C. atys

Assuming unequal variances

Difference	20.0184	t Ratio	2.164118
Std Err Dif	9.2502	DF	51.98229
Upper CL Dif	38.5804	Prob > |t|	0.0351*
Lower CL Dif	1.4565	Prob > t	0.0175*
Confidence	0.95	Prob < t	0.9825

(b)

Figure CS1: **Even with inclusion of the outlier in the *C. atys* glenohumeral extension data, the distribution was symmetrical and unimodal, indicating a meaningful mean and relative normality based on the CLT (n = 33).** Additionally, the p-value was 0.018. The outlier was excluded from the reported analysis for the purpose of a more conservative analysis, based on its potential to be an influential observation.

CODING DOCUMENTATION

Figure 3.1: Mangabeys vs Chimpanzee Upclimbs (Ulnohumeral)

```
#open data file#

cercs <- read.delim(file = "~/Downloads/Approximate Angle Measures (Manual).txt", sep = "\t",
header = TRUE)
chimps <- read.delim (file = "~/Downloads/Approximate Angle Measures (Manual2).txt", sep =
"\t", header = TRUE)
chimpup <- subset(chimps, Up.Down == "up")
chimpdown <-subset(chimps, Up.Down == "down")

#2-sample T#
res <- t.test (cercs$Elbow, chimpup$Elbow)
res

#remove NAs#
cercs1 <- na.exclude(cercs$Elbow)
chimpup1 <- na.exclude(chimpup$Elbow)

#visualize boxplot#
names <- c(rep("C. atys", 40), rep("P. troglodytes", 32))
value <-c(cercs1, chimpup1)
data <- data.frame(names, value)

boxplot(data$value ~ data$names,
        xlab = "Species",
        ylab = "Degrees",
        main = NA)

#add p-value & significance#
text(x = 2, y = 75, labels = "t = 1.10, p = 0.276")

#add jitter
mylevels <- levels(data$names)
levelProportions <- summary(data$names)/nrow(data)
for (i in 1:length(mylevels)) {
  thislevel <- mylevels[i]
  thisvalues <- data[data$names==thislevel, "value"]

  myjitter <-jitter(rep(i, length(thisvalues)), amount=levelProportions[i]/2)
  points(myjitter, thisvalues, pch = 20, col=rgb(0,0,0,0.9))

}
```

Figure 3.2: Mangabeys vs Chimpanzee Downclimbs (Ulnohumeral)

```
#open data file#

cercs <- read.delim(file = "~/Downloads/Approximate Angle Measures (Manual).txt", sep = "\t",
header = TRUE)
chimps <- read.delim (file = "~/Downloads/Approximate Angle Measures (Manual2).txt", sep =
"\t", header = TRUE)
chimpdown <- subset (chimps, Up.Down == "down")

#2-sample T#
res <- t.test(cercs$Elbow, chimpdown$Elbow)
res

#remove NAs#
cercs1 <- na.exclude(cercs$Elbow)
chimpdown1 <- na.exclude(chimpdown$Elbow)

#visualize boxplot#
names <- c(rep("C. atys"), rep("P. troglodytes"))
value <-c(cercs1, chimpdown1)
data <- data.frame(names, value)

boxplot(data$value ~ data$names,
        xlab = "Species",
        ylab = "Degrees",
        main = NA)

#add p-value & significance#
text(x = 1.9, y = 75, labels = "t = -4.22, p < 0.0001")

#add jitter
mylevels <- levels(data$names)
levelProportions <- summary(data$names)/nrow(data)
for (i in 1:length(mylevels)) {
  thislevel <- mylevels[i]
  thisvalues <- data[data$names==thislevel, "value"]

  myjitter <-jitter(rep(i, length(thisvalues)), amount=levelProportions[i]/2)
  points(myjitter, thisvalues, pch = 20, col=rgb(0,0,0,0.9))

}
```

Figure 3.3: Chimpanzee Upclimbs vs Chimpanzee Downclimbs (Ulnohumeral)

```
#open data file#

cercs <- read.delim(file = "~/Downloads/Approximate Angle Measures (Manual).txt", sep = "\t",
header = TRUE)
chimps <- read.delim (file = "~/Downloads/Approximate Angle Measures (Manual2).txt", sep =
"\t", header = TRUE)
chimpup <- subset (chimps, Up.Down == "up")
chimpdown <- subset (chimps, Up.Down == "down")

#2-sample t-test#
res <- t.test(chimpup$Elbow, chimpdown$Elbow)
res

#remove NAs#
chimpup1 <- na.exclude(chimpup$Elbow)
chimpdown1 <- na.exclude(chimpdown$Elbow)

#visualize boxplot#
names <- c(rep("P. troglodytes (up)", 55), rep("P. troglodytes (down)", 23))
value <-c(chimpup1, chimpdown1)
data <- data.frame(names, value)

boxplot(data$value ~ data$names,
        xlab = "Species",
        ylab = "Degrees",
        main = NA)

#add p-value & significance#
text(x = 1.9, y = 75, labels = "t = -6.25, p < 0.0001")

#add jitter
mylevels <- levels(data$names)
levelProportions <- summary(data$names)/nrow(data)
for (i in 1:length(mylevels)) {
  thislevel <- mylevels[i]
  thisvalues <- data[data$names==thislevel, "value"]

  myjitter <-jitter(rep(i, length(thisvalues)), amount=levelProportions[i]/2)
  points(myjitter, thisvalues, pch = 20, col=rgb(0,0,0,0.9))

}
```

Figure 3.4: Mangabeys vs Chimpanzee Upclimbs (Glenohumeral)

```
#open data file#

cercs <- read.delim(file = "~/Downloads/Approximate Angle Measures (Manual).txt", sep = "\t",
header = TRUE)
chimps <- read.delim (file = "~/Downloads/Approximate Angle Measures (Manual2).txt", sep =
"\t", header = TRUE)
chimpup <- subset (chimps, Up.Down == "up")
chimpdown <- subset (chimps, Up.Down == "down")

#2-sample t-test#
res <- t.test(cercs$Shoulder, chimpup$Shoulder)
res

#remove NAs#
cercs2 <- na.exclude(cercs$Shoulder)
chimpup2 <- na.exclude(chimpup$Shoulder)

#visualize boxplot#
names <- c(rep("C. atys"), rep("P. troglodytes"))
value <-c(cercs2, chimpup2)
data <- data.frame(names, value)

boxplot(data$value ~ data$names,
        xlab = "Species",
        ylab = "Degrees",
        main = NA)

#add p-value & significance#
text(x = 1.9, y = 30, labels = "t = -0.758, p = 0.452")

#add jitter
mylevels <- levels(data$names)
levelProportions <- summary(data$names)/nrow(data)
for (i in 1:length(mylevels)) {
  thislevel <- mylevels[i]
  thisvalues <- data[data$names==thislevel, "value"]

  myjitter <-jitter(rep(i, length(thisvalues)), amount=levelProportions[i]/2)
  points(myjitter, thisvalues, pch = 20, col=rgb(0,0,0,0.9))

}
```

Figure 3.5: Mangabeys vs Chimpanzee Downclimbs (Glenohumeral)

```
#open data file#

cercs <- read.delim(file = "~/Downloads/Approximate Angle Measures (Manual).txt", sep = "\t", header = TRUE)
chimps <- read.delim (file = "~/Downloads/Approximate Angle Measures (Manual2).txt", sep = "\t", header = TRUE)
chimpup <- subset (chimps, Up.Down == "up")
chimpdown <- subset (chimps, Up.Down == "down")

#2-sample t-test#
res <- t.test(cercs$Shoulder, chimpup$Shoulder)
res

#remove NAs#
cercs2 <- na.exclude(cercs$Shoulder)
chimpup2 <- na.exclude(chimpup$Shoulder)

#visualize boxplot#
names <- c(rep("C. atys"), rep("P. troglodytes"))
value <-c(cercs2, chimpup2)
data <- data.frame(names, value)

boxplot(data$value ~ data$names,
        xlab = "Species",
        ylab = "Degrees",
        main = NA)

#add p-value & significance#
text(x = 1.9, y = 30, labels = "t = -0.758, p = 0.452")

#add jitter
mylevels <- levels(data$names)
levelProportions <- summary(data$names)/nrow(data)
for (i in 1:length(mylevels)) {
  thislevel <- mylevels[i]
  thisvalues <- data[data$names==thislevel, "value"]

  myjitter <-jitter(rep(i, length(thisvalues)), amount=levelProportions[i]/2)
  points(myjitter, thisvalues, pch = 20, col=rgb(0,0,0,0.9))

}
```

Figure 3.6: Chimpanzee Upclimbs vs Chimpanzee Downclimbs (Glenohumeral)

```
#open data file#

chimpupsep <- read.delim(file = "~/Downloads/Approximate Angle Measures (P. troglodytes
up).txt", sep = "\t", header = TRUE)
chimpdownsep <- read.delim(file = "~/Downloads/Approximate Angle Measures (P. troglodytes
down).txt", sep = "\t", header = TRUE)

#2-sample t-test#
res <- t.test(chimpupsep$Shoulder, chimpdownsep$Shoulder)
res

#remove NAs#
chimpupsep2 <- na.exclude(chimpupsep$Shoulder)
chimpdownsep2 <- na.exclude(chimpdownsep$Shoulder)

#visualize boxplot#
speciesname <- c(rep("Up", 39), rep("Down", 23))
values <- c(chimpupsep2, chimpdownsep2)
data <- data.frame(values, speciesname)
character <-as.data.frame.character(speciesname)

boxplot(data$values ~ data$speciesname,
        xlab = "P. troglodytes Climbing Direction",
        ylab = "Degrees",
        main = NA)

text(x = 2.0, y = 75, labels = "t = -1.90, p = 0.033")

#add jitter
mylevels <- levels(data$speciesname)
levelProportions <- summary(data$speciesname)/nrow(data)
for (i in 1:length(mylevels)) {
  thislevel <- mylevels[i]
  thisvalues <- data[(data$speciesname)==thislevel, "values"]

  myjitter <-jitter(rep(i, length(thisvalues)), amount=levelProportions[i]/2)
  points(myjitter, thisvalues, pch = 20, col=rgb(0,0,0,0.9))

}
```

Figure 3.7: DBH vs Ulnohumeral (Mangabeys)

```
cercsplot <- read.delim (file = "~/Downloads/Approximate Angle Measures (Manual).txt", sep =
"\t", header = TRUE)

#elbow#
plot(cercsplot$DBH, cercsplot$Elbow,
    xlab = "Diameter at Breast Height (cm)",
    ylab = "Elbow Angle (degrees)",
    main = NA)
```

Figure 3.8: DBH vs Glenohumeral (Mangabeys)

```
cercsplot <- read.delim (file = "~/Downloads/Approximate Angle Measures (Manual).txt", sep =
"\t", header = TRUE)

#shoulder#
plot(cercsplot$DBH, cercsplot$Shoulder,
    xlab = "Diameter at Breast Height (cm)",
    ylab = "Shoulder Angle (degrees)",
    main = NA)
```

Figure 3.9: DBH vs Ulnohumeral (Chimpanzees)

```
chimpupplot <- read.delim (file = "~/Downloads/Approximate Angle Measures (P. troglodytes
up).txt", sep = "\t", header = TRUE)

#elbow#
plot(chimpupplot$DBH, chimpupplot$Elbow,
    xlab = "Diameter at Breast Height (cm)",
    ylab = "Elbow Angle (degrees)",
    main = NA)
```

Figure 3.10: DBH vs Glenohumeral (Chimpanzees)

```
chimpupplot <- read.delim (file = "~/Downloads/Approximate Angle Measures (P. troglodytes
up).txt", sep = "\t", header = TRUE)

#shoulder#
plot (chimpupplot$DBH, chimpupplot$Shoulder,
     xlab = "Diameter at Breast Height (cm)",
     ylab = "Shoulder Angle (degrees)",
     main = NA)
```

*Portions of code from the first six figures modified from the work of Yan Holtz (2018), https://www.r-graph-gallery.com/96-boxplot-with-jitter.html.

ACKNOWLEDGEMENTS

I would like to thank the Dartmouth Anthropology Department, J. DeSilva, L. Fannin, N. Dominy, S. McGraw, and many Taï field assistants for their input, support, and feedback. Funding for data collection was provided by the Explorers' Grant (to LDF) and for part of the initial analysis by the James O. Freedman Presidential Research Scholarship (to MSJ).

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