Form and Function of the Primate Cervical Vertebral Column

by

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ABSTRACT

As the junction between the head and the trunk, the neck functions in providing head stability during behaviors like feeding to facilitating head mobility during behavior like grooming and predator vigilance. Despite its importance to these vital behaviors, its form and function remain poorly understood. Fossil hominin cervical vertebrae preserve a striking diversity in form despite the commitment to orthograde bipedality. Do these differences in cervical vertebral form correspond to functional variations among our recent ancestors? This dissertation attempts to understand 1) how does the neck function in head stability and mobility 2) how do these functions relate to cervical vertebral form. Kinematic and passive range of motion studies were conducted in several species of primate to obtain measures of function which were subsequently related to skeletal form.

Results show that cervical vertebral morphology does not significantly covary with differences in joint mobility. Rather, they implicate the critical role of ligaments and muscles in facilitating head mobility. Results of the kinematics study show that the neck plays a role in maintaining head stability during locomotion. However, the kinematic data do not significantly correlate with morphological variation among primate species. Given the negative results of the extant morphological analyses, it is difficult to apply them to the fossil record. As such, the functional significance of the disparate morphologies found in the hominin fossil record remain ambiguous.

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Chapter 1 Introduction

The neck is the junction between the head and trunk. As such, it transmits mechanical loads from the head to the trunk, allows for a mobile visual field, and acts as a conduit for vessels and nerves, as well as a home for digestive and respiratory organs. One of the primary functions of the neck is to help maintain a stable head, which is essential during locomotion because visual and vestibulocochlear inputs are required for efficient navigation through complex environments (Dunbar et al., 2008). Despite its manifest importance, the relationship between primate vertebral form and neck function is understudied. The morphology of the cervical vertebrae should be adapted to their function. The loads experienced are often higher in the postcrania during locomotion than during other behaviors (Preuschoft, 2004). Therefore, variation primate cervical vertebral form should theoretically reflect differences in locomotor and postural behaviors. Primates, as a whole, practice a large range of locomotor modes and postural repertoires. As such, exploring the diversity in their neck function can give insight into how the spine may be adapted those functions. The aim of this research is to understand how cervical vertebral form is adapted to providing head stability and facilitating mobility during locomotion and its implications for locomotor evolution within hominins.

The head and neck are traditionally modeled as a bow and string with the neck muscles supporting vertebral position through tension (Slijper, 1946). Under this model, species with more pronograde necks (those whose necks are habitually positioned more perpendicular to the force of gravity) require greater support than those with more orthograde necks (which are more aligned with the gravity vector). To maintain pronograde postural function, either the muscular effort must be larger, or the muscle force vectors must be oriented in a more mechanically advantageous direction. The shift to orthograde bipedality affects the gravitational loading of the spine and, therefore, how the neck maintains the position of the head. Therefore, differences in posture should affect the form cervical vertebral column (Shapiro, 1991; Nalley and Grider-Potter, 2015). While this bow-and-string model is informative it neglects the dynamic manner in which head stability is maintained during habitual locomotion. The neck's maintenance of head stability should also influence vertebral morphology.

During locomotion, the neck controls head balance, which is vital for a stable field of vision. Efficient locomotion requires visual stability in order to see and respond to substrate variation (Assaiante and Amblard, 1993; Dunbar et al., 2008). Axial movement during locomotion varies among species and among locomotor modes (Dunbar, 2004b; Hirasaki and Kumakura, 2004; Dunbar et al., 2008; Xiang et al., 2008). Primates also normally adjust their visual fields to reflect the orientation of the substrate, or suprastrate (Strait and Ross, 1999; Hirasaki and Kumakura, 2004; Stevens and Heesy, 2013). Because the movement of the trunk differs between locomotor modes and the position of the head varies with substrate position, how the neck maintains head stability should also vary. In turn, the spine should be adapted to maintaining that stability during locomotion.

Very few studies have attempted to relate primate cervical vertebral form to function (Schultz, 1942, 1961; Toerien, 1961; Ankel, 1972; Gommery, 2000; Aiello and Dean, 2002; Manfreda et al., 2006; Parks, 2012; Gómez-Olivencia et al., 2013; Nalley, 2013; Meyer et al., 2018). Several of these studies have proposed hypotheses about the effects of cervical form in balance of the head or in locomotor function (Schultz, 1961; Toerien, 1961; Ankel, 1972; Aiello and Dean, 2002; Gommery, 2006). These have not been empirically tested. Others have been hindered by their use of broad locomotor categories, such as 'quadruped' (Manfreda et al., 2006; Parks, 2012; Nalley, 2013), to classify cervical function rather. These broad locomotor categories are problematic in that they do not reflect the nuances of actual locomotion. Overall, there are many gaps in understanding the functional morphology of the cervical vertebrae that require further investigation.

To establish form-function relationships, the many functions of the head-neck complex must be explored. Neck postural data during locomotion have been collected from a variety of primate species (Strait and Ross, 1999). Strait and Ross (1999) measured the external inclination of the neck in the sagittal plane during mid-stance or mid-swing (see Fig. 1.1). Though this study includes a diverse array of primate species, the zoo animals used were unshaven. The presence of fur likely introduced a large amount of error into their data. This measure also omits the variation in flexion-extension across the gait cycle and excludes lateral flexion and rotation. The neck functions in all three planes and in order to understand postural stability of the head, neck motion needs to be understood in three dimensions. Despite these limitations, these data have used to successfully establish form-function relationships in the cervical spine (Nalley and Grider-Potter, 2015, 2017). Absolute head and neck range of motion (ROM) has also been quantified in only four species of non-human primates (Graf et al., 1995). These data are sparse in their quantity of subjects and in their number of primate species. A greater breadth and depth of taxonomic sampling would allow functional relationships to be elucidated.

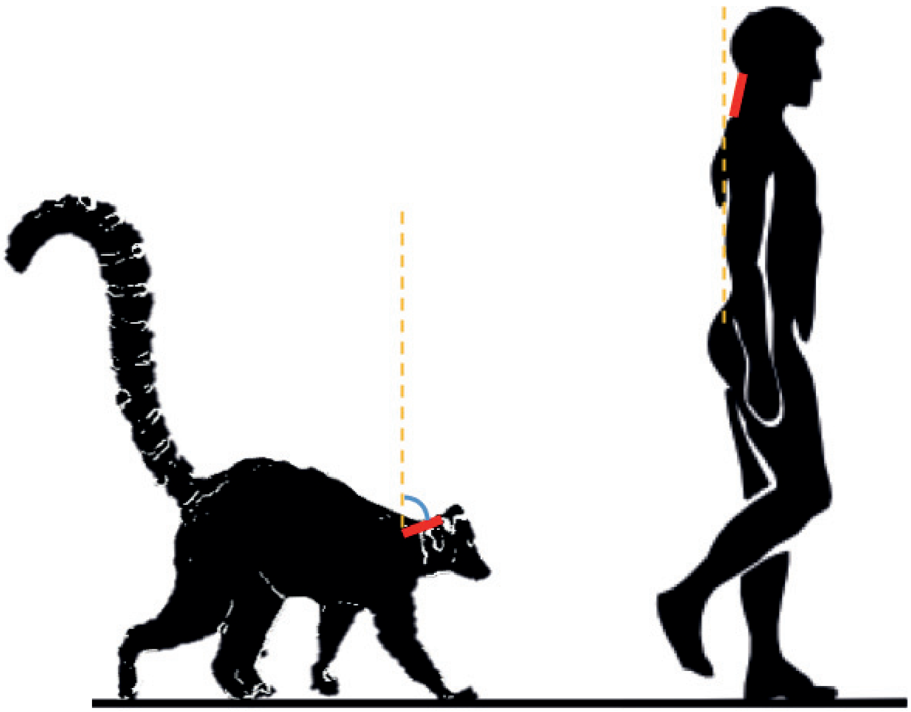

Figure 1.1: Strait and Ross's (1999) measure of neck inclination during mid-stance/mid-swing is the angle (blue) between the neck (red) relative to the vertical line of gravity (yellow) in Lemur catta *(left) and* Homo sapiens *(right).*

Previous research has linked cervical form to neck locomotor function (Nalley and Grider-Potter, 2015, 2017). The primitive morphology found in early hominins likely indicates functional differences among these species. In particular, *Australopithecus* vertebral specimens show long spinous processes, small centra, and curved atlantooccipital joint (Nalley, 2013). These morphologies are associated with more pronograde neck postures in extant primates (Nalley and Grider-Potter, 2015, 2017). Even later *Homo* does not possess the same pattern as modern *Homo sapiens* of large centra, small, bifurcated spinous processes and flat atlantooccipital joints(Lordkipanidze et al., 2007; Gómez-Olivencia et al., 2013). These variations likely demonstrate not only differences in function, but also the piecemeal manner in which the hominin skeleton adapted to bipedal locomotion.

The goal of this dissertation is to understand how craniocervical form is adapted to maintaining head stability during locomotion. Once understood, these relationships will be applied to fossil specimens in order to illuminate the evolution of the spine in primates. Biomechanical principles will be used to create specific sets of predictions relating form and function of the head and neck in a diverse group of primate taxa. Neck function will be assessed through kinematic studies and radiographic imaging by measuring both range of head and neck motion during frequent modes of locomotion and maximum ROM respectively. Craniocervical form will be measured using 3D surface scans. These data will be used to elucidate the relationships between form and function in extant species. Results of such a study are applicable to the mammalian clade as a whole as the cervical column is understudied in most taxa but will be immediately applied to the problem of how the hominin neck evolved in response to the advent of habitual bipedality.

1.1 Basicranial Form and Function

Numerous synapomorphies separate primates from other mammals, including larger brains, decreased facial length, and convergent orbits (Preuschoft et al., 2002), all of which should affect head stability and its maintenance. Unlike most other primates, *Homo sapiens* possess an anteriorly positioned foramen magnum (see Russo and Kirk, 2013 for review). Historically, the anterior position and ventral orientation of the foramen magnum is potentially related to orthograde posture and balancing the head on an erect spinal column (Schultz, 1942); however, little empirical evidence demonstrates the function of that relationship (Russo and Kirk, 2013, 2017). Recent research suggests that both the advent of bipedal locomotion as well as increased brain size influence the position and orientation of the foramen magnum (Spoor, 1997; Strait and Ross, 1999; Lieberman et al., 2000; Bastir et al., 2010; Kimbel and Rak, 2010; Russo and Kirk, 2013). Both Spoor (1997) and Bastir (2010) showed that increased brain size is correlated with stronger basicranial flexion (i.e. flexion between basion, sella, and the foramen caecum) and a more inferiorly inclined foramen magnum. However, foramen magnum angulation is thought to be a product of brain size rather than basicranial flexion (Lieberman et al., 2000; Bastir et al., 2010). It is important to note that neck posture, as measured by Strait and Ross (1999), is not related to foramen magnum angulation (Strait, 1998). The exact relationship between the location and orientation of the foramen magnum and inclination of the cervical spine is unknown.

Despite this gap in knowledge, we know that changes in hominin foramen magnum position affects the mechanics of balancing the head on the neck and trunk (Demes, 1985). In combination with an enlarged braincase and retracted face, the alteration of the craniocervical junction causes the cranium’s center of gravity to be shifted further towards the middle of the head (Demes, 1985; Kapandji, 2008). The anterior location of the foramen magnum requires nuchal musculature to pull the cranium ventrally and caudally rather than dorsally and caudally in more posterior condition (Fig. 1.2; Demes, 1985). The head has been modeled as a first class lever, with the fulcrum at the occipital condyles. The repositioning of the foramen magnum brings the head’s center of gravity closer to the fulcrum, creating a mechanical environment where balancing the head requires little muscular effort.

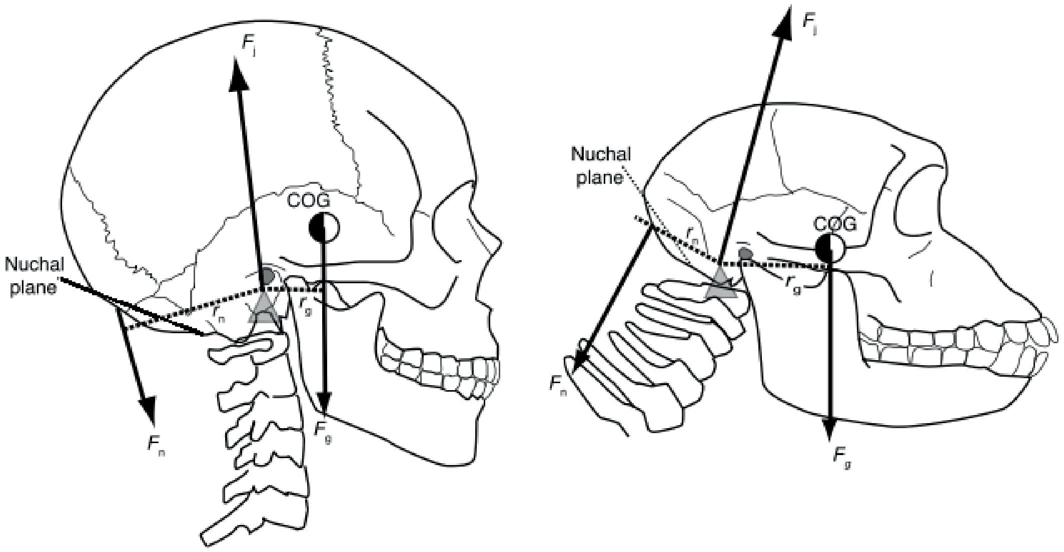

Figure 1.2 Differences in forces at the craniocervical junction in a human (left) and chimpanzee (right). Balance of the head is dependent upon orientation of the center of gravity, position and orientation of the foramen magnum, and neck posture. Taken from Lieberman (2011).

Angulation of the nuchal plane should also influence how the head is balance. Nuchal muscles maintain equilibrium through balancing the pre-condylar weight of the skull. The manner in which the head is balanced is affected by direction and magnitude of nuchal forces (Demes, 1985). In *Pan troglodytes*, and presumably most mammalian quadrupeds, the nuchal plane is inclined posteroinferiorly while it is directed inferiorly in humans (Nevell and Wood, 2008). Increasing the distance between the atlantooccipital joint (the fulcrum) and the site of muscular insertion lengthens the lever arm thereby decreasing the required muscular effort (Strait and Ross, 1999; Preuschoft and Witzel, 2002).

Muscles with greater cross-sectional area are capable of producing larger forces (Brand et al., 1986) and muscles with greater cross-sectional area are correlated with larger skeletal areas for attachment (Dean, 1985). Kunimatsu (1992) explored the size of primate nuchal plane area, finding that all primates within his sample, with the exemption of humans, had relatively similar nuchal plane areas. This exception is likely because the human head has a center of gravity almost directly superior to its spinal support, causing spinal compression rather than bending (Slijper, 1946; Aiello and Dean, 2002; Kapandji, 2008). Due to the more balanced relationship between the head and spinal column, large neck muscles are superfluous in species with orthograde neck postures. The reduction in nuchal musculature present in humans is also presumed in fossil hominins (as measured by dimensions of the nuchal plane of the occipital bone, for example) (Kunimatsu, 1992), possibly indicating the presence of neck orthogrady as early as *Australopithecus*.

1.2 Upper Cervical Spine Form and Function

The goal of this section is to review what is known about mammalian cervical vertebral form and how it is influenced by function. The eutherian cervical spine is predominately composed of seven vertebrae. The overwhelming majority of investigations into the biomechanics of the cervical spine pertain to the human neck, though few non-human mammalian studies do exist within anthropological and veterinary literature (Slijper, 1946; Fleagle, 1977; Penning and Badoux, 1987; Vidal et al., 1988; Milne, 1991; Gál, 1993a; b; Graf et al., 1995; Keshner and Delp, 1997; Cullinane et al., 1998; Strait and Ross, 1999; Choi et al., 2003b; a; Lu et al., 2005; Rhodin, 2008; Sheng et al., 2010; Pierce et al., 2011; Farshadmanesh et al., 2013). The upper cervical spine (C0-C2) is functionally and anatomically distinct from the lower cervical spine, Fig. 1.3 (White and Panjabi, 1990; Kapandji, 2008). The atlas is an unusual vertebra in that it lacks a weight-bearing vertebral body, which has been incorporated into the axis as the dens (Jenkins, 1969). Anterior and posterior arches connect the articular facets and possess a circular odontoid facet anteriorly and a small spinous process posteriorly. The occiput (C0), atlas (C1), and axis (C2) tend to couple, or move as a group, during lateral bending and axial rotation (White and Panjabi, 1990). This pattern also occurs between C2-C5, C5-T1, T1-T4, and T4-T8 (White and Panjabi, 1990), highlighting the importance of considering these vertebrae as skeletal units, or parts of an integrated whole.

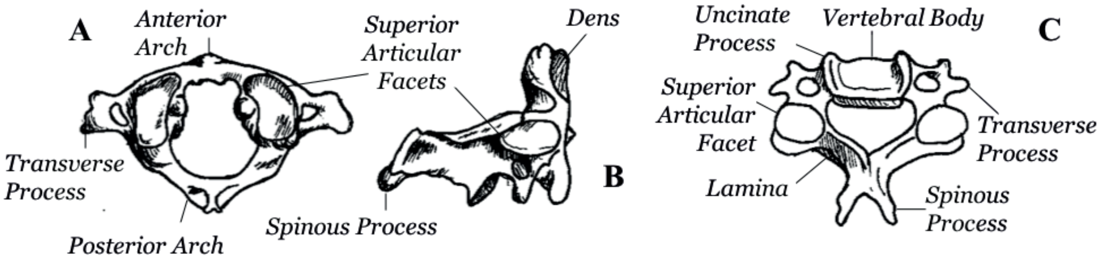

Figure 1.3 Human cervical vertebrae including A) the atlas or C1, B) the axis or C2, and C) a typical lower cervical vertebra C3-C7. Adapted from Gray's Anatomy (1918).

Recently, Villamil (2018) concluded a study of morphological integration in the hominoid cervical column. Her results show several interesting patterns of integration and evolvability in the cervical metrics of *Homo*, *Pan*, and *Hylobates*. C1 is both highly integrated with other craniocervical elements and highly evolvable; this means its morphology covaries with the morphology of the other cervical vertebrae but also responds to natural selection most rapidly in comparison to other cervical levels (Villamil, 2018). This result implicates C1 as the most valuable for functional analyses in both extant and fossil species. Her results also demonstrate distinct units of integration including C0-C1, C2, C3-C4-C5, and C6-C7. She also hypothesizes that the small degree of integration found within C2 and C7 may be due to the transitional nature of these vertebrae from upper to lower cervical column and from cervical to thoracic or perhaps the differences in forces experienced at these levels. These patterns are similar to the functional groups observed by (White and Panjabi, 1990).

In mammals, the occipital's articulation with the cervical spine occurs between the paired occipital condyles (C0) and the concave superior articular facets of the atlas (C1). The paired articulations are more or less symmetrical and act together as a unit during motion. In humans, this joint allows for 25-30° of flexion-extension and 3-4° of lateral flexion (Bogduk and Mercer, 2000; Kapandji, 2008). Slight rotation at the atlantooccipital joint is possible through ipsilateral translation and contralateral lateral flexion, but only in conjunction with atlantoaxial rotation (White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008). Flexion of the atlantooccipital joint is inhibited by contact between the anterior aspect of the foramen magnum and the dens of the axis while the tectorial membranes and alar ligaments restrict extension and lateral flexion, respectively (see Fig. 1.4). In addition, these joints are also stabilized by their joint capsules (White and Panjabi, 1990).

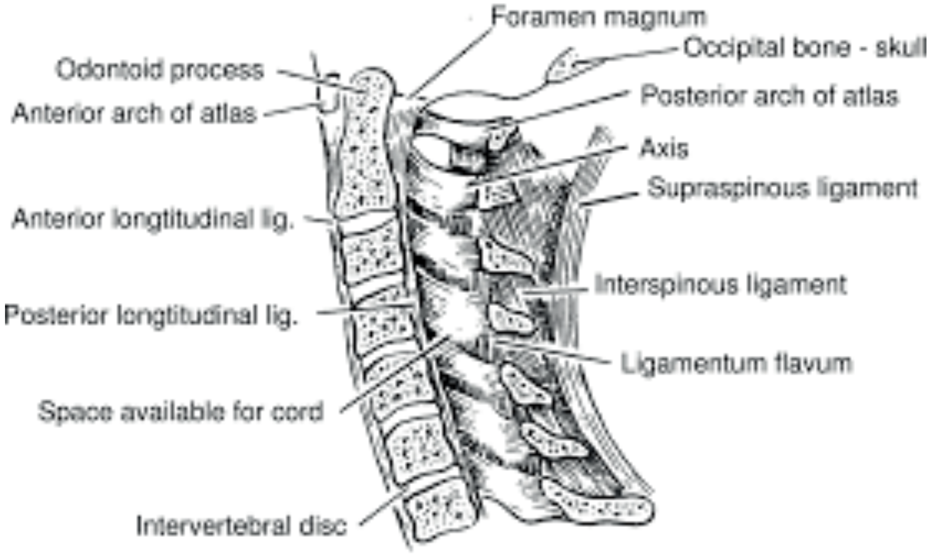

Figure 1.4: Ligaments of the cervical spine, taken from (Crosby, 2006).

Graf and colleagues (1995) conducted one of the few joint-motion studies that included non-human mammals. Using radiographs and dissections, they determined that non-primate quadrupeds (*Lepus*, *Felis*, and *Cavia*) have atlantooccipital joints with passive ranges of motion averaging between 92-106° of flexion-extension. The two macaque species used in the study, *M. fascicularis* and *M mulatta*, have disparate atlantooccipital flexion-extension ranges of only 1.5° and 32°, respectively, with *Saimiri* falling in between them at 19° ±15° (Graf et al., 1995). Humans, in comparison, have ~25-30° of flexion-extension at the atlantooccipital joint (White and Panjabi, 1990; Panjabi et al., 1991). The human atlantoaxial joint has a range of flexion-extension of 20° and can rotate 40°; its lateral flexion is negligible (White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008). Graf and colleagues (Graf et al., 1995) showed that the flexion-extensions range of motion of *Macaca* is between 1-3° while that of *Saimiri* is 16°. The range of flexion-extension for cats and rabbits is roughly 20° and guinea pig is greatest at 39° (Graf et al., 1995). Domestic dogs range from 15-35° in flexion (Penning and Badoux, 1987).

Do these differences in range of motion relate to cervical vertebral form? It is difficult to draw general conclusions about the relationship between mammalian cervical form and cervical function from a study of very few individuals from a scatter of mammalian species. Aiello and Dean (2002) suggested that the concavity of the atlantooccipital joint reflects range of motion, but Manfreda and colleagues (2006) indicated that joint curvature may correlate with locomotor mode. In a geometric morphometric study, Manfreda et al. (2006) correlated atlas morphology to locomotor categories and body size. Their analyses show some differences in overall atlas shape based on the type of habitual locomotion. The articular facet angle in nine species of primate varies between the curved facets (109°) in *Papio* and *Ateles* and the flatter facets (145°) of *Homo sapiens*. However, this variation in curvature fails to correlate with locomotor mode frequencies. Nalley and Grider-Potter (2017) have also investigated the function of atlantooccipital joint curvature. They related the curvature to Strait and Ross' (1999) measure of neck posture during locomotion. Specifically, they found that the atlantooccipital joint tends to be more curved in species with more pronograde neck postures (Grider-Potter and Hallgren, 2013; Nalley and Grider-Potter, 2017).

Other aspects of atlas morphology are also functionally relevant. Within primates, the posterior arch becomes more robust with increasing body size (Manfreda et al., 2006). In addition, other dimensions of the anterior and posterior arches and transverse process length have an isometric relationship with body and head size. This increase in robusticity is likely related to the relative increase in size of nuchal muscles as well as the increased forces associated with supporting a heavier head (Nalley and Grider-Potter, 2017). It is important to note, however, that body mass affects the locomotor repertoire of an animal. For example, smaller-bodied primates tend to locomote above branch while larger-bodied primates locomote below branch (Doran, 1993, 1997; McGraw, 1998). Therefore, these observed changes could relate to locomotor or postural differences inherent in large or small-bodied primates. For example, The transverse processes also become inclined more cranially with increasing body mass in primates (Manfreda et al., 2006).

The vertebral arteries pass through the transverse processes via the transverse foramina ubiquitously present in C1-C6 and thus, the morphology of these structures likely influences arterial function. Though arteries are elastic, arterial blood flow between the human atlas and axis significantly diminishes after 30^o of rotation contralaterally and 45^o ipsilaterally (White and Panjabi, 1990). Notably, *Tarsius* can rotate its head 180^o on its trunk. Ankel-Simons and Simons (2003) attribute this ability to the unusual coronal orientation of its zygapophyseal joints. Looking outside Mammalia, owls also have extreme degrees of axial rotation and they possess several anatomical adaptations to accommodate this behavior (Kok-Mercado et al., 2013). Their transverse foramina, for example, are roughly ten times larger than the vertebral artery passing through them. Additionally, their carotid arteries anastomose in the hypophyseal fossa above the sphenoid allowing significant collateral flow from the unobstructed vertebral artery, preventing the cessation of blood flow during extreme rotation (Kok-Mercado et al., 2013). Tarsiers show similar adaptations: their C1 foramen is relatively larger and their vertebral arteries have much smaller cross-sectional areas throughout the cervical column (Nalley and Grider-Potter, 2015; Nalley et al., 2019).

The atlantoaxial joint is composed of two paired zygapophyseal joints and the medial dens facet. The zygapophyseal joints are slightly convex dorsoventrally, and are stabilized by the articular capsules, which are elastic in order to facilitate ranges of motion (White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008). The dens is anchored to the anterior arch by the transverse ligament of the atlas which runs between its left and right tubercles. Superiorly, the apical ligament of the dens attaches to the ventral aspect of the foramen magnum (Jenkins, 1969; White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008). Its elastic nature implies that it may not significantly aid in stability (White and Panjabi, 1990). The alar ligaments run between the dorsolateral surface of the dens and the medial portion of the occipital condyle. These ligaments serve to limit rotation (Jenkins, 1969; White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008).

Many of the morphologies found in the axis correlate with both body size as well as Strait and Ross's (1999) measure of neck inclination. Dimensions of the C2's pedicle and lamina are strongly and isometrically correlated with skull geometric mean to the exclusion of neck inclination. The C2 spinous process length also does not correlate with neck inclination as it does in the lower cervical levels (Nalley and Grider-Potter, 2015, 2017). Perhaps this result is not surprising given that few nuchal muscles attach to the spinous process or laminae of the axis. Axis spinous process length does, however, have a positively allometric relationship with body mass. Both the angle of the dens and the angle of the superior articular facets correlate with neck inclination. As the neck becomes increasingly vertical, the dens becomes more dorsally inclined. This angle results in the neutral orientation of the C0 and C1 to be more dorsally oriented, which better supports the head by positioning it over the neck. As neck posture becomes more horizontal, the articular facets become more caudally oriented. The flatter facet found in primates with more orthograde necks may be an adaptation to withstanding the increased compressive forces of gravity (Nalley and Grider-Potter, 2017).

1.3 Lower Cervical Spine Form and Function

Eutherian lower cervical vertebrae comprise two components: the centrum and the neural arch (Fig. 1.3). This composition is highly conserved within the mammalian clade, unlike other vertebrates. The exception to this conservation is the presence of uncinate processes on the cranial aspect of the centrum, which are found in the occasional marsupial, some rodents, and most primates (Hall, 1965). The raised sides of the centrum form a saddle-shape joint unique to cervical vertebrae. In humans, uncinate processes project most markedly in C3-C5 and sequentially decrease in height from C6-T1 (Milne, 1991). These uncinate processes inhibit true lateral flexion, instead necessitating rotation and extension at the joint to laterally flex the neck (Kapandji, 2008). Within primates, the great apes have the largest uncinate processes (Toerien, 1961; Hall, 1965). In humans, width of the vertebral body and laminae has been shown to increase from C2 to C7 (Gaughran, 1954; Milne, 1991). Facet width and vertebral body size are also thought to play a role in resistance to lateral flexion (Milne, 1991)or the ability to bear greater load in more orthograde postures (Cartmill and Brown, 2014).

Between adjacent vertebral bodies are the intervertebral discs. These structures resist compressive forces and permit movement. Bending forces that likely occur in the pronograde are counteracted by the tension produced by the vertebral ligaments in order to maintain posture (Slijper, 1946; Jenkins, 1969; Putz, 1992; Preuschoft and Gunther, 2012). Discs have three major components: the central nucleus pulposus, the surrounding annulus fibrosis, and the cartilaginous end plates. The nucleus pulposus is gelatinous and contains 70-90% water (White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008). Between these structures and the vertebral body lies the cartilaginous end plate adhering the layers to each other (White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008). Dissection of macaque spines revealed that the craniocaudal height of the nucleus pulposus increases caudally (Longo et al., 2006). However, in humans the nucleus pulposus is thickest in the lumbar region but thinnest in the thoracic region (Cramer, 2013). This variation in thickness is unexpected. Axial loading increases caudally in orthograde postures due to body mass (Boszczyk et al., 2001; Cartmill and Brown, 2014). Thus, one would expect thickness to increase caudally in order to combat increased axial loading. Further study is required to understand how the thoracic region is compensating for relatively thin discs. Gál (1993a) found that the nucleus pulposus varies in position within mammals and is typically located slightly dorsal to the center of the vertebral body. In humans, the cervical nucleus pulposus is located centrally while its more dorsal in the lumbar region. Peripherally, the concentric layers of the annulus fibrosus are composed of obliquely alternating fibers. The annulus fibrosis is thickened ventrally in terrestrial mammals, likely indicating a habitual loading regime (Gál, 1993a).

The neural arches are predominately sites of muscular attachment and often act as bony levers (White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008).

Because of their function, the neural arch structures are of particular interest to functional morphological studies. The pedicles are struts connecting the centrum to the neural arch. As struts, they are thought to transmit compressive loads between the neural arches and the vertebral bodies, especially when the pedicles are oriented parallel to the line of gravity (Pal and Routal, 1986). Because of this, their cross-section areas increase from the first thoracic vertebra to the last (Shapiro, 1993a) and cross-sectional area positively scale with body mass (Shapiro, 1993a; Nalley, 2013).

The transverse processes are also largely sites of muscular attachment, particularly for muscles that laterally flex the neck. In the mid-cervical column, the transverse processes have an anterior root and a posterior root surrounding the transverse foramina. The anterior root of the transverse process branches from the root of the pedicle. The anterior root of the C3 transverse process is oriented at a 60^o angle from the sagittal plane and a 15^o angle from a transverse plane in humans (Kapandji, 2008). Soricid, or shrew, transverse processes are more craniocaudally oriented in C3 and progressively become more ventrodosally inclined in C7 within the cervical column (Gaughran, 1954). It is likely that this orientation is associated with the direction of the force vectors of the muscles attached to it (Slijper, 1946; Shapiro, 1995; Pierce et al., 2011), and thus, variation in orientation should reflect functional differences. The posterior root of the transverse process originates from the pillar of the articular facets. The two roots are bridged by superiorly concave groove on top of which lies the spinal nerve. Both the posterior and anterior roots contain tubercles that serve as attachment sites for the scalene muscles (Kapandji, 2008). In most primates, C2-C7 possess transverse foramina through which the vertebral arteries pass. This foramen is occasionally bipartite primates. In a small percentage of human C2 (3-5%), the transverse foramen is incomplete, or open. This anomaly is not known to occur in other primates. The lack of transverse foramen is much more common in C7, especially in humans (Rios et al., 2014). The presence of the anterior root of the transverse process at C7 seems to vary phylogenetically; it is absent in strepsirrhines, possessed by few platyrrhines, and habitually present in catarrhines (Rios et al., 2014).

Immediately posterolateral to the pedicle is the pillar of the articular facets. Human cranial and caudal articular (zygapophyseal) facets on the pillar are angled at between 30°-50° relative to the ventral vertebral body margin. The facets become increasingly more dorsal as they approach the cervicothoracic border (Harrison et al., 2005). The orientation of these zygaphophyseal joints affects their ranges of motion (Slijper, 1946; Milne, 1991; Russo, 2010; Pierce et al., 2011). It has been suggested that the more cranial orientation of upper cervical articular facets is associated with larger ranges of motion within the joints of C1 and C2 (Milne, 1991), but empirical studies do not suggest a significant craniocaudal gradient in range of motion (White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008). This pattern of increasingly dorsal facets holds true for most, if not all, primates (Toerien, 1961).

Variations in articular facet orientation do not appear to affect the degree cervical lordosis, at least in humans (Harrison et al., 2005). Gommery (2000) posits that the orientation of the superior articular facets of the axis significantly contribute to a lordotic cervical spine. This lordosis is thought to increase spinal flexibility and its capacity for shock absorption (White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008). The caudal articular facet of a cranial vertebra abuts the cranial articular facet of the caudally adjacent vertebra. A capsular ligament unites these articular facets to form a zygophophyeal joint and is generally looser in the cervical region than the thoracolumbar portion of the spine (White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008). These joints also transmit loads through the vertebral column (Pal and Routal, 1986; White and Panjabi, 1990; Shapiro, 1993a). The orientation of these joints throughout the spine reflects the types of motion that can be accommodated and how much load they can dissipate (because the load must be normal to the joint surface). The craniodorsal positioning of cervical articular facets facilitates flexion-extension, lateral flexion, and axial rotation (Milne, 1991; Kapandji, 2008). Whereas the dorsoventral orientation of the thoracic facets generally facilitates lateral flexion and rotation and the mediolateral orientation lumbar facets restricts much of the motion to flexion-extension (White and Panjabi, 1990; Kapandji, 2008).

Human C4-C5 and C5-C6 zygopophyseal joints generally have large ranges of motion: 20° of flexion-extension, 10° of lateral flexion, and 7° of axial rotation (White and Panjabi, 1990; Bogduk and Mercer, 2000; Mercer and Bogduk, 2001; Kapandji, 2008). Though each zygophphyseal joint has its own average range of motion, one joint rarely, if ever, moves in isolation. As previously discussed, the spine can be functionally subdivided into motion segments: C0-C2, C2-C5, C5-T1, and T1-T4. During human lateral flexion and rotation, these segments tend to move as a unit (White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008). These motion segments are important because they indicate the that the greatest ranges of lateral flexion and rotation should be found in the C2, C5, and T1 joints. During flexion the cranial vertebra translates ventrally and angles cranially, leaving a gap on the dorsal side of the joint. The posterior longitudinal ligament runs along the dorsal surface of the vertebral bodies, within the vertebral canal. This position allows the ligament to impede cervical flexion. Conversely, extension occurs predominately through caudal angular motion and slight dorsal translation, creating a gap at the ventral portion of the joint surface. Extension is inhibited by both the anterior longitudinal ligament. Collision of the spinous process of the superiorly adjacent vertebra has also been shown to inhibit extension in the lower cervical spine (Kapandji, 2008). Most agree that lateral flexion and axial rotation are coupled (White and Panjabi, 1990; Mercer and Bogduk, 2001; Kapandji, 2008). There is debate to whether the orientation of the articular facets (Milne, 1991; Kapandji, 2008) or the uncinate processes (Mercer and Bogduk, 2001) restrict pure lateral flexion and rotation.

Medial to the articular pillars, forming the dorsal margin of the bony vertebral canal, are the laminae, to which many of the neck muscles attach. These plank-like structures serve as attachment sites for the ligamenta flava, which occupy the area between adjacent laminae. This ligament has a resting tension which slightly compresses the intervertebral disc, potentially offering stability (White and Panjabi, 1990). It also functions in resisting flexion and rotation (Putz, 1992; Kapandji, 2008). The laminae meet medially where the spinous process originates. In humans, the spinous process is bifurcated in C3-C6 with interspinous ligaments running between them, with which the supraspinous ligament is continuous. The interspinous ligaments appear particularly elastic in monkeys in comparison to humans (Slijper, 1946). This is of interest because musculo-ligamentous variation among primate spines is relatively understudied. If little significant differences are found between skeletal form and function, then soft tissues are the next avenue to explore.

It is likely that the inclination and length of the spinous process is indicative of the magnitude and direction of the forces produced by associated nuchal muscles. Most primate spinous processes tend to lengthen from C3 to C7, within an individual. Apes tend to have relatively longer spinous processes than other primates (Toerien, 1961; Shapiro, 1993a). Additionally, the inclination of the spinous process relative to the ventral surface of the vertebral body tends to about perpendicular. More cranial inclinations are seen *Gorilla*, *Macaca*, and *Papio*. Notably, *Homo* and *Alouatta* exhibit the most cranially inclined cervical spinous processes (Toerien, 1961). Toerien (1961) has also observed a rough correlation between the changes in spinous processes inclination and articular facet orientation within a vertebral column, but more recent, empirical studies have yet to be conducted.

The nuchal ligament runs craniocaudally from the external occipital protuberance and crest along the cervical spinous process and terminates at the seventh cervical vertebra in humans–the first thoracic in ungulate and canids (White and Panjabi, 1990; Mercer and Bogduk, 2003; Konig and Liebich, 2006; Lieberman, 2011). The nuchal ligament does not appear to be present in non-human primates. Old World monkeys have a midline raphe that seems to be less robust than the human ligament (Choi, Keshner, and Peterson 2003a, unpublished dissections). Histologically, however, the human nuchal ligament is much more raphe-like than the robust ligament found in ungulates (Johnson et al., 2000; Mercer and Bogduk, 2003). In humans, the nuchal ligament serves as an attachment site for cranial trapezius, rhomboid minor, splenius capitis, and serratus posterior superior. This ligament is thick and elastic; it largely functions in maintaining head stability and is likely important during rapid locomotion (Rhodin, 2008; Lieberman, 2011). Takeshita and colleagues (2004) conducted an empirical study using human cadaveric spines. By resecting the nuchal ligament, they found that cervical spines exhibited larger ranges of flexion and decreased stiffness, indicating that the ligament provides stability to the cervical spine during flexion (Takeshita et al., 2004). The ligament's evolution within the hominin lineage could be related to maintaining head stability during running. If this is the case, reduced flexion may simply be a by-product of selection for the nuchal ligament. To the exclusion of humans, apes lack a well-developed nuchal ligament (Lieberman, 2011). Its absence in most mammals suggests independent evolution within *Homo*, Ungulata, and Canidae

(Slijper, 1946) but whether it is an adaptation to reducing head movement during locomotion in all these taxa is unclear.

1.4 Maintenance of Head Stability during Locomotion

Maintaining balanced, relatively immobile head (i.e. head stability) is a crucial component of locomotion as the head houses the organs involved in spatial orientation, navigation, and whole-body balance. Primates also normally adjust their visual fields to reflect the orientation of the substrate, or suprastrate (Strait and Ross, 1999; Hirasaki and Kumakura, 2004; Stevens and Heesy, 2013). The maintenance of head posture is related to vertebral form (Nalley, 2013). Somewhat simplistically, the head has been modeled as a lever with the atlantooccipital joint as the fulcrum (Demes, 1985). The force of the neck muscles, the weight of the head, and the lengths of both the moment and load arms affect balance of the head. Decreasing the length of the face can shorten the load arm while moving the atlantooccipital joint rostrally moves the head's center of mass closer to the fulcrum, creating a scenario where the head is balanced with relatively little muscular force (Fig. 1.2). While load arm length is important to understanding head balance, head center of mass is also useful. Within the first class lever model, the closer the center of mass is to the fulcrum, the less muscular effort is needed to maintain balance.

Under this head-balancing model, taxa with more projecting faces (longer load arms) require greater torque to maintain head balance (Demes, 1985; Jaanusson, 1987; Nalley, 2013). Research suggests that cervical vertebral morphology is adapted to maintaining balance of a head in more prognathic species. For example, greater laminar cross-sectional area is likely an adaptation to increased bending loads associated with larger muscle forces. Longer spinous processes lengthen the moment arm, thereby increasing the mechanical advantage. Longer spinous processes may also increase the area available for muscular attachment, potentially increasing the muscular cross-sectional area (Nalley, 2013; Nalley and Grider-Potter, 2015). Other adaptations to increased muscular effort, such as a greater craniovertebral area for muscular attachment, should also be found in more pronograde species but this hypothesis has yet to be tested.

This traditional head-balancing model fails to take into account the effects differences in posture or locomotion may have on head balance. Slijper (1946) modeled the cervical spine as a bow and string. The vertebral column acts as the bow, with vertebral positions maintained through the tension of the string (the muscles and ligaments). The amount of tension required differs between orthograde and pronograde primates. Orthograde primates require less muscular effort to maintain head balance than pronograde primates because neck muscles are advantageously oriented to counteract the vertical force of gravity. Human heads are unique among primates in that they are aided by the nuchal ligament, which helps maintain balance with little muscular effort. In pronograde primates, the cervical spine is oriented perpendicular to the force of gravity. This position is less mechanically advantageous than the orthograde condition; it requires greater muscular force to maintain the appropriate orientation of the head. Thus, both facial projection and posture should influence the muscular effort needed to maintain head stability. This, in turn, will affect basicranial and cervical vertebral morphology.

Using this biomechanical model, Nalley and Grider-Potter (2015, 2017) found correlations between Strait and Ross's (1999) measure of neck posture and cervical vertebral morphology. As previously discussed, Strait and Ross (1999) measured the dorsal inclination of the superficial neck during locomotion in several species of primate. These data are valuable in that they provide a quantified measure of neck function during locomotion. Nalley and Grider-Potter (2015, 2017) found that spinous process are relatively longer in primate species with more pronograde neck postures. In addition, more pronograde species tend to have laminae with greater cross-sectional areas. We conclude that longer spinous processes offer greater mechanical advantage to the nuchal muscles and more robust laminae better resist higher muscular loads. More pronograde postures require greater muscular effort to maintain and, thus, the cervical spine shows adaptations to mitigating those forces. In addition, the study found that articular facets are more coronally oriented in species with more pronograde neck postures. It is possible that this orientation functions in load transmission along the neural arch. This relationship, however, was only significant in C4 and C7. There was also a significant relationship between vertebral body height and posture. More pronograde species tend to have taller vertebral bodies, which could aid in lordosis formation or

In addition to the morphology and orientation of the head and neck, the thoracolumbar spine should also affect how head stability is maintained. Previous research has variation among the movement of the head and trunk in primates (Dunbar, 2004a; Hirasaki and Kumakura, 2004; Dunbar et al., 2008; Xiang et al., 2008; Thompson, 2016). Because the movement of the trunk differs between primates (Dunbar, 2004a; Dunbar et al., 2008; Xiang et al., 2008) and the position of the head varies with substrate position (Strait and Ross, 1999; Stevens and Heesy, 2007), how the neck maintains head stability should covary. In turn, the cervical spine should be adapted to maintaining a relatively immobile, balanced head during locomotion. As primates are highly variable in the postural habits and locomotor modes, they are the ideal subjects to test this hypothesis. The function of the neck during locomotion is poorly understood. Elucidating its function in extant primates and relating that function to the morphology of the cervical vertebrae will allow us to retrodict the neck function and its evolution in fossil hominins.

1.5 Fossil Primate Vertebral Morphology

Most early hominin vertebrae are described as ape-like rather than *Homo*-like (Coroner and Latimer, 1991; Gommery, 2000; Kikuchi et al., 2012). Many cervical elements are rarely pictured or described in the literature making superficial evaluation of morphology and preservation difficult. For example, ASI-VP-2 from *Australopithecus anamensis* (White et al., 2006), DIK-1-1 *Australopithecus afarensis* (Alemseged et al., 2006), SKW 3342 and KNM-ER 164c from *Homo sp*. (Day and Leakey, 1974; Susman et al., 2001), and several specimens from *Homo antecessor* (Carretero et al., 1999) have been reported in the literature have yet to be described or published with an informative photograph.

Several *Australopithecus* cervical vertebrae are well known in the literature: A.L. 333-83, A.L. 333-101, A.L. 333-106, SK 4776 and SKW 854. The atlas belonging to *Australopithecus afarensis*, A.L. 333-83, preserves the right articular facets, lateral mass, and a fragment of the posterior arch and dates to ~3.2mya. Notably, the atlantooccipital joint has a highly curved, apelike morphology (Coroner and Latimer, 1991; Gommery, 1996; Aiello and Dean, 2002) which could potentially indicate a more pronograde neck posture (Nalley and Grider-Potter, 2017). A more pronograde neck posture is unexpected in hominins because it is assumed that neck orthogrady likely co-evolved with trunk orthogrady and bipedal locomotion. The implications of the curved atlantooccipital joint present a puzzle. Axes A.L. 333-101 and SKW 854, *A. afarensis* from Hadar and *A. robustus* from Swartkrans respectively, are somewhat damaged. The fossil atlantooccipital joints are more curved than humans but are flatter than chimpanzees, with that of A.L. 333-101 falling within the lower range of variation for humans (Gommery, 2006). The 2mya SK 4776 from *A. robustus* is likely C3 or C4 and seems to be most similar to *Pan*. A.L. 333-106 is most likely the sixth cervical vertebra morphologically most similar to *Pan* with a long spinous process and large cross-sectional area of the spinous process (Nalley, 2013).

Recently, field work at Woranso-Mille, Ethiopia recovered a nearly complete (C2-C7) australopith cervical column (Meyer, 2016) dating to ~3.5mya (Haile-Selassie et al., 2016). Overall, the KSD-VP-1/1 vertebrae show a mixture of human-like and ape-like morphologies. In particular, the vertebral bodies of the lower levels are absolutely larger than both the human and the slightly younger A.L. 333 material. Their whole-vertebra geometric means are more similar to that of *Gorilla* (Meyer, 2016). This is unexpected because as a weight-bearing structure vertebral body size correlates strongly with body mass and *Australopithecus* was much smaller than extant *Gorilla*. However, vertebral canal area, another variable strongly correlated with body mass (MacLarnon, 1995), is more similar to humans than it is to gorillas and chimpanzees. Relative centrum height of the australopith specimens is more similar to humans than to the great apes, unlike the C6, A.L. 333-101. The vertebral bodies also possess wedging in similar degrees to that found in other hominoids (Meyer, 2016) but intervertebral discs likely play a greater role in creating cervical lordosis than bony morphology (Johnson and Shapiro, 1998) and thus reconstructing cervical lordosis in fossil species is difficult. In addition, these vertebrae preserve low, human-like uncinate processes. These low margins potentially facilitated ranges of rotation and lateral flexion greater than that found in other great apes (Meyer, 2016) but cervical ROM has not been measured in non-human apes.

Four cervical specimens of *Australopithecus sediba* dating to ~2mya have also been recently described by Meyer and colleagues (Meyer et al., 2017). The overall size is smaller than humans both absolutely and relative to the reconstructed body mass. It is difficult to interpret the implications of such a result given the combination of the subadult and adult specimen in both the vertebral analyses as well as the body size reconstruction. The spinous processes appear shorter than chimpanzees, the facets are angled acutely (relative to midline), and uncinate processes are tall and sharp, and the anterior tubercle of the transverse process is robust (Meyer et al., 2017). Similar to other hominin specimens, *A. sediba* preserves a mosaic morphology of ape-like and human-like features, suggesting differences in cervical function. Following Nalley and Grider-Potter (2015), one could interpret the short spinous processes and vertebral bodies as evidence of orthograde posture. Incorporating these fossils into a broader data set could further elucidate behaviors of extinct species.

1.6 Research Goals

This dissertation aims to build upon previous work to elucidate many of the numerous functions of the neck, understand how these functions influence vertebral morphology, and retrodict those functions within the hominin lineage. Specifically, it explores 1) maximum ranges of motion of the primate head and neck and 2) locomotor kinematics of the head, neck, and trunk and their influence on vertebral form. Why does human cervical morphology diverge so significantly from that of other primates? If the neck has a significant locomotor function, then can we attribute this divergence to the advent orthograde posture necessitate by the reliance on habitual bipedality? If, on the other hand, facilitating head mobility is a driving selective force on cervical form, then can variation in cervical morphology be attributed to intervertebral ranges of motion.

The following chapters of this dissertation test the hypothesis that head stability and head mobility both influence cervical form. This hypothesis is tested using two specific aspects of neck function in primates: passive range of motion (i.e. facilitating head mobility) and locomotor kinematics (i.e. maintaining head locomotor stability). The first study investigates the relationship between maximum ranges of head and neck motion and cervical morphology. After establishing these baseline maximum ranges of motion (ROM), the second study will attempt to understand the influence of range of axial motion during habitual locomotion on cervical morphology.

Vertebrae may be adapted to the most frequent modes of locomotion as they are the most consistent loads the bones must withstand. It is also possible that the vertebrae are adapted to rare but critical loading regimes associated with activities such as predator vigilance that require full ranges of motion. Here, both the habitual ROMs associated with locomotion as well as the behaviorally rarer maximum ROMs will be quantified. It is expected that the species will not use its maximum ROM during locomotion but that there will be greater absolute mobility in species that rely on that particular ROM during locomotion (e.g., if a gibbon relies on significant degrees if rotation during locomotion will also have a large range of maximum rotation) in order to prevent soft tissue damage or joint dislocation. Vertebral morphology is likely a compromise between many different functions. Balancing the head is likely just as important, if not more so, as allowing head mobility. As such, morphologies affecting head balance will also be tested. Overall, this dissertation attempts to understand the functional influences on vertebral form in the hopes of shedding light on anomalous shape of human cervical vertebrae and their evolution within the hominin fossil record.

1.7 Hypothesis and Predictions

This dissertation is divided into two distinct studies that test how the degree to which the vertebral shape is influenced by facilitating head mobility and providing head stability. The first study tests the degree to which cervical vertebrae are adapted to facilitating or inhibiting maximum ranges of motion. For example, protruding bony processes can offer greater mechanical advantage but could potentially collide in maximal positions. From this hypothesis stem several predictions:

P1a: Spinous processes physically inhibit extension (Kapandji, 2008). Therefore, I predict that spinous processes will be shorter in vertebral levels with greater maximum ranges of extension (see Fig. 1.5).

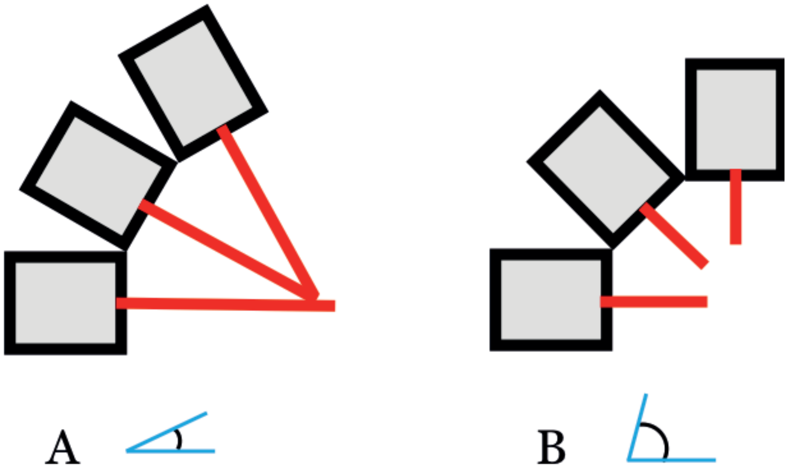

Figure 1.5 Long vertebral processes (red, A) should collide at maximum ranges of motion, inhibiting range of motion but short vertebral processes will not, Predictions 1a and 1b

P1b: Transverse processes will be both shorter and more cranially inclined in vertebral levels with greater ranges of lateral flexion. Long transverse processes should physically inhibit lateral movement, but more cranially oriented processes should provide greater mechanical advantage for the lateral flexors of the neck (see Fig. 1.5).

P1c: Uncinate processes are known to physically inhibit lateral flexion (Kapandji, 2008). Thus, vertebrae with taller, more medially-oriented uncinate processes will have smaller ranges of lateral flexion (see Fig. 1.6).

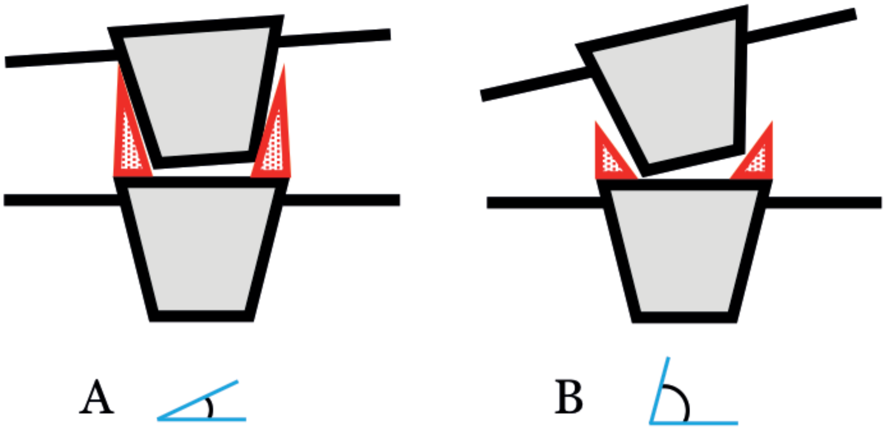

Figure 1.6 Tall uncinate processes (red, A) should inhibit large ranges of lateral flexion in comparison to shorter processes, Prediction 1c.

P1d: Relatively larger joint surfaces should be associated with an increased the range of motion at those joints. Thus, cranio-caudally taller articular facets should facilitate greater ranges of flexion (see Fig. 1.7).

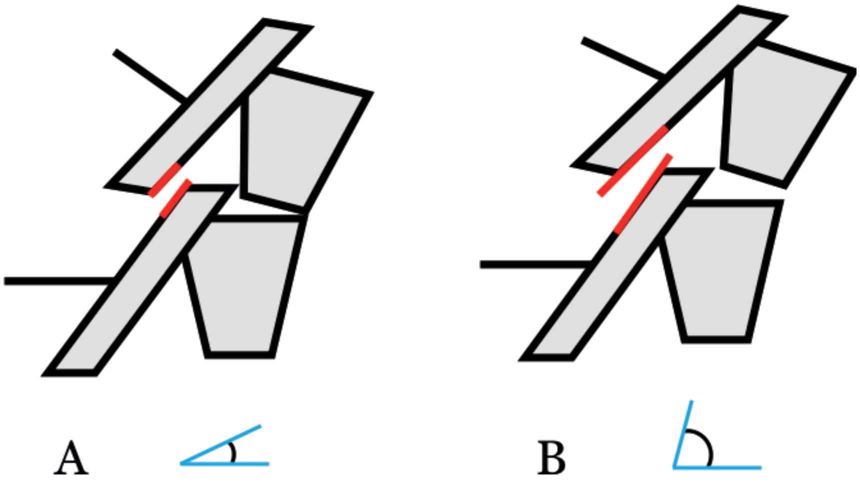

Figure 1.7 Craniocaudally shorter articular facets facilitate lesser ranges of flexion (red, A) in comparison to taller facets, Prediction 1d.

P1e: Craniocaudally short vertebrae decrease the overall displacement of the vertebral column (Ward, 1993; Breit and Künzel, 2004). Therefore, the range of whole-neck flexion-extension will be greater in species with craniocaudally taller vertebral bodies (see Fig. 1.8).

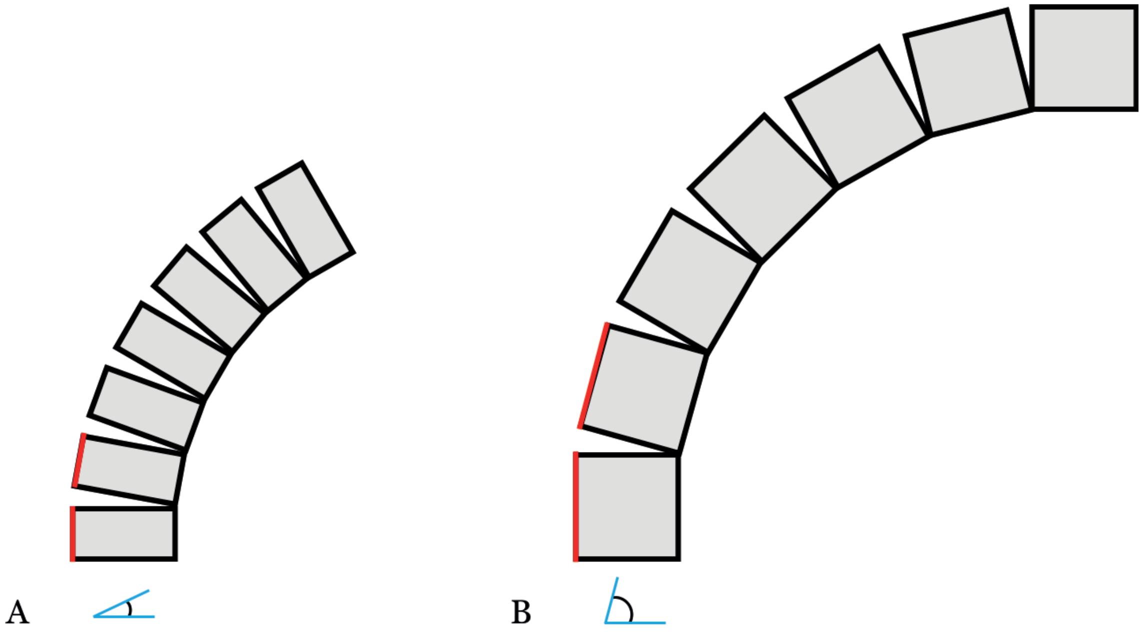

Figure 1.8 After Ward (1993), craniocaudally tall vertebral bodies (B), should facilitate large ranges of flexion-extension in comparison to shorter vertebral bodies.

P1f: Greater curvature in 'female' joint surfaces (e.g., acetabulum and lunate bone) should be associated with increased range of motion and multidirectional loading (Hamrick, 1996; Aiello and Dean, 2002). Therefore, greater curvature in the caudal portion of the atlantooccipital joint (i.e. smaller angular relationship between the ventral and dorsal aspects of the facet) should correspond to larger ranges of flexion-extension at that joint (see Fig. 1.9).

These predictions will be tested by comparing morphological measurements of cervical vertebrae and to their joint ranges of motion.

Figure 1.9 Joint curvature should correlate with habitual, normal loading of the joint surface, and therefore, the range of motion the joint can accommodate. Large curvature (B) should be associated with large range of motion, Prediction 1f.

The goal of the second study is to understand the locomotor function of the neck and how that function influences cervical vertebral morphology. Specifically, how does the neck function in maintaining head balance.

P2a: Trunk kinematics vary among species during locomotion. In order to maintain head stability, variation in trunk kinematics will, in turn, affect neck kinematics. Therefore, trunk movement during a stride will correlate with neck movement, but not head movement.

P2b: Trunk kinematics varies among species during locomotion. In order to maintain head stability, this variation will, in turn, affect neck kinematics. Therefore, trunk movement during a stride will correlate with neck movement, but not head movement.

P2c: If head stability is the goal and the neck's function is to counteract the movements of the trunk in order to maintain that stability, then there should be a proximodistal decrease in locomotor range of motion in each axial segment (i.e., head<C3<C5<C7<T1) in all species regardless of locomotor mode.

P2d: Trunk kinematics varies among species. Therefore, head-neck angular kinematics should covary with trunk angular kinematics. As locomotor trunk range of motion increases, so should neck range of motion in order to counteract the movement of the trunk and maintain head stability.

These predictions will be assessed using axial kinematic data collected from four species of lemur during their primary modes of locomotion (see Table 2.6).

The second set of predictions will also be tested using locomotor range of motion in order to understand the degree to which cervical vertebral morphology is adapted to facilitating ranges of motion during locomotion. By incorporating both maximum and locomotor ranges of motion, I will compare how both rare (but potentially vital) and frequent behaviors shape vertebral morphology. This hypothesis will be tested using the same set of predictions as the passive ROM study (e.g. **P1a**=**P3a**) with the addition of another:

P3g: Articular facets will be oriented more cranially (i.e. more parallel with the cranial surface of the vertebral body) in species with larger ranges of rotation. The effects of articular facet orientation on ROM are known within the human vertebral column (White and Panjabi, 1990). A cranially oriented facet, like that found in the joint between C1 and C2, facilitates larger rotational ROM while a facet that is oriented parallel with the dorsal surface allow larger ranges of rotation. As it is difficult to measure rotation using radiographs (Graf et al., 1995), this prediction cannot be tested with maximum intervertebral rotation.

These predictions will be tested using the kinematic data of axial segments during habitual locomotion from four species of lemur and comparing it to cervical morphology. If both maximum and locomotor ROM are significantly correlated with the strength of each influences will be compared using AIC values gather from the statistical models. These hypotheses will be rejected if no significant correlations are found between cervical form and neck function, at a significance level of $p>0.05$. Particular attention will be paid to the pattern of significance. For example, if only one vertebral level correlates with a specific functional measure, the results will be interpreted with greater caution than a correlation that is found in all vertebral levels. If locomotor ROM predictions are supported but ROM predictions are rejected (or vice versa) then the I would conclude that habitual loading regimes more strongly influence vertebral form than rarer behaviors. If both locomotor and maximum ROM predictions are rejected, future investigations into muscle and ligament morphology and properties would likely prove beneficial as it is possible that soft tissues more strongly influence vertebral ROM than skeletal morphology. If both ROM and head balancing predictions are supported, then corrected Akaike Information Criterion (AICc) values will be calculated for each analysis and used to determine what function the morphology best predicts. AICc values are commonly used to determine which model best fits the data. Significant results will then be used to interpret the morphology found in fossil primate specimens.

Chapter 2 Materials and Methods

2.1 Morphological data

To test these hypotheses, both morphological and functional data were collected. Morphological data were collected from 676 vertebral specimens (C1-T1) of 15 primate species housed at the American Museum of Natural History (New York, New York), National Museum of Natural History (Washington DC), Muséum national de'Histoire naturelle (Paris, France), and Field Museum of Natural History (Chicago, IL) (see Table 2.1 for complete list). Taxa were chosen in order to complement the functional data collected for this study as well as those available from the literature. Chosen species encompass the diverse range locomotor repertoires, and postural habits found in extant primates. Maturity of individuals was determined based on the fusion of annular rings; only adult specimens were used in the analyses. Because all functional data came from captive individuals, no attention was paid to the geographic origin of the specimens.

Table 2.1 Species used in the morphological analyses and the number of individuals

Species	**n**
Lemur catta	7
Eulemur mongoz	6
Varecia variegata	9
Propithecus verreauxi	9
Otolemur crassicaudatus	8
Macaca fascicularis	7
Macaca fuscata	2
Macaca mulatta	15
Sapajus apella	8
Saimiri sciureus	9
Hylobates lar	8
Pan troglodytes	13
Homo sapiens	6

Morphometric data were collected from surface scans of skeletal museum specimens using an Einscan 3Ds (Shining 3D) white-light scanner. This scanner was chosen for both its economy and accuracy (<0.05mm). Landmarks were taken from these three-dimensional surface scans using the Rhinoceros (McNeel & Associates) CAD software. Landmarks of interest were placed on scans and lengths measured between these landmarks (see Fig. 2.1, Table 2.2). These data were complemented by digitized 3D coordinate data collected from skeletal specimens using a Microscribe digitizer (Immersion Corp.). The landmarks were then used to measure the morphologies of interest (see Fig. 2.1, Table 2.3). In some cases, mostly C6, the vertebrae have both posterior and anterior transverse processes. In this case, the anterior transverse process was used for analysis because it is almost universally the longer and more robust of the two. Measurements were taken from the left side unless absent or degraded; then, the right side was used.

Table 2.2 Description of skeletal landmarks digitized for morphological analyses.

Landmark	Level	Description
1	C1-T1	Dorsal-most extent of the spinous process; In the case of bifurcated spinous processes, the point was taken on each bifurcation and the midpoint between the two used
2	C1-T1	Cranial-most aspect of the lamina, midway between the articular pillar and spinous process
3	C1-T1	Dorsal-most aspect of the lamina, midway between the articular pillar and spinous process
4	C1-T1	Caudal-most aspect of the lamina, midway between the articular pillar and spinous process
5	C1-T1	Ventral-most aspect of the lamina, midway between the articular pillar and spinous process
6	C1-T1	Cranial-most aspect of the transverse process
7	C1-T1	Lateral-most aspect of the transverse process
8	C1-T1	Dorsal-most extent of the vertebral canal
9	C1-T1	Ventral-most extent of the vertebral canal
10	C1-T1	Lateral-most extent of the vertebral canal, bilateral
11	C1-T1	Cranial-most extent of the joint surface of the superior articular facet
12	C1-T1	Caudal-most extent of the joint surface of the superior articular facet
13	C2-T1	Cranioventral-most extent of the vertebral body
14	C2-T1	Caudoventral-most extent of the vertebral body
15	C3-T1	Points along the margin of the cranial plateau of the vertebral body, excluding uncinate processes
16	C3-T1	Cranial-most extent of the uncinate process
17	C2	Cranial-most extent of the dens, or odontoid process
18	C1	Ventral-most extent of the joint surface of the superior articular facet
19	C1	Point of greatest curvature between the two aspect of the superior articular facet
20	C1	Dorsal-most extent of the joint surface of the superior articular facet

Figure 2.1 Landmarks taken from vertebral specimens. C1 (left), C2 (center), and lower cervical (C4, right) of Lemur catta. See Table 2.2 for description. Colors correspond to linear measurements taken (see Figure 2.2).

Angular measurements were taken relative to the plane created by 8-12 points along the margins of the cranial surface of the vertebral body for C3-T1. Because C2 lacks this cranial surface, its angular measurements were taken relative to a line between the inferior-most and superior-most aspect of the vertebral body on the ventral surface at midline. The atlas lacks a centrum entirely; thus, only the angular relationship between the two aspects of the superior articular facet was measured (see Fig. 2.2, Table 2.3).

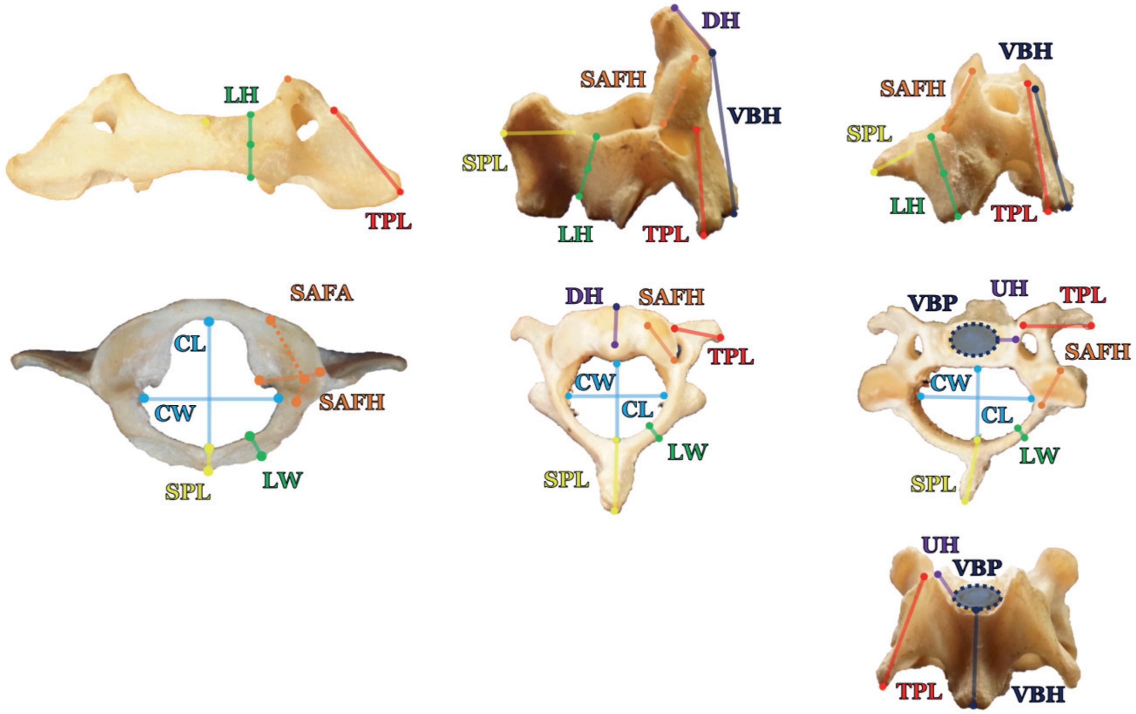

Figure 2.2 Variables measured from skeletal material. Linear measurements calculated based on distances between landmarks. Angular measurements calculated between vertebral body plane (C3-T1), VBH line (C2), and relative to itself (C1, superior articular facet).

Table 2.3 Morphological variables measured from the skeletal landmarks and their abbreviations.

Measurement	Abbreviation	Description
Vertebral Body Plane	VBP	Plane created from points (Point 15) along the margin of the cranial aspect of the vertebral body
Spinous Process Length	SPL	Maximum length of the spinous process; distance between Point 1 and Point 8
Spinous Process Angle	SPA	Craniocaudal orientation of the spinous process; angle between the SPL line and VBP (C3-T1) or VBH (C2)
Lamina Height	LH	Maximum height of the lamina; distance between Point 2 and Point 4
Lamina Width	LW	Maximum width of the lamina; distance between Point 3 and Point 5

Transverse Process Length	TPL	Maximum length of the transverse process; distance between Point 6 and Point 7
Transverse Process Angle	TPA	Craniocaudal orientation of the transverse process; angle between the TPL line and VBP (C3-T1) or VBH (C2)
Canal Length	CL	Maximum length of canal at midline; distance between Point 8 and Point 9
Canal Width	CW	Maximum width of vertebral canal; distance between Points 10 bilaterally
Superior Articular Facet Height	SAFH	Maximum height of the superior articular facet; distance between Point 11 and Point 12
Superior Articular Facet Angle	SAFA	Craniocaudal orientation of the transverse process; angle between the SAFH line and the VBP (C3-T1), VBH (C2), or itself (C1)
Vertebral Body Height	VBH	Maximum height of the ventral aspect of the vertebral body; distance between Point 13 and Point 14
Uncinate Process Height	UH	Maximum height of the uncinate process; distance beteen Point 16 and the nearest Point 15
Dens Height	DH	Maximum height of the dens; distance between Point 13 and Point 17

2.2 Maximum Range of Motion

Maximum intervertebral passive ranges of motion data were measured from seven primate species (n=18) at three institutions. Following methods approved by Institutional Animal Care and Use Committees (Protocol# A141-16-06), individuals were anesthetized. They were gently, but firmly moved into their maximum ranges of flexion, extension, and lateral flexion, held in place with sand bags, and radiographed. Because the anesthesia mask often prohibited the chin from touching the chest, it was momentarily removed for positioning and exposure during maximum flexion. To be able to separate flexion and extension, a neutral posture was also radiographed. This neutral posture was achieved by orienting the neck parallel to the trunk and allowing the head to fall naturally. The Duke Lemur Center (DLC) possesses a digital x-ray machine and thus the strepsirrhine images are higher quality than those of the gibbon (Osaka University) or chimpanzees (Stony Brook University) were taken on traditional film and scanned. In addition, the chimpanzee radiographs were taken by Dr. Nathan Thompson (Department of Anatomy, New York Institute of Technology College of Osteopathic Medicine) and do not include a neutral posture or lateral flexion.

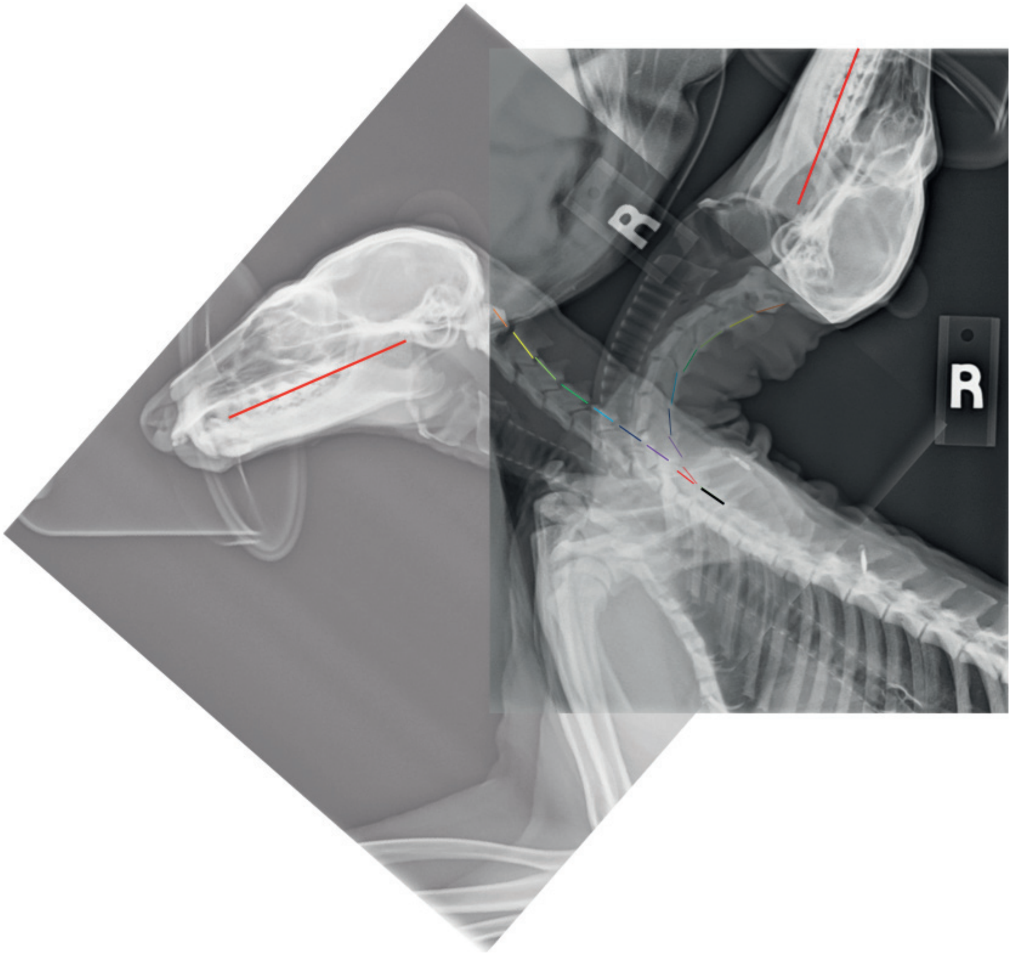

Figure 2.3 Varecia variegata *(Kizzy) radiographs of neutral posture (left) and extension (right) overlain at T2. Images were imported into ImageJ to measure the angles between lines.*

To measure range of motion in the sagittal plane, maximum flexion and extension radiographs were overlain with the neutral posture at T2. Lines were drawn along the articular pillars, which are quite dense and thus easily visible. Angles were taken between the same vertebrae in these different positions using ImageJ (Wayne

Rasband) to obtain intervertebral ranges of motion. The neutral position in the coronal plane was assumed to be at midline. Thus, angles were measured between vertebrae at maximum lateral flexion (see Fig. 2.3).

Limited range of motion data are also available in the literature. Human ROM is well established and taken from White and Panjabi (1990). As discussed in the Chapter 1, Graf and colleagues (1995) have measure intervertebral ranges of motion in four species of primate: *Sapajus apella*, *Macaca mulatta*, *Macaca fascicularis*, and *Saimiri scuireus*. These data were also taken from radiographs of anesthetized animals and, with the exception of the C0-C1 joint, appear equivalent to the data collected for this thesis. Due to the logistical difficulty and expense of irradiating captive primates (including humans), these published data were included in the analyses. See Table 2.4 for a complete list.

Table 2.4 Species used for range of motion analyses and their number of individuals. Graf et al. did not report sex or number of individuals per species. They report ten primate individuals total and one individual of Sapajus apella. *Therefore, the other species must be between 2-4.*

Species	**n**	**Source**
Sapajus apella	1	Graf et al. 1995
Macaca mulatta	~3	Graf et al. 1995
Macaca fascicularis	~3	Graf et al. 1995
Saimiri sciureus	~3	Graf et al. 1995
Eulemur mongoz	3	Duke Lemur Center
Lemur catta	3	Duke Lemur Center
Propithecus verreauxi	3	Duke Lemur Center
Otolemur crassicaudatus	1	Duke Lemur Center
Varecia variegata	3	Duke Lemur Center
Hylobates lar	1	Osaka University
Pan troglodytes	2	Stony Brook University
Homo sapiens		White and Panjabi, 1990

Phylogenetic generalized least squares (PGLS) regression was used to test for correlations between vertebral morphology and intervertebral ROM. Most morphological variables of interest should affect range of motion of the more cranial intervertebral joint. For example, the uncinate processes of C3 should influence the range of lateral flexion in the C2-C3 joint. Thus, all morphological variables were tested against their cranial joint's ROM with the exception of spinous process length and angle, which should more strongly correlate with the inferior joint. Although some variables (e.g. vertebral body height) have no reason to more strongly influence either superior or inferior joint, they were regressed against the superior joint for consistency. Linear measurements were size adjusted using the square root of vertebral canal area, which is known to strongly correlate with body mass (MacLarnon, 1996). In addition, the relationship between canal area and species mean body mass (Smith and Jungers, 1997) was confirmed within the sample used for this dissertation. Phylogenetic generalized least squares regressions demonstrate aa strongly significant relationship for all vertebral level and both sexes (see Fig 2.4, Table 2.5). In addition, this has been used to scale primate cervical vertebrae in other studies (Nalley, 2013). This allowed the dimensions to be scaled per vertebral specimen rather than relying on species averages. In addition, these values were logarithmically transformed prior to analysis in order to comply with parametric assumptions. Consensus trees used in the analyses were downloaded from 10ktrees.nunn-lab.org (Arnold et al., 2010). Analyses were conducted in R using the packages ape (Paradis et al., 2018), geiger (Harmon et al., 2015) and caper (Orme et al., 2013).

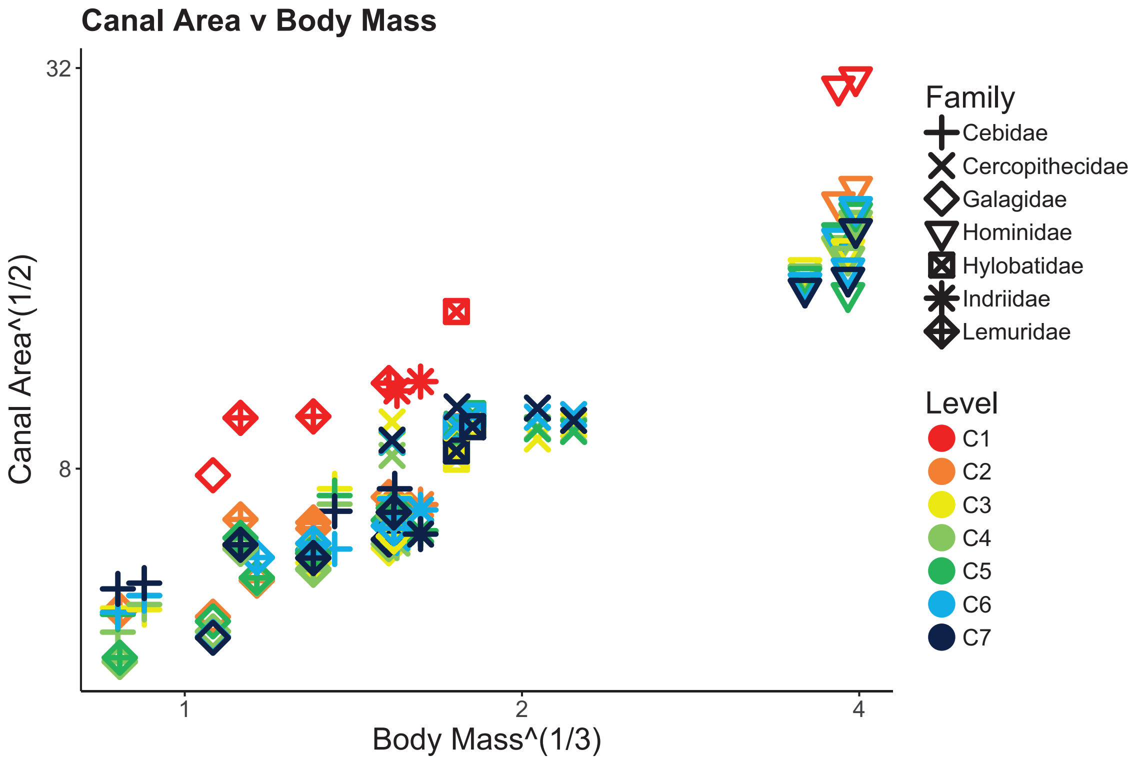

Figure 2.4 Relationship between cervical canal area and species means of body mass within this sample. PGLS analyses were conducted per level for each sex. Figure shows all levels and both sexes.

Table 2.5: Results of the PGLS regressions of species means of body mass on canal area for each cervical level.

Y	X	Level	Lambda	Adj. r^2	p
Square Root Canal Area	Cube Root Body Mass	C1 male	0	0.987	0.0004
Square Root Canal Area	Cube Root Body Mass	C2 male	0	0.977	0.0001
Square Root Canal Area	Cube Root Body Mass	C3 male	0	0.954	0.0000
Square Root Canal Area	Cube Root Body Mass	C4 male	0	0.948	0.0000
Square Root Canal Area	Cube Root Body Mass	C5 male	0	0.945	0.0000
Square Root Canal Area	Cube Root Body Mass	C6 male	0	0.965	0.0000
Square Root Canal Area	Cube Root Body Mass	C7 male	0	0.940	0.0000
Square Root Canal Area	Cube Root Body Mass	C1 female	1	0.996	0.0013
Square Root Canal Area	Cube Root Body Mass	C2 female	0	0.990	0.0000
Square Root Canal Area	Cube Root Body Mass	C3 female	0.252	0.918	0.0000
Square Root Canal Area	Cube Root Body Mass	C4 female	0.552	0.960	0.0000
Square Root Canal Area	Cube Root Body Mass	C5 female	0.216	0.968	0.0000
Square Root Canal Area	Cube Root Body Mass	C6 female	0.309	0.952	0.0000
Square Root Canal Area	Cube Root Body Mass	C7 female	1	0.779	0.0023

2.3 Kinematics: Locomotor Range of Motion

Kinematic data focus on four species of lemur: *Varecia variegata*, *Lemur catta*, *Eulemur mongoz*, and *Propithecus verreauxi* (n=12, see Table 2.4). Strepsirrhines are well-suited to investigate the relationship between cervical form and function because they practice a diversity of locomotor modes and postural repertoires. This diversity offers a natural experiment on locomotor diversity within a single clade. By confining the sample to lemurs, we are minimizing the potentially confounding effects of significant differences in cranial morphology and phylogenetic distance. More importantly, these species are readily available for kinematic research at the Duke Lemur Center. Ethics committee approval was obtained prior to data collection.

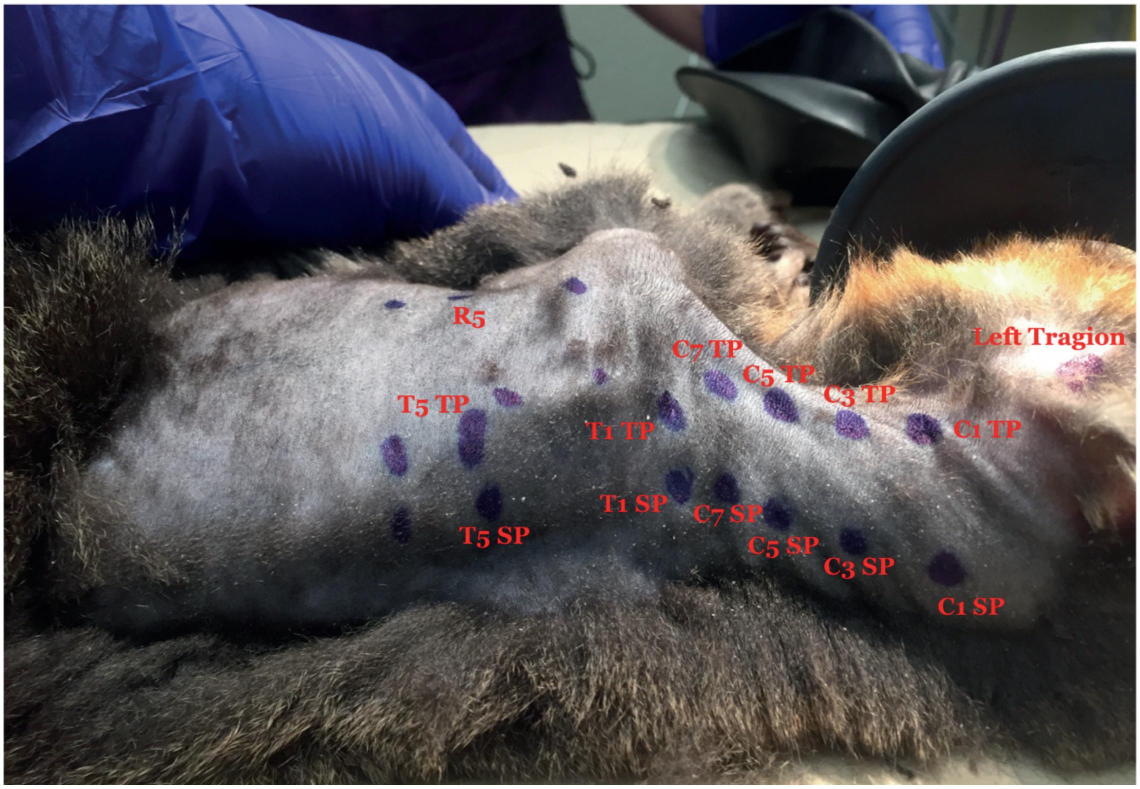

Figure 2.5 Axial landmarks used in the kinematics study (Eulemur mongoz, Oscar).

While under anesthesia for radiographic data collection, individuals were shaved and marked with permanent marker at palpable craniocervical landmarks (see Fig. 2.5).

Three-dimensional kinematics requires at least three landmarks to define xyz coordinate systems. The head segment was defined by bilateral tragion and bilateral lateral canthus landmarks. The cervical column was divided into three sections: upper (C1 spinous process, C1 transverse process, C3 spinous process), middle (C3 spinous process, C5 transverse process, and C5 spinous process), and lower (C5 spinous process, C7 spinous process, and C7 transverse process). The upper trunk segment was defined by: T1 spinous process, T5 spinous process, and the lateral-most aspect of rib 5 landmarks. The left side of the body was arbitrarily chosen for transverse process and rib landmarks. These sections correspond to functional division of the vertebral column found in the human spine (White and Panjabi, 1990).

Kinematic data were collected in the experimental space at the Duke Lemur Center. Individuals were brought from their enclosures and manually restrained while I re-highlighted the landmarks using white, non-toxic paint pens because the permanent marker, though visible, was often faded.

Substrates were constructed with the assistance of David Brewer, the research technician at Duke Lemur Center. He and the lemur center staff are experienced conducting locomotor experiments and are familiar with the habits and capabilities of their animals. Thus, both their expertise as well as previously published naturalistic studies were relied upon to construct locomotor substrates to achieve the desired mode of locomotion. In addition, Drs. Angel Zeininger and Daniel Schmitt were immensely helpful and advised in all aspects of the experiments.

At most, six cameras (GoPro Hero4, GoPro Inc., borrowed from the Animal Locomotion Lab at Duke University) were used to capture locomotor bouts. Each was modified with a BackBone Rib Cage (Ribcage, v1.0; Back-Bone, Ottawa, ON) in order to eliminate the distortion inherent in the default fish-eye lens. These cameras were placed at strategic locations in order to best capture landmarks from at least two angles. The species' most frequent mode of locomotion was used for the experiment (see Table 2.6). If the neck is adapted to providing head stability during locomotion, then the most frequent modes should give the strongest morphological signal.

Table 2.6 Species used in the kinematics study and their most frequent mode of locomotion.

Species	**n**	**Primary mode of locomotion**	**Frequency**	**Source**
Propithecus verreauxi	3	Vertical clinging and leaping (VCL)	68%	Gebo, 1987
Eulemur mongoz	3	Horizontal leaping	37%	Gebo, 1987
Varecia variegata	3	Arboreal Quadrupedalism	35%	Gebo, 1987
Lemur catta	3	Terrestrial Quadrupedalism	51%	Gebo, 1987

Terrestrial quadrupedalism (*Lemur catta*): The experimental room is floored with plastic tiles adhered to a wooden base. Although this substrate doesn't occur naturally, the plastic allows for easy cleaning and, therefore, prevention of disease transfer. In addition, all individuals included in this study are accustomed to the room and its flooring. To confine mediolateral movement, a wooden board adhered to cinderblocks acted as the substrate. The measurement space was placed in the middle such that the individual had at least one gait cycle prior to entering it. Five cameras were placed anteriorly, laterally, and superiorly to best capture axial landmarks from multiple views (see Fig. 2.6a). Video recordings were taken at 120f/s, 720p to best capture the speed of locomotion at the highest possible quality.

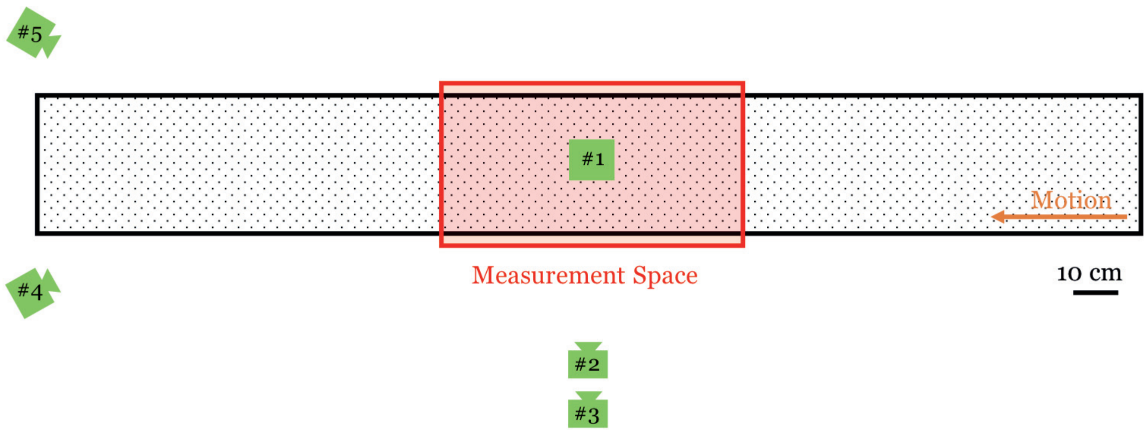

Figure 2.6 Terrestrial Quadrupedalism experimental setup; A wooden substrate (black) was adhered to cinderblocks .2m above the floor with a measurement space (red) in the center, to scale. Camera #1 was placed 2.3m above the substrate at a 90º angle (i.e. looking straight down). Camera #2 (distance not to scale) was placed 1.25m outside the enclosure level with the measurement space to capture a sagittal view. Camera #3 (distance not to scale) was placed 1.35m outside the enclosure 1.3m above the substrate, 30º from the vertical. Cameras #4 and #5 were placed 30º from the direction of motion, level with the substrate.The size measurement space reliably allowed for one half of a gait cycle. Although the traditional time frame of kinematic analysis is one entire gait cycle, the markers were too small to differentiate when the size of the space was increased to accommodate a full gait cycle. Because axial markers lie in the midline, we can assume the second half of the gait cycle will be the mirror image of the first half. To combat this, only trials which began with left forelimb touchdown were used for analysis.

<u>Arboreal quadrupedalism (*Varecia variegata*)</u>: Arboreal and terrestrial quadrupedalism were quite similar in their experimental setups. Individuals walked between two raised platforms along a wooden pole. The same measurement space was again placed in the middle of the pole and cameras were placed in similar positions (see Fig. 2.7). Videos were recorded at 120f/s, 720p.

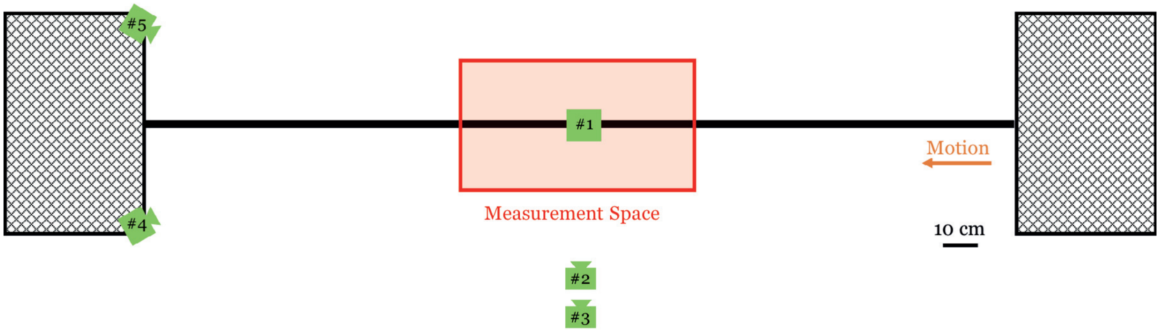

Figure 2.7 Arboreal locomotion setup; a 3.2cm diameter wooden pole was placed between two platforms 45cm above the floor. Platforms and pole were weighted with cinderblocks to create a stable substrate. Camera #1 was placed 2.1m above the substrate at a 90° angle. Camera #2 (distance not to scale) was placed 1.25 outside the enclosure level with the measurement space. Camera #3 (distance not to scale) was placed 1.35m outside the enclosure 1m above the substrate, 30° from the vertical. Cameras #4 and #5 were placed 30° from the direction of motion, level with the substrate.

Horizontal leaping (*Eulemur mongoz*): Two raised platforms were placed 0.75m apart. This distance was chosen because it is easily accomplished by the individuals, so to not tire them out or encourage them to jump down to the floor then up to the second platform. It is also not close enough to where they can bridge the gap with forelimbs and hindlimbs on either side. This distance has also been used in previous lemur kinematic studies (Demes et al., 1995). The size of the measurement space was increased in order to accommodate this distance (see Fig. 2.8). In addition, videos were recorded at a higher frame rate (240f/s) and, thus, lower quality (WVGA). One complete gait cycle was analyzed for this mode of locomotion beginning with right forelimb take-off and ending with hindlimb touchdown.

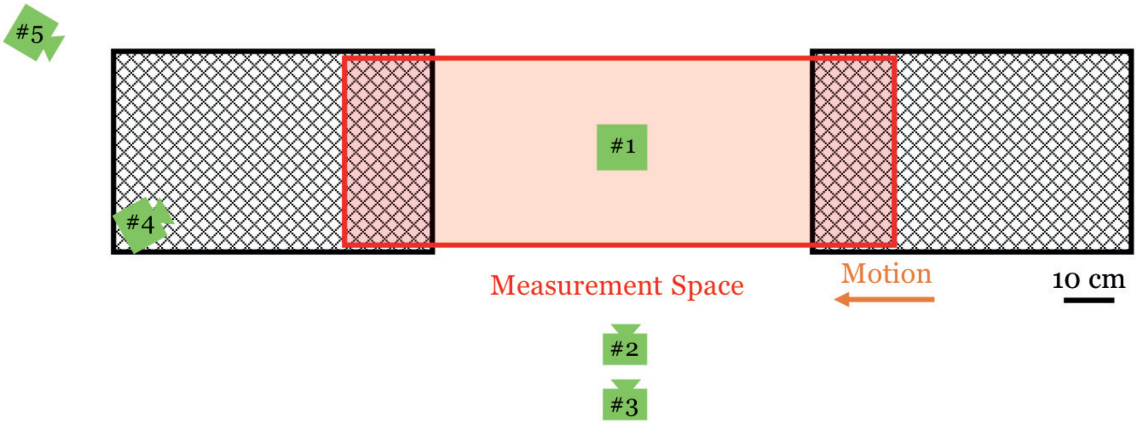

Figure 2.8 Horizontal leaping setup; two 0.45m tall platforms were placed 0.75m apart and weighted with cinderblocks. Camera #1 was placed 2.1m above the substrate at a 90° angle. Camera #2 (distance not to scale) was placed 1.21m outside the enclosure level with the measurement space. Camera #3 (distance not to scale) was placed 1.37m outside the enclosure 1m above the substrate, 10° from the vertical. Camera #4 was placed 30° from the direction of motion, level with the substrate. Camera #5 (distance not to scale) was mounted 0.77m above the platforms and angled inferiorly 20°.

Vertical clinging and leaping (*Propithecus verreauxi*): Two PVC poles were placed 1m apart. This distance was chosen because it was easily accomplished by subjects with minimal reliance on the floor as an intermediate between the two (see Fig. 2.9). The gait cycle was defined by right forelimb release to right forelimb touchdown. Videos were recorded at 240f/s, WVGA.

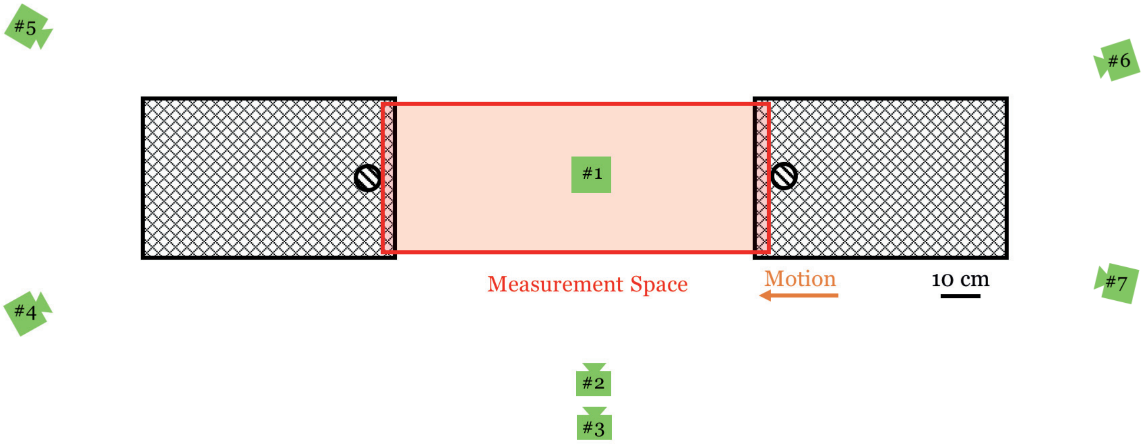

Figure 2.9 Vertical clinging and leaping setup, camera distances not to scale; 1.65m tall, 6cm diameter PVC pipes were bolted to the 0.45m platforms and stabilized with cinderblocks. Camera #1 was mounted 2.7m above the floor looking straight down. Camera #2 was placed in lateral view 2m from the measurement space. Camera #3 was placed 2m from the measurement space and oriented 10º inferiorly. Camera #4 was placed 1.35m from the floor, 1.5m from the measurement space, and directed 30º from line of motion. Camera #5 was mounted 1.55m from the floor, 1.5m from the measurement space, and oriented 10º inferiorly. Cameras #6 and #7 were mounted 2.1m from the floor, 1.65m from the measurement space, and oriented 20º inferiorly.

In all modes of locomotion, substrates were weighted such that compliance was minimal. All but one subject had previously been used for locomotor studies in the research room and have been trained with whistles. They were enticed with food rewards with the trainer holding the reward at the end of the substrate at roughly eye level if reluctant. Otherwise, the treat was not shown until they completed the pass. With this behavior, I hoped to minimize any artificial head postures resulting from the animal focusing on the treat.

Landmark Processing and Analysis: The Matlab (The Mathworks, Inc.) package, DLT data viewer (Hedrick, 2008), was used to obtain three-dimensional movement from the two-dimensional videos. Objects of known dimensions (Zometool) were built and placed in the experimental spaces before and after subjects' trials and filmed with cameras in position. These objects were used to calibrate the measurement space using the program. After calibration, landmarks were hand digitized per gait cycle (or half gait cycle) per frame for each camera and trial. At least five trials per individual, per mode of locomotion were digitized. Three-dimensional motion of each landmark was then exported.

With the assistance of Dr. Matt O'Neill (Department of Anatomy, Midwestern University), the Matlab package Kinemat (Reinschmidt and van den Bogert, 1997) was tailored to the data and used to create coordinate systems for each body segment. The angular motion (i.e., cardan angles) of each axial coordinate system was calculated relative to both the global coordinate system and the adjacent, proximal coordinate system (e.g. motion of the head in space and relative to the C3 segment was calculated). Both relative measures are important as the former allows us to understand the locomotor movement of the axial skeleton and the latter how much of that motion is dependent upon trunk movement. Data were then smoothed with a low-pass Butterworth filter in accordance with suggested industry standards (Winter et al., 1974) with a cutoff frequency of 6Hz depending upon which visually seemed to best suit the data.

2.4 Statistical Analyses

These angular data (i.e., cardan angles) for head-neck-trunk segments for each frame from each trial were used to test Prediction 2a and 2b. The angular data were then used to calculate locomotor range of motion (maximum-minimum) for each segment (head, C3, C5, C7, T1, neck, and trunk) for each trial. These trial ranges of motion were used to test the Predictions 2c and 2d.

Kinematic and kinematic-morphology predictions were tested linear mixed-effect models (LMM) in R. LMMs were used because it allowed me to control for 1) the variation in speed between trials and locomotor modes, 2) variations in sex of the individuals, as well as 3) repeatedly measuring the same individual. In addition, LMM avoids issue with multiple testing (see Peres-Neto, 1999 and Lane, 2013 for review) and issues with uneven sample sizes (a problem inherent in ANOVA). The motion of each axial segment was analyzed with the morphology of the motion of the origin of its coordinate system. For example, the neck segment is defined by C1 and C7 spinous processes and C7 transverse process landmarks and, therefore, the neck was statistically compared to C7 morphology. However, it is important to note that this type of analysis does not allow for the control of non-independence among the data due to phylogenetic relationships. Thus, the hope is that focusing on one clade (strepsirrhines) reduces any confounding results phylogeny may have.

Chapter 3 Influences of passive range of motion on cervical vertebral form

The goal of this thesis is to understand the various functional influences on cervical vertebral form. This chapter specifically investigates the effects of passive, intervertebral range of motion (ROM) has on bony morphology. To test Predictions 1-5, passive, intervertebral range of motion data were collected from radiographs of living primate specimens and morphological measurements collected from skeletal specimens (see Tables 3.1 and 3.2). In the cases of mixed sex samples (i.e. strepsirrhines), no significant differences were found between male and female morphology (relative to vertebral canal area) or intervertebral ranges of motion. In the case of range of motion data from the literature, sex was not specified. In these instances, sexes were pooled for analysis. Range of motion predictions were tested for each intervertebral joint using phylogenetic generalized least squares (PGLS) regression (see Chapter 2 for details). Thus, the strength of the support for the hypothesis will be analyzed not only through which test are significant, but how many vertebral levels demonstrate significance. For example, significant relationships between ROM and morphology in five out of seven cervical levels demonstrates much greater support than significant relationships in only two cervical levels. If there is a biological relationship between morphology and range of motion, it should hold true for multiple vertebral levels. This method has been previously used in vertebral functional morphological analyses (Nalley and Grider-Potter, 2015, 2017). In addition, the potential error (Type I) associated with multiple comparisons was corrected for using false discovery rate (FDR). Because these types of analyses (Bonferroni etc.) can increase Type II error, the tables report both the raw p-values as well FDR-corrected p-values. The p-values were only adjusted within each prediction (e.g. lateral flexion v. transverse process length) because each set of analyses is independent. It would also create an unreasonably low p-value to correct for each analysis separately, regardless of prediction or vertebral level.

3.1 Results and Discussion

Spinous Process Length and Angle

P1a: Spinous processes are known to physically inhibit extension (Kapandji, 2008). I expect spinous processes to be shorter and more cranially oriented in vertebral levels with greater maximum degrees of extension.

Results of the PGLS analyses comparing spinous process lengths (SPL) and angles (SPA) are reported in Table 3.1. Significant, negative correlations between SPL and intervertebral range of extension were found in the C5-6 and C7-T1 joints (Fig. 3.1). In both these joints, range of extension decreases with increasing process length. These results are only significant C7-T1, and approaches significance in C5-C6, which isn't terribly surprising. Spinous processes tend to become longer in more inferior cervical levels and it is likely that there is a length threshold for inhibiting extension. Spinous process angle does not significantly correlate with range of extension (Table 3.1). Anecdotally, spinous processes only appear to collide during extension in the chimpanzee. Given these mixed results, I conclude that, overall, this prediction is weakly supported for spinous process length (but not angle), and only after a certain length threshold is reached.

Table 3.1 Results of the PGLS analyses for range of motion and skeletal morphology. Significant correlations in bold ($p<0.05$) and those approaching significance italicized ($0.1>p>0.05$).

Joint	Motion	Morph	λ	Slope	Adj. r^2	p	Adj. p
C1-C2	Extension	SPL	0	0.008	-0.136	0.838	0.838
C2-C3	Extension	SPL	0	0.006	-0.111	0.667	0.838
C3-C4	Extension	SPL	0	-0.008	-0.086	0.656	0.838
C4-C5	Extension	SPL	0	0.010	-0.076	0.599	0.838
C5-C6	Extension	SPL	0	-0.351	0.368	**0.028**	*0.099*
C6-C7	Extension	SPL	0.122	0.012	-0.052	0.494	0.838
C7-T1	Extension	SPL	0	-0.039	0.606	**0.005**	**0.034**
C2-C3	Extension	SPA	0	2.694	-0.035	0.420	0.627
C3-C4	Extension	SPA	0	-0.552	-0.090	0.627	0.627
C4-C5	Extension	SPA	1	-0.968	0.031	0.289	0.627
C5-C6	Extension	SPA	0	0.614	-0.068	0.533	0.627
C6-C7	Extension	SPA	1	-1.304	0.241	0.085	0.324
C7-T1	Extension	SPA	1	0.801	0.220	0.114	0.302
C0-C1	Lateral Flexion	TPL	0.435	0.010	-0.200	0.970	0.970
C1-C2	Lateral Flexion	TPL	0	0.078	0.213	0.166	0.221
C2-C3	Lateral Flexion	TPL	0	-0.247	0.061	0.291	0.110
C3-C4	Lateral Flexion	TPL	1	-0.303	0.606	**0.024**	*0.064*
C4-C5	Lateral Flexion	TPL	0.974	-0.226	0.421	*0.068*	0.110
C5-C6	Lateral Flexion	TPL	1	-0.460	0.682	**0.014**	*0.055*
C6-C7	Lateral Flexion	TPL	1	-0.493	0.709	**0.011**	*0.055*
C7-T1	Lateral Flexion	TPL	1	0.093	-0.236	0.843	0.844
C1-C2	Lateral Flexion	TPA	0	0.093	-0.199	0.961	0.678
C2-C3	Lateral Flexion	TPA	0	7.964	0.470	*0.054*	0.125
C3-C4	Lateral Flexion	TPA	0	-2.813	0.050	0.303	0.425
C4-C5	Lateral Flexion	TPA	0.932	-3.119	0.778	**0.005**	*0.069*
C5-C6	Lateral Flexion	TPA	0	-6.273	0.521	**0.041**	0.125
C6-C7	Lateral Flexion	TPA	1	-3.499	0.321	0.108	0.425
C7-T1	Lateral Flexion	TPA	0	2.424	-0.186	0.666	0.678
C2-C3	Lateral Flexion	UH	0	0.081	-0.128	0.595	0.821
C3-C4	Lateral Flexion	UH	0	0.045	-0.167	0.722	0.821
C4-C5	Lateral Flexion	UH	0	0.051	-0.158	0.688	0.821
C5-C6	Lateral Flexion	UH	0	-0.039	-0.187	0.821	0.821
C6-C7	Lateral Flexion	UH	0	-0.092	-0.159	0.691	0.821
C7-T1	Lateral Flexion	UH	0	-0.057	-0.306	0.817	0.821
C0-C1	Flexion	SAFH	0	0.027	0.786	0.920	0.920
C1-C2	Flexion	SAFH	0	0.003	-0.151	0.783	0.895
C2-C3	Flexion	SAFH	0	0.006	-0.034	**0.004**	**0.030**

C3-C4	Flexion	SAFH	0.281	0.023	0.310	*0.064*	0.170
C4-C5	Flexion	SAFH	0	0.014	0.599	**0.010**	**0.038**
C5-C6	Flexion	SAFH	0.33	0.008	0.018	0.313	0.603
C6-C7	Flexion	SAFH	0.487	0.006	-0.011	0.385	0.603
C7-T1	Flexion	SAFH	0	-0.015	-0.060	0.453	0.603
C2-C3	Pitch	VBH	0	0.028	-0.156	0.680	0.877
C3-C4	Pitch	VBH	0	0.109	0.646	**0.010**	*0.069*
C4-C5	Pitch	VBH	0	0.039	0.003	0.345	0.877
C5-C6	Pitch	VBH	0	-0.022	-0.126	0.752	0.877
C6-C7	Pitch	VBH	0	0.027	-0.015	0.379	0.877
C7-T1	Pitch	VBH	0	-0.013	-0.169	0.730	0.877
C0-C7	Sum (Pitch)	Sum (VBH)	0	-0.001	-0.198	0.938	0.920
C0-C1	Pitch	SAFA	0	-0.222	-0.200	0.673	0.673

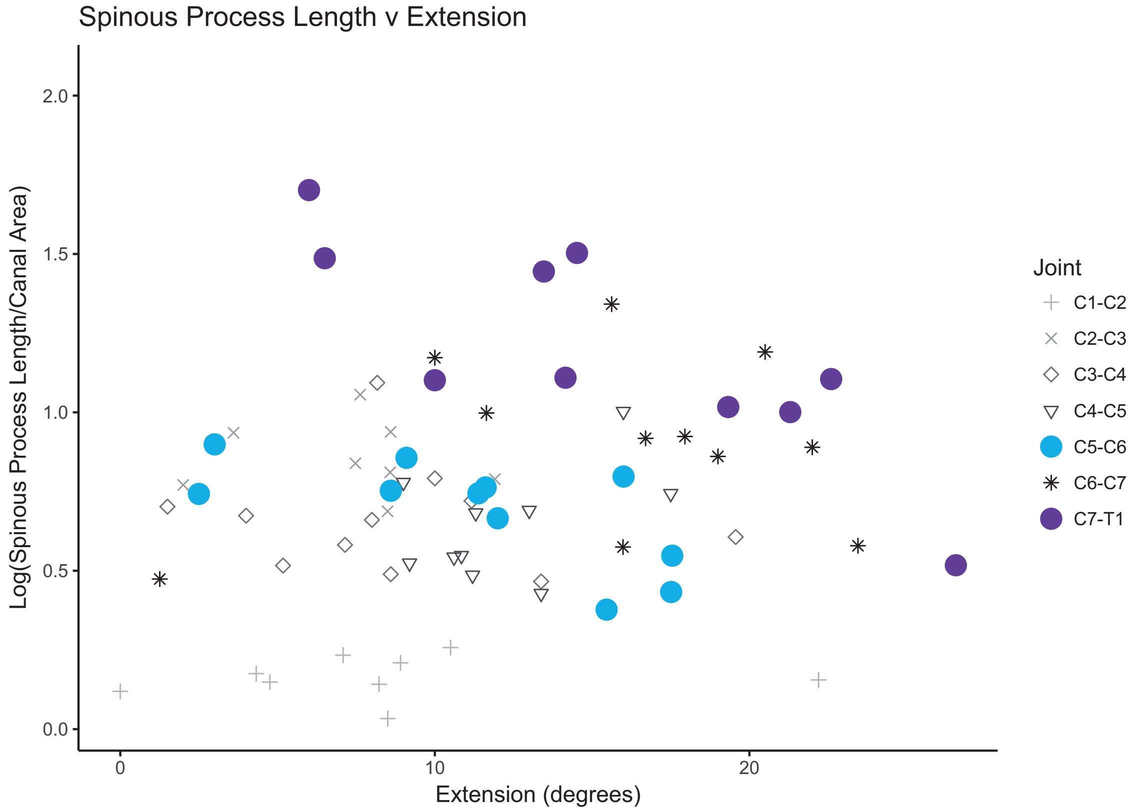

Figure 3.1 PGLS results of Spinous Process Length (SPL) on flexion per vertebral level. Significant results (C7-T1) and those approaching significance (C5-C6) are colored and insignificant results are shades of grey.

Nalley and Grider-Potter (2015) also found that neck inclination (as measured by Strait and Ross (1999)) also strongly correlates with spinous process length in C3-C7 vertebrae. From these analyses, we concluded that longer spinous processes are found in primates with more horizontal neck postures in order to increase the mechanical advantage of the nuchal musculature. These correlations were significant (with high correlation coefficients) across all levels. This indicates that neck posture may more strongly influence cervical morphology than ROM, but additional analyses incorporating both functional variables would be able to further elucidate the relative influence of each function.

Transverse Process Length and Angle

P1b: Transverse processes will be shorter and more cranially oriented in vertebral levels with greater ranges of lateral flexion. Long transverse processes should physically inhibit lateral movement, but more cranially oriented processes should provide greater mechanical advantage.

The C6 typically has anterior and posterior roots of the transverse processes. Both processes are also occasionally present in C5 and C7 levels as well. In the case of C5 and C6, the anterior process was used for analysis because it is always longer and more robust, whereas the reverse is true for C7. The longer process was used for analysis because if one is going to more strongly inhibit or facilitate range of motion, it should be the longer of the two. The longer one is more likely to collide with adjacent vertebrae than the shorter one.

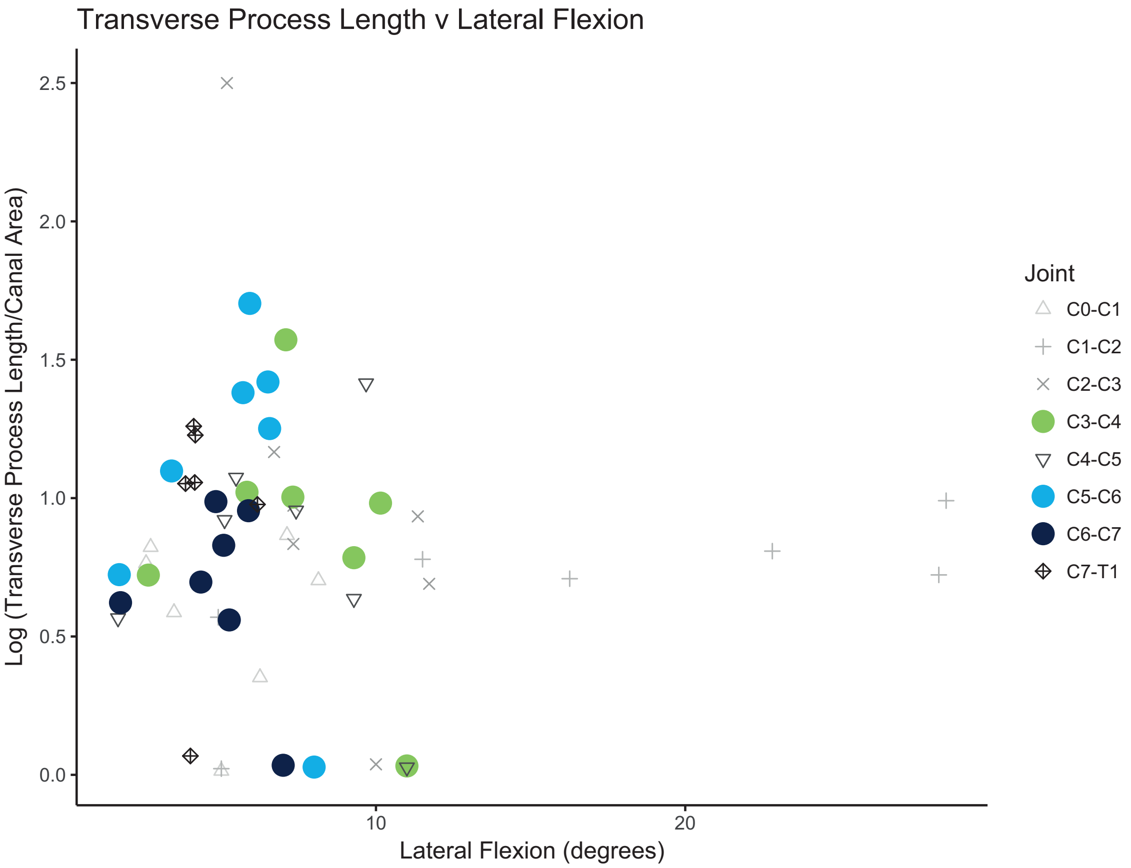

Figure 3.2 PGLS results of Transverse Process Length (TPL) on lateral flexion per vertebral level. Results approaching significance (C3-C4, C5-C6, and C6-C7) are colored and insignificant results are shades of grey.

Results demonstrate that, contrary to predictions, longer transverse processes actually facilitate greater ranges of lateral flexion in three intervertebral joints (C3-C4, C5-C6 and C6-C7, see Figure 3.2). Even though this result only approaches significance at these levels, it potentially indicates that in the lower cervical vertebrae, longer transverse processes offer greater mechanical advantage during ipsilateral lateral flexion. This measure of motion is passive, meaning the muscles aren't active. However, in order to provide greater ranges of lateral flexion via muscle action, the joints need to be able to accommodate that motion.

Transverse process angle is also weakly correlated with degree of lateral flexion (Table 3.1, Figure 3.3). This relationship is significant for C4-C5 joint. The more caudal joints seem to support the predictions: the transverse processes become more cranially oriented with increasing ranges of lateral flexion. Overall the results do not strongly support this prediction.

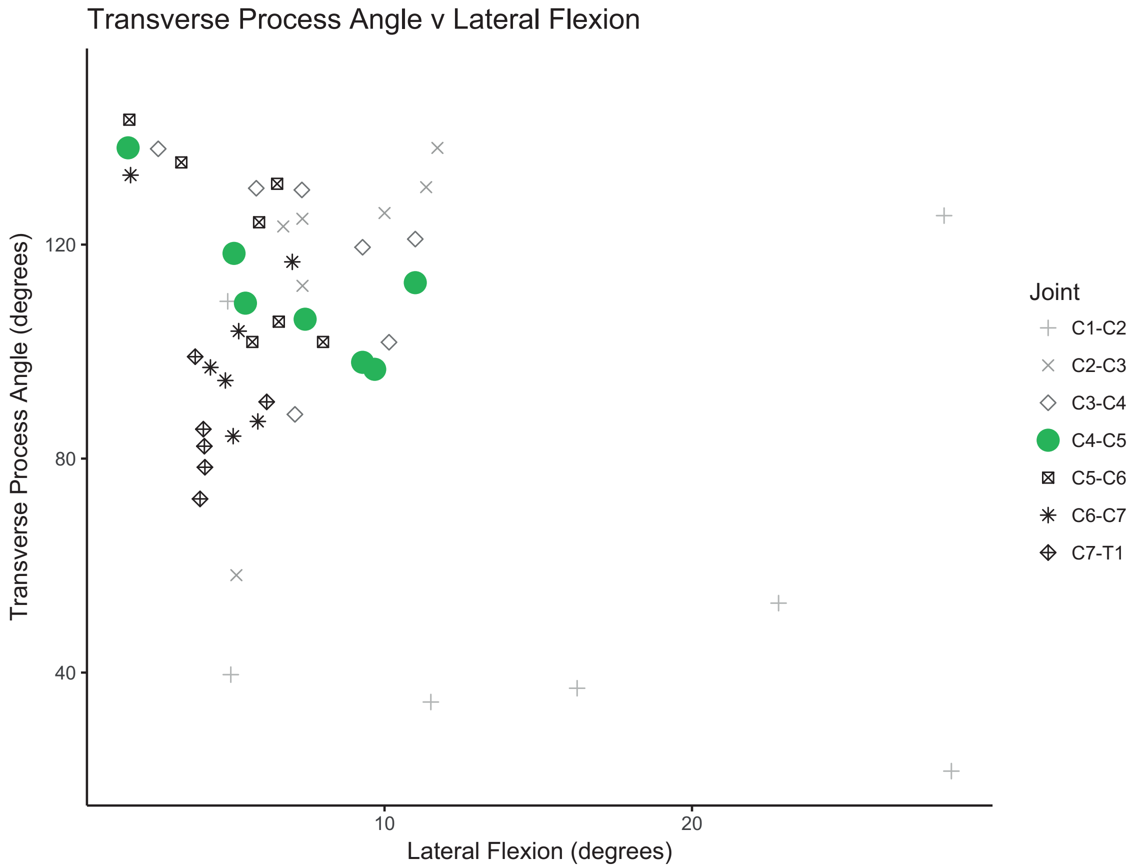

Figure 3.3 PGLS results of Transverse Process Angle (TPA) on lateral flexion per vertebral level. Significant results (C4-C5 and C5-C6) and those approaching significance (C2-C3) are colored and insignificant results are shades of grey.

Uncinate Process Height

P1c: Uncinate processes create a U-shape which is thought to stabilize the joint. Therefore, craniocaudally taller uncinate processes should restrict the range of lateral flexion.

Results of the PGLS regressions demonstrate no significant correlations between lateral flexion and uncinate process height or angle (Table 3.1). Thus, this prediction is not supported. It is likely that the intervertebral discs and associated ligaments restrict motion to a greater degree than bony morphology.

Meyer and colleagues (2018) recently published an analysis of uncinate process morphology in primates. The results indicate that uncinate process height is negatively allometric, larger primates tending to have much less prominent processes than do smaller-bodied species. Unsurprisingly, morphology does not correlate with locomotor category. Further work using methods such as x-ray reconstruction of moving morphology (XROMM) could further elucidate the role of the uncinate processes in a comparative sample, because it would allow us to see the exact pattern of motion between vertebrae during lateral flexion and rotation.

Superior Articular Facet Height

P1d: Relatively large joint surface areas should increase the range of motion. Therefore, craniocaudally taller facets should correlate with increased ranges of flexion.

Results show that C2-C3 and C4-C5 joint ranges of motion are significantly positively correlated with articular facet height. This indicates that increasing facet height in these two joint increases range of flexion (see Table 3.1, Figure 3.4). Overall, this prediction is weakly supported.

Nalley and Grider-Potter (2015, 2017) observed a significant influence of neck posture on articular facet orientation but did not investigate its influence on height. Specifically, they found that more coronal orientations were common in more pronograde species, but only at the C4 and C7 vertebral levels. They concluded that these orientations might offer greater resistance to displacement in these taxa. It is likely that both these variables are important functional influences on vertebral form.

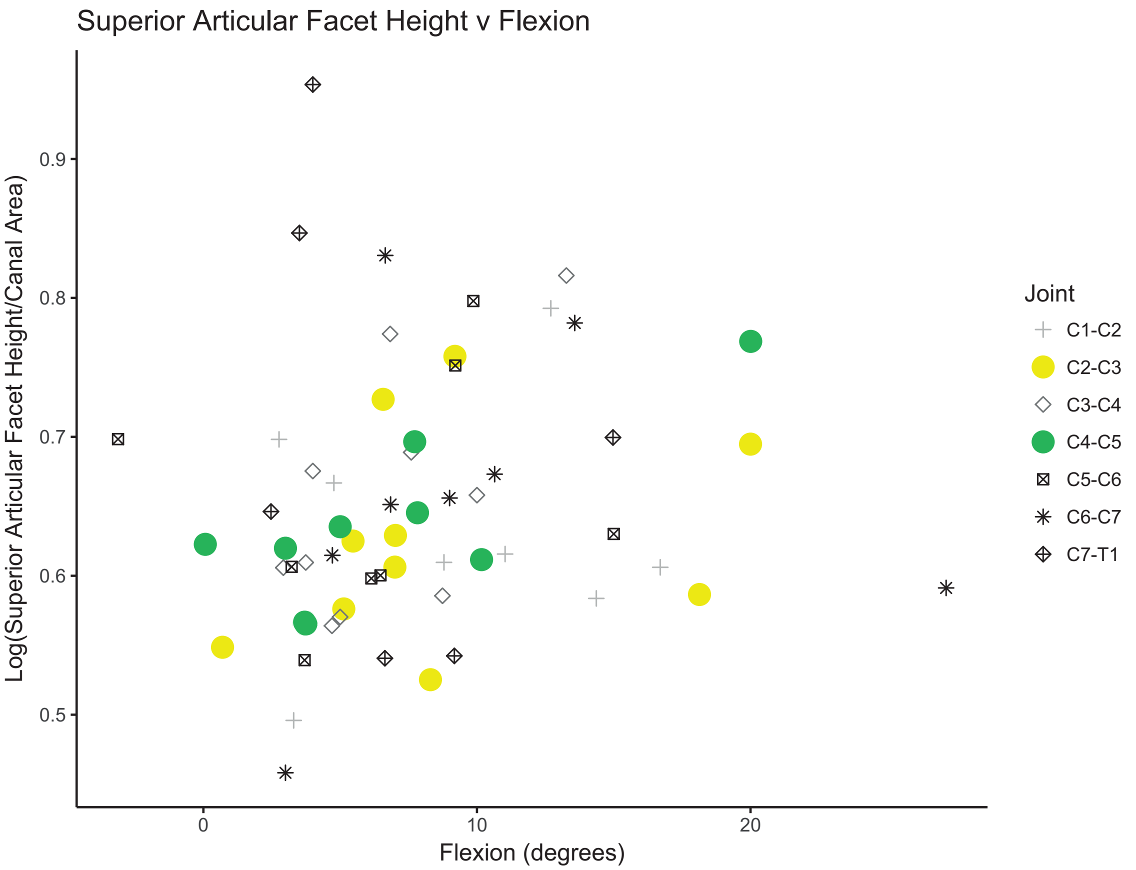

Figure 3.4 PGLS results of Superior Articular Facet Height (SAFH) on flexion per vertebral level. The results approaching significance (C4-C5) are colored and insignificant results are shades of grey.

Cervical Column Height

P1e: A taller column should increase its overall angular displacement. Thus, range of whole-neck flexion-extension will be greater in species with craniocaudally taller cervical columns.

To test this prediction skeletal measures of vertebral body heights (C2-C7) were summed and compared to the summed range of motion for total range of head and neck motion in addition to the intervertebral correlations. Results demonstrate no significant correlation between column height and range of flexion-extension, and only one vertebral level, C3-C4, is approaching significance and positively correlated with range of motion (Figure 3.5, Table 3.1). It may be that intervertebral discs and their associated ligaments more strongly constrain vertebral motion.

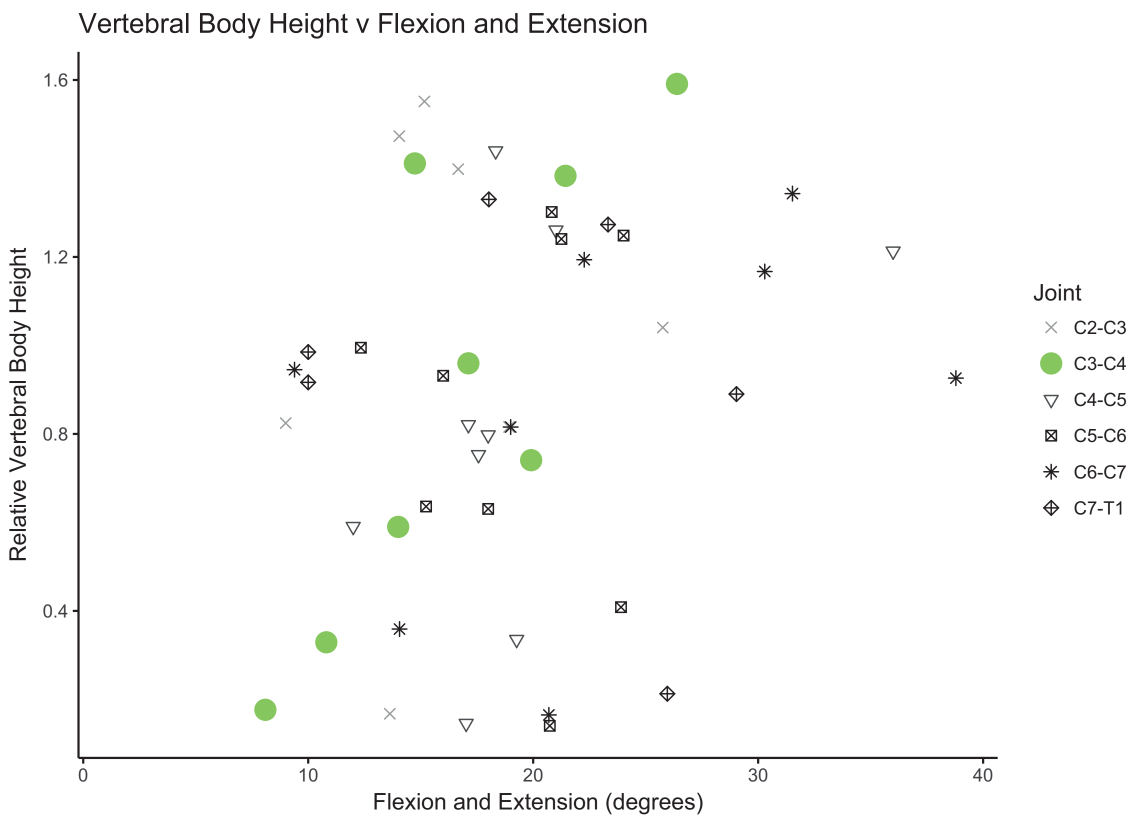

Figure 3.5 PGLS results of Vertebral Body Height (VBH) on flexion-extension. Results approaching significance (C3-C4) are colored and insignificant results are shades of grey.

Ward (1993) suggested that craniocaudally taller vertebral bodies should be associated with larger degrees of angular excursion at the intervertebral joints. These results suggest otherwise: total column length is not correlated with total of head-neck motion and vertebral body height is only significantly correlated with flexion-extension at one vertebral level. Nalley and Grider-Potter (2015) also found correlations between vertebral body height and neck posture. They concluded that this might increase lordotic curvature formation or maintenance because longer vertebrae would increase the total amount of flexion at each joint in a resting posture. However, these results indicate that might not be the case. Because vertebral body height is not strongly associated with maximum range of flexion, it likely does not influence lordosis. It could be possible that longer vertebral bodies offer greater area for force dissipation, thereby more efficiently resisting the bending moments associated with more pronograde postures.

Atlantooccipital Joint Curvature

P1f: Larger curvature of the atlantooccipital joint facilitates greater range of flexion-extension.

Regression results indicate that the curvature is not related to range of flexion-extension in the atlantooccipital joint. This is contrary to the hypothesis put forth by Aiello and Dean (2002) for the atlantooccipital joint .

Previous analyses conducted by Nalley and Grider-Potter (2017) have shown significant correlations between atlantooccipital joint curvature and neck posture. However, this relationship is largely driven by changes in the ventral aspect of the facet. The ventral aspect becomes oriented more dorsally in more pronograde species (Grider-Potter, 2013). It is possible that this orientation better protects the joint from multidirectional forces and increasing curvature is not adapted to any particular increase in ROM. The results of this study demonstrate that this variation does not affect joint range of motion. Hamrick's (1996) study on primate carpals suggests that joint curvature reflects habitual loading patterns. A relatively flat facet (e.g., the tibial plateau) is adapted to dissipating unidirectional loads whereas a more curved joint (e.g., the acetabulum) may habitually dissipate loads from many directions. Stability in multiple directions may not be as important in more orthograde species whose atlantooccipital joints largely combat unidirectional compression.

3.2 Discussion

Skeletal inhibition of motion

Overall, these results do not strongly support the hypothesis that vertebral morphology is correlated with intervertebral range of motion. Some vertebral levels show significant correlations between ROM and morphology; however, no correlation is significant across all vertebral levels. Longer spinous processes appear to inhibit range of extension in the lower vertebral levels. This isn't surprising because spinous processes tend to be longer in the lower levels, and thus, these lower levels pass the threshold needed to inhibit motion. Anecdotally, the middle and lower spinous processes only appear to touch bone-to-bone in the radiographs taken from *P. troglodytes*, which also have relatively longer spinous processes. It is likely that spinous processes in the upper cervical levels are too short in the species included here to inhibit range of extension.

It's also important to note that these variables tested are isolated; meaning, they don't take into account how the morphologies might influence each other. For example, both the length of the transverse process and angle of the transverse process influence the range of motion in tandem (e.g. a more coronally oriented process may allow for a longer process without inhibiting motion). In addition, the inhibition of motion is likely influenced by the length of the transverse process and height of the vertebral body in tandem; the transverse process can be longer when the vertebral body is craniocaudally taller. Future work should investigate these variables in tandem in order to understand their collective influences on range of motion.

Contrary to the prediction, longer transverse processes seem to facilitate greater ranges of lateral flexion rather than inhibiting it. Longer processes move the muscular action further from the joint center, thereby creating greater mechanical advantage: less muscular force is required to laterally flex in species with longer transverse processes. Although these ranges of motion are passive (i.e. muscles are inactive), the range of motion should still be large, so that the muscles can facilitate the lateral neck flexors (e.g. the scalenes, spinalis capitis, iliocostalis cervicis, and longissimus cervicis) originate on these processes in humans, this result could be explained in terms of increasing mechanical advantage of these muscles. These results further indicate that skeletal morphology does not strongly correlate with motion motion.

Uncinate process height demonstrated no correlation with range of lateral flexion. Spinal fusion is commonly practiced in the medical field to inhibit motion at particular vertebral joints. Research has demonstrated that when a vertebral joint is fused, the superior joint often exhibits an increased range of motion and concomitant disc degeneration (Chow et al., 1996; Kumar et al., 2001; Eck et al., 2002; Hilibrand and Robbins, 2004; Rohlmann et al., 2006). Cleary, the fibrocartilaginous annulus fibrosis plays a critical role in providing joint stability. What, then, is the role of an uncinate process? It is possible that it inhibits range of rotation, rather than lateral flexion. It is commonly cited in the literature that the uncinate processes require humans to extend and laterally flex their cervical vertebrae in order to accomplish neck rotation. It may also be that hard tissues only inhibits motion if soft tissue degenerates or fails.

Recently, Manafzadeh and Padian (2018) conducted a study investigating the degree to which ligaments restrain hip mobility in quail in an effort to retrodict hip posture in fossil ornithodirans. They obtained an osteological measure of hip ROM by overlaying 3D scans of the hip and femur and eliminating those overlays in which bones touched or the joint was dislocated. Ligamentous ROM was measured through manipulating dissected specimens and manipulating them in front of an x-ray reconstruction of moving morphology (XROMM) system. They then mapped the ligamentous point cloud of possible osteological and ligamentous positions and found that ligaments restrict bony movement to 5.28% of the morphospace. This immense reduction in ROM underscores the function of ligaments: to provide joint stability. Coupled with the results of this study, it would appear that skeletal morphology rarely provides a bony stop for range of motion and, therefore, should not be used to reconstruct ROM in fossil taxa.

Chapter 4 Axial kinematics and neck function during locomotion

The overarching goal of this dissertation is to understand the functional relationships of vertebral morphology. However, this chapter is dedicated to understanding how the neck functions during locomotion. One must first recognize function before understanding the relationship between form and function. This study tests the hypothesis that the locomotor function of the neck is to maintain head stability. To test this hypothesis, kinematic data were collected using videos taken from four species of strepsirrhines (*Eulemur mongoz*, *Lemur catta*, *Propithecus verreauxi*, and *Varecia variegata*) during their primary modes of locomotion: horizontal leaping, terrestrial quadrupedalism, vertical clinging and leaping, and arboreal quadrupedalism respectively (Gebo, 1987; Table 2.6; see Table 4.1 for average range of motion of each body segment relative to the global coordinate system and Chapter 2 for description of methods).

These data were collected in order to test the hypothesis that the neck functions to maintain head stability by counteracting the movements of the trunk during locomotion. From this hypothesis stem several predictions: a) trunk kinematics varies due to locomotor mode, b) trunk movement influences neck movement, but not head movement, during locomotion , c) there is a proximodistal increase in locomotor range of motion of each axial segment, and d) neck range of motion increases with increases trunk range of motion during locomotion (see Chapter 2). These predictions were tested using linear mixed models in order to incorporate differences in speed as a fixed effect as well as repeatedly measuring the same individual and species. Depending on the prediction, models used: 1) cardan angles for head-neck-trunk segments across trials within the global coordinate system, 2) range of motion (max angle-min angle) of the head-neck-trunk segment for each trial within the global coordinate system, or 3) range of motion (max cardan angle-min cardan angle) of the head and vertebral segments (C3, C5, C7, and T1) for each trial within the global coordinate system (see Chapter 2 for details). Cardan angles are the angular motions of pitch (rotation in the sagittal plane), roll (rotation in the quadruped transverse plane), and yaw (rotation in the quadruped frontal plane). Speed was calculated using the distance traveled by the tragion landmark and divided by the time of the gait cycle. Speed was included as a fixed effect in all models. These kinematic data were then correlated with morphometric data using in order to understand how locomotor range of motion influences cervical vertebral morphology. In light of the results of these analyses, additional linear mixed models were conducted in order to understand the variation in morphology across the sample.

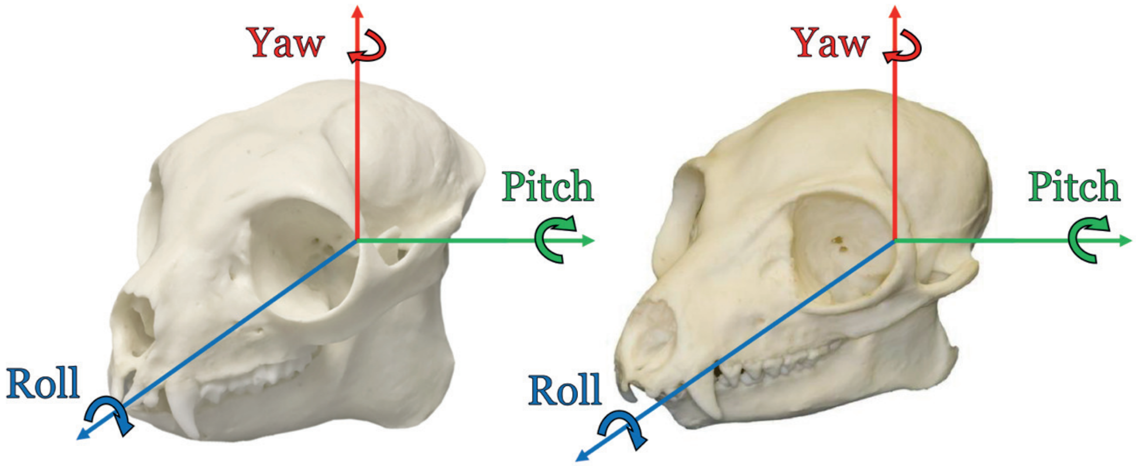

Figure 4.1 Directions of angular motion in an orthograde sifaka and pronograde ring-tailed lemur.

Species	Mode	N_{trial}	Speed (m/s)			Level	Pitch (deg)			Yaw (deg)			Roll (deg)		
E. mongoz	HL	11	8.261	(+/-)	1.227	Head	45.3	(+/-)	24.0	53.3	(+/-)	33.6	21.5	(+/-)	12.9
						C3	58.7	(+/-)	39.1	53.3	(+/-)	45.3	59.3	(+/-)	32.6
						C5	50.4	(+/-)	32.0	38.1	(+/-)	28.5	46.6	(+/-)	43.7
						C7	50.0	(+/-)	36.0	56.7	(+/-)	52.1	58.1	(+/-)	36.9
						Neck	19.9	(+/-)	8.4	25.9	(+/-)	13.4	25.6	(+/-)	17.0
						T1	40.7	(+/-)	19.0	35.8	(+/-)	29.2	40.3	(+/-)	18.7
						Trunk	28.7	(+/-)	18.8	39.0	(+/-)	24.6	40.3	(+/-)	24.6
L. catta	TQ	9	1.903	(+/-)	0.446	Head	26.6	(+/-)	12.7	59.7	(+/-)	29.3	86.5	(+/-)	54.7
						C3	22.9	(+/-)	16.0	12.7	(+/-)	9.1	22.0	(+/-)	14.2
						C5	38.1	(+/-)	24.4	11.3	(+/-)	6.6	22.2	(+/-)	12.4
						C7	31.8	(+/-)	17.8	24.9	(+/-)	32.8	24.1	(+/-)	15.6
						Neck	13.0	(+/-)	5.1	16.1	(+/-)	13.1	12.3	(+/-)	5.6
						T1	24.3	(+/-)	14.6	12.0	(+/-)	4.9	25.1	(+/-)	10.7
						Trunk	10.5	(+/-)	6.9	22.1	(+/-)	20.9	22.2	(+/-)	17.0
P. verreauxi	VCL	7	14.846	(+/-)	1.019	Head	29.4	(+/-)	26.3	63.0	(+/-)	59.5	67.2	(+/-)	61.0
						C3	61.2	(+/-)	22.6	78.2	(+/-)	61.9	36.6	(+/-)	21.7
						C5	39.7	(+/-)	33.9	31.4	(+/-)	33.0	30.3	(+/-)	26.0
						C7	36.7	(+/-)	18.7	31.1	(+/-)	28.7	24.5	(+/-)	19.9
						Neck	54.1	(+/-)	17.3	80.1	(+/-)	44.3	34.9	(+/-)	20.7
						T1	39.3	(+/-)	14.2	55.0	(+/-)	44.6	40.9	(+/-)	26.5
						Trunk	36.4	(+/-)	23.4	28.5	(+/-)	16.7	21.3	(+/-)	10.7
V. variegata	AQ	12	2.986	(+/-)	0.681	Head	9.8	(+/-)	5.9	11.0	(+/-)	13.7	12.4	(+/-)	12.5
						C3	43.8	(+/-)	20.2	33.7	(+/-)	6.4	18.9	(+/-)	16.3
						C5	32.9	(+/-)	35.1	40.7	(+/-)	19.8	15.0	(+/-)	10.2
						C7	21.1	(+/-)	21.8	43.1	(+/-)	22.4	11.0	(+/-)	4.2
						Neck	22.5	(+/-)	17.1	26.2	(+/-)	21.2	14.6	(+/-)	11.5
						T1	29.2	(+/-)	23.6	49.0	(+/-)	16.1	16.6	(+/-)	23.4
						Trunk	12.5	(+/-)	11.9	17.9	(+/-)	6.7	19.5	(+/-)	9.6

Table 4.1 Average ranges of segment motion across gait cycles for each species (horizontal leaping =HL, terrestrial quadrupedalism =TQ, vertical clinging and leaping = VCL, arboreal quadrupedalism =AQ).

4.1 Results-Kinematics

Trunk Kinematics vs. Species

P2a: Trunk kinematics varies among primate species during their primary mode of locomotion.

Linear mixed models were conducted using both cardan angles of the trunk during each frame of each trial as well as the resulting range of angular motion per trial. Both sets of kinematic data demonstrate significant differences in trunk motion among species. Both *Eulemur* and *Propithecus* experience larger ranges of pitch and yaw during leaping than do *Lemur* and *Varecia* during quadrupedalism (see Table 4.2). Variation in trunk yaw across the gait cycle does not seem to be vary due to species (p=0.135), but the range of yaw does (p=0.011). Intuitively, this result makes sense: a sifakas' trunk during vertical clinging and leaping should move differently than a ring-tailed lemur's during terrestrial quadrupedalism. Given that it has been demonstrated that trunk motion varies among species, I can now use it as the basis for subsequent predictions.

Table 4.2 Results of the linear mixed models among both global segment angles and global segment range of motion. Significant correlations in bold (p<0.05).

Y: Segment Angle or ROM	X	X2	Random Effects	r^2	p_X	p_{X2}
Trunk Yaw	Species	Speed	Indv (Trial (Frame))	0.104	0.135	0.563
Trunk Roll	Species	Speed	Indv (Trial (Frame))	0.601	**0.000**	0.313
Trunk Pitch	Species	Speed	Indv (Trial (Frame))	0.243	**0.011**	0.546
Trunk Yaw ROM	Species	Speed	Indv (Trial (Frame))	0.330	**0.011**	0.533
Trunk Roll ROM	Species	Speed	Indv (Trial (Frame))	0.334	**0.011**	0.544
Trunk Pitch ROM	Species	Speed	Indv (Trial (Frame))	0.510	**0.014**	0.558

Table 4.3 Prediction 2b results of the linear mixed models. Significant correlations in bold ($p<0.05$).

Y	**X1**	**X2**	**Random Effects**	**r^2**	**p_X**	**P_{X2}**
Head Yaw	Trunk Yaw	Speed	Species(Individual (Trial))	0.099	**0.000**	0.317
Head Roll	Trunk Roll	Speed	Species(Individual (Trial))	0.008	**0.000**	**0.022**
Head Pitch	Trunk Pitch	Speed	Species(Individual (Trial))	0.054	0.276	0.338
Head Yaw	Neck Yaw	Speed	Species(Individual (Trial))	0.065	0.583	0.216
Head Roll	Neck Roll	Speed	Species(Individual (Trial))	0.002	0.388	0.845
Head Pitch	Neck Pitch	Speed	Species(Individual (Trial))	0.076	**0.000**	**0.213**
Neck Yaw	Trunk Yaw	Speed	Species(Individual (Trial))	0.260	**0.000**	**0.006**
Neck Roll	Trunk Roll	Speed	Species(Individual (Trial))	0.320	**0.000**	**0.000**
Neck Pitch	Trunk Pitch	Speed	Species(Individual (Trial))	0.424	**0.000**	**0.023**

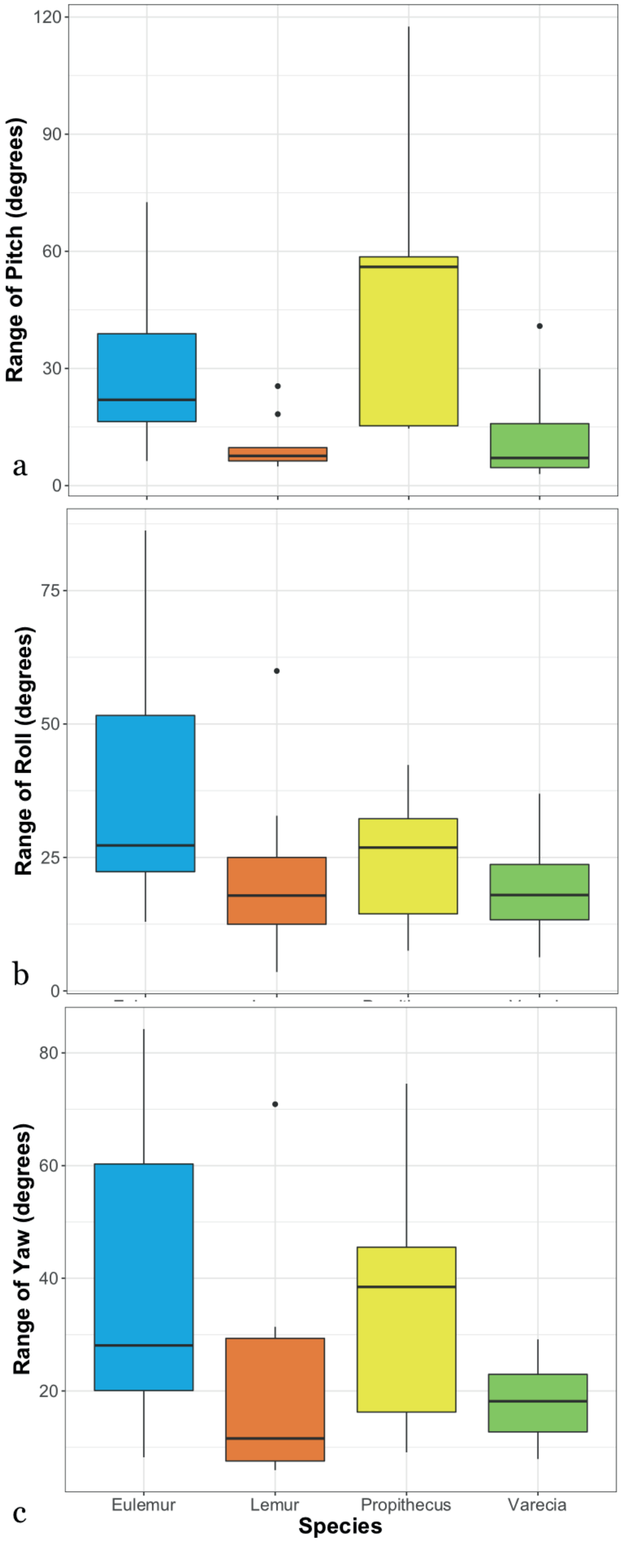

Figure 4.2 Trunk range of pitch (a), roll (b), and yaw (c) during primary mode of locomotion in four species of lemur: Eulemur mongoz, Lemur catta, Propithecus verreauxi*, and* Varecia variegata.

Trunk vs. Neck Kinematics

P2b: In order to maintain head stability, variation in trunk kinematics will, in turn, affect neck kinematics. Therefore, trunk movement during a stride will predict neck movement, but not head movement.

The data demonstrate variation in how the axial segments move with and opposite each other during locomotion. These linear mixed models were conducted by correlating cardan angles of the head, neck, and trunk in the global coordinate system per frame of each trial (see Table 4.3 for model specifics). Trunk movement does predict a significant, but minute amount of head yaw or roll during a gait cycle ($r^2_{yaw}=0.099$ and $r^2_{roll}=0.008$, $p<0.001$, see Table 4.3). However, trunk pitch significantly predicts head pitch, contrary to the predictions ($p_{pitch}=0.2761$). Conversely, neck yaw and roll does not predict head yaw or roll ($p_{yaw}=0.5825$, $p_{roll}=0.3877$) but does weakly predict head pitch ($r^2_{pitch}=0.076$, $p_{pitch}<0.001$).

The neck and trunk are much more highly correlated with each other than the head and trunk ($r^2_{yaw}=0.260$, $r^2_{roll}=0.320$, $r^2_{pitch}=0.424$, $p<0.001$). This implies that during locomotion the head pitches with the neck but rolls and yaws with the trunk. As a whole, these correlations indicate that trunk movement influences neck movement but also weakly influences head movement.

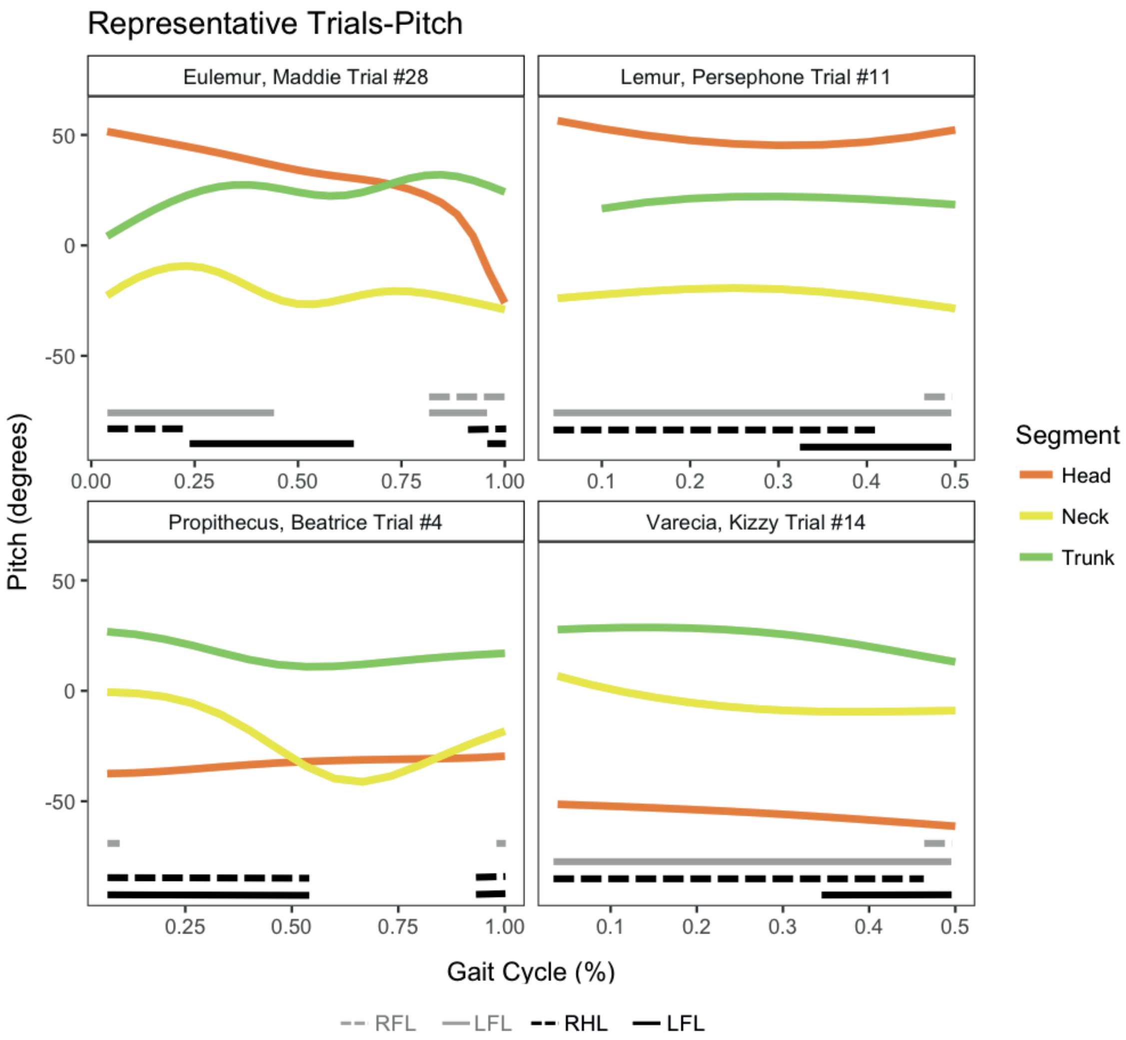

Figure 4.3 Representative pitch of the head, neck, and trunk segments across the gait cycle. Statistical analyses demonstrated variation in angular motion due to speed and thus, representative trials are depicted rather than averages.

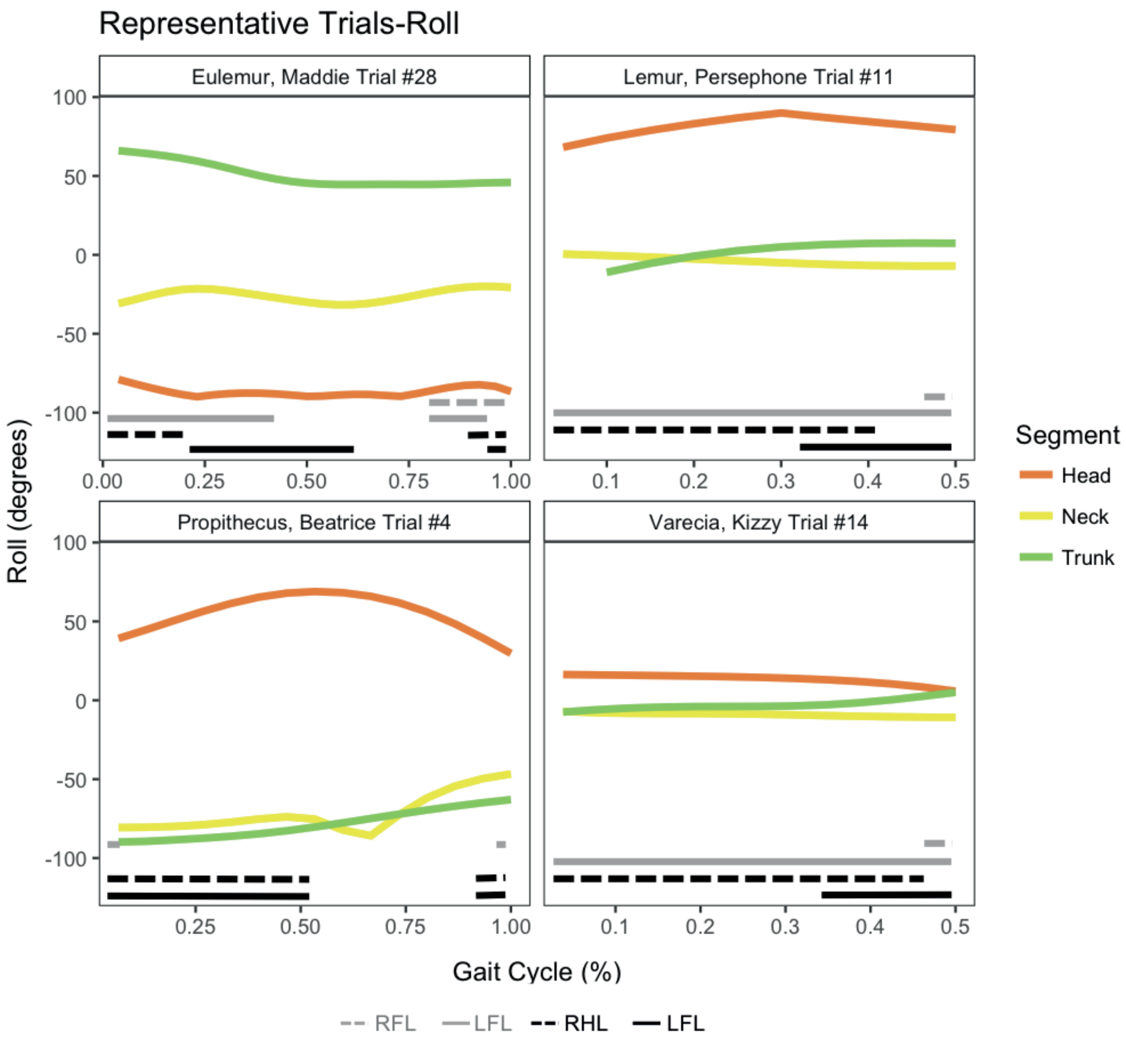

Figure 4.4 Representative roll of the head, neck, and trunk segments across the gait cycle.

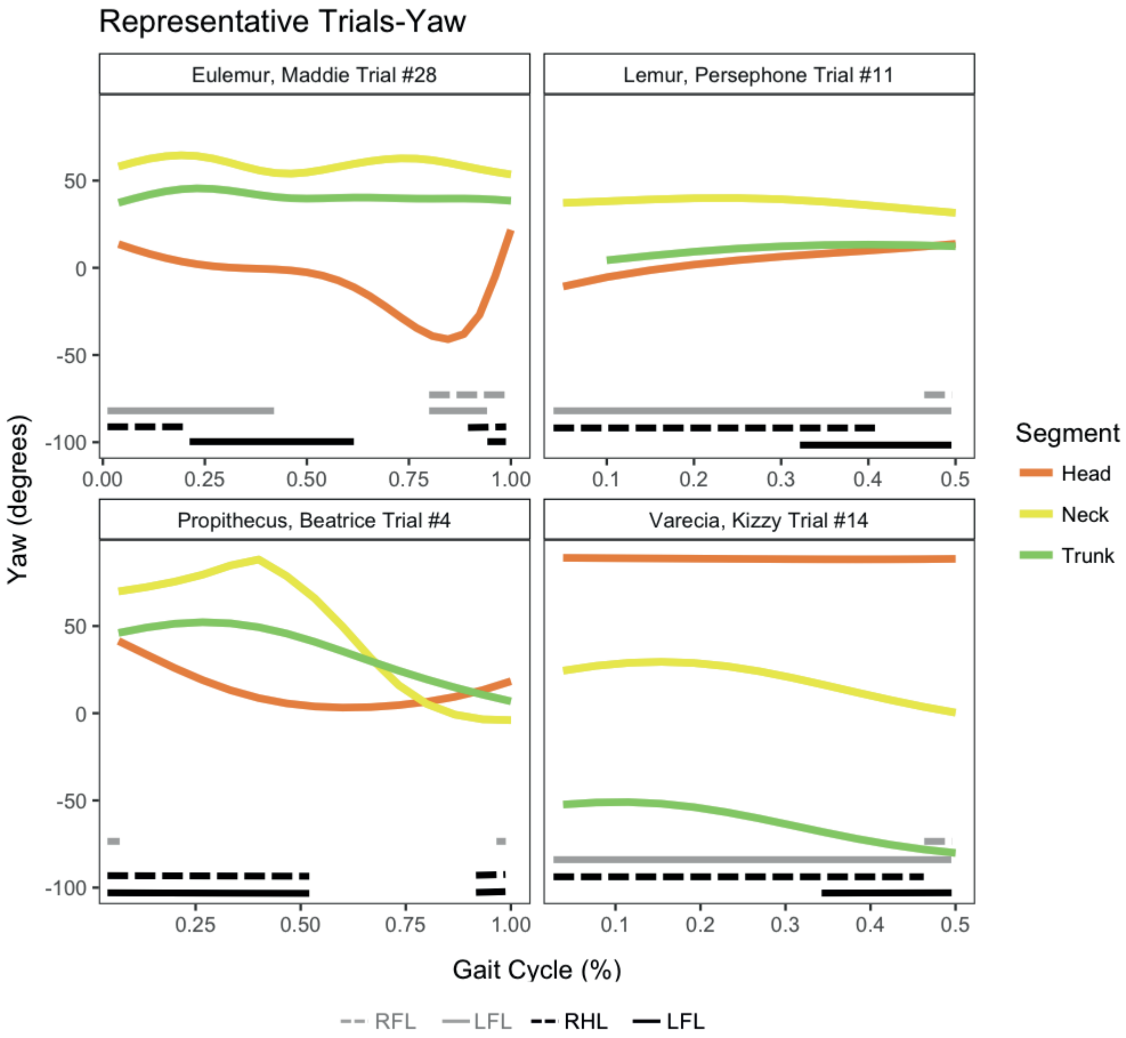

Figure 4.5 Representative yaw of the head, neck, and trunk segments across the gait cycle.

Segmental Stability

P2c: If head stability is the goal and the neck's function is to counteract the movements of the trunk in order to maintain that stability, then there should be a proximodistal decrease in locomotor range of motion in each axial segment (i.e. Head<C3<C5<C7<T1).

To test this prediction, models incorporated the ranges of motion of each vertebral segment across one trial. The vertebral segment data demonstrate unbelievably large ranges of motion during locomotion (see Table 4.1). In many cases these locomotor ranges of motion are larger than the passive range of motion found at those segments, which leads be to believe that these data are not accurate. It is possible that methodological error in the vertebral segment data are confounding the results. Specifically, skin artifact likely plays a role in this error, see discussion below. Thus, the analyses were also conducted using segment ranges of motion but found no difference in significance. Results demonstrate very little support for this prediction: models for movement in all planes are not significant (p_{yaw}=0.094, p_{roll}=0.438, p_{pitch}=0.493, see Table 4.4). Post-hoc analyses show only one significant difference: C3-C7 yaw (see Table 4.5 and Figure 4.6). This result is surprising. If head stability is an important aspect of locomotion, then the neck should act to minimize its motion.

Table 4.4 Prediction 2c linear mixed model results for the vertebral segments (head, C3, C5, C7, and T1) as well as the axial segments (head, neck, trunk). Significant correlations in bold (p<0.05) and those approaching significance italicized (0.1>p>0.05).

Y: ROM	X	X2	Random Effects	r^2	p_X	p_{X2}
Yaw	Vertebral Segment	Speed	Individual (Trial)	0.07	*0.09*	0.19
Roll	Vertebral Segment	Speed	Individual (Trial)	0.04	0.44	0.27
Pitch	Vertebral Segment	Speed	Individual (Trial)	0.03	0.49	0.42
Yaw	Whole Segment	Speed	Individual (Trial)	0.14	0.41	**0.00**
Roll	Whole Segment	Speed	Individual (Trial)	0.07	0.15	*0.07*
Pitch	Whole Segment	Speed	Individual (Trial)	0.20	0.35	**0.00**

Table 4.5 Post-hoc results (Tukey HSD) for prediction 2c testing for differences among levels, p-values corrected using Bonferroni's method. Significant correlation in bold (p<0.05).

	Head-C3	Head-C5	Head-C7	Head-T1	C3-C5	C3-C7	C3-T1	C5-C7	C5-T1	C7-T1
Yaw	0.42	1.00	0.80	1.00	0.27	**0.04**	0.31	0.95	1.00	0.88
Roll	0.94	1.00	0.84	0.94	0.95	1.00	0.56	0.85	0.95	0.37
Pitch	0.93	0.98	0.85	1.00	0.68	0.38	0.84	0.99	1.00	0.93

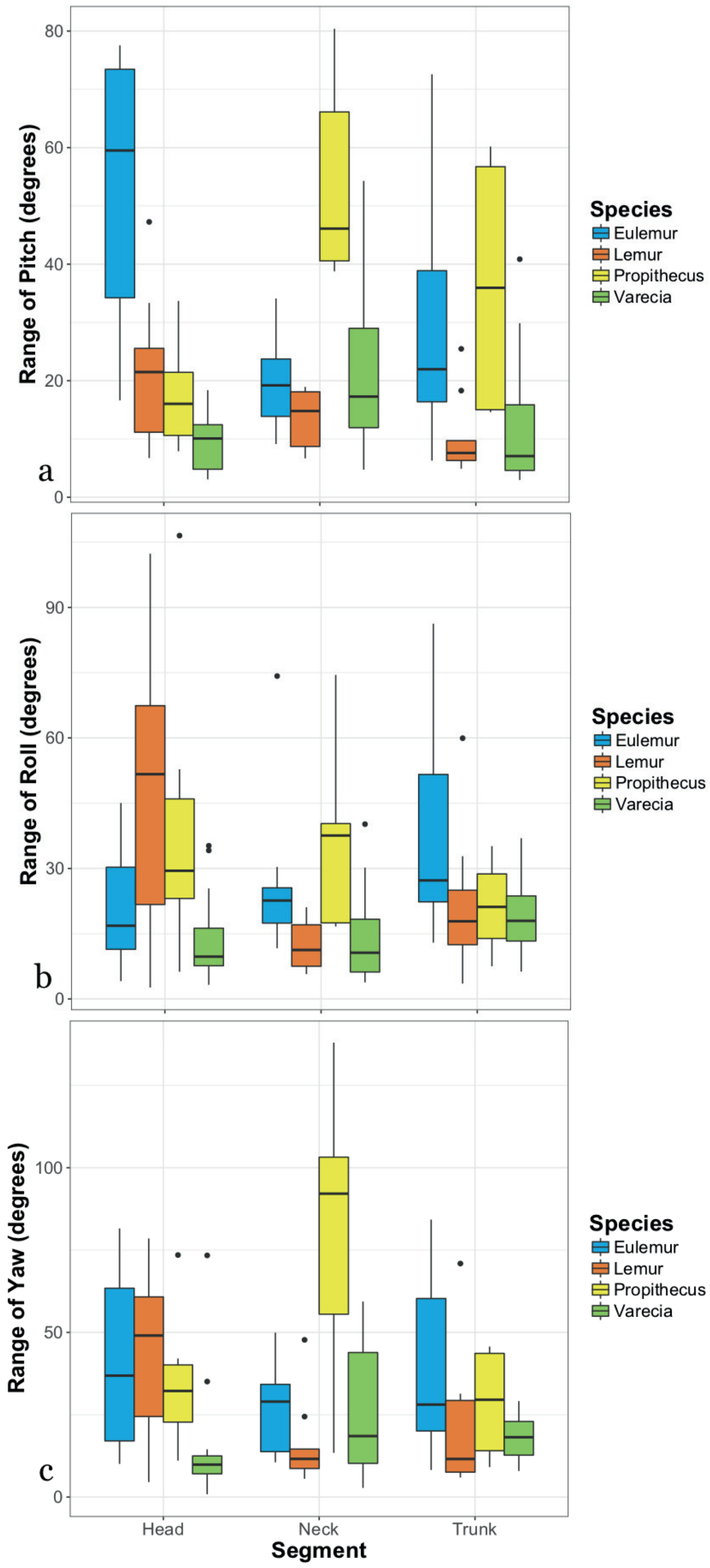

Figure 4.6 Species variation in locomotor ranges of pitch (a), roll (b), and yaw (c). No significant differences were found.

Species-specific kinematics

P2d: As locomotor trunk range of motion increases, so should neck range of motion in order to counteract the movement of the trunk.

Models were conducted using head-neck-trunk segment ranges of motion per trial to test this prediction. No significant results were found among species, but results for roll and pitch approach significance (p_{roll}=0.051, p_{pitch}=0.080, see Table 4.6). Post-hoc analyses show an interesting pattern of significance differences: *Eulemur* has significantly different pitch than *Lemur* (p=0.0195) or *Varecia* (p=0.0224), but not *Propithecus*. While *Varecia* has significantly different ranges of roll than *Lemur* or and *Eulemur*, see Table 4.7 and Figure 4.5a-c. This grouping is likely influenced by their locomotor modes: *Eulemur* and *Propithecus* group together as leapers in their high degrees of flexion-extension.

Table 4.6 Prediction 2d results of the linear mixed models. Significant correlations in bold (p<0.05).

Y: ROM	**X**	**X2**	**Random Effects**	**r^2**	**p_X**	**p_{X2}**
Yaw	Species	Speed	Individual (Trial)	0.1490	0.4284	**0.0004**
Roll	Species	Speed	Individual (Trial)	0.1155	*0.0509*	0.1177
Pitch	Species	Speed	Individual (Trial)	0.2541	*0.0802*	**0.0001**

Table 4.7 Post-hoc test results (Tukey HSD) testing for significant differences between species, p-values corrected using Bonferroni's method. Significant correlations in bold (p<0.05) and those approaching significance italicized (0.1>p>0.05).

	Em-Lc	**Em-Pv**	**Em-Vv**	**Lc-Pv**	**Lc-Vv**	**Pv-Vv**
Yaw	0.6510	0.4220	0.3350	0.4690	0.4560	0.3220
Roll	0.3714	0.3004	*0.0572*	0.2734	*0.0600*	0.1061
Pitch	**0.0195**	0.6122	**0.0224**	0.1242	0.9979	0.1306

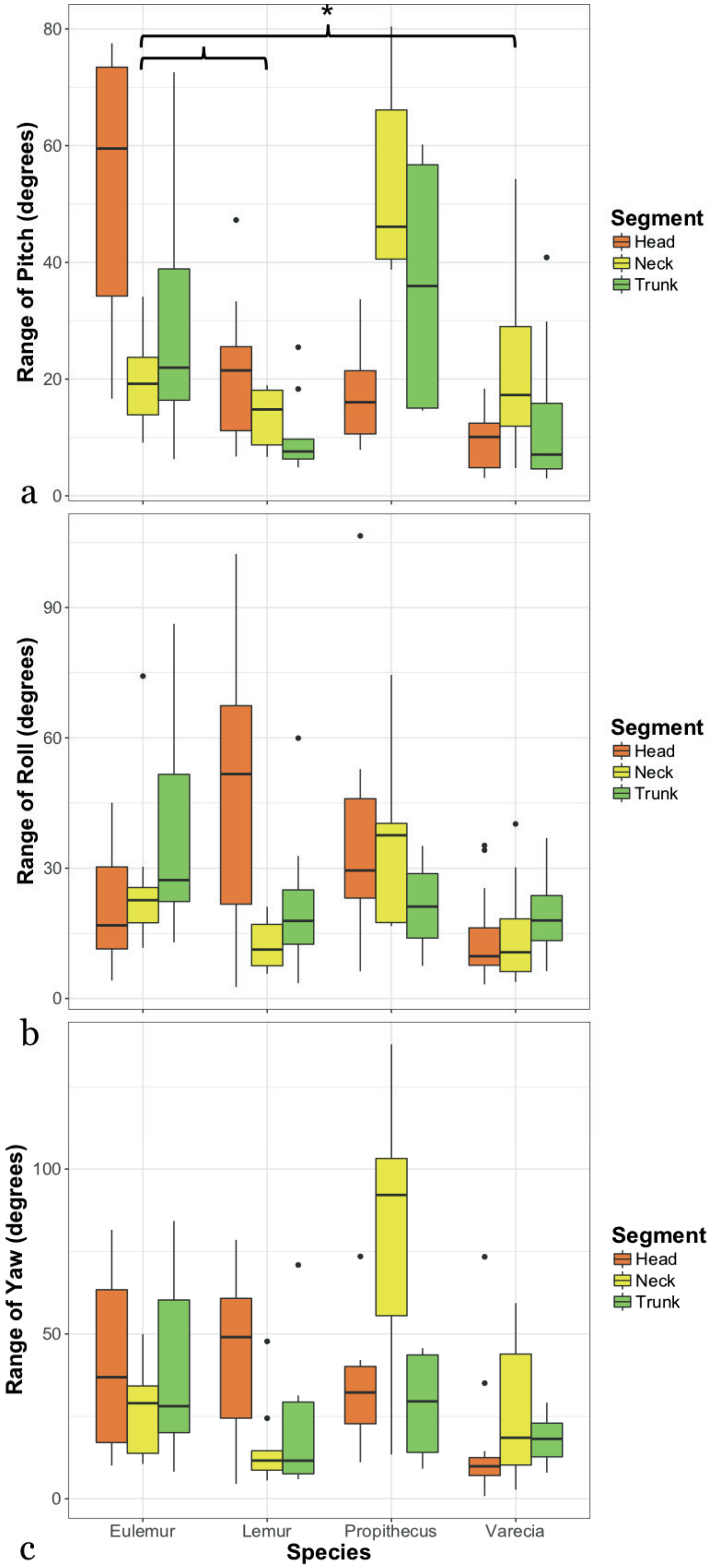

Figure 4.7 Species differences in ranges of pitch (a), roll (b), and yaw (c) within one gait cycle. Significant differences were found between Eulemur *and* Lemur *as well as* Eulemur *and* Varecia.

4.2 Results-Morphology

The results of the kinematic analyses demonstrate that the intervertebral kinematics had too much methodological error to be considered realistic (see Section 4.1). Thus, it is difficult to apply locomotor ranges of motion to each vertebral level. Instead, head-neck-trunk segment motion (yaw, pitch, and roll) was applied to C1, C7, and T5 morphology respectively (see Table 4.8). In the case of sifakas, who are habitually orthograde, yaw and roll were switched such that yaw corresponds to lateral flexion and roll corresponds to axial rotation in all species (see Figure 4.8). Linear mixed models were used to correlate average segment range of motion per species to vertebral morphology in order to test the hypothesis that locomotor range of motion influences vertebral morphology, see Chapter 2: **P1a-g**. Linear mixed models were chosen in order to avoid issues with multiple comparison. However, these analyses ignore potential similarity within the data due to close phylogenetic relationships.

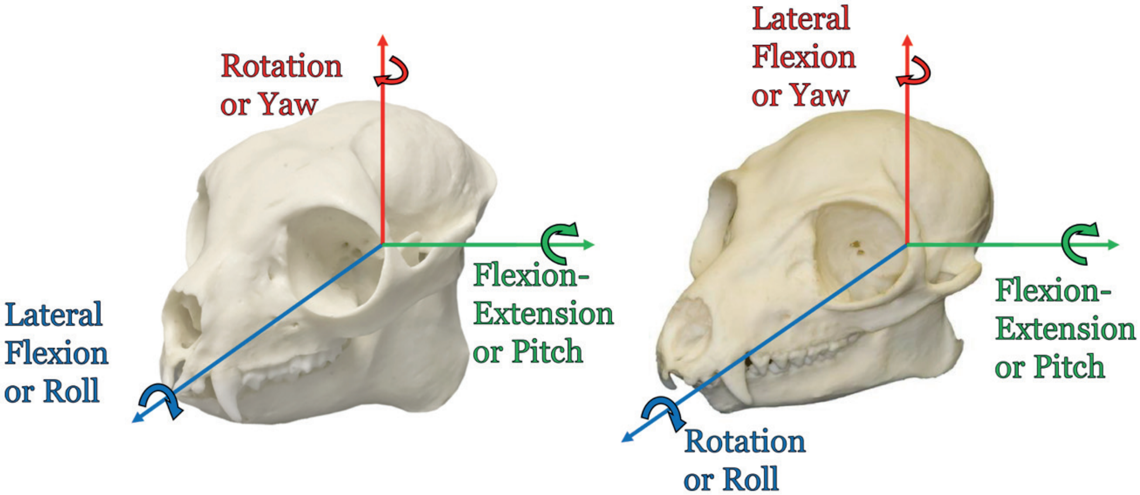

Figure 4.8 Directions of anatomical motion in an orthograde sifakas (left) and pronograde ring-tailed lemur (right).

As a whole, the results of the linear mixed models demonstrate very little support for these predictions (see Table 4.8). The only significant result is that of transverse process length and locomotor range of lateral flexion. Contrary to predictions, transverse process length increases with decreasing range of lateral flexion. However, this contrary result was also found for maximum range of motion (Table 3.1). Thus, it is unlikely that transverse processes hinder movement during locomotor range of motion but not maximum range of motion. The results of the kinematic analyses demonstrate no significant differences in range of head and neck motion among species (see Table 4.4); meaning, there is no difference in head and neck locomotor function within the sample. Because there is no difference in function, it becomes difficult to relate any morphological differences to that function. Therefore, both the results of the kinematics analyses and the morphological analyses indicate that range of motion during the primary mode of locomotion does not influence vertebral morphology. Given the negative results of these analyses, what can we say about the influences on morphological variation within these four species?

Additional analyses were subsequently conducted to understand how morphology varies among species. To assess the morphological variation among species, linear mixed models were conducted to understand differences in specific morphological variables at each vertebral level among species (e.g. the differences among species' spinous process lengths per vertebral level). These analyses were chosen in order to account for any potential variation due to sex as well as to avoid issues associated with uneven sample sizes and multiple comparisons. Results of these analyses show some interesting patterns of variation (see Table 4.9, 4.10 and Figure 4.9 and 4.10). *Varecia* has significantly longer spinous processes than *Lemur* and *Eulemur*, but not *Propithecus*. *Varecia* also has significantly longer transverse processes than all other species. Longer processes are thought to offer greater mechanical advantage for the nuchal musculature by increasing the distance from the joint center of rotation as well as offering greater area for muscular attachment, potentially increasing the muscle PCSA.

Table 4.8 Prediction 3 descriptions and results.

Prediction	Description	Model	Result
3a	Range of extension is smaller in species with relatively larger spinous processes	log(spl/sqrt(ca))~pitch + 1|level/species	n.s.
3b	Range of lateral flexion is smaller in species with longer transverse processes	log(tpl/sqrt(ca))~roll + 1|level/species)	p=0.02
3c	Range of lateral flexion will decrease with increasing uncinate process height	Unable to test in C1, C7, and T5	-
3d	Range of flexion should be larger in species with craniocaudally taller articular facets	log(safh/sqrt(ca)) ~ pitch + 1|level/Species	n.s.
3e	Range of flexion-extension should be larger in species with taller vertebral bodies	log(sum(vbl/sqrt(ca))) ~ neck pitch + 1|level/Species	n.s.
3f	Range of flexion-extension should be larger in species with more curved atlantooccipital joints	safa (c1) ~ head pitch + 1|level/Species	n.s.
3g	Range of rotation should be larger in species with more cranially-oriented articular facets	safa (c7t5) ~ (neck, trunk) yaw + 1|level/Species	n.s.

Table 4.9 Results of the linear mixed models testing for morphological variations among species. Significant correlations in bold (p<0.05).

Morphology	X	Random	r^2	p_X
SPL	Species	Level (Species (ID))	0.024	**0.015**
TPL	Species	Level (Species (ID))	0.203	**0.001**
SAFH	Species	Level (Species (ID))	0.238	**0.001**
UH	Species	Level (Species (ID))	0.0936551	**0.0335**
VBH	Species	Level (Species (ID))	0.213	**0.001**
SAFA	Species	Level (Species (ID))	0.005	**0.021**

Table 4.10 Post-hoc results (Tukey HSD) of the linear mixed models testing for morphological differences between species, p-values reflect Bonferroni corrections. Significant correlations in bold (p<0.05).

Species	**Em-Lc**	**Em-Pv**	**Em-Vv**	**Lc-Pv**	**Lc-Vv**	**Pv-Vv**
SPL	0.975	0.242	**0.007**	0.462	**0.025**	0.535
TPL	0.999	0.844	**0.000**	0.893	**0.000**	**0.000**
SAFH	0.996	**0.001**	**0.001**	**0.001**	**0.001**	0.326
UH	0.252	**0.005**	**0.027**	0.368	0.697	0.963
VBH	**0.000**	**0.000**	**0.000**	0.413	0.480	0.998
SAFA	0.758	0.370	0.439	0.910	**0.047**	**0.007**

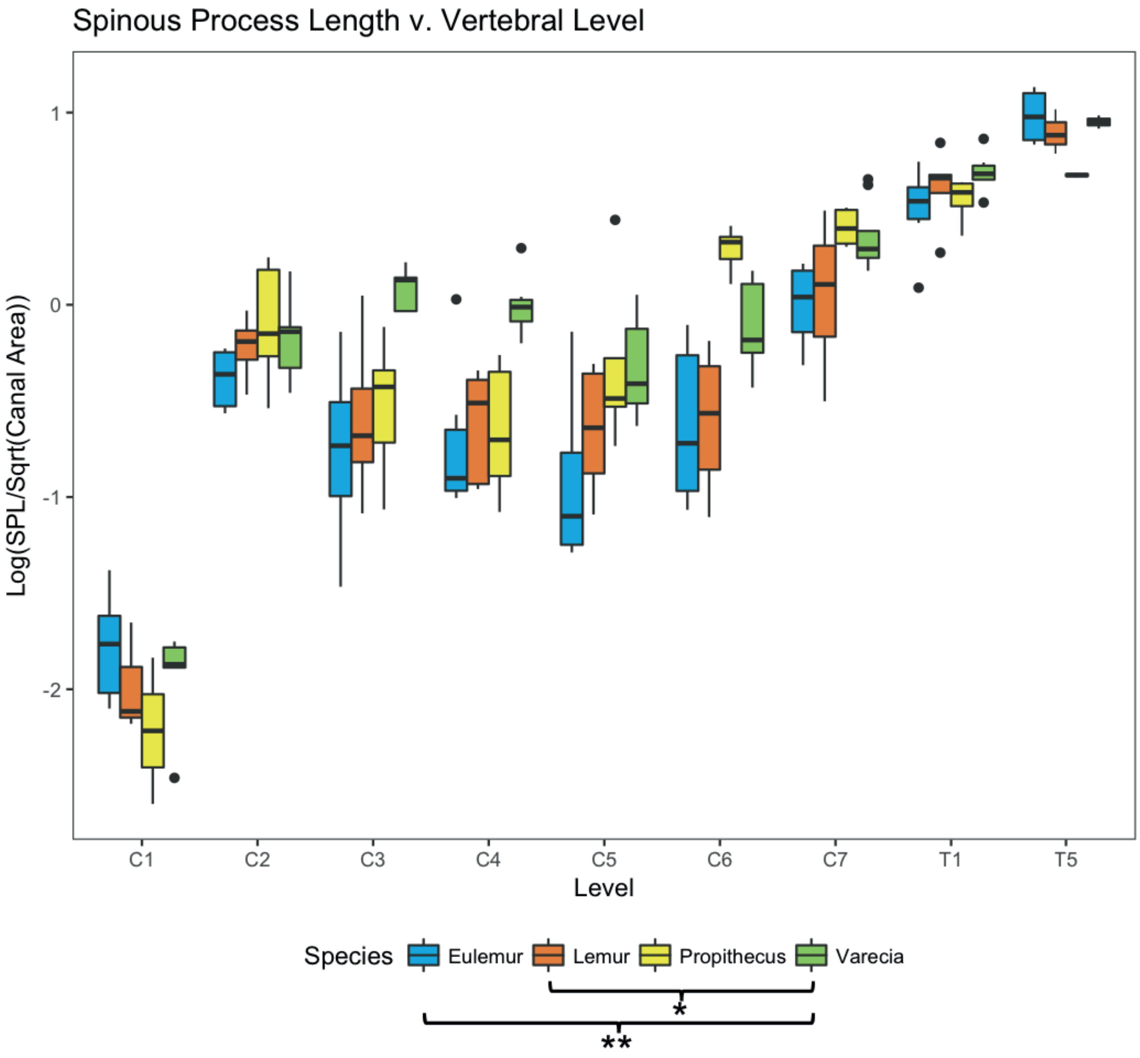

Figure 4.9 Results of the linear mixed models demonstrate significant differences between Varecia *and* Lemur *and* Varecia *and* Eulemur *in relative spinous process length within each vertebral level.*

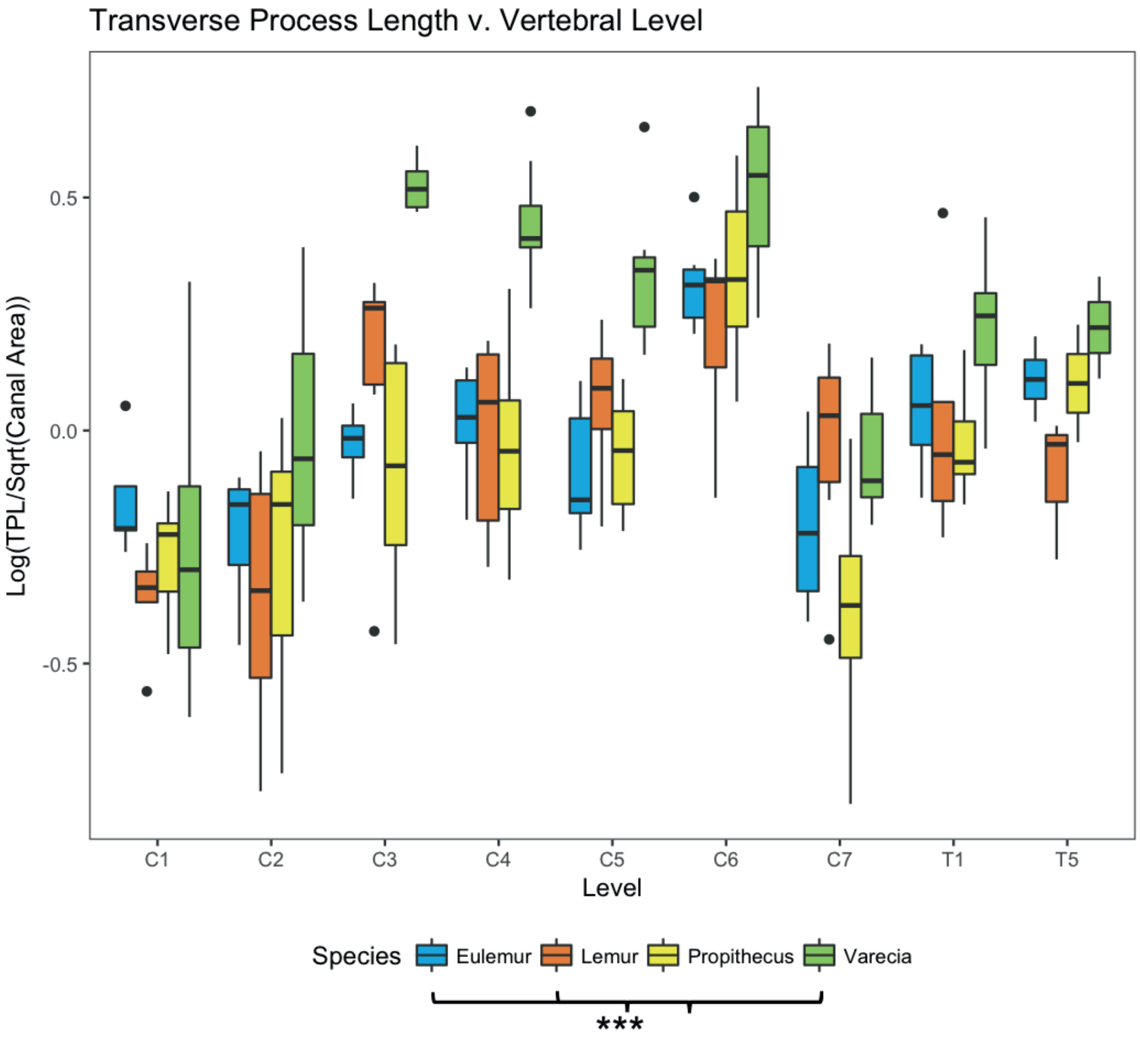

Figure 4.1 Results of the linear mixed models demonstrate significant differences between Varecia *and all other species in relative transverse process length at each vertebral level.*

Eulemur and *Lemur* have significantly smaller articular facets than *Propithecus* and *Varecia*. Larger articular facets are thought to transmit higher loads (Parr et al., 2011; Yapuncich and Boyer, 2014). *Eulemur* also has significantly smaller uncinate processes than both *Varecia* and *Propithecus* (see Figures 4.11 and 4.12). Taller uncinate processes have been purported to offer greater neck stability (Kotani et al., 1998), however the results of Chapter 3 do not lend support to this hypothesis.

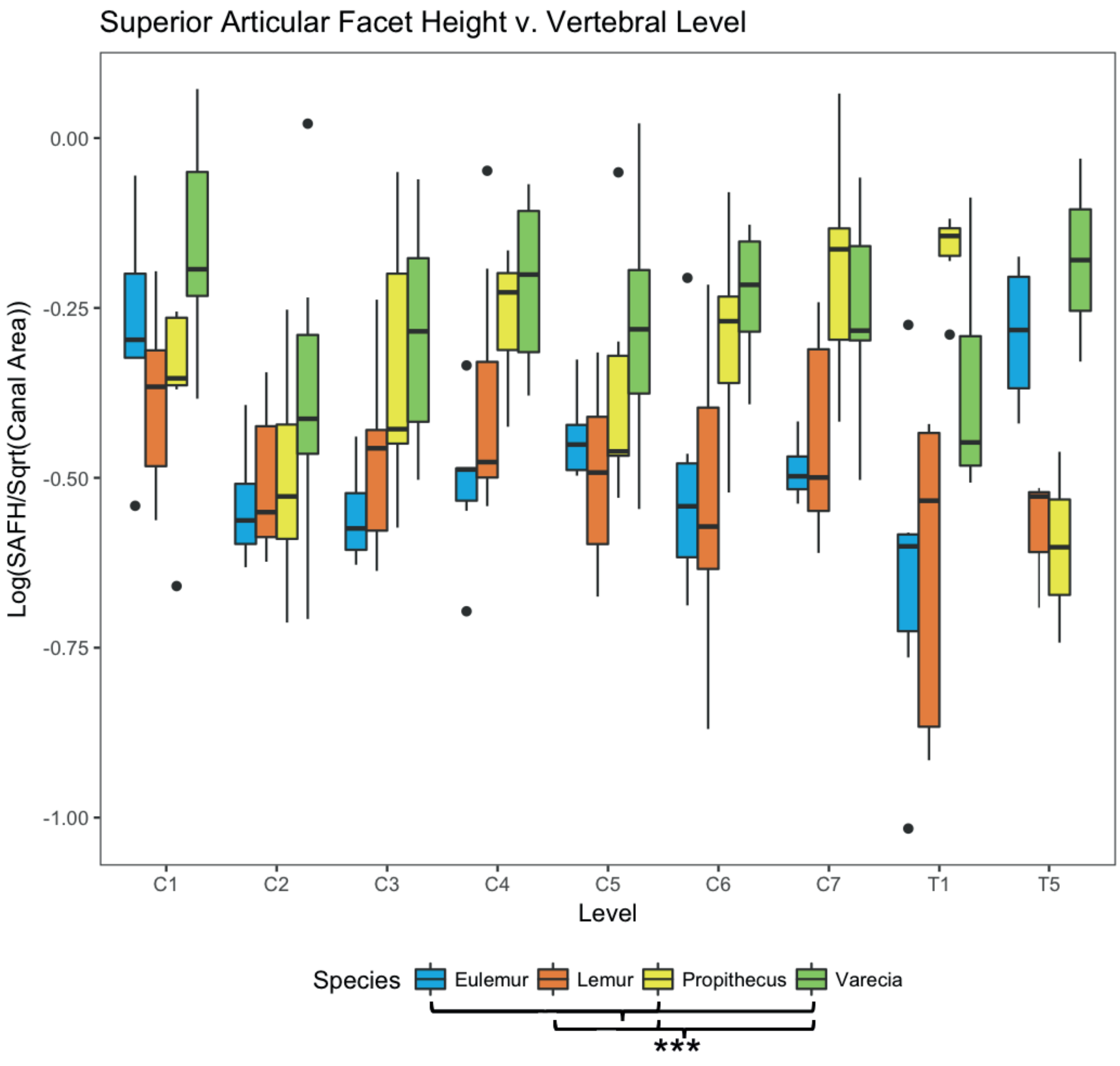

Figure 4.2 Results of the linear mixed models demonstrate Eulemur *and* Lemur *have significantly shorter articular facets than do* Propithecus *and* Varecia *with vertebral levels.*

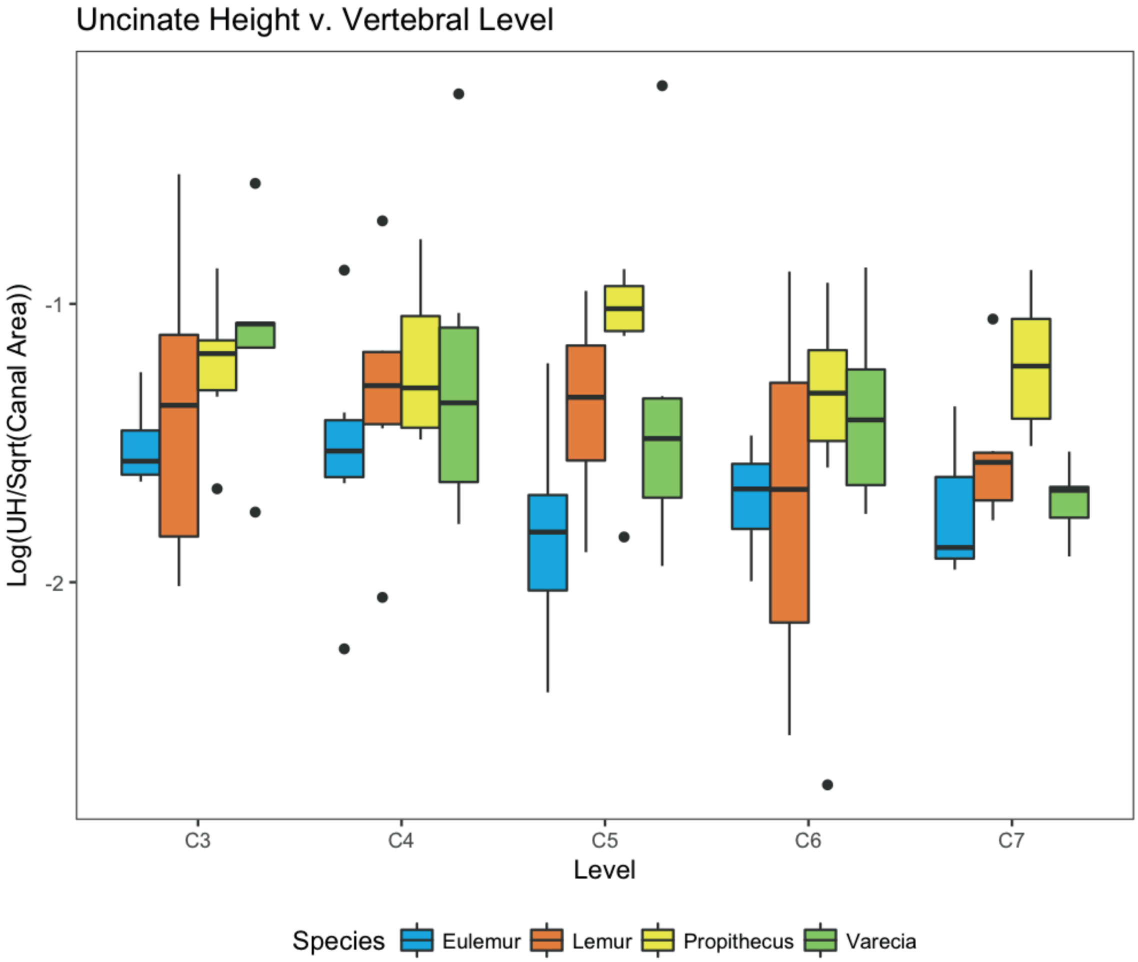

Figure 4.3 Eulemur *possesses significantly shorter uncinate processes than both* Propithecus *and* Varecia.

Eulemur also has shorter vertebral bodies than the other species. Longer vertebral bodies could offer greater resistance to bending moments in more pronograde species (see Fig. 4.13). Longer bodies are also thought to increase range of whole spine motion; however, no support was found for this hypothesis (see Chapter 3). *Varecia* has more cranially oriented articular facets than both *Lemur* and *Propithecus* (see Fig. 4.14).

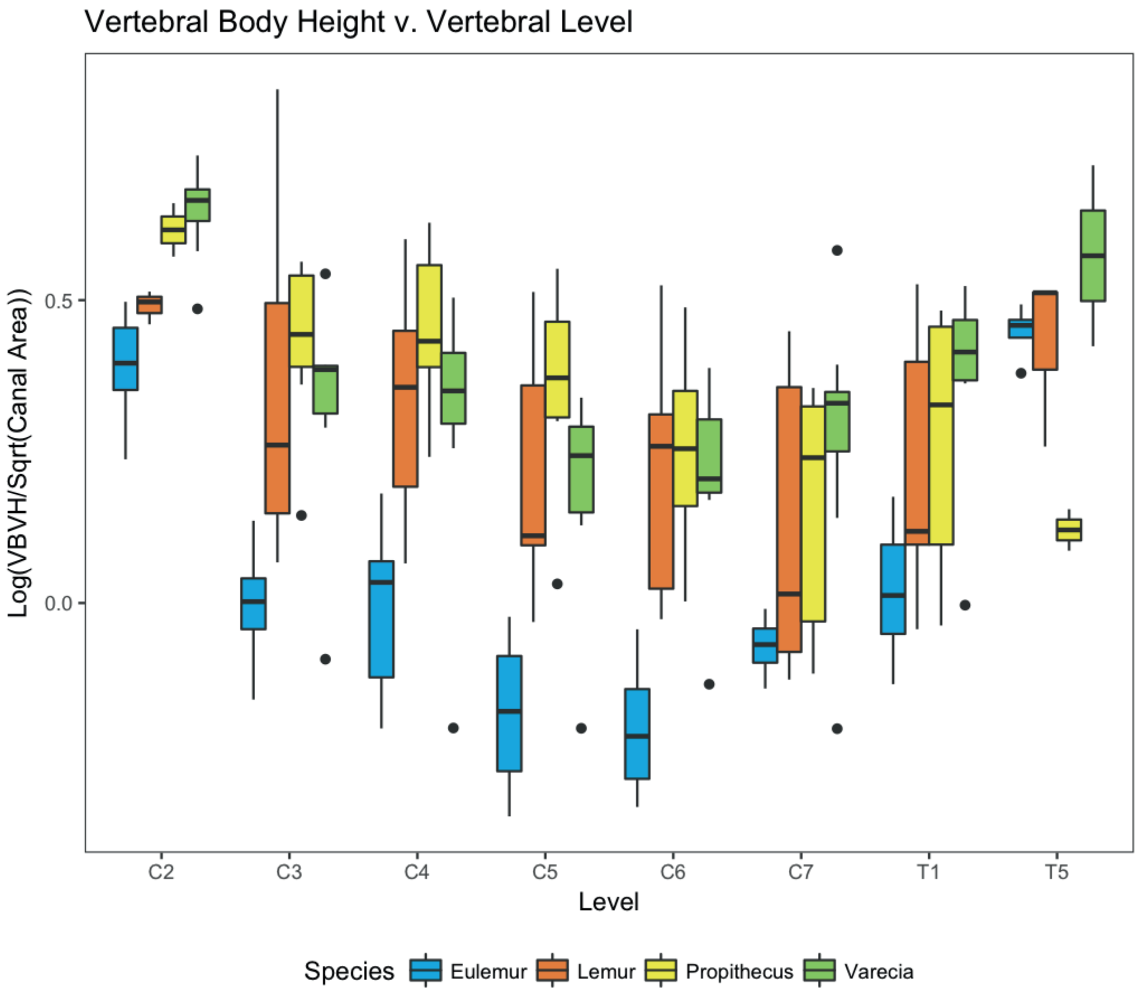

Figure 4.4 Eulemur *has significantly shorter vertebral bodies than the other species.*

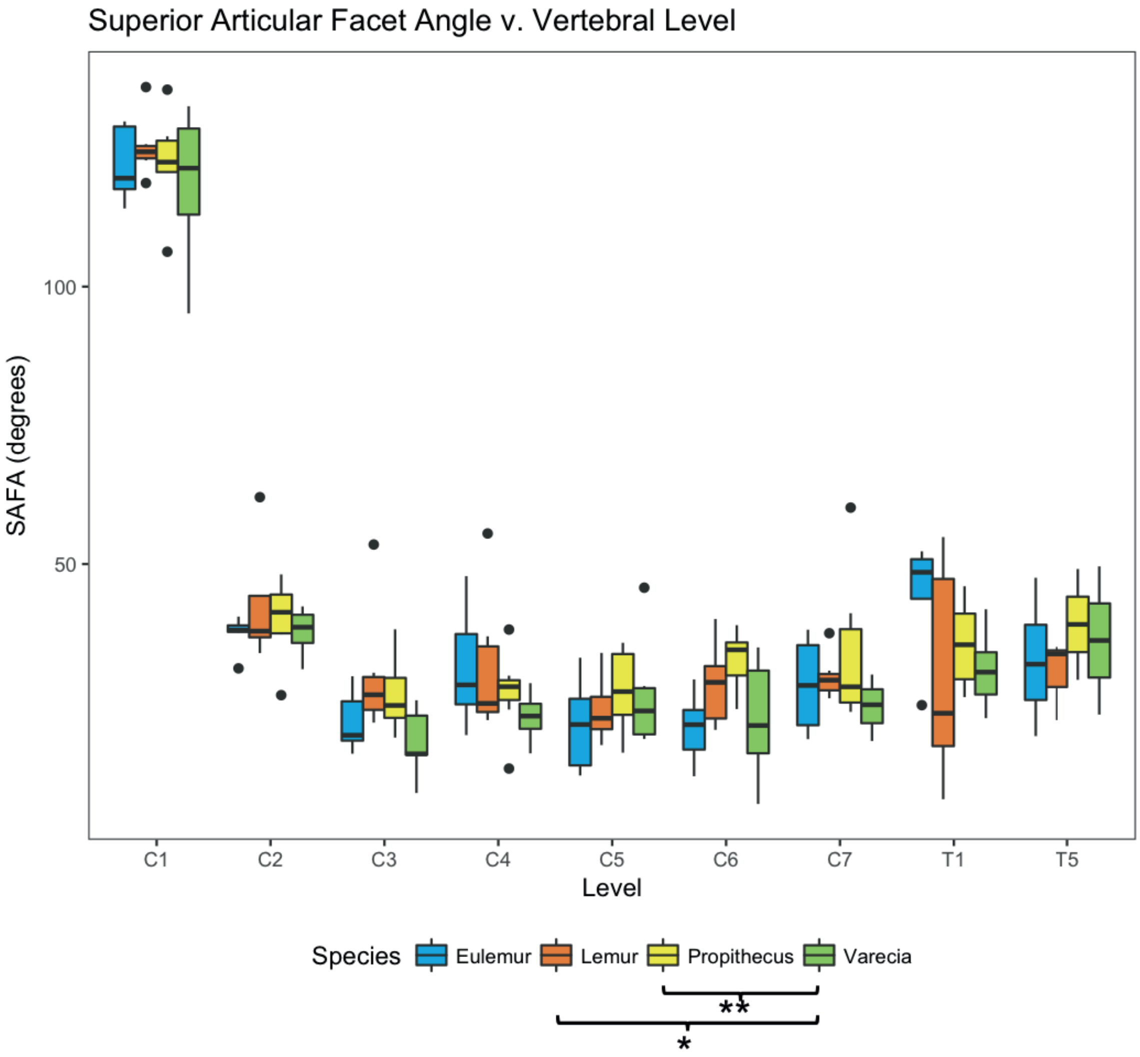

Figure 4.5 Varecia *has more coronally oriented facets per vertebral level than both* Lemur *and* Propithecus.

4.3 Discussion

Speed

Speed was a fixed effect in all of these analyses (see Tables 4.2-4.4 and 4.6). If the purpose of head stability during locomotion is to navigate through a complex environment, stability should increase with speed because the need to react to a more quickly to changing substrate should also increase. However, speed did not demonstrate a consistent pattern of significance within the models (see Tables 4.2-4.4 and 4.6). Thus, post-hoc analyses were conducted specifically testing the effects of speed on segmental motion across the gait cycles (see Table 4.11, Fig 4.8a-d). These results demonstrate that speed predicts range of motion of the neck (in all planes) as well as trunk pitch. These results are similar to that found in the literature: there is a significant increase in trunk pitch with increasing speed, but head pitch is unaffected (see Table 4.12 and discussion below).

Table 4.11 Effects of speed on locomotor segment range of motion. Significant correlations in bold (p<0.05).

Y: ROM	X	Random Effects	r^2	p_X
Head Yaw	Speed	Species (Individual)	0.071281	0.1709
Head Roll	Speed	Species (Individual)	2.64E-05	0.9855
Head Pitch	Speed	Species (Individual)	0.01773	0.599
Neck Yaw	Speed	Species (Individual)	0.35734	**9.00E-04**
Neck Roll	Speed	Species (Individual)	0.222221	**0.0073**
Neck Pitch	Speed	Species (Individual)	0.27027	**0.0231**
Trunk Yaw	Speed	Species (Individual)	0.109576	0.1257
Trunk Roll	Speed	Species (Individual)	0.061382	0.2879
Trunk Pitch	Speed	Species (Individual)	0.481145	**1.00E-04**

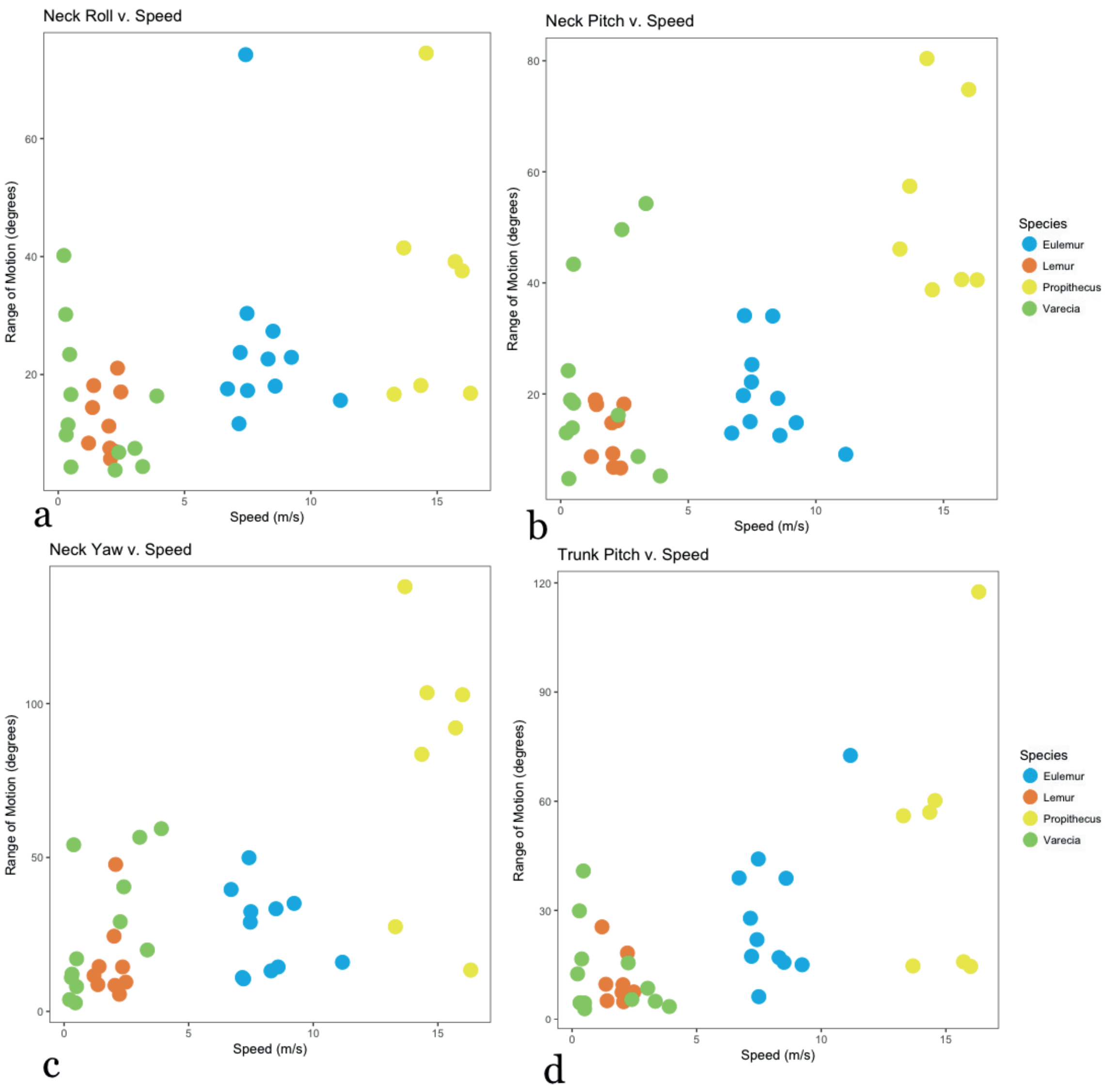

Figure 4.6 Speed significantly predict neck range of pitch (a), roll (b), and yaw (c) as well as trunk pitch (d), but species also (locomotor mode) demonstrate differences in speed.

Dunbar and colleagues (2008) conducted a kinematic study of sagittal-plane motion of the horse head, neck, and trunk during walking, trotting, and cantering. Their data demonstrate that the head during walking and cantering has a similar range of head pitch (9° and 10° respectively) as well as trunk pitch (6° and 8° respectively), see Table 4.12. Vertical translation was also analyzed for these trials. Their analyses demonstrate that there is an inverse relationship between vertical translation and head pitch: when the head translates superiorly, it also angles inferiorly. The effect of this relationship is likely to maintain a steady gaze. The similarity in head pitch between walking and cantering would seem to indicate, at least in horses, that speed has little effect. However, there is a large increase in vertical translation of the head between walking (12cm) and cantering (23cm) (Dunbar et al., 2008). Given the relationship between translation and angular movement, it would seem that there is a decrease angular movement relative to head displacement. Because head displacement increases during cantering, this increase in head angular stability could potentially decrease gaze stability, contrary to the hypothesis tested in this chapter.

However, more recent research has suggested that ungulates possess different head-neck kinematics than other mammals (Loscher et al., 2016). Loscher et al. (2016) have shown that long-necked ungulates time their head movements in order to decrease energy expenditure. Short-necked primates (cercopithecids) and felids moved their head and trunk together during locomotion. However, the heads of long-neck ungulates are out of phase with the trunk. They appear to time the oscillations of the head and neck such that the greatest force is being transmitted during the single support phase. This timing likely decreases the change in center of mass, thereby decreasing energy expenditure (Loscher et al., 2016). These results imply that mechanisms of head stability may be derived in ungulates, in comparison to primates, and that Dunbar et al.'s (2008) results may not be directly applicable to primates.

Table 4.12 Ranges of segment motion during one gait cycle, adapted from Dunbar (2008).

Displacement	Pitch Angle						Vertical Translation		
Speed	Slow			Fast			Slow		Fast
Segment	Head	Neck	Trunk	Head	Neck	Trunk	Head	Trunk	Head
Horse[1]	9 (+/-4)	10 (+/-3)	6 (+/-2)	10 (+/-4)		8 (+/-1)	12 (+/-4)	10(+/-2)	23(+/-5)
Giraffe[2]		4 (+/-1)							
Langur[1]	17(+/-5)		10 (+/-3)	15 (+/-2)		42 (+/-4)	7 (+/-2)		19 (+/-4)
Vervet[1]	15(+/-7)		6 (+/2)			14 (+/-7)			
Macaque[1]	13 (+/-4)		13 (+/-3)	13 (+/-3)		30 (+/-8)	7 (+/-2)		11 (+/-5)
Macaque[3]	5 (+/-2)		7 (+/-2)						
Gibbon[4]	4(+/-1)						2 (+/-1)		
Chimpanzee[5]	12 (+/-5)			17 (+/-7)					
Human[6]	12 (+/-3)	18 (+/-4)	7 (+/-2)						
Human[7]	9 (+/-3)			14 (+/-4)			5-9		7-16
Eulemur				53(+/-23)	20 (+/-8)	29(+/-19)			
Lemur	21(+/-13)	13 (+/-5)	11 (+/-7)						
Propithecus				17 (+/-9)	54(+/-17)	36(+/-23)			
Varecia	10 (+/-5)	23(+/-17)	13(+/-12)						

[1]Dunbar 2008, [2]Basu et al. 2019, [3]Xiang 2008, [4]Hirasaki and Kumakura 2004, [5]Thomson 2016, [6]Cromwell 2001, [7]Pozzo 1990

However, Dunbar conducted similar studies on several species of cercopithecids (Dunbar, 2004a; b). The primate head and trunk kinematics show a pattern similar to horses: there is little difference in range of pitch between speeds, but an increase in vertical displacement. Unlike horses, non-human primates increase trunk pitch with increasing speed (see Table 4.12). This increase in trunk pitch likely results in the increased vertical displacement of the head. In their analysis of macaque quadrupedalism, Xiang et al. (2008) found a slight decrease in head yaw with increasing speed (0.4-1.0m/s) but not pitch or roll. The authors noted that trial-specific head yaw tended to be larger trunk yaw and both head roll and pitch was smaller than that of the trunk. These patterns were not subjected to statistical analyses, however.

Pozzo and colleagues (1990) also investigated head stabilization during locomotion in humans both in lit and unlit conditions They found that both angular pitch and vertical displacement of the head increases with locomotor speed. However, the effects of speed were diminished in the darkness trials (Pozzo et al., 1990). This likely indicates that maintaining gaze stability is an underlying influence on angular head movements during locomotion.

Pozzo et al.'s (1990) human results, Dunbar's (2004a; b) results, and Xiang et al.'s (2008) results seem to contradict each other. Pozzo et al.'s (1990) humans increase head pitch with faster speeds, Xiang and colleagues' (2008) macaques decrease head yaw with increasing speed, speed doesn't seem to affect Dunbar's (2004a; b) Old World monkey head pitch. The results of this dissertation show that speed doesn't predict head motion in any plane (see Table 4.11). The lemur kinematic data, however, do show that neck motion increases with speed as well as trunk pitch. Increases in trunk pitch were also demonstrated in Dunbar's data set, see Table 4.12. The data presented in this dissertation, however, are not ideally suited to test the effects of speed because locomotor mode seems to influence speed. For example, leaping (horizontal and vertical) trials are much faster than the quadrupedal trials. Body size can also affect speed as well as the kinematics used to attain faster locomotion (Gatesy and Biewener, 1991). Speed was self-selected in all trials as well; therefore, differences between individuals is also confounding. Additional, treadmill-based experiments within one mode of locomotion would better facilitate our understanding the kinematic effects of speed.

Literature values and data accuracy

Very little has been published on the locomotor kinematics of the primate neck, so it is difficult to ground the results of this dissertation in existing literature. However, we can compare axial segment pitch for the few species that have been studied (see Table 4.12). Overall the head data seem comparable. The ranges of variation exhibited by *Lemur*, *Propithecus*, and *Varecia* appear similar to that of other primate species: ~10-20° of pitch. However, head pitch in *Eulemur* is higher than all other values (53° +/- 23°). Horizontal leaping involves a fair amount of whole-body flexion-extension, which could explain these outlying results. Literature neck pitch values are only available for human walking and so there is only one value to compare, rather than a pattern among species. Ranges of pitch overlap for all species except *Propithecus*, which has a much greater range of neck pitch than the other speices (54° +/- 17°). However, as a whole, lemur trunk pitch appears to mirror data found in the literature: faster modes of locomotion (e.g. leaping) have larger ranges of pitch than slower one (i.e. walking). The trunk values for *Eulemur* and *Propithecus* (29° and 36° respectively), seem to match those found in langurs and macaques locomoting at fast speeds while those of *Lemur* and *Varecia* (11° and 13°, respectively) are similar to langurs and macaques walking at slow speeds (see Table 4.12).

Leaping is a dynamic mode of locomotion and thus one would expect large ranges of segment motion. Given the data, it appears that *Eulemur* has much greater pitch in its head than its neck during locomotion, while *Propithecus* has a much greater range in its neck than its head. This may indicate species- or locomotor-specific strategies in mitigating trunk motion and maintaining gaze stability. *Eulemur* has a much greater range of passive motion than *Propithecus* at the atlantooccipital joint (61° vs. 26°, see Table 6.2). It is likely that this difference in range of passive motion influences the locomotor kinematics. This difference in range of motion does not seem to be reflected in skeletal morphology (see Fig. 4.14). Because *Eulemur*'s craniovertebral junction can accommodate such a large range of pitch, the head moves much more than the neck during leaping. It is possible that in order to maintain gaze and balance, other anatomical variations compensate, such as increased eye range of motion or larger semicircular canals.

In comparison with the literature values, however, the standard deviations for my values tend to be much higher (10°-30°) than previous studies (1°-10°), see Table 4.12. This brings into question sources of variation in the data both inherent in the head-neck complex as well as that due to methodological error. It is possible that movement of the axial skeleton during locomotion is less stereotyped than the appendicular skeleton; meaning, it is inherently variable.

It could also be that the variability is due to methodological error. The minimal data available from the literature hint that the noise in this dataset is more likely due to error. Specifically, it is possible that the error in the data come from skin-motion artifacts, or the non-congruency of skin motion and skeletal motion. These artifacts are common sources of error for any kinematic analysis that relies on superficial markers and has been well-studied in human lower limbs (reviewed in Peters et al., 2010; Fukui et al., 2016). These error tend to increase with increasing soft tissue coverage of the bone (Taylor et al., 2005). Analysis comparing skeletal movement to that of dermal markers has recently demonstrated that that the human lower cervical spine (C6) is more vulnerable to error during flexion-extension while the upper cervical spine (C2) has greater error in lateral flexion (Wang et al., 2016). These data suggest that soft tissue artifact plays a role in the error found in these data. Future work should focus on methods, such as XROMM (X-ray motion of moving morphology) in order to satisfactorily understand intervertebral locomotor kinematics.

The kinematics of the vertebral segments seem much more prone to error than that between head, neck, and trunk segments (see Table 4.1). They have much larger ranges of motion and much larger standard deviations. These errors are so large that the render the vertebral motion data suspect. For example, the pitch of the neck in *Eulemur* averages 19.9° +/- 8.4° (see Table 4.1). This is a reasonable value, comparable to those of other segments found in the literature. However, the average range of pitch for the C5 segment is 50.4° +/- 32° , far exceeding the both range of motion for the entire neck as well as the passive range of motion for the C3-C4 and C4-C5 joints combined. The same is true for the motion of many vertebral segments. This error could be due to several factors, but soft tissue artifact likely plays a role.

For this study, gaze is a particular concern for head range of motion. Lemurs were enticed with food rewards to walk through the measurement space. An effort was made by the handlers to position the food at roughly eye level. However, this position may have affected head range of motion. In particular, *Lemur*, head roll and yaw seem high (see Figs. 4.4 and 4.5). This larger range of motion could be the result of looking at the food or the handler.

It may also be error in digitizing. Markers were occasionally difficult to see and sometimes obscured by fur; this is especially true of the C1 spinous process marker. In addition, the DLTdv Matlab package that was used to digitize the videos creates confidence intervals around the digitized point. These intervals often overlapped between adjacent landmarks due to the low magnification of the image. Camera zoom could have been increased for the experiments. However, increased zoom would have sacrificed the percentage of stride available for digitization. Overall, these sources of error lead me to believe that the kinematics of the vertebral segments do not reflect reality and, therefore, cannot be used for subsequent analyses. It also calls into question the results of the analyses used to test the predictions P2c and P2d that were obtained using vertebral segment motion. Only the results using head, neck, and trunk segment motion should be considered. Attention in future analyses will be focused on the kinematics and range of motion of the head, neck, and trunk segments.

Further kinematic analyses

Axial translation is likely an important factor in rotation movement. Several works have previously demonstrated the importance of including translation when considering head rotational motion (Pozzo et al., 1990; Hirasaki and Kumakura, 2004; Xiang et al., 2008; Thompson, 2016). This is especially true of leaping behaviors. In the videos, it appears as the individual reaches the peak of its leap, the head and neck are angled downward in order to maintain visual contact with their landing point (or the food reward being held by the handler).

Future work should explore the influence of appendicular kinematics on axial kinematics. Locomotor speed, for example, affects stride length and stride frequency. Perhaps the effects of speed on neck and trunk movement (see Table 4.12) are consequences of stride differences. It is also important to consider the timing of the limb kinematics. Loscher and colleagues (2016) demonstrated in ungulates, timing of the support can affect the energetics of axial kinematics. In addition, a diagonal sequence gait was used in both arboreal and terrestrial quadrupedal trials (see Fig. 4.4). It would be beneficial to compare the axial kinematics between diagonal and lateral sequence gaits. It could be that gait sequence affects center of mass position, and therefore influences head-neck-trunk ranges of motion during locomotion. Future work will investigate these questions both within this dataset as well as through new experiments.

Neck function

Results for the vertebral segments exhibit far too much error to be confidently used for analysis. Instead, I will focus on the results using the head-neck-trunk segment data in order to understand how the neck's locomotor function can be applied to vertebral morphology. Overall, the data indicate minimal species-specific differences in locomotor kinematics. However, it is difficult to discern the distinction between species and locomotor mode because each species practices a different primary mode of locomotion. This decision was by design because the ultimate goal of this dissertation is to understand how different locomotor modes may affect vertebral morphology. However, all these species practice more than one mode of locomotion. The experiments conducted here relied on the assumption that habitual loading influences vertebral morphology. However, behaviors which are rare but important (and produce much higher loads) should also influence vertebral morphology. Future work will explore intraspecific locomotor variation and the relative influences of species and locomotor mode on axial kinematics.

Results indicate that trunk motion varies among species (Table 4.2) and that trunk motion significantly predicts neck motion (Table 4.3). This implies that axial segments may be under different biomechanical constraints during different modes of locomotion and these constraints should influence vertebral form.

Morphological variation

The range of motion in the neck during locomotion does not vary significantly within this sample. Thus, it is unlikely to correlate with any morphological variation among these species. It is possible that function does not vary enough in the sample to give a strong signal. Meaning, that the neck balances the head in similar ways regardless of locomotor mode. Lemurs, in particular, are capable of locomoting a variety of different ways. All species practice varying frequencies of leaping, climbing, and quadrupedalism (Gebo, 1987). It may be that vertebral morphology is adapted to dissipating many different kinds of forces from a variety of locomotor and postural modes. Large forces occur during locomotion and should, therefore, most strongly influence skeletal morphology (Preuschoft, 2004).

It may be that the locomotor signal is lost within the noise of other functional influences on cervical vertebral morphology. The neck functions during many other behaviors, such as feeding and foraging, grooming, predator vigilance, etc. All of these behaviors are likely under selective pressures and, thus, so is the vertebral morphology required to accomplish these behaviors. It is possible that vertebral morphology is generalized in order to function many different ways.

Some of the morphological variables appear to separate out based on body size despite the size-adjustment. Craniocaudal vertebral body height, for example, is significantly smaller in *Eulemur* in comparison to the other species, which also has the smallest body mass of the sample (Figure 4.13). In comparison to the larger *Propithecus* and *Varecia*, the smaller *Eulemur* and *Lemur* have craniocaudally shorter articular facets (see Figure 4.11). These indicate that these morphologies may not scale isometrically with body mass. Perhaps, larger species require greater stability via relatively larger joint surfaces or craniocaudally taller vertebral bodies.

The lack of correlation between locomotor range of motion and skeletal morphology may indicate locomotor neck function more strongly influences soft tissue morphology rather than bony vertebral shape. For example, spinous process length doesn't correlate with range of extension. Instead of increasing the mechanical advantage of the nuchal musculature by increasing spinous process length, the cross-sectional area of the muscles could increase.

Chapter 5 Discussion

5.1 Summary of Results

As the junction between the head and the trunk, the neck serves many different functions. The primary functions investigated in this dissertation were head-neck mobility and head-neck stability during locomotion. The hypothesis that vertebral morphology influences head-neck mobility was tested using intervertebral joint ranges of motion collected from radiographs. Regression results indicate little support for the predictions, see Table 3.1. Therefore, I conclude that ligaments and muscle offer greater stability to the joints than skeletal anatomy.

To understand how locomotion influences cervical vertebral morphology, I first tested the hypothesis that the neck functions in providing head stability during locomotion. This hypothesis was tested by collection axial kinematic data from four species of lemur during the species' primary mode of locomotion. The methods used provided values too coarse to satisfactorily gauge intervertebral kinematics and ranges of motion during locomotion. Analyses using axial segments (head, neck, and trunk) demonstrated that the locomotor mode influence trunk movement and that the movement of the trunk predicts neck movement in all planes as well as head roll and yaw, but neck pitch predicts head pitch. These results imply that the neck has a significant locomotor function. The last hypothesis attempted to understand the influence of locomotor axial kinematics on vertebral morphology. Due to the coarseness of the intervertebral results, however, axial segment ranges of motion could only be applied to C1, C7, and T5. These analyses, unsurprisingly, did not produce significant results. Thus, additional post-hoc analyses were conducted trying to understand how vertebral morphology varied between species. Results showed significant variations among species in all vertebral measurements. These significant differences appear to be influenced by body size, despite the data being size adjusted. It is likely that these morphological variables do not scale isometrically.

5.2 Neck Function

The neck originates with the advent of terrestrial tetrapods (see Ericsson et al., 2013 for review). A neck decouples the head from the trunk. This decoupling has led to a variety of exaptations; although it may not have evolved for the express purpose of grooming or feeding, the neck plays an important role in those behaviors. The neck's function in feeding has been well-documented in reptiles (Summers et al., 1998; Jones et al., 2009; Taylor et al., 2011; Snively et al., 2014), but also of note in mammals (Dumont, 1999; Anton et al., 2003; Salesa et al., 2005; Van Valkenburgh, 2006; Simmons and Altwegg, 2010). The neck's function in feeding behaviors is understudied in primates, but primates are known to manipulate objects with their head and neck (e.g. Torigoe, 1985) and anecdotally involve the neck in feeding behaviors (e.g. bark stripping or fruit/nut peeling). The neck is also useful in other behaviors such as grooming (Richmond et al., 1992) or predator vigilance. Behaviors like grooming and vigilance should, theoretically, select for large ranges of motion, potentially facilitating head-neck instability. Although the neck functions in these behaviors, I find it unlikely that they strongly select for cervical vertebral morphology within the hominin lineage. Becoming bipedal freed the hands from their locomotor function and, in turn, facilitated the increased manual dexterity (Kivell, 2015) for functions like feeding and grooming. It is more likely that the morphological differences found among fossil hominins (see Nalley, 2013 for review) stem from posture or locomotor selective pressures.

By decoupling the head from the trunk during locomotion the head is no longer required to move strictly in concert with the trunk. Separating the head from the pectoral girdle allowed for head stability during locomotor tasks and head mobility for behaviors such as predation, feeding, and grooming. Work on salamanders has demonstrated that the neck muscles are much more active during terrestrial locomotion than in aquatic locomotion (Frölich and Biewener, 1992). These data lend support to the idea that the neck originally evolved for balancing the head during locomotion. The link between terrestrial locomotion and neck evolution is further supported by the presence of cervical fusion (syncervical vertebrae) in cetaceans, especially those that swim in the open ocean rather than shallow waters (e.g. river dolphins). It is likely that this fusion functions in stabilizing the neck for hydrodynamic swimming (Vanburen and Evans, 2017). Syncervical vertebrae found in ricochetal rodents (as well as shortened cervical vertebrae) are also thought to limit head motion during locomotion but the functional advantage of this has not been demonstrated (Vanburen and Evans, 2017). The presence of syncervical vertebrae in ricochetal rodents is counterintuitive to the hypothesis that neck mobility aids in head balance; this warrants further study.

Strait and Ross (1999) measured the average inclination of the neck during mid-stance or mid-swing in a wide sample of primates. There is no correlation between this measure of neck posture and the mode of locomotion in which it was collected. The values during quadrupedal locomotion, for example, range from 48° to 108° from the vertical line of gravity. However, species with locomotor modes requiring orthograde trunk postures (brachiation, suspension, bipedalism) tend to have more orthograde necks (18° -50° from vertical). This variation implies that neck function differs among modes of locomotion, but further research is required to understand the correlation between postural variation and locomotor function. Furthermore, locomotion places much higher loads on the skeleton than other behaviors (Preuschoft, 2004), such as grooming, and, therefore, should have greater influence on postcranial form.

If the neck functions to counteract movements of the trunk, then what variation is present among trunk motion due to locomotor mode? According to the results of this thesis research, range of whole-trunk pitch does not seem to exceed 20° normal walking of large-bodied mammals (see Table 4.12). However, these ranges are much larger during faster modes of locomotion both in the dataset collected for this dissertation as well as those collected by Dunbar et al. (2008). The results of this dissertation demonstrate cautious support for the hypothesis that speed influences axial kinematics. Speed is a significant predictor of range of trunk pitch and all ranges of neck motion (see Table 4.11). But because speed was self-selected by the animal locomoting, an experiment controlling for both locomotor mode and speed would better be able to understand the relationship between speed and axial kinematics.

Very few studies have investigated neck kinematics during locomotion. Data are available for horses (Dunbar et al., 2008) and giraffes (Basu et al., 2019), but work by Loscher and colleagues (2016) suggest that ungulates have derived locomotor head-neck kinematics and, therefore, might not be useful for describing the general mammalian condition. Cromwell et al. (2001) studied movement of the human head, neck, and trunk in the sagittal plane during bipedal walking. The trunk, defined by landmarks at the lumbosacral and cervicothoracic junctions, demonstrated the least angular motion and the neck had the greatest range of motion, see Table 4.12 for (Cromwell et al., 2001) Their results further reveal that the neck acts in opposition to the trunk. As the trunk extends during double limb support, the head and neck flex. They conclude that this oppositional movement allows for continued head balance and gaze stabilization.

Results of this thesis exhibit a similar pattern: the neck and the trunk move opposite each other. Statistical analyses demonstrate that trunk motion predicts neck motion in all planes of movement: yaw, pitch, and roll. Neck pitch also predicts head pitch while trunk roll and yaw predict head roll and yaw, see Table 4.3. Visual inspection of the data do not reveal as clear a pattern as Cromwell and colleagues' (2001) study, see Table 4.12. The neck and trunk appear to oppose each other in pitch, likely in order to stabilize the head. In roll, the neck appears intermediate between the head and trunk; it moves with neither. During quadrupedal trials, the neck and trunk move together in yaw.

The strepsirrhine ranges of motion also tell a complex story. The human neck ranges of motion are almost three times greater than those of the trunk, see Table 4.12 (Cromwell et al., 2001). This pattern is seen in both *Propithecus* VCL and *Varecia* arboreal quadrupedalism. For *Lemur* and *Eulemur*, however, the greatest range of motion is in the head. This could indicate differences in mechanisms of head stabilization. However, vertebral morphology does not statistically correlate with these differences. Perhaps those species have different semicircular canal morphology or larger eye range of motion or there are differences in muscular morphology.

The semicircular canals have historically been associated with locomotion because they function in both the vestibulo-ocular reflex (VOR) and the vestibulo-collic reflex (VCR), the reflexes stabilizing the eyes and head respectively. Both reflexes are important aspects of head and gaze stabilization. The neural mechanisms of the VOR are well understood: as fluid moves within the canal it activates the cranial nerves that control ocular muscles, but the pathway for the VCR still remains nebulous but should act to stabilize the head in space via neck musculature (Goldberg and Cullen, 2011). Experimental work has demonstrated that these reflexes are vital in maintaining stability during involuntary head movements, but usually don't operate during voluntary head and eye movements (Pozzo et al., 1989; Hirasaki et al., 1999; Goldberg and Cullen, 2011). In comparison to birds, the mammalian VCR is relatively weak but the converse is true of the VOR (Goldberg and Cullen, 2011). It seems that mammals stabilize gaze by stabilizing the eyes and birds stabilize gaze by stabilizing the head (Goldberg and Cullen, 2011). Whether this difference is due to phylogenetic inertia or selection on whole-head stability isn't understood but the dichotomy exemplifies the importance of gaze stability during involuntary movements.

Regardless of which reflex is employed, the semicircular canals clearly function in locomotion in stabilizing the eyes and head. Research has linked larger canals to increased locomotor agility (Spoor et al., 2007) and more recently canal orthogonality to rotational head angular velocity during locomotion (Malinzak et al., 2012). Malinzak and colleagues (2012) found a significant, inverse correlation between the angular relationship between semicircular canals and the magnitude of the angular velocity of the head during locomotion. When compared to head and neck pitch, semicircular canal size and orientation does not seem to be correlated with axial movement during the primary mode of locomotion within the sample, see Table 5.1. *Lemur* and *Eulemur* have larger semicircular canals than *Propithecus* or *Varecia*. It is possible the larger canal size allows for smaller neck movements (and, therefore, larger head movements) during locomotion but further research on a greater number of taxa would be required to satisfactorily answer this question. This thesis only included one mode of locomotion. Malinzak suggests semicircular canals morphology could be adapted to high-risk locomotor behaviors. It is very unlikely that the slow-paced quadrupedal locomotion of *Lemur* and *Varecia* is the riskiest behavior in which they engage. Thus, it might also be useful to study head-neck motion in a variety of locomotor modes both common and rare (but risky).

Table 5.1 Head-neck kinematic values and semicircular canal morphology. Data taken from [1]Spoor et al. (2007) and [2]Malinzak et al. (2012).

Species	**Mode**	**Head Pitch**	**Neck Pitch**	**Canal Radius[1]**	**Agility score[1]**	**90var[2]**	**Angular Velocity[2]**
Eulemur	HL	45 (+/-24)	20 (+/-8)	0.196	medium	77.9	78
Lemur	TQ	26 (+/-12)	13 (+/-5)	0.161	medium	52.6	94
Propithecus	VCL	29 (+/-26)	54 (+/-17)	0.149	fast	27.7	124
Varecia	AQ	9 (+/-5)	23 (+/-17)	0.145	medium	55.6	56

Habitual posture during locomotion could be important for proper function of the vestibulo-collic reflex. Differences in head, neck and trunk postures have been shown affect the timing and activation of neck musculature (Thomson et al., 1996; McCluskey and Cullen, 2007; Corneil et al., 2013). These differences in muscular activation, in turn, affect the how the vestibulo-collic reflex operates. It is likely that these postures fall within the ideal range for muscular activation. Strait and Ross's (1999) dataset included several platyrrhine species under different modes of locomotion. The intraspecific difference between these modes is minimal (<20°). It could be that the VCR operates in an ideal postural range and that range explains the variation in neck posture despite similar modes of locomotion.

Differences in ocular mobility could also explain the smaller neck ROM, in comparison to head ROM, found in *Lemur* and *Eulemur*. Larger ocular ranges of motion could compensate for larger head movements. The human eye can move 89° in adduction-abduction, elevate 28°, depress 47°, and 7° in both intorsion and extorsion (Kushner and Kraft, 1983; Shin et al., 2016). Comparative data are not available for non-human primates, but future work should investigate the differences in primate eye function and anatomy and its bearing on the VOR and VCR.

Proprioception could also play a role in these large head movements. All individuals were locomoting on stable, stiff substrates. They habituated to the space and substrates prior to data collection. It is possible that substrate compliance affects head mechanics. Compliant substrates have been shown to affect limb and trunk kinematics in primates. As a whole, these studies demonstrate that primates tend to reduce whole-body center of mass when locomoting on less stable substrates (Demes et al., 1995; Young, 2008; Channon et al., 2011; Young et al., 2016). Kinematic differences due to substrate compliance should also affect the head and neck. If the lemurs are on a stiff, familiar substrate, head stability may be less important. They do not need to look where they are going because they know where the substrate in relation to their bodies.

The results of this dissertation, coupled with previously conducted research, demonstrate that the neck has an important locomotor function: to facilitate head balance and gaze stability. The influence this function has on morphology, however, is more ambiguous.

5.3 Functional Influences on Vertebral Morphology

This dissertation aimed to understand the relative influences of both passive and locomotor range of motion on vertebral morphology. As a whole, the results demonstrate little support for either hypothesis. It is more likely that ligamentous anatomy constrains passive range of motion. The human spinal ligaments and their contributions to spinal stability are well described in the medical literature (reviewed in White and Panjabi, 1990; Jaumard et al., 2011). For example, intraspecific analysis has indicated that intervertebral discs with smaller areas offer greater mobility (Natarajan and Andersson, 1999). However, comparative data on morphological, histological and mechanical differences in mammalian spinal ligaments are quite limited (Little et al., 1981), but see

Long et al.'s (1997) study in dolphins. Given the negative results of this dissertation research, it is difficult to apply them to the fossil record, but we can attempt to apply what is already known about functional morphology of the spine.

Other attempts have been made to reconstruct joint range of motion in fossil specimens (Hutson and Hutson, 2012; Hammond, 2013; Kambic et al., 2017; Manafzadeh and Padian, 2018) and they similarly conclude the important of soft tissue in providing joint stability. Discussed previously, was the study conducted by Manafzadeh and Padian (2018) which found incredible expansion in avian hip ROM after ligamentous removal. They, and others, also highlight the necessity of studying range of motion in three-dimensions (Kambic et al., 2017; Manafzadeh and Padian, 2018). A species rarely moves in one plane at a time. This is especially true of the neck: the uncinate processes purportedly require lateral flexion and extension in order to accomplish joint rotation (Kapandji, 2008). The 3D morphospace of possible movements could inform the study of cervical vertebral morphology and its potential effects on range of motion. The head and neck rarely move in one plane (e.g. flexion-extension). Rather, movement is often three-dimensional. For example, the potential range of rotation likely differs between maximum flexion and neutral postures. If both passive and locomotor range of motion fail to impart a functional signal, then what can we say about the vertebral morphology found within fossil hominoids?

The vertebral body is the primary weight-bearing vertebral structure. However, in humans, it has been demonstrated that cervical neural arch bears as much as 36% of the compressive loads applied to them (Pal and Sherk, 1988). It would be informative to conduct similar experiment on a range of species and loading regimes, especially applying tensile loads to primates with more pronograde neck postures. Because the vertebral body functions significantly in weight-bearing, its dimensions are highly correlated with body mass (Rose, 1975; Shapiro, 1993b; Shapiro and Simons, 2002; Nakatsukasa and Hirose, 2003; Chen et al., 2005; Cotter, 2011; Nalley and Grider-Potter, 2015). In the lower vertebral levels, expansion of vertebral body diameter has been associated with increased compressive loading in orthograde trunk postures (Rose, 1975; Shapiro and Simons, 2002; Chen et al., 2005). The cervical vertebrae, however, do not show a correlation between neck orthogrady and centrum surface expansion. Instead, they demonstrate a significant link between pronograde posture and craniocaudally longer vertebral bodies (Nalley and Grider-Potter, 2015). It is likely that vertebral bodies experience greater bending moments in more pronograde postures and, therefore, increasing length increases the area over which to distribute these loads. Work across mammals by Arnold et al. (2017) has revealed that cervical body length has a negatively allometric relationship with body mass and they reason that stouter vertebrae can better accommodate the larger forces associated with increasing body mass. Similar results have been demonstrated for primate lumbar vertebrae (Shapiro and Simons, 2002). Centrum length was also analyzed in this dissertation as a correlate of range of flexion-extension with minimal success. It is likely that the relative size of the intervertebral discs is also an important factor in flexion-extension movement (Breit and Künzel, 2004).

Uncinate processes are also important as they are thought to offer joint stability. This hypothesis is logical: a U-shaped joint and supported by human research (Kapandji, 2008), the analyses conducted as a part of this dissertation found no relationship between relative uncinate height and passive range of lateral flexion. Uncinate height and “roundness” has also been shown to be highly correlated with body size (Meyer et al., 2018). Uncinate processes are relatively taller in smaller primates (Meyer et al., 2018). The functional significance of this pattern is not clear.

The spinous process has received much attention in investigations of functional morphology because it is the attachment site of the head-neck extensors. Longer, more caudally oriented processes are thought to provide greater mechanical advantage to the nuchal musculature because they extend the moment arm of the neck extensors further from the joint's center of rotation (Shapiro, 1993b; Nalley and Grider-Potter, 2015). Spinous process length has been shown to scale with positive allometry, potentially indicating the necessity for relatively greater muscular output to maintain stability in larger animals (Shapiro and Simons, 2002; Arnold et al., 2016). In addition, Nalley and Grider-Potter (2015) established a significant correlation between relative spinous process length and neck posture. Species with have more pronograde neck postures during locomotion have relatively longer spinous processes. This is likely due to the need for greater force needed to balance the head in more pronograde neck postures (Nalley and Grider-Potter, 2015). This dissertation provided little evidence longer spinous processes result in either reduced ranges of extension through skeletal inhibition of motion or increased ranges of flexion by lengthening the moment arm.

The cross-sectional area of the neural arch (i.e. pedicles, laminae, processes) is also of interest. Relatively larger cross-section area should offer increased resistance to deformation under loading (reviewed in Lieberman et al., 2004). Increased pedicle dimensions are found in the lower lumbar vertebrae of more orthograde primate taxa (Shapiro, 1993a), likely in response to greater compressive loading. The cross-sectional area of cervical laminae was found to correlate with neck inclination in C4 and C5, as well, but no other neural arch area correlations proved significant in the primate cervical spine (Nalley and Grider-Potter, 2015).

Morphology of the articular facets should also affect the motion and loading patterns that occurs between intervertebral joints. The angle of the facets within the spinal column varies: lumbar facets are positioned medially to limit rotation, thoracic facets are oriented ventro-dorsally to limit lateral flexion, and cervical facets are angled cranially in order to facilitate greater freedom of motion (Kapandji, 2008). Despite these known, gross differences in facet orientation and range of motion, no interspecific correlation between the two was found in primate cervical vertebrae in this dissertation. Neck posture, however, has been shown to correlate with facet orientation. More orthograde primates possess more coronally oriented facets. This is likely an adaptation to increasing compressive forces associated with neck orthogrady (Nalley and Grider-Potter, 2015). In addition, pronograde primates tend to have much greater curvature of the atlantooccipital joint, possibly to combat increased multidirectional loading (Hamrick, 1996; Grider-Potter and Hallgren, 2013; Nalley and Grider-Potter, 2017).

Results of this dissertation also demonstrate little support for the prediction that increased joint size equates to increased ranges of motion. This is likely due to stability offered by the joint capsular ligaments. Articular facet size has been implicated in habitual loading patterns (Breit and Kunzel, 2002; Meyer, 2016). Given that the articular pillars can dissipate up to 1/3 of vertebral loading, it is possible that articular facet size correlates with habitual posture. One would expect joint surface size to increase with the large compressive loads associated with orthograde neck posture.

5.4 Implications for fossil hominin species

This research attempted understand the functional influences on cervical vertebral form in order to retrodict the behaviors of extinct species. The vertebrae of fossil hominins are particularly puzzling as they preserve human-like and ape-like morphologies. If form follows function, this implies concomitant human-like and ape-like functions. Specimens from several species of hominin have been described in the literature.

Australopithecus afarensis

A C1, C2, and C6 from Hadar (Lovejoy et al., 1982), as well as the mostly complete column (C2-C7) from Woranso-Mille (Meyer, 2016) have been unearthed. Relative vertebral body height of the specimens is similar to that found in modern *Homo sapiens* and shorter than that found in *Pan*, but not outside the values found in hylobatids (Nalley, 2013; Meyer, 2016). The Hadar C6 (A.L. 333-106) possesses a long, robust spinous process, similar to that found in *Pan*, more robust laminae than humans (but not apes), and taller articular facets. No spinous processes are preserved from the KSD-VP 1/1 series. However, the laminae are more robust than in modern humans. The lower cervical articular facets of the KSD-VP 1/1 vertebrae are oriented more obliquely (relative to midline) than in modern humans but the facets have similar relative heights.

A partial atlas of *A. afarensis* has been recovered, A.L. 333-83 (Lovejoy et al., 1982). Similar to that found in more pronograde species, the atlantooccipital joint is highly curved. Highly curved joints should offer greater stability under multidirectional loading (Hamrick, 1996), e.g. different head-neck postures. The axes from Hadar and Woranso-Mille also present disparate morphologies. The Hadar specimen, A.L. 333-101, preserves articular facets that are flat (similar to humans) and a dens that lacks the dorsal inclination found in some non-human primates. The articular facet orientation is potentially a response to increased compressive loading associated with orthogrady (Gommery, 2006). In contrast, the KSD-VP 1/1 C2 has highly angled superior articular facets, similar to that found in New World monkeys, but lacks a dens (Meyer, 2016). This variation is surprising. The Hadar specimen has significant taphonomic damage to the articular facets, which could explain the variation in this specific variable. As a whole, however, the apparently incongruent morphologies between the A.L. 333-101 and KSD-VP 1/1 specimens are cause for concern. The linear measurements from KSD-VP 1/1 are not scaled with a consistent measure of size, which could be obfuscating a pattern, but this wouldn't account for disparities in angular measurements. Future work should investigate the intraspecific variation found in ape cervical morphology and if these specimens fall outside the expected range of variation within one species.

The robusticity of the spinous process imply that like great apes, *A. afarensis* benefitted from increased force output of the nuchal musculature. Similarly, the morphologies indicate adaptations to habitually large, multidirectional loading of the cervical spine (e.g. robust laminae and spinous processes, curved atlantooccipital joint). Therefore, it is likely that *A. afarensis'* neck posture was not as orthograde as that of modern humans.

Australopithecus sediba

Several cervical vertebrae of *A. sediba* have been discovered: a C3 and C7 from a subadult MH1 and a C3 and C6 from the adult MH2 (Berger et al., 2010). They have subsequently been analyzed by (Meyer et al., 2017). Both individuals are absolutely smaller than modern humans in vertebral body and canal dimensions. According to the analyses conducted by Meyer et al. (2017), articular facet height does not fall outside the range of human values but is angled much more acutely relative to midline. This angulation is similar to that found in extant apes as well as A.L. 333-106 (but not KSD-VP 1/1). The relative spinous process lengths of MH2 are not significantly different from humans. All relative linear values are not significantly different in Meyer et al.'s (2017) analyses, with the exception of uncinate 'roundness' and a ratio of centrum to neural arch mass in C3, but not C6. In addition, the spinous processes of C6 are much more inferiorly inclined than in anatomically modern humans, which could offer nuchal musculature greater mechanical advantage during extension. The articular facets appear more coronally oriented, in comparison to humans, which could indicate greater compression in the articular pillars. Additionally, Meyer et al. (2017) show that in comparison to humans, *A. sediba* has a more robust, inferiorly inclined transverse process as well as more vertical uncinate processes. The transverse process robusticity could, according to the results of this dissertation, relate to increased mechanical advantage of the lateral neck flexors. Overall, these morphologies appear very similar to that of *H. sapiens*, which may indicate similarities in head balance mechanisms and neck posture. However, additional measurements (such as lamina cross-sectional area and articular facet angle in the sagittal plane) would further elucidate the functional implications of the preserved morphology.

Homo erectus

Two subadult cervical specimens from Dmanisi, C2 and C3, are described in the literature (Meyer, 2005). Meyer (2005) reported absolute values. For purposes of comparison, I scale his data to vertebral canal area and compared to species ranges from Nalley (2013), which were previously scaled to vertebral canal area. The C2 preserves laminae with relative thickness just outside the range of adult human variation. Its spinous process is relatively long, similar to that found in *Gorilla* and *Pongo*. Given that this specimen is immature, it is likely that these values would be on the lower end of the species values. The articular facets are oriented 53° from the plane of the vertebral body. Its uncinate processes are short and angled (unlike those found in the *A. sediba* specimens). The relative thickness of the lamina is slightly thinner than the human and chimpanzee values found for adult C3. The relative height of the vertebral body falls within the range of the extant *H. sapiens*. Its pedicles are absolutely shorter than both the adult and subadult specimens from Malapa (Meyer, 2005; Meyer et al., 2017). These specimens, although immature, reveal an interesting pattern. Despite lacking annular ring fusion, the C2 is more robust. However, the C3 appears more gracile. Cranial vertebrae reach maturity earlier than more caudal vertebrae (Scheuer and Black, 2000; Altan et al., 2012). Thus, these differences could be due to ontogeny: C2 is at a later stage of maturation than C3. The robusticity found C2 would seem to indicate greater loading associated with pronograde postures. However, it is difficult to partition functional variation from ontogentic variation in these subadult specimens.

A subadult C7 attributed to *Homo erectus*, KNM-WT 15000r, has also been described in the literature (Brown et al., 1985; Latimer and Ward, 1993). Its annular rings are also unfused. The vertebral body of the specimen is craniocaudally shorter than that of *Homo sapiens* but does not differ significantly in any other linear metric (Nalley, 2013; Meyer et al., 2018). However, this could also be attributed to its immaturity.

Homo neanderthalensis

Many more cervical vertebral specimens of Neanderthals have been found which allows for both greater statistical power as well as an improved understanding of variation within the extinct species. Neanderthal cervical vertebral morphology and its implications was reviewed by (Gómez-Olivencia et al., 2013). They conducted their analyses using raw measurements. At all levels, dorsoventral diameter of the vertebral canal is not significantly different from that of humans, but the transverse diameter of the canal is significantly larger. Correcting for body size would improve the comparisons made here. Their analyses show that Neanderthals have significantly longer, and more horizontally oriented spinous processes as well as thicker laminae, in comparison to modern humans in the lower cervical vertebrae (C5-C7). The ventral aspect of the vertebral body is significantly short in all levels. The uncinate processes do not differ in height, nor do the pedicle dimensions. The robusticity of the vertebrae is expected in Neanderthals, who are a robust species in many other aspects. The robusticity of the neural arch is likely an adaptation to creating and transmitting high muscular loads. It may be that the robust skull found in Neanderthals requires and equally robust neck to balance it.

5.5 Future Directions

The results of this research show that both passive and locomotor range of motion have little influence on cervical vertebral morphology. Very few functional influences on cervical vertebral morphology have been identified. Analyses testing the influences of locomotor mode on cervical morphology have had mixed success in previous studies (Manfreda et al., 2006; Nalley, 2013; Arlegi et al., 2017; Meyer et al., 2018; Villamil, 2018), but most are unsatisfactory in that they use of categorial variables. These categories often ignore or reduces critical, explanatory variation. Quadrupedalism, for example, encompasses a range of neck inclinations (Strait and Ross, 1999), positional behaviors, and locomotor behaviors (Hunt et al., 1996). This category obscures meaningful behavioral variation found within it. This dissertation attempted, in part, to quantify locomotor variation in neck function via axial kinematics rather than relying on broad, often meaningless, categories. Results demonstrate that the neck is an active participant in locomotion. Locomotor behavior should, consequently, be reflected in vertebral morphology. However, methodological issues prevented intervertebral kinematics from being successfully applied to vertebral morphology. Future work would benefit from more refined methods of skeletal kinematic data collection (i.e. XROMM). It is also important to collect data from a variety of locomotor modes, especially those that are rare but induce high loads or are potentially risky. This will facilitate understanding species-specific vs. locomotion-specific behaviors of the axial skeleton. Kinematic analyses would also benefit from a more controlled study of speed. Understanding the influence of soft-tissue anatomy on cervical morphology is a large gap in the literature. This gap is overly apparent in the discussion of passive range of motion and its inhibitors. Detailed studies of muscular and ligamentous morphology and histology would greatly benefit our understanding of neck form and function.

This dissertation quantified the locomotor function of the primate neck: to balance the head and counteract the movements of the trunk. This is a critical step towards understanding the neck's myriad of functions and how they influence its form. Although this measure of locomotor function did not correlate with skeletal morphology, habitual neck posture during locomotion has previously been shown to influence it (Nalley and Grider-Potter, 2015, 2017). Future work would benefit from furthering our understanding of axial kinematics in a variety of species and their numerous modes of locomotion and other behaviors (e.g. feeding). In understanding this, we may shed light on the selective pressures that shape the disparate vertebral morphologies found in the hominin fossil record.

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APPENDIX A

DATA TABLES

Table 0.1 Species averages of morphological measurements

Species	Level	CA	SPL	SAFH	ATPL	PTPL	UH	VBVH	SPA	SAFA	ATPA	PTPA
S. apella	C1	108.19	1.72	5.71	4.82					161.28		
E. mongoz	C1	81.52		4.29	7.00					153.93		
H. sapiens	C1	450.03	7.51	17.20	13.23					126.36		
H. lar	C1	136.37	2.85	6.36	6.19					139.89		
L. catta	C1	69.18		5.22	7.11					163.05		
M. mulatta	C1	175.54	2.85	5.19	5.62					143.78		
O. crassicaudatus	C1	28.78	1.78	4.57	4.48					149.37		
P. verreauxi	C1	86.52		5.24	9.13					153.82		
S. sciureus	C1	54.41		2.70	4.86					160.83		
V. variegata	C1	86.19	1.71	8.20	9.43					159.28		
S. apella	C2	55.01	6.55	5.61	5.58		5.29	7.85	88.24	59.02	66.96	
E. mongoz	C2	34.95	4.86	4.53	5.19		3.28		135.54	20.21	97.20	112.30
H. sapiens	C2	445.23	15.78	16.27	9.57		15.55	17.18	117.16	53.82	131.42	113.00
H. lar	C2	90.33	7.78	6.83	6.04		5.12	11.43	107.80	26.03	103.91	131.75
L. catta	C2	39.83	6.11	4.62	5.10		4.39	6.68	111.61	32.09	86.40	120.78
M. mulatta	C2	79.67	9.03	6.93	5.51		6.34	9.43	107.82	47.52	50.01	69.28
O. crassicaudatus	C2	30.74	4.85	2.82	3.24		3.40	6.88	134.79	26.64	94.96	93.88
P. verreauxi	C2	42.00	7.11	5.45	6.82		4.80	8.92	115.30	27.23	90.22	
S. sciureus	C2	30.69	3.64	4.15	4.15		2.78		175.69	27.11	54.43	
V. variegata	C2	52.37	6.49	5.50	7.74		5.79	6.56	101.21	25.10	128.39	96.04
S. apella	C3	86.62	5.10	4.10	7.01		2.37	5.20	130.11	59.44	131.78	128.39
E. mongoz	C3	36.72	3.57	3.67	5.96		1.10	7.62	140.15	31.80	135.06	112.45
H. sapiens	C3	411.82	12.13	10.72	12.32	6.47	5.24	14.16	121.76	52.62	125.61	115.90
H. lar	C3	82.66	6.01	5.45	6.45		3.41	8.94	111.17	33.95	118.68	103.77
L. catta	C3	39.11	3.56	3.84	6.80		1.68	9.14	125.26	29.97	61.59	129.91

M. fascicularis	C3	72.26	5.99	4.69	5.30	5.08	3.58		137.93	27.56	140.60	141.61
M. mulatta	C3	83.07	6.80	5.94	7.04	5.30	3.94	6.97	126.78	23.48	103.67	99.52
O. crassicaudatus	C3	35.71	2.08	2.63	3.73		1.10	8.19	120.63	31.24	130.78	98.42
P. troglodytes	C3	89.83	19.72	8.54	8.90	6.36	5.30		140.14	26.80	135.20	149.11
P. verreauxi	C3	39.89	4.42	4.58	7.49		2.08	10.20	135.75	31.50	102.39	
S. sciureus	C3	75.28	2.41	2.69	4.88		1.60	5.59	147.24	30.52	134.10	134.08
V. variegata	C3	43.08	5.44	4.88	13.25		2.44	8.75	107.95	26.49	39.90	92.12
C. apella	C4	93.63	5.54	4.40	6.06	4.44	2.34	4.87	126.17	78.09	121.24	129.97
E. mongoz	C4	34.04	3.41	4.08	6.28	5.73	1.52	7.02	130.04	15.88	109.67	131.00
H. sapiens	C4	389.44	14.17	12.05	10.67	6.25	4.93	14.33	130.27	50.27	112.26	101.66
H. lar	C4	893.14	7.49	5.55	7.35	3.94	3.39	7.89	117.60	29.91	141.50	136.72
L. catta	C4	41.45	3.59	4.32	5.98		1.58	8.07	103.68	29.76	80.72	
M. fascicularis	C4	83.52	5.67	4.84	5.79	2.88	3.40		126.16	29.64	135.96	137.23
M. mulatta	C4	93.53	6.37	6.00	5.93	4.63	3.96	7.20	125.89	30.13	122.64	106.73
O. crassicaudatus	C4	30.79	1.91	2.72	3.50		1.15	7.53	130.73	28.62	149.82	101.25
P. troglodytes	C4	109.20	23.87	8.70	8.97	7.22	5.28		133.62	26.01	139.86	144.45
P. verreauxi	C4	40.62	4.11	4.82	7.79		2.04	10.30	128.69	29.35	77.77	
V. variegata	C4	46.02	5.82	5.14	9.22	1.71	2.30	9.10	99.17	28.97	36.31	87.62
S. apella	C5	89.47	6.12	4.24	3.92	4.11	2.47	4.90	126.96	61.80	85.70	123.10
E. mongoz	C5	37.27	3.43	4.18	5.62	2.76	1.22	6.37	146.75	21.45	83.85	114.94
H. sapiens	C5	410.77	16.85	11.74	9.61	7.44	5.40	11.84	128.84	52.86	99.63	117.67
H. lar	C5	101.20	8.23	6.08	5.80	3.75	3.28	8.45	111.68	35.87	141.63	128.84
L. catta	C5	39.46	3.64	3.97	6.26	4.21	1.59	7.56	112.29	27.46	110.81	114.42
M. fascicularis	C5	59.52	6.69	4.91	3.97	3.93	3.10		135.89	12.74	112.23	130.34
M. mulatta	C5	94.20	7.41	5.67	4.31	5.03	3.53	6.42	127.20	29.46	115.85	111.46
O. crassicaudatus	C5	34.86	1.75	2.63	2.95	1.17	0.97	7.37	124.42	29.06	131.44	94.13
P. troglodytes	C5	111.93	26.33	8.57	7.38	7.07	5.16		137.47	25.23	123.90	146.26
P. verreauxi	C5	41.53	5.75	4.82	7.03	4.54	2.10	9.56	143.73	23.69	112.27	
S. sciureus	C5	69.05	3.41	2.85	3.32	2.85	1.41	4.20	140.54	29.66	135.17	140.62
V. variegata	C5	53.47	5.33	5.37	9.01	5.14	2.33	7.92	124.70	28.33	39.11	70.80
S. apella	C6	86.50	8.02	4.15	9.25	4.14	2.36	5.35	121.89	41.90	126.68	123.90

E. mongoz	C6	37.59	4.06	4.25	8.39	2.29	1.22	6.27	132.52	29.44	126.16	113.82
H. sapiens	C6	421.16	21.89	12.05	10.13	7.12	5.23	13.46	128.65	43.57	125.09	104.54
H. lar	C6	93.16	9.66	5.77	6.79	3.19	3.16	7.38	114.66	25.96	147.55	129.71
L. catta	C6	40.08	4.36	4.04	7.70	3.39	1.44	8.89	119.12	30.89	62.35	122.22
M. fascicularis	C6	55.73	8.01	4.65	7.04	4.16	3.05		147.09	23.75	103.16	119.12
M. mulatta	C6	96.41	8.60	5.63	8.66	5.18	3.82	7.34	126.18	28.91	118.59	113.25
O. crassicaudatus	C6	31.45	2.08	3.06	4.84	1.56	0.93	7.02	128.23	30.86	128.23	91.14
P. troglodytes	C6	123.70	28.13	9.02	8.79	6.45	5.50		128.79	26.79	129.43	136.59
P. verreauxi	C6	41.82	9.58	5.11	10.45	3.49	1.75	8.77	145.57	24.83	115.90	
S. sciureus	C6	43.03	4.33	2.66	5.69	2.46	1.23	4.51	140.43	19.55	120.33	
V. variegata	C6	63.13	6.42	5.34	10.75	4.68	1.67	8.34	117.56	38.37	89.54	79.68
S. apella	C7	93.09	11.51	4.15	4.80	5.07	1.96	5.38	116.72	66.52	147.14	118.15
E. mongoz	C7	31.92	5.91	3.85		4.60	1.17	6.11	139.78	24.16	141.53	122.66
H. sapiens	C7	320.93	29.82	11.41	10.62	11.90	5.79	11.23	128.96	55.32	121.35	111.78
H. lar	C7	96.20	11.94	5.20	5.39	5.38	3.12	7.70	110.08	35.42	140.99	123.14
L. catta	C7	37.26	7.03	3.83		5.74	1.25	7.89	133.52	28.08	82.35	100.82
M. fascicularis	C7	54.29	9.04	4.27	4.34	6.16	3.33		141.14	29.50	120.18	128.71
M. mulatta	C7	84.41	10.37	5.47		6.71	3.47	6.17	127.61	27.42	119.97	110.44
O. crassicaudatus	C7	27.64	2.27	2.96		2.46	0.76	7.36	122.41	28.09	125.54	108.02
P. troglodytes	C7	140.75	29.09	8.91		10.65	6.23		131.89	24.56	141.99	151.62
P. verreauxi	C7	39.48	9.98	5.17	4.82	4.37	1.60	8.38	154.90	21.23	129.81	
S. sciureus	C7	4097.57	5.92	2.55		2.98	1.26	4.71	127.56	28.87	125.04	129.71
V. variegata	C7	50.87	9.07	5.03		5.89	1.35	7.79	110.94	29.79	27.19	88.02
S. apella	T1	35.34	12.99	3.77		4.94		6.25	117.66	80.04		94.36
E. mongoz	T1	27.31	8.65	3.17		4.84		5.94	129.76	34.60	102.65	117.36
H. sapiens	T1	384.88	32.03	12.50		19.71	5.02	16.31	128.19	52.14	109.05	107.04
H. lar	T1	67.11	12.57	5.61		6.84	1.23	7.82	131.37	18.99		96.07
L. catta	T1	36.23	9.56	3.06		5.16	1.14	8.63	128.98	29.02	61.95	115.09
M. mulatta	T1	72.69	17.25	4.51		8.35	3.38	7.19	124.32	37.58	38.48	92.21
O. crassicaudatus	T1	27.42	7.28	2.52		4.65	1.06	7.67	128.27	33.23	138.46	105.56
P. verreauxi	T1	33.56	9.92	4.47		4.84	1.16	7.61	144.25	33.24	109.77	

S. sciureus	T1	23.76	7.57	2.26		3.37		4.79				
V. variegata	T1	44.08	11.41	4.36		6.79	0.71	7.86	120.93	34.83	31.35	98.65

Table 0.2 Ranges of intervertebral motion.

Species	**Joint**	**Source**	**Extension**	**Flexion**	**Flexion-Extension**	**Lateral Flexion**
Sapajus apella	C0-C1	Graf et al. 1995	107.50			
Eulemur mongoz	C0-C1	Duke Lemur Center	35.44	25.94	61.38	7.12
Homo sapiens	C0-C1	White and Panjabi, 1990	12.40	14.40	26.80	5.00
Hylobates lar	C0-C1	Osaka University	11.61	3.18	14.79	6.25
Lemur catta	C0-C1	Duke Lemur Center	8.94	16.82	25.76	8.14
Macaca mulatta	C0-C1	Graf et al. 1995	137.00	105.00	242.00	
Macaca mulatta	C0-C1	Graf et al. 1995	119.30	118.00	237.30	
Otolemur crassicaudatus	C0-C1	Duke Lemur Center	5.72	13.04	7.33	3.47
Propithecus verreauxi	C0-C1	Duke Lemur Center	9.51	19.33	27.22	2.57
Pan troglodytes	C0-C1	Stony Brook University			8.76	
Saimiri sciureus	C0-C1	Graf et al. 1995	116.40	106.70	223.10	
Varecia variegata	C0-C1	Duke Lemur Center	34.40	21.67	56.07	2.71
Sapajus apella	C1-C2	Graf et al. 1995	0.00			
Eulemur mongoz	C1-C2	Duke Lemur Center	4.32	14.36	18.69	22.82
Homo sapiens	C1-C2	White and Panjabi, 1990	10.50	12.70	23.20	5.00
Hylobates lar	C1-C2	Osaka University	8.91	4.77	13.68	4.90
Lemur catta	C1-C2	Duke Lemur Center	8.23	16.70	24.93	28.20
Macaca mulatta	C1-C2	Graf et al. 1995	3.00	0.00	3.00	
Macaca fascicularis	C1-C2	Graf et al. 1995	7.00	5.30	12.30	
Otolemur crassicaudatus	C1-C2	Duke Lemur Center	7.08	8.79	1.71	16.26
Propithecus verreauxi	C1-C2	Duke Lemur Center	8.50	11.03	18.35	11.51
Pan troglodytes	C1-C2	Stony Brook University			16.07	

Saimiri sciureus	C1-C2	Graf et al. 1995	222.20	3.30	225.50	
Varecia variegata	C1-C2	Duke Lemur Center	4.76	2.77	7.52	28.44
Sapajus apella	C2-C3	Graf et al. 1995	0.00			
Eulemur mongoz	C2-C3	Duke Lemur Center	8.50	5.13	13.63	7.33
Homo sapiens	C2-C3	White and Panjabi, 1990	2.00	7.00	9.00	10.00
Hylobates lar	C2-C3	Osaka University	11.91	7.02	18.93	11.72
Lemur catta	C2-C3	Duke Lemur Center	8.58	5.47	14.05	6.71
Macaca mulatta	C2-C3	Graf et al. 1995	4.00	20.00	24.00	
Macaca fascicularis	C2-C3	Graf et al. 1995	16.00	8.30	24.30	
Otolemur crassicaudatus	C2-C3	Duke Lemur Center	7.63	18.14	25.76	7.33
Propithecus verreauxi	C2-C3	Duke Lemur Center	8.60	6.57	15.17	11.35
Pan troglodytes	C2-C3	Stony Brook University			1.65	
Saimiri sciureus	C2-C3	Graf et al. 1995	3.60	0.70	4.30	
Varecia variegata	C2-C3	Duke Lemur Center	7.47	9.19	16.67	5.18
Sapajus apella	C3-C4	Graf et al. 1995	1.50			
Eulemur mongoz	C3-C4	Duke Lemur Center	5.17	2.92	8.10	5.83
Homo sapiens	C3-C4	White and Panjabi, 1990	4.00	10.00	14.00	11.00
Hylobates lar	C3-C4	Osaka University	11.17	8.74	19.91	2.64
Lemur catta	C3-C4	Duke Lemur Center	7.14	7.60	14.74	7.31
Macaca mulatta	C3-C4	Graf et al. 1995	10.00	4.00	14.00	
Macaca fascicularis	C3-C4	Graf et al. 1995	8.00	5.00	13.00	
Otolemur crassicaudatus	C3-C4	Duke Lemur Center	13.38	3.74	17.12	
Propithecus verreauxi	C3-C4	Duke Lemur Center	19.57	6.83	26.39	10.15
Pan troglodytes	C3-C4	Stony Brook University			10.81	
Saimiri sciureus	C3-C4	Graf et al. 1995	8.60	4.70	13.30	

Varecia variegata	C3-C4	Duke Lemur Center	8.17	13.27	21.44	7.09
Sapajus apella	C4-C5	Graf et al. 1995	0.00			
Eulemur mongoz	C4-C5	Duke Lemur Center	9.20	7.83	17.02	5.11
Homo sapiens	C4-C5	White and Panjabi, 1990	9.00	3.00	12.00	11.00
Hylobates lar	C4-C5	Osaka University	17.50	0.07	17.57	1.66
Lemur catta	C4-C5	Duke Lemur Center	10.85	10.17	21.01	5.48
Macaca mulatta	C4-C5	Graf et al. 1995	13.00	5.00	18.00	
Macaca fascicularis	C4-C5	Graf et al. 1995	11.30	0.00	11.30	
Otolemur crassicaudatus	C4-C5	Duke Lemur Center	13.38	3.74	17.12	9.29
Propithecus verreauxi	C4-C5	Duke Lemur Center	10.61	7.72	18.33	7.42
Pan troglodytes	C4-C5	Stony Brook University			19.27	
Saimiri sciureus	C4-C5	Graf et al. 1995	11.20	3.70	14.90	
Varecia variegata	C4-C5	Duke Lemur Center	15.99	20.01	36.00	9.68
Sapajus apella	C5-C6	Graf et al. 1995	2.50			
Eulemur mongoz	C5-C6	Duke Lemur Center	17.51	3.23	20.74	5.70
Homo sapiens	C5-C6	White and Panjabi, 1990	3.00	15.00	18.00	8.00
Hylobates lar	C5-C6	Osaka University	9.10	6.14	15.24	1.70
Lemur catta	C5-C6	Duke Lemur Center	17.55	6.47	24.02	6.56
Macaca mulatta	C5-C6	Graf et al. 1995	16.00	0.00	16.00	
Macaca fascicularis	C5-C6	Graf et al. 1995	8.60	0.00	8.60	
Otolemur crassicaudatus	C5-C6	Duke Lemur Center	15.46	-3.12	12.34	3.39
Propithecus verreauxi	C5-C6	Duke Lemur Center	11.62	9.21	20.83	6.51
Pan troglodytes	C5-C6	Stony Brook University			23.90	
Saimiri sciureus	C5-C6	Graf et al. 1995	12.00	3.70	15.70	
Varecia variegata	C5-C6	Duke Lemur Center	11.39	9.87	21.25	5.92

Sapajus apella	C6-C7	Graf et al. 1995	20.50			
Eulemur mongoz	C6-C7	Duke Lemur Center	15.98	4.72	20.70	5.08
Homo sapiens	C6-C7	White and Panjabi, 1990	10.00	9.00	19.00	7.00
Hylobates lar	C6-C7	Osaka University	11.64	27.15	38.79	1.74
Lemur catta	C6-C7	Duke Lemur Center	23.45	6.84	30.29	4.82
Macaca mulatta	C6-C7	Graf et al. 1995	22.00	0.00	22.00	
Macaca fascicularis	C6-C7	Graf et al. 1995	16.70	0.00	16.70	
Otolemur crassicaudatus	C6-C7	Duke Lemur Center	1.26	10.65	9.39	5.26
Propithecus verreauxi	C6-C7	Duke Lemur Center	15.62	6.65	22.27	4.34
Pan troglodytes	C6-C7	Stony Brook University			14.06	
Saimiri sciureus	C6-C7	Graf et al. 1995	19.00	3.00	22.00	
Varecia variegata	C6-C7	Duke Lemur Center	17.95	13.57	31.53	5.88
Sapajus apella	C7-T1	Graf et al. 1995	6.50			
Eulemur mongoz	C7-T1	Duke Lemur Center	19.33	6.64	25.96	4.14
Homo sapiens	C7-T1	White and Panjabi, 1990	6.00	4.00	10.00	4.00
Hylobates lar	C7-T1	Osaka University				2.25
Lemur catta	C7-T1	Duke Lemur Center	14.15	9.17	23.33	3.84
Macaca mulatta	C7-T1	Graf et al. 1995	10.00	0.00	10.00	
Macaca fascicularis	C7-T1	Graf et al. 1995	21.30		21.30	
Otolemur crassicaudatus	C7-T1	Duke Lemur Center	26.57	2.47	29.04	4.16
Propithecus verreauxi	C7-T1	Duke Lemur Center	14.52	3.51	18.03	6.17
Saimiri sciureus	C7-T1	Graf et al. 1995	22.60	3.00	25.60	
Varecia variegata	C7-T1	Duke Lemur Center	13.47	14.97	28.44	4.11
Eulemur mongoz	C0-C7	Duke Lemur Center	115.45	70.76	186.21	63.12
Homo sapiens	C0-C7	White and Panjabi, 1990	56.90	75.10	132.00	61.00

Hylobates lar	C0-C7	Osaka University	81.84	57.07	138.91	32.86
Lemur catta	C0-C7	Duke Lemur Center	98.88	79.25	178.13	71.06
Otolemur crassicaudatus	C0-C7	Duke Lemur Center	90.47	57.45	119.81	58.44
Propithecus verreauxi	C0-C7	Duke Lemur Center	98.54	70.85	166.58	60.00
Varecia variegata	C0-C7	Duke Lemur Center	113.60	105.32	218.92	69.00

APPENDIX B

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE APPROVAL

Institutional Animal Care and Use Committee (IACUC)
Office of Research Integrity and Assurance
Arizona State University
660 South Mill Avenue, Suite 315
Tempe, Arizona 85287-6111
Phone: (480) 965-4387 *FAX:* (480) 965-7772

Animal Protocol Review

ASU Protocol Number:	**16-1519TK**
Protocol Title:	**Form and Function of the Primate Cervical Spine and Hominin Postural Evolution**
Principal Investigator:	**Neysa Grider-Potter**
Date of Action:	**6/28/2016**

The animal protocol review was considered by the Committee and the following decisions were made:

This tracking protocol has been approved for work being covered under Duke University protocol A141-16-06.

If you have not already done so, documentation of Level III Training (i.e., procedure-specific training) will need to be provided to the IACUC office before participants can perform procedures independently. For more information on Level III requirements see https://researchintegrity.asu.edu/training/animals/levelthree.

Protocol Approval Period: **6/28/2016 – 6/27/2019**

Signature: SAugustowski for C Johnson Date: 6/20/2016
IACUC Chair or [✓ Designee]

Cc: IACUC Office
IACUC Chair