

DIMORPHISM AND INTEGRATION IN THE Pelves OF ANTHROPOID
PRIMATES

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Doctor of Philosophy

By
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DIMORPHISM AND INTEGRATION IN THE PELTS OF ANTHROPOID PRIMATES

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This work is dedicated to Lloyd and Victoria Moffett, for their unceasing support

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS	ii
LIST OF FIGURES	viii
LIST OF TABLES	xiii
ABSTRACT	xvii
CHAPTER ONE: Introduction.....	1
Cephalopelvic proportions and birth in anthropoids	1
Factors hypothesized to influence pelvic dimorphism	7
Modularity and integration in the primate pelvis	14
CHAPTER TWO: Dimorphism in the size and shape of the birth canals of anthropoid primates	24
Background.....	24
Hypotheses	31
Materials and methods.....	33
Results	44
Discussion and conclusions.....	57

CHAPTER THREE: Dimorphism in relative sacral breadth among Catarrhine

primates	92
Background.....	92
Materials and methods.....	97
Results	107
Discussion and conclusions	109

CHAPTER FOUR: Dimorphism in non-obstetric pelvic morphology in anthropoid

primates	126
Background.....	126
Hypotheses	128
Materials and methods.....	129
Results	134
Discussion and conclusions.....	137

CHAPTER FIVE: Integration in the anthropoid birth canal and non-obstetric pelvis... 157

Background.....	157
Hypotheses	162
Materials and methods.....	164

Results	175
Discussion and conclusions	180
CHAPTER SIX: Summary and Future Directions	195
WORKS CITED	207
APPENDIX A	243
VITA.....	252

LIST OF FIGURES

Figure 1.1: Cephalopelvic proportions in primates	18
Figure 1.2: Superior view of a fetal skull showing relative anteroposterior and mediolateral dimensions	19
Figure 1.3: Relationship between maternal and neonatal body size in anthropoid primates	20
Figure 1.4: Allometry of primate brain development.....	21
Figure 1.5: The three planes of the birth canal – inlet, midplane, and outlet	22
Figure 1.6: Fetal head aligning with the pelvic inlet	22
Figure 1.7: Fetal rotation in humans versus non-human primates	23
Figure 2.1: Landmarks collected on the birth canal	63
Figure 2.2: Linear distances of the birth canal	64
Figure 2.3: Birth canal shape overlap between sexes.....	82
Figure 2.4a: Principal components analysis of birth canal shape in <i>Homo sapiens</i>	83
Figure 2.4b: Euclidean distance matrix analysis of birth canal shape in <i>Homo sapiens</i> ..	83
Figure 2.5a: Principal components analysis of birth canal shape in <i>Hylobates lar</i>	84

Figure 2.5b: Euclidean distance matrix analysis of birth canal shape in <i>Hylobates lar</i> ...	84
Figure 2.6a: Principal components analysis of birth canal shape in <i>Macaca mulatta</i>	85
Figure 2.6b: Euclidean distance matrix analysis of birth canal shape in <i>Macaca mulatta</i>	85
Figure 2.7a: Principal components analysis of birth canal shape in <i>Nasalis larvatus</i>	86
Figure 2.7b: Euclidean distance matrix analysis of birth canal shape in <i>Nasalis larvatus</i>	86
Figure 2.8a: Principal components analysis of birth canal shape in <i>Papio anubis</i>	87
Figure 2.8b: Euclidean distance matrix analysis of birth canal shape in <i>Papio anubis</i> ...	87
Figure 2.9a: Principal components analysis of birth canal shape in <i>Saimiri sciureus</i>	88
Figure 2.9b: Euclidean distance matrix analysis of birth canal shape in <i>Saimiri sciureus</i>	88
Figure 2.10a: Principal components analysis of birth canal shape in <i>Gorilla gorilla</i>	89
Figure 2.10b: Euclidean distance matrix analysis of birth canal shape in <i>Gorilla gorilla</i>	89
Figure 2.11a: Principal components analysis of birth canal shape in <i>Pan troglodytes</i>	90
Figure 2.11b: Euclidean distance matrix analysis of birth canal shape in <i>Pan troglodytes</i>	90
Figure 2.12a: Principal components analysis of birth canal shape in <i>Alouatta seniculus</i> .	91
Figure 2.12b: Euclidean distance matrix analysis of birth canal shape in <i>Alouatta seniculus</i>	91

Figure 3.1: Scatter plots of (A) body mass dimorphism index versus lumbar vertebral body dimorphism index and (B) body mass dimorphism index versus cephalopelvic proportions.....	119
Figure 3.2: Measurements of the (A) sacrum and (B) lumbar vertebra	120
Figure 3.3: Anterior views of male and female sacra of: (a) <i>Hylobates lar</i> ; (b) <i>Nasalis larvatus</i> ; (c) <i>Homo sapiens</i> ; (d) <i>Gorilla gorilla</i>	125
Figure 4.1: Landmarks of the non-obstetric pelvis.....	143
Figure 4.2: Overlap between the sexes in non-obstetric pelvis shape.....	146
Figure 4.3a: Principal components analysis of non-obstetric pelvis shape in <i>Homo sapiens</i>	148
Figure 4.3b: Euclidean distance matrix analysis of non-obstetric pelvis shape in <i>Homo sapiens</i>	148
Figure 4.4a: Principal components analysis of non-obstetric pelvis shape in <i>Hylobates lar</i>	149
Figure 4.4b: Euclidean distance matrix analysis of non-obstetric pelvis shape in <i>Hylobates lar</i>	149
Figure 4.5a: Principal components analysis of non-obstetric pelvis shape in <i>Macaca mulatta</i>	150

Figure 4.5b: Euclidean distance matrix analysis of non-obstetric pelvis shape in <i>Macaca mulatta</i>	150
Figure 4.6a: Principal components analysis of non-obstetric pelvis shape in <i>Nasalis larvatus</i>	151
Figure 4.6b: Euclidean distance matrix analysis of non-obstetric pelvis shape in <i>Nasalis larvatus</i>	151
Figure 4.7a: Principal components analysis of non-obstetric pelvis shape in <i>Papio anubis</i>	152
Figure 4.7b: Euclidean distance matrix analysis of non-obstetric pelvis shape in <i>Papio anubis</i>	152
Figure 4.8a: Principal components analysis of non-obstetric pelvis shape in <i>Saimiri sciureus</i>	153
Figure 4.8b: Euclidean distance matrix analysis of non-obstetric pelvis shape in <i>Saimiri sciureus</i>	153
Figure 4.9a: Principal components analysis of non-obstetric pelvis shape in <i>Gorilla gorilla</i>	154
Figure 4.9b: Euclidean distance matrix analysis of non-obstetric pelvis shape in <i>Gorilla gorilla</i>	154

Figure 4.10a: Principal components analysis of non-obstetric pelvis shape in <i>Pan troglodytes</i>	155
Figure 4.10b: Euclidean distance matrix analysis of non-obstetric pelvis shape in <i>Pan troglodytes</i>	155
Figure 4.11a: Principal components analysis of non-obstetric pelvis shape in <i>Alouatta seniculus</i>	156
Figure 4.11b: Euclidean distance matrix analysis of non-obstetric pelvis shape in <i>Alouatta seniculus</i>	156
Figure 5.1: Landmarks of the birth canal and non-obstetric pelvis	187
Figure 5.2: Linear distances of the birth canal	188
Figure 5.3: Linear distances of the non-obstetric pelvis	189

LIST OF TABLES

Table 2.1: Numbers of individuals, body mass dimorphism, and cephalopelvic proportions.....	62
Table 2.2: Birth canal landmarks.....	63
Table 2.3: Birth canal dimension calculations	64
Table 2.4: Reduced major axis regressions of natural logged birth canal size against S1 body breadth	65
Table 2.5: Reduced major axis regression of natural logged birth canal dimensions against S1 body breadth.....	65
Table 2.6: Student’s t-tests for dimorphism in absolute and relative birth canal size.....	66
Table 2.7: Student’s t-tests for dimorphism in absolute and relative birth canal dimensions	71
Table 2.8: Student’s t-tests results for differences between males and females in residuals from reduced major axis regressions of pelvic size variables with S1 body breadth	74
Table 2.9: Dimorphism index ranks	77
Table 2.10: Results for discriminant function analysis of the influence of sex on intraspecies principal components scores for birth canal shape	79

Table 2.11: Student’s t-tests for dimorphism in birth canal shape along each principal component	80
Table 2.12: Euclidean distance matrix analysis FORM test of male and female differences in overall birth canal shape within species	80
Table 2.13: Shape of the pelvic planes in female and male anthropoids	81
Table 2.14: Shape overlap between sexes	81
Table 3.1: Sampled taxa	118
Table 3.2: Isometry test results.....	121
Table 3.3: Hypotheses and predictions outlined in text	122
Table 3.4: Randomization tests (2-tailed) for sexual dimorphism in vertebral measurements	123
Table 3.5: Randomization test results for sexual dimorphism in relative sacral and relative lumbar breadths	124
Table 4.1: False pelvis landmarks	143
Table 4.2: Reduced major axis regressions of natural logged non-obstetric pelvis dimensions against logged S1body breadth	144
Table 4.3: Dimorphism in non-obstetric pelvic size: Student’s t-tests on residuals	144
Table 4.4: Magnitude of dimorphism ranks for the non-obstetric pelvis	145

Table 4.5: Shape overlap between sexes	146
Table 4.6: Student’s t-tests for dimorphism in birth canal shape	147
Table 4.7: Euclidean distance matrix analyses of male and female differences in overall non-obstetric pelvs shape within species.....	147
Table 5.1: Hypotheses and predictions.....	186
Table 5.2: Landmarks of the birth canal.....	187
Table 5.3: Landmarks of the non-obstetric pelvis	187
Table 5.4: Modularity testing for birth canal and non-obstetric pelvis	190
Table 5.5: Magnitudes of integration in birth canal linear distances across anthropoids	191
Table 5.6: Difference of means test of difference in integration magnitudes between taxa for birth canal distances	191
Table 5.7: Differences in the magnitudes of integration in birth canal linear distances between males and females across anthropoids	191
Table 5.8: Magnitudes of integration in non-obstetric pelvic linear distances.....	192
Table 5.9: Similarity in integration magnitudes between taxa for non-obstetric pelvic distances	192
Table 5.10: Differences in the magnitudes of integration in non-obstetric linear distances between males and females across anthropoids.....	192

Table 5.11: Mantel tests of matrix similarity in interspecies integration patterns between birth canal traits.....	193
Table 5.12: Similarity in birth canal integration patterns between males and females..	193
Table 5.13: Mantel tests of matrix similarity in integration patterns between non- obstetric pelvic traits.....	194
Table 5.14: Similarity in non-obstetric integration patterns between males and females	194

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ABSTRACT

The link between obstetric demand (natural selection for birth) and pelvic morphology in anthropoids has remained ambiguous for the past century. Though it is assumed that the dramatic sexual dimorphism seen in modern human pelvis is due to obstetric demand, this does not explain why other primates that give birth to relatively small neonates also exhibit pelvic dimorphism. This thesis explores the correlation between obstetric demand and dimorphism and morphological integration in anthropoid pelvis. Dimorphism in birth canal and non-obstetric pelvic morphology is present across most primates regardless of obstetric demand, but those primates that give birth to relatively large babies have the most pelvic sexual dimorphism. Sexual dimorphism in sacral breadth is likewise most apparent in species that give birth to large neonates relative to the maternal birth canal. In species that give birth to large neonates, females also have higher magnitudes of integration in birth canal morphology compared to males, but this is not true in species that give birth to small neonates. This study demonstrates a clear link between obstetric demand, pelvic dimorphism, and the magnitudes of pelvic integration in anthropoid primates.

CHAPTER 1: INTRODUCTION

Reproductive success is one of the most important requirements of any animal's biology - unsuccessful birth immediately and dramatically affects the fitness of both mother and offspring. Therefore, obstetric (birth-related) selection likely has considerable effects on pelvic morphology in species with a tight fit between the maternal pelvis and neonate. However, the extent to which obstetric selection has shaped the primate pelvis is poorly characterized - as important as birth is hypothesized to be in shaping pelvic morphology, we actually know relatively little about how birth affects primate pelvic morphology in anthropoid primates. How do the three dimensional shapes of the pelvis differ between males and females due to obstetric selection? What different patterns of pelvic sexual dimorphism evolved across anthropoid species in response to obstetric demand? Are primate pelvic integration patterns influenced by obstetric demand? These gaps in our knowledge limit the inferences we can make about the functional morphology of the pelvis, sexual dimorphism, and the evolution of cephalopelvic proportions in primates.

The purpose of this thesis is to address the effects of obstetric demand on sexual dimorphism and integration in the pelves of anthropoids. Chapter 2 quantifies the patterns of sexual dimorphism in the birth canals of anthropoid taxa and the effects of obstetric demand on the magnitudes of birth canal dimorphism seen in these taxa. Chapter 3 further assesses the effects of obstetric demand on sexual dimorphism in the

sacrum of anthropoids. Then, Chapter 4 quantifies the extent of sexual dimorphism in parts of the pelvis not directly related to the birth canal (termed here the “non-obstetric pelvis”) and how these relate to obstetric demand. Finally, Chapter 5 quantifies the effects of obstetric demand on the patterns and magnitudes of morphological integration (covariation between various individual parts) of anthropoid pelvises.

I. CEPHALOPELVIC PROPORTIONS AND BIRTH IN ANTHROPOIDS

Cephalopelvic proportions - the ratio of neonatal head diameters to maternal birth canal dimensions (Schultz, 1949; Leutenegger, 1982; Rosenberg, 1992; Li, 2002; Rosenberg and Trevathan, 2002) – are the metric by which obstetric demand is frequently quantified in primates (Schultz, 1949; Leutenegger 1970, 1974; Lindburg, 1982; Stoller 1995). Large cephalopelvic proportions, or large neonatal head size compared to maternal pelvic diameters, are common among primates (Schultz, 1949; Leutenegger, 1970, 1974; Stoller, 1995), especially among monkeys. Among New World monkeys, *Ateles* and *Saimiri* are known to have large cephalopelvic proportions, while *Alouatta* has smaller proportions than *Ateles* or *Saimiri* (Schultz 1949; Leutenegger 1970, 1974; Stoller 1995). Among Old World monkeys, *Papio*, *Nasalis*, and *Macaca* have large cephalopelvic proportions (Schultz 1949; Leutenegger 1970, 1974; Stoller 1995); there are no known Old World monkeys with small proportions. In contrast, the living apes generally tend to have small cephalopelvic proportions (Figure 1.1); two notable exceptions include *Hylobates* and *Homo* (Schultz, 1949; Leutenegger, 1982). Birthing large-headed newborns has further been shown to lead to

strenuous labors in nonhuman primates (Bowden et al., 1967; Hopf, 1967; Schultz, 1969; Brandt and Mitchell, 1971; Christen, 1974; Phillips, 1976). For example, squirrel monkeys (*Saimiri sciureus*) have a prolonged and difficult birth process (Bowden et al., 1967; Hopf, 1967), with dystocia, or a mismatch between neonatal head size and maternal birth canal size, occurring in roughly 25% of labors (Rasmussen et al., 1980). In contrast, large-bodied apes such as *Pongo* and *Gorilla* have small cephalopelvic proportions (Schultz, 1949; Leutenegger, 1982) and relatively easy labors compared to humans (Brandt and Mitchell, 1971).

Neonatal head size shape will obviously affect both neonatal head dimensions and cephalopelvic proportions. In all primates, the sagittal (anteroposterior) dimension of the neonatal cranium is larger than the transverse (mediolateral) dimension (Figure 1.2; Schultz, 1949; Leutenegger, 1974), and the widest transverse diameter of the neonatal cranium is near the occiput (Figure 1.2). Brain size and body size are negatively allometric across mammals (and primates), such that smaller animals have relatively larger brains (Jerison, 1973). There is also a negatively allometric relationship between neonatal body weight and maternal body weight (Figure 1.3; slope=0.69, $r^2=0.98$), such that the relative size of the neonate becomes disproportionately larger as maternal body size decreases (Leutenegger, 1982; Wells et al., 2012), although humans have a larger neonatal size than is predicted based upon maternal body size (Leutenegger, 1982; DeSilva and Lesnik, 2008). Moreover, neonatal brain mass scales negatively with adult brain mass in primates (Martin, 1983; DeSilva and Lesnik, 2008; DeSilva, 2011), meaning that in large-bodied apes, more brain development occurs postnatally compared to smaller-bodied monkeys (Figure

1.4). These allometric relationships may account for the small cephalopelvic proportions found in non-human large-bodied apes.

The shape and dimensions of the maternal bony birth canal will also affect cephalopelvic proportions. There are three areas of constriction in the birth canal traditionally defined for humans and other primates (Figure 1.5): the pelvic inlet, midplane, and outlet (see also Rosenberg, 1992). These “planes” (though not actually planar in all primates) define areas of the pelvis that are common sites of cephalopelvic disproportion, or a mismatch between the neonatal head and birth canal (Leutenegger, 1974; Lindburg, 1982; Trevathan, 1987; Tague, 1991; Rosenberg, 1992; Rosenberg and Trevathan, 2002). The inlet is bounded anteriorly by the superior pubic symphysis and pectineal line, laterally by the linea arcuata, and posteriorly by the superior sacral alae and anterior first sacral vertebral body. The midplane is bounded anteriorly by the inferior pubic symphysis, laterally by the ischial spines, and posteriorly by the mid-sacrum. The outlet is bounded anteriorly by the inferior pubic symphysis, laterally by the postero-medial ischial tuberosities, and posteriorly by the inferior sacrum. In all primates besides hominins, the dorsoventral dimensions of all three planes exceed the transverse dimensions (Schultz, 1949; Leutenegger, 1974). In monkeys, the broadest part of the birth canal is in the dorsal portion of the birth canal (creating a dorsally capacious but ventrally compressed birth canal), whereas humans also have ventrally widened birth canals such that the entire birth canal is rounded (Rosenberg and Trevathan, 2002).

How the neonatal head engages the birth canal during birth also influences cephalopelvic proportions. Generally, the fetus will orient itself so that the maximum

diameter of the cranium (dorsoventral) is aligned with the maximum diameter of the maternal pelvic planes (Joulin, 1864). Accordingly, in non-human primates, the neonate modally enters the birth canal facing ventrally (relative to the mother), such that the longest cranial dimension (dorsoventral) is aligned with the largest diameter of the birth canal (also dorsoventral) and the broadest part of the cranium (near the occiput) is near the dorsal portion of the birth canal (Figure 1.6). The neonate remains in this position to emerge face-forward (Figure 1.7; Brandt and Mitchell, 1971; Lindburg, 1982; Rosenberg, 1992; Rosenberg and Trevathan, 1996; Trevathan, 1996; Rosenberg and Trevathan, 2002). In contrast, humans have birth canals in which the maximum diameter of the inlet (the transverse diameter) is rotated 90 degrees (Figure 1.7) compared to those of the midplane and outlet (the dorsoventral diameters) (Schultz, 1949; Lindburg, 1982; Tague and Lovejoy, 1986; Trevathan, 1987; Rosenberg, 1992; Ruff, 1995; Rosenberg and Trevathan, 1996; Trevathan, 1996; Rosenberg and Trevathan, 2002; Walrath, 2003; Franciscus, 2009; Brown, 2011). Therefore, in humans the head engages the inlet facing laterally (i.e., with the dorsoventral cranial dimension aligned with the transverse pelvic inlet diameter; Figure 1.6), but when the head reaches the midplane, it rotates (Figure 1.7) so that the dorsoventral cranial dimension engages the dorsoventral diameter of the midplane (Lindburg, 1982; Tague and Lovejoy, 1986; Trevathan, 1987; Rosenberg, 1992; Rosenberg and Trevathan, 1996; Trevathan, 1996; Rosenberg and Trevathan, 2002). Then, because humans have a ventrally expanded midplane and outlet compared to other primates, the broadest portion of the neonate cranium (near the occiput) aligns with the ventral part of the midplane and outlet, and the neonate emerges from the birth

canal facing dorsally (Brandt and Mitchell, 1971; Lindburg, 1982; Trevathan, 1987; Rosenberg and Trevathan, 1996; Trevathan, 1996; Walrath, 1997; Rosenberg and Trevathan, 2002; Franciscus, 2009).

Cephalopelvic proportions in primates have previously been calculated between the neonatal head and maternal pelvic inlet using what are assumed to be the most common birth orientations (Figure 1.6; Schultz, 1949; Leutenegger, 1970, 1974; Stoller, 1995). Any alternative alignments of neonates in the birth canal would change how the neonatal cranium engages the birth canal. In fact, it has been observed that many human neonates do not rotate in the traditionally described manner (Caldwell and Moloy, 1933; Caldwell et al., 1934; Calkins, 1939; Steele and Javert, 1942; Walrath, 2003), and fetal rotation sometimes occurs in both *Saimiri* and *Papio* such that neonates engage the inlet in an oblique orientation (Stoller, 1995). Nonetheless, because current models of cephalopelvic proportions assume that the dorsoventral diameter of the fetal head is oriented so that it aligns with the maximum diameters of the birth canal, these models provide conservative estimates of cephalopelvic proportions in primates.

One limiting factor of using cephalopelvic proportions to quantify obstetric demand is that diameters of the birth canal and neonatal head may not be static during birth. Birth canal size may be able to increase during birth due to ligamentous deformation – the result of the hormone relaxin (Thorp and Fray, 1938; Hartman and Straus, 1939; Weiss et al., 1981; Fuchs and Fuchs, 1984; Weiss, 1984; Germain and Ferre, 1987; Sherwood, 1988; MacLennan, 1991; Goldsmith et al., 1995). Further, in humans the neonatal head can deform during birth due to the presence of cranial

fontanelles in human neonates (Aisenson, 1950; Acheson and Jefferson, 1954; Popich and Smith, 1972; Davies et al., 1975; Faix, 1982; Duc and Largo, 1986; Malas and Sulak, 2000; Faro et al., 2005; Paladini et al., 2008; Shajari et al., 2011). However, it is unknown how consistent ligamentous and neonatal cranial deformation are within primate species, and whether or not these phenomena are pervasive across taxa. Future studies should aim to quantify ligament and neonatal head deformation and their effects on cephalopelvic proportions.

Another factor influencing obstetric selection is the relative size and rigidity of the shoulders of the neonate (Trevathan and Rosenberg, 2000). Shoulder dystocia, or mismatch between the size of the shoulders and the birth canal, is known to occur in humans (Benedetti and Gabbe, 1978; Acker et al., 1985; Gross et al., 1987; Nocon et al., 1993). However, rates of shoulder dystocia among non-human primates are not well-studied, and how the shoulders are able to deform in the birth canal during birth across primates is unexplored. Because much more is known about cephalopelvic proportions in anthropoids (Schultz, 1949; Leutenegger, 1970, 1974; Stoller, 1995), cephalopelvic proportions are a more frequently-used metric to evaluate obstetric difficulty in primates.

II. FACTORS HYPOTHESIZED TO INFLUENCE PELVIC DIMORPHISM

Birth and the “obstetric dilemma”

Sexual dimorphism is a difference in morphology between males and females within a single species (Darwin, 1896). Dimorphism can arise by sexual selection (i.e.,

one sex selecting for a specific morphology in the opposite sex) or by differing selective pressures on sexes imposed by their environments or biological requirements (Darwin, 1896; Rensch, 1960; Lande, 1980b; Hedrick and Temeles, 1989; Shine, 1989; Plavcan, 2001; Fairbairn and Blanckenhorn, 2007; Plavcan, 2011). The magnitude of dimorphism in any structure can be thought of as a result of selection on both male and female traits (Plavcan, 2011).

In *Homo*, both males and females are argued to be under selection for reduced distances between the acetabulae and between the acetabular joints and sacrum (Washburn, 1950, 1960; Pinkerton, 1973; Zihlman, 1978) because this decreases the required hip abductor forces during bipedal locomotion (Ruff, 1995). However, females are also hypothesized to experience birth-related selection to maintain an obstetrically sufficient bony pelvis for passage of a relatively large-headed neonate (Washburn, 1960). This conflict between selection on the pelvis for narrower dimensions to facilitate bipedalism and selection for a larger birth canal to allow birth has been coined the “obstetric dilemma” (Washburn, 1960).

This “obstetric dilemma” in females has been hypothesized to be a primary factor driving dimorphic pelvic morphology in humans (Berge et al., 1984; Tague and Lovejoy, 1986; Abitbol, 1987b; Hager, 1989; Rosenberg, 1992; Abitbol, 1996; Rosenberg and Trevathan, 2002; but see Dunsworth et al., 2012; Wells et al., 2012). Indeed, human females have been found to exhibit relatively (controlling for body size) larger transverse and dorsoventral dimensions of the pelvic inlet (Thoms and Greulich, 1940; Young and Ince, 1940; Segebarth-Orban, 1980) and midplane (Holland et al., 1982; Abitbol, 1988, Hager, 1989; Tague, 1992; Correia, 2005; Kurki, 2007; Brown,

2011), as well as for the transverse diameters of the pelvic outlet (Holland et al., 1982; Hager, 1989; Tague, 1992; Correia, 2005; Brown, 2011). Females also have relatively longer pubic bones (Washburn, 1948) and relatively wider sacra (Tague, 2007; Moffett et al., 2013). Additionally, humans are dimorphic in some aspects of the pelvis which are not directly part of the birth canal, including biacetabular (Tague, 1992) and biiliac breadth (Ruff and Hayes, 1983; Ruff, 1987, 1995; Lovejoy, 2005), and it is presumed that these dimorphisms are a consequence of dimorphism in the bony birth canal.

In addition to influencing modern human pelvic dimorphism, it has been argued that our species' strenuous obstetric demand was a primary factor influencing pelvic form during the Pleistocene (Ruff, 1995; Lovejoy, 2005). In fact, it is hypothesized that a tight fit between the neonatal head and maternal birth canal similar to modern humans could have evolved among *Homo erectus* (Walker and Ruff, 1993; Ruff, 1995; Simpson et al., 2008; but see DeSilva, 2011), and it almost certainly present among early *H. sapiens* and Neandertals (Arsuaga et al., 1999; Rosenberg et al., 2006; Ponce de León et al., 2008; Franciscus, 2009; Weaver and Hublin, 2009).

Our species' difficult birth has also been related to the evolution of other unique human traits and social behaviors including obligate birth assistance from other humans, increased infant dependency after birth, and increased cooperative behaviors during and after pregnancy (Trevathan, 1996; Rosenberg and Trevathan, 2002). Humans also give birth to young with a relatively lower percentage of prenatal brain growth completed before birth compared to other primates (Krogman, 1951; Washburn, 1960; Lovejoy, 1981; Rosenberg, 1992). Thus, this "obstetric dilemma" has

historically been thought to be a key feature of our lineage, impacting our morphology, developmental trajectories, and sociality.

However, recent research questions whether the “obstetric dilemma” is actually a contributing factor to pelvic dimorphism and secondary altriciality in our species (Dunsworth et al., 2012; Wells et.al, 2012). Instead, it has been argued that our secondary altriciality is due to the metabolic constraints of gestating a large fetus (Dunsworth et al., 2012), and that the extremely tight fit between the birth canal and neonatal head in modern humans is a result of a shift to agricultural subsistence (Wells et al., 2012), and populations dependent on foraging and/or hunting (the context in which modern humans first evolved) should not exhibit such an extreme obstetric dilemma. Further, it has recently been argued that the overall wider pelvis of females does not negatively impact locomotor efficiency (Warrener et al., 2015). Last, it has been questioned whether the “obstetric dilemma” is even a uniquely human feature (Wells et al., 2012), as females exhibit relatively larger birth canals than males in many mammalian species (Gardner, 1936; Schultz, 1949; Dunmire, 1955; Crelin and Newton, 1969; Leutenegger, 1970, 1973; Chapman et al., 1994; Tague, 2003; Berdnikovs et al., 2007; Schutz et al., 2009a; Schutz et al., 2009b).

Yet, regardless of whether the “obstetric dilemma” is uniquely human or even whether it exists at all, the highly dimorphic morphology of the pelvis in our species is typically attributed to selection for birth (Turner, 1885; Paterson, 1893; Derry, 1912; De Souza, 1913; Emmons, 1913; Trotter, 1926; Caldwell and Moloy, 1933; Howells and Hotelling, 1936; Thoms, 1937; Greulich, 1938; Thoms and Greulich, 1940; Young and Ince, 1940; Letterman, 1941; Nicholson and Allen, 1945; Heyns, 1947; Flander,

1978; Flander and Corruccini, 1980; Segebarth-Orban, 1980; Abitbol, 1988; Hager, 1989; Milne, 1990; Tague, 1992; Arsuaga and Carretero, 1994; LaVelle, 1995; Abitbol, 1996; Hager, 1996; Walrath, 1997; Tague, 2000; Walrath, 2003; Correia et al., 2005; Kurki, 2007; Novak, 2007; Tague, 2007; Benazzi et al., 2009; Kurki, 2011; Novak et al., 2012; Moffett et al., 2013).

The presence of a range of cephalopelvic proportions across anthropoid primates (Figure 1.1) provides an excellent opportunity to test the hypothesis that large cephalopelvic proportions influence dimorphism in the pelvis. Yet, previous research has not resolved whether large cephalopelvic are the primary cause of dimorphism in the birth canal across anthropoid primates (Schultz, 1949; Leutenegger, 1970; Mobb and Wood, 1977; Steudel, 1981b; Wood and Chamberlain, 1986; Li, 2002; Tague, 2005). Therefore, it is critical to quantify the patterns of dimorphism in the birth canal across anthropoids as well as quantify the role of obstetric selection in shaping pelvic dimorphism both within and across anthropoids.

Body size and body size dimorphism

Some previous research has implicated allometric scaling in influencing pelvic dimorphism across primates (Schultz, 1949; Steudel, 1981b, 1984; Tague, 2005). Ischial length, pubic length, lower iliac height, and sagittal inlet diameter scale with negative allometry across primates (Steudel, 1984; but see Lewton, 2015 for ischial length). Accordingly, there is an overall evolutionary trend within primates for ischial length, pubic length, lower iliac height, and sagittal inlet diameter, to become relatively

smaller as animals become larger. In species in which males are much larger than females for body size, it is plausible that allometric scaling may account for sexual dimorphism in these pelvic morphologies (Steudel, 1981b).

Sexual differences in ecology or locomotor repertoire

The pelvis serves as an attachment site for the hindlimbs as well as for muscles related to locomotion. Muscles which govern hindlimb and trunk movement attach to the pelvis. To the pubis, adductors attach along the caudal portion, while abdominal muscles attach to the superior portion. The quadratus lumborum, abdominal muscles and latissimus dorsi muscles also attach to the superior portion of the ilium, whereas iliacus, lateral hip rotators, and hip abductors attach to the posterior and lateral portions of the ilium in hominids. Hip flexors attach at the anterior portion of the ilium, and hip extensors attach to the posterior and caudal portions of the ischium. The pelvic floor muscles attach to the caudal and posterior ischium as well as the caudal pubis. The stresses and strains associated with locomotion will affect pelvic form (Badoux, 1974; Dalstra and Huijkes, 1995; Lewton, 2010), and pelvic morphology is thus hypothesized to be related to habitual or obligate locomotor repertoires assumed by primates (Waterman, 1929; Steudel, 1981; Ward, 1991, 1993; MacLatchy, 1998; Lewton, 2010).

Primates exhibit a range of positional and locomotor behaviors, including pronograde and orthograde, suspension, clinging and leaping, bipedalism, and terrestrial and arboreal quadrupedalism. Humans, who are bipeds, have a

craniocaudally compressed pelvis, reduced inferior iliac height, and laterally flaring ilia compared to other primates (Johanson et al., 1982; Tague and Lovejoy, 1986; Lovejoy et al., 1999; Lovejoy, 2005), as well as enlarged and medially protruding ischial spines (Abitbol 1988; Lovejoy 2005) and widened sacra (Robinson, 1972; Leutenegger and Kelly, 1977; Abitbol, 1987a; Lovejoy, 2005) compared to other primates. Primates which use suspensory locomotion have wide and coronally-oriented iliac blades (Waterman, 1929; Schultz, 1930; Reynolds, 1931; Reynolds and Hooton, 1936; Schultz, 1936, 1961; Benton, 1967; Ward, 1991; Lycett and von Cramon-Taubadel, 2013; Lewton, 2015; Morgan et al., 2015), small iliac tuberosities (Waterman, 1929; Ward, 1991), greater lumbar entrapment and cranio-caudally expanded pelves compared to quadrupeds. In contrast, quadrupedal primates tend to have more sagittally-oriented iliac blades, a narrower posterior ilium, and large ischial tuberosities (Waterman, 1929; Schultz, 1930; Reynolds, 1931; Schultz, 1936, 1961; Benton, 1967; Ward, 1991) compared to bipedal and suspensory primates.

In primates, especially in species that have high levels of body size dimorphism like gorillas, males and females may use different frequencies of various locomotor behaviors (Remis, 1995). Thus, disparities in male and female pelvic morphology may be due to differences in biomechanics and/or slight locomotor differences between males and females of disparate body sizes within a single species (Studel, 1981b; 1984). Pelvic dimorphism, although usually thought to result from selection on the pelves of females, may also be the result of selection on males, especially within species which are largely divergent in body size and may exhibit slight differences in

locomotor behaviors due to such large body size dimorphism (Moffett et al., 2013), such as gorillas.

III. MODULARITY AND INTEGRATION IN THE PRIMATE PELVIS

Defining modularity and integration

Modularity and integration describe processes by which evolution shapes biological complexity and imposes constraints upon the forms of organisms. Morphological integration (Olson and Miller, 1951; Olson and Miller, 1958), or covariation between phenotypic traits, is the result of either selection for covariation of these phenotypes and/or a pleiotropic (i.e., one gene affecting multiple traits) linkage of these phenotypes (Lande, 1979, 1980a). Selection for covariation may alter the *magnitude* of covariation among traits (i.e, increase covariation of morphological traits), or alter a *pattern* of morphological integration (i.e., alter which traits covary) (Cheverud, 1996; Ackermann and Cheverud, 2000; Marroig and Cheverud, 2001).

As it is currently used, the term “modularity” describes a unit or number of units of a phenotype which: 1) collectively serve a primary functional role (Wagner, 1996); 2) are integrated morphologically, genetically, functionally, and/or developmentally (Cheverud, 1988, 1996; Wagner, 1996; Klingenberg, 2008); 3) are somewhat independent (uncorrelated) of other such units (Wagner, 1996; Klingenberg, 2008); and 4) exhibit hierarchical levels of interaction with other sets of traits (Wagner and Altenberg, 1996; Magwene, 2001). Thus, selection on one module can produce changes within the module that do not greatly affect other modules (Wagner, 1996;

Wagner and Altenberg, 1996; Magwene, 2001; Wagner et al., 2007; Klingenberg, 2008; Klingenberg and Marugán-Lobón, 2013). For example, if we envision that the ilium is a separate module from the pubis, selection for increased iliac breadth should not produce a correlated change in the length of the pubis. However, selection for increased iliac breadth could produce a correlated change in iliac neck thickness because these two traits are within the same (hypothetical) module.

While any modular system must necessarily have integration between the traits within that module, integrated traits are not necessarily modular. To illustrate this point, imagine six separate linear distances. In the first instance, three of these traits tightly covary with one another, and the other three traits also tightly covary with one another. However, the three traits in the first group do not covary with the three traits in the second group. In this first instance, these sets of traits can be categorized as modular. Now envision that all six linear distances strongly covary with one another. In this case, these linear distances would be said to be integrated, but they are not arranged into modules.

The effects of obstetric selection on pelvic integration in anthropoids

It is possible that obstetric demand influences integration and modularity in the primate pelvis (Lewton, 2013). The primate pelvis has been characterized as being comprised of two modules, the ilium and the ischiopubis (Lewton, 2013). The ischiopubic region participates heavily in the birth canal, while the ilium does not (excepting the *linea arcuata*), so it is possible that these two modules are differentially

affected by obstetric selection. Compared to other apes (which have smaller cephalopelvic proportions), humans have increased modularity (reduced covariation) between the linear distances within the birth canal and other pelvic traits (Grabowski, 2013). Increased modularity in the human pelvis compared to other apes could be the result of increased obstetric selection in humans (compared to other apes) (Grabowski et al., 2011; Grabowski, 2013). If this is the case, other primates with large cephalopelvic proportions should also exhibit reduced integration (and increased modularity) between the birth canal and non-obstetric pelvis. However, previous studies have not tested this hypothesis.

It should be expected that any birth-related selection should lead to increased integration (and less variation) within the birth canal among species with large cephalopelvic proportions, because traits within the birth canal should be under co-selection. For example, if obstetric selection increases pubic length, sacral breadth, and inlet breadth among all species with large cephalopelvic proportions, these traits may be more highly integrated among species with large cephalopelvic proportions than in species with small cephalopelvic proportions. Evidence indicates that *Hylobates* and *Homo* have increased birth canal integration compared to other apes (Grabowski, 2013), and these two taxa also have large cephalopelvic proportions compared to other apes. This result could indicate that the selective pressure exerted by large cephalopelvic proportions results in higher correlations among obstetrically-relevant traits. This hypothesis should be further examined across anthropoids.

Because all primates are under selection for locomotion (regardless of cephalopelvic proportions) it might be expected that integration within the non-

obstetric pelvis should either be unaffected or decreased by obstetric selection. For example, the covariation between ischium length, acetabular size, and iliac breadth should not be affected by relative neonate size, so integration levels between these distances should be similar across taxa regardless of obstetric demand.

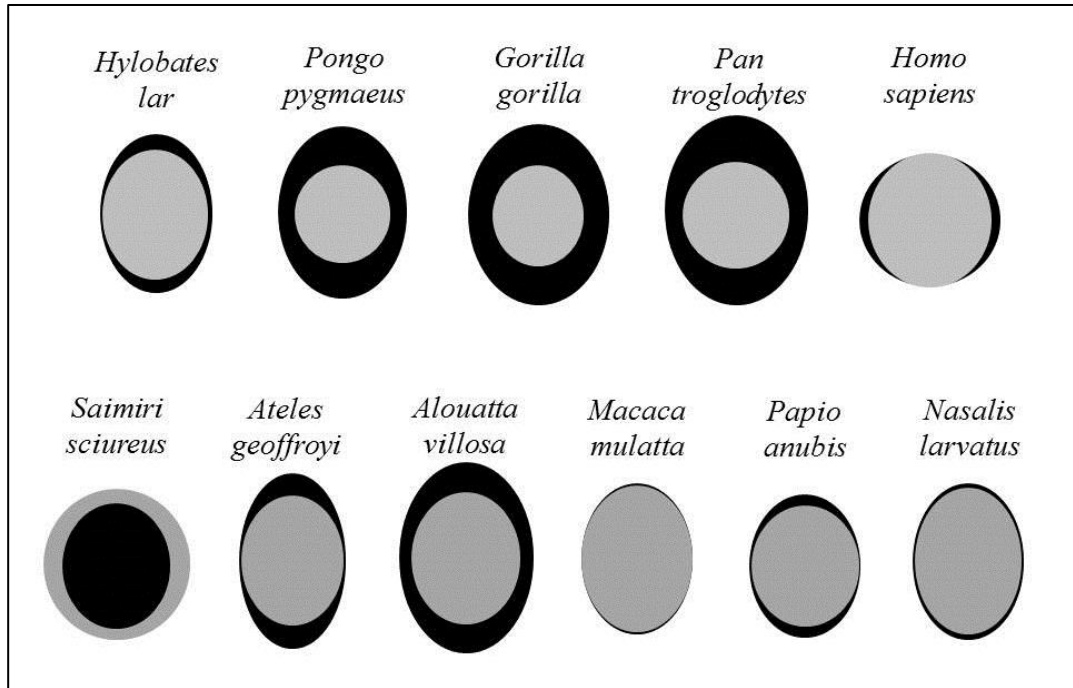


Figure 1.1: Cephalopelvic proportions in primates. Gray represents neonatal head diameters and black represents maternal pelvic inlet diameters at the time of birth. Figure modified from Schultz (1949); data for cephalopelvic proportions in *Alouatta*, *Papio*, *Saimiri* from Leutenegger (1982) and Stoller (1995).

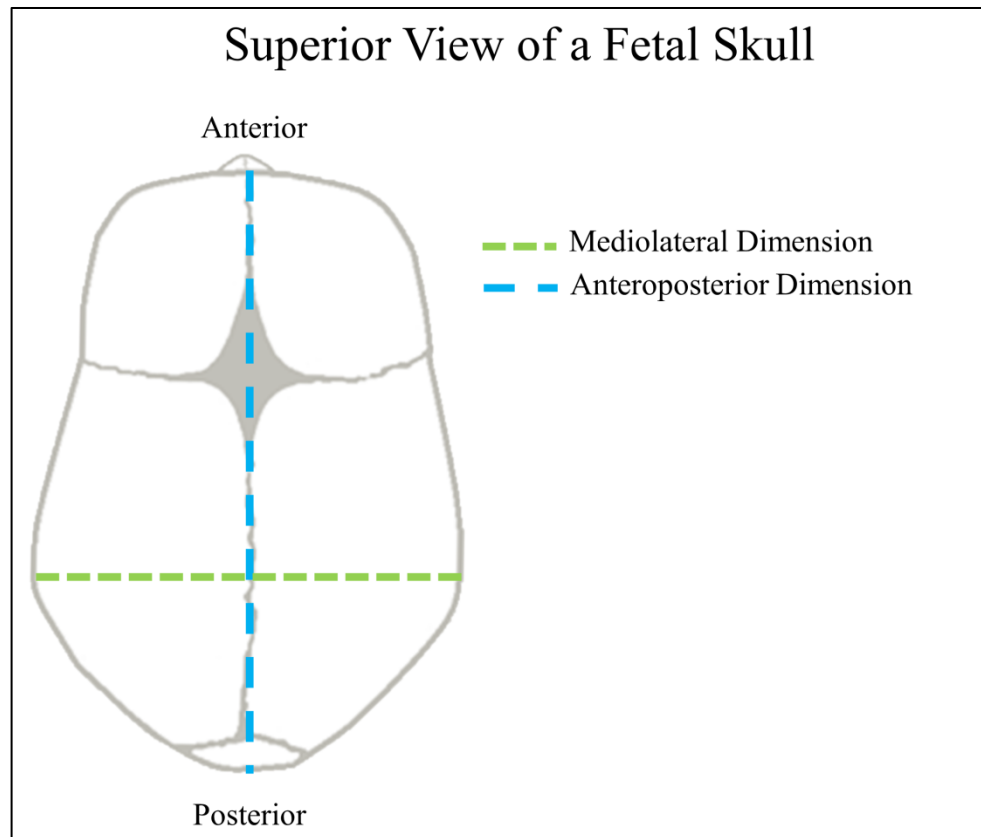


Figure 1.2: Superior view of a fetal skull showing the relative anteroposterior and mediolateral dimensions of the skull. Figure modified from Moffett and Aldridge (2013).

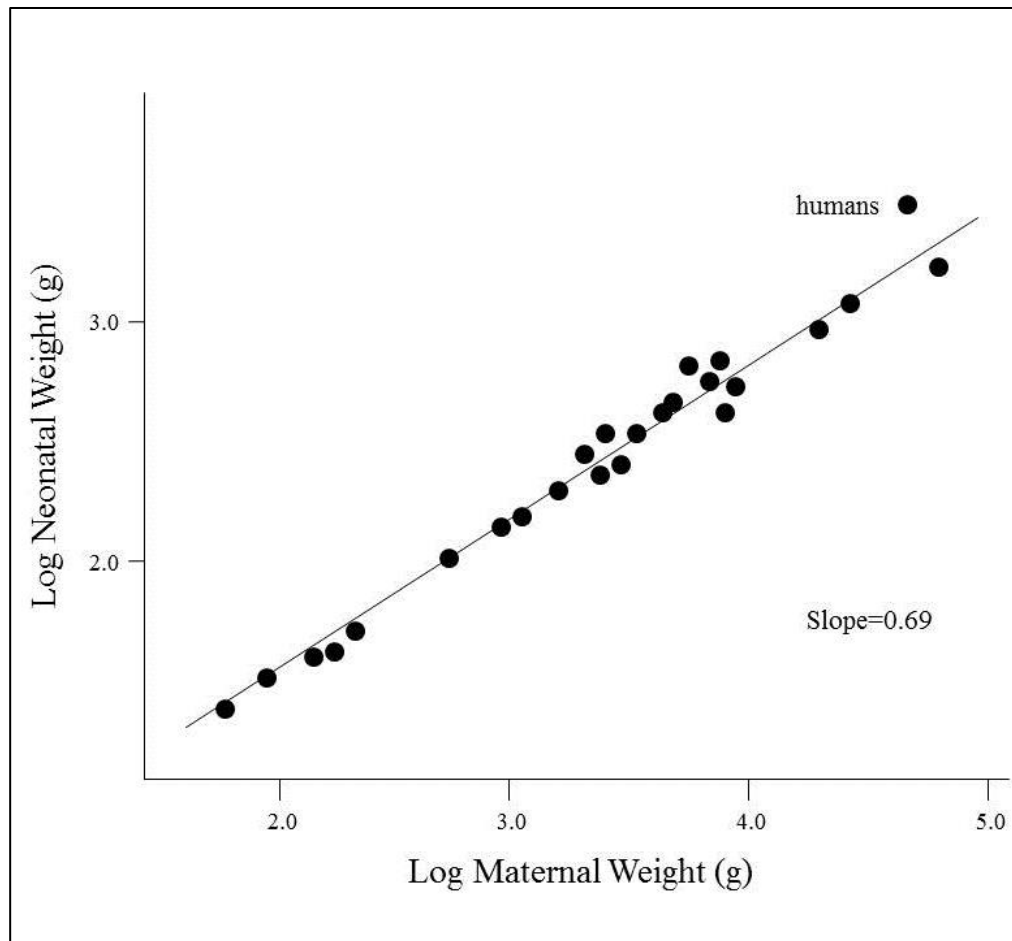


Figure 1.3: Relationship between maternal and neonatal body size in anthropoid primates. Figure adapted from Leutenegger (1982).

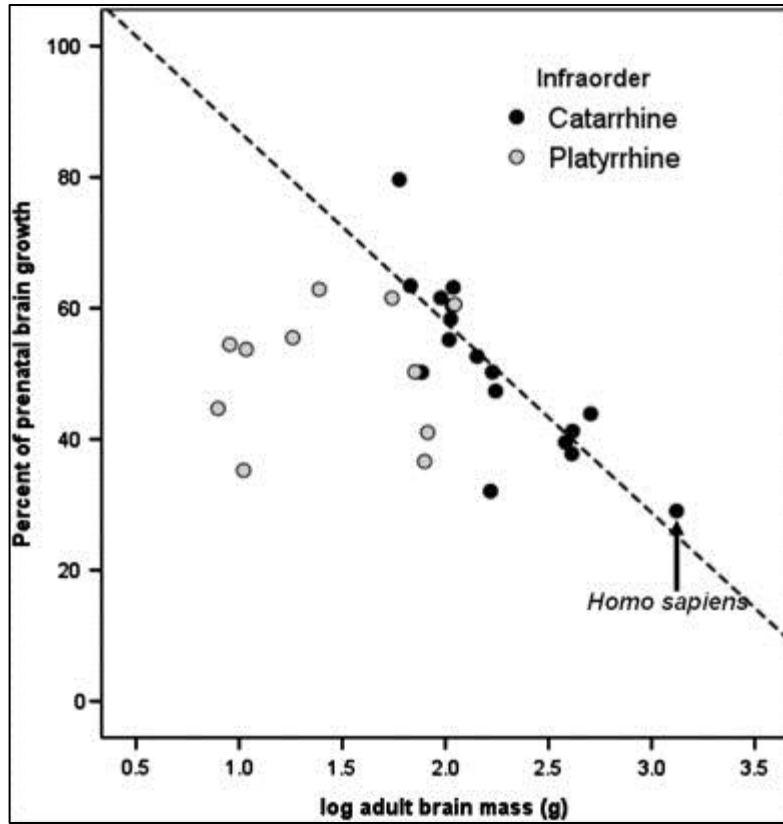


Figure 1.4: Allometry of primate brain development ($r^2=0.66$). Figure modified from DeSilva and Lesnik (2008). Note the negatively allometric relationship between prenatal brain growth and total adult brain mass among Catarrhines.

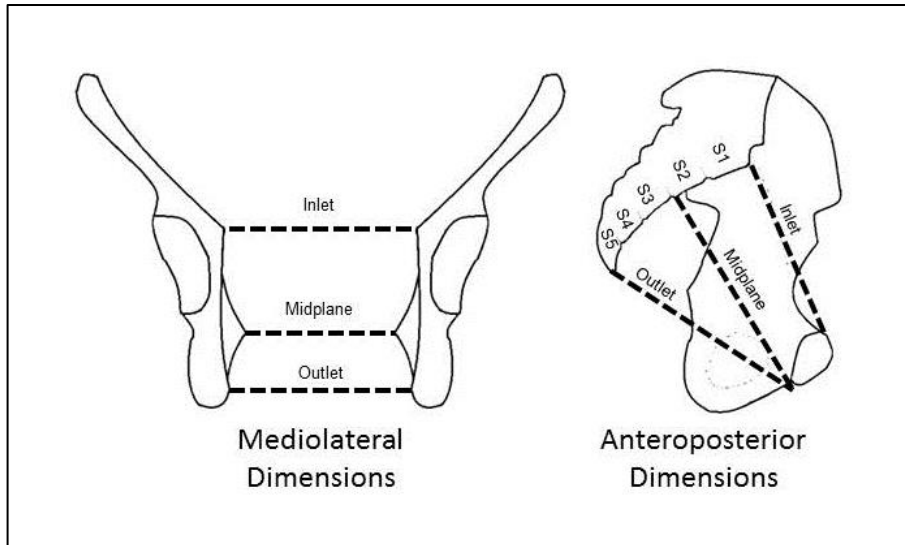


Figure 1.5: The three planes of the birth canal – inlet, midplane, and outlet. Figure modified from Rosenberg (1992).

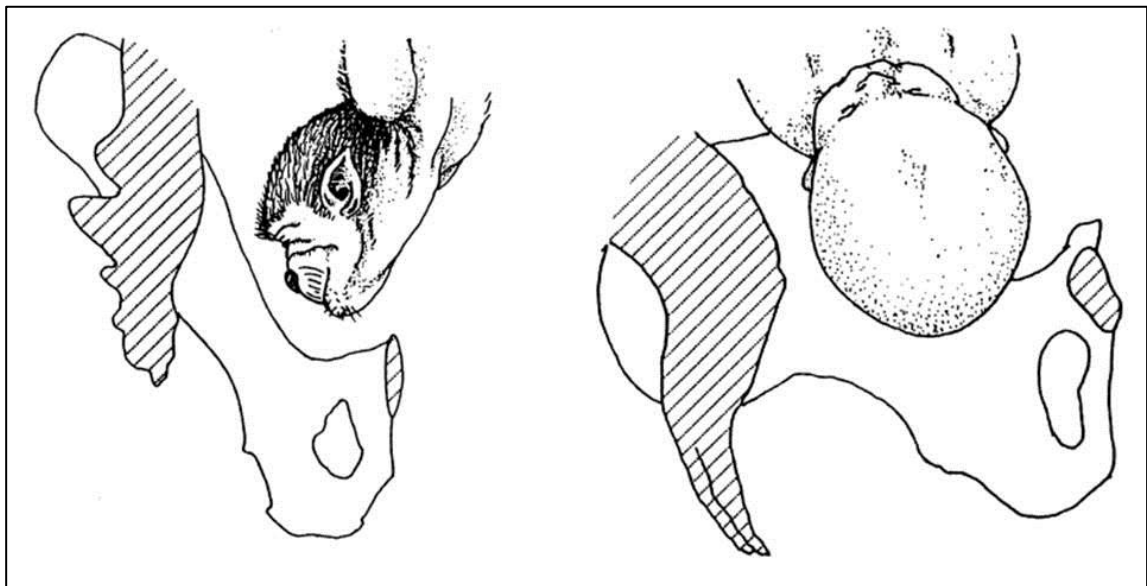


Figure 1.6: Fetal head aligning with the pelvic inlet in (a) non-human primates; and (b) humans. Figure modified from Trevathan (1987), original artwork by Aldine de Gruyter.

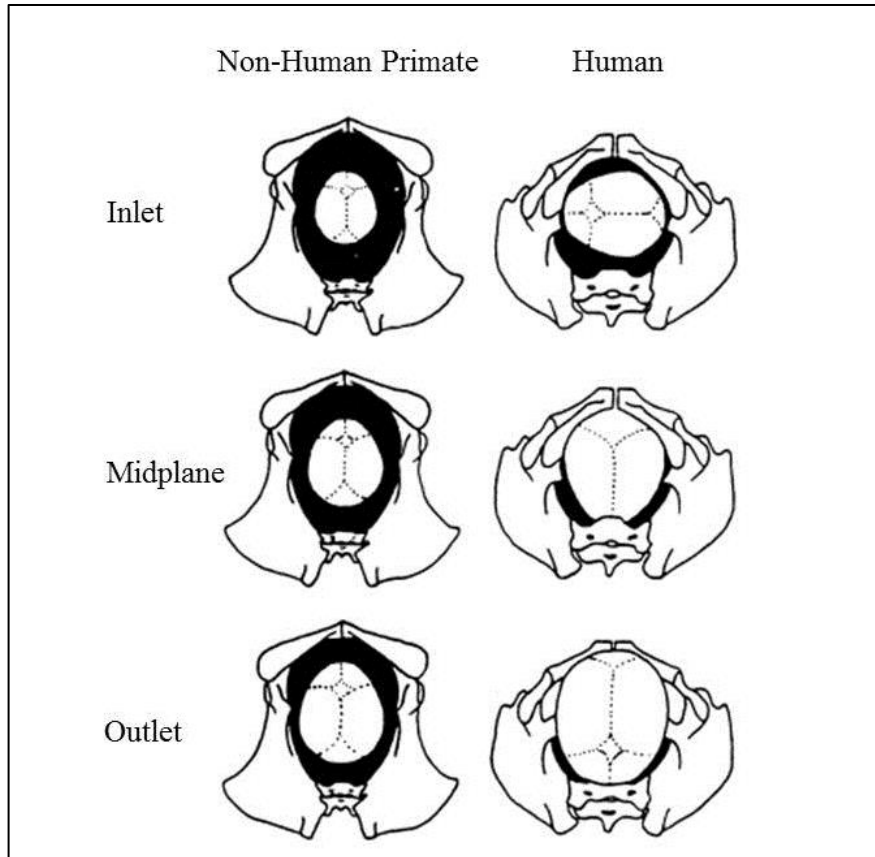


Figure 1.7: Fetal rotation in humans versus non-rotation in non-human primates. Figure modified from Lovejoy (2005).

CHAPTER 2: DIMORPHISM IN THE SIZE AND SHAPE OF THE BIRTH CANALS OF ANTHROPOID PRIMATES

I. BACKGROUND

Human females give birth to large neonates relative to maternal body and birth canal size (Schultz, 1949; Leutenegger, 1974), and the hypothesis that the female pelvis is adapted to the selective pressures of giving birth to such large neonates appears well-supported (Washburn, 1948; Tague, 1989, 1992; Lovejoy, 2005). Although females are smaller than males for both stature and body mass, females have a more spacious birth canal than males (Turner, 1885; Caldwell and Moloy, 1933; Greulich, 1938; Young and Ince, 1940; Coleman, 1969; Krogman and Işcan, 1986; Hager, 1989; Tague, 1989, 1992; Walrath, 1997; Correia et al., 2005; Kurki, 2007; Brown, 2011; Kurki, 2011). Across human populations, females have larger circumferences of the pelvic inlet, midplane, and outlet than males, both absolutely and relative to body size (Tague, 1992). Females also have mediolaterally wider midplanes (Holland et al., 1982; Hager, 1989; Tague, 1991; 1992; Correia, 2005; Brown, 2011) and outlets (Holland et al., 1982; Hager, 1989; Tague, 1992; Correia, 2005; Brown, 2011; but see Krogman and Işcan, 1986) than males relative to body size.

Because humans, who are bipeds, are thought to be under selection for smaller biacetabular breadths and distances between the sacroiliac and acetabular joints (Washburn, 1950, 1960; Pinkerton, 1973; Zihlman, 1978; Ruff, 1995; Lovejoy, 2005),

and because iliac breadth is assumed to be under stabilizing selection in humans for thermoregulatory imperatives (Ruff, 1993), it is usually presumed that dimorphism in human pelvis is due to an “obstetric dilemma” in females (Washburn, 1960). Because selection for obstetric imperatives in females should increase the size of the maternal birth canal (Berge et al., 1984; Tague and Lovejoy, 1986; Abitbol, 1987b; Hager, 1989; Rosenberg, 1992; Abitbol, 1996; Rosenberg and Trevathan, 2002), female pelvic form is hypothesized to represent a tradeoff between selection for obstetric demand and selection for locomotor efficiency and/or thermoregulation (Ruff, 1995; Lovejoy, 2005). Further, this “obstetric dilemma” is thought to alter the timing of birth so that humans have a truncated gestational period (and consequently give birth to neonates with a smaller proportion of brain growth completed) compared to other apes (Washburn, 1960; DeSilva and Lesnik, 2006) as a result of locomotor selection limiting the size of the birth canal. However, recent research indicates that the “obstetric dilemma” may not exist in humans. Wider interacetabular distances in females may not pose an energetic cost compared to males (Warrener et al., 2015), and it is possible that maternal metabolic constraints rather than pelvic constraints alter the timing of birth in humans (Dunsworth et al., 2012). Further, the prevalence of cephalopelvic disproportion (mismatch between the neonatal head and maternal birth canal) in modern humans might be the result of the transition to agricultural subsistence and increased nutrition during pregnancy (Wells et al., 2012) and therefore might be unrelated to the adoption of bipedalism (Wells et al., 2012; Warrener et al., 2015).

These results present a conundrum – if there is no “obstetric dilemma”, why are human pelvises so dimorphic? It is possible that dimorphism in the birth canal is simply

the result of obstetric selection on females (rather than a “tradeoff” between obstetrics and locomotion in females). If this were the case, it would be expected that other primate taxa that give birth to large neonates relative to maternal body size should also exhibit dramatic dimorphism in the birth canal. Though humans are the only extant bipedal primates, large cephalopelvic proportions, in which neonatal head size is large compared to maternal pelvic diameters, are common among primates (Schultz, 1949; Leutenegger, 1970, 1974; Stoller, 1995), especially among monkeys (Table 2.1). In contrast, the living apes (with the exception of *Homo* and *Hylobates*) have small cephalopelvic proportions (Table 2.1; Schultz, 1949; Leutenegger, 1982). The variation in cephalopelvic proportions that exists across anthropoid primates presents an opportunity to test the hypothesis that the existence of large cephalopelvic proportions within anthropoid species results in dimorphism in the size or shape of the birth canal.

a. Which aspects of birth canal morphology should be the target of obstetric selection?

Obstetric selection should hypothetically influence birth canal size, shape, or a combination of both, leading to dimorphism in the size or shape of the female birth canal compared to the bony equivalent in males. Though males obviously do not possess a birth canal, they do possess a negative space of the pelvis which is the bony equivalent of the female birth canal. For brevity, the bony equivalent of the female birth canal that exists in males will be referred to as the “birth canal” in males (even though a neonate does not pass through this structure in males).

It is possible that only birth canal *size* is the target of obstetric selection because obstetric selection should be concerned principally with creating adequate space for the passage a neonate (Tague, 1991). Birth canal size can be increased in females by selection for an isometrically bigger birth canal in females compared to males. Alternatively, selection to increase the circumference of one or more pelvic planes - the pelvic inlet, midplane, and/or outlet - in females compared to males would lead to dimorphism in the size of these planes.

It is also possible that obstetric selection modifies birth canal *shape*. If there is no change in the circumference of the birth canal planes (i.e., absolute size), selection for a rounder birth canal – in which the mediolateral diameters of the pelvic planes approximate or exceed the dorsoventral diameters - may facilitate birth, because a comparatively larger neonatal head can fit through a rounder canal compared to a more ellipsoid one. Such selection should correspond to a mediolaterally wider birth canal in females compared to males.

Males and females may also differ in the *size and shape* of the birth canal. For the birth canal, selection on size and selection on shape are related, such that any increase in the mediolateral or dorsoventral (or both) diameters of each plane increase the circumference of that plane. However, if only the mediolateral or dorsoventral diameter increases, the shape of the birth canal changes. An increase in only the mediolateral dimension of the birth canal leads to a rounder or more transversely oval canal, whereas an increase in only the dorsoventral dimension creates a more dorsoventrally ellipsoid canal. A concurrent increase in the mediolateral and dorsoventral diameters of the birth canal increases circumference, but it does not change

the shape of the canal. Thus, the mediolateral and dorsoventral diameters of the birth canal represent both aspects of size and shape.

Because there are many ways to create an obstetrically-sufficient birth canal (selection on size, selection on shape, selection on both), and because size and shape differences between males and females can be achieved through selection for dimorphism in different parts of the pelvis (sacrum, pubis, ilium, ischium), it is possible that there is not one ‘pattern of dimorphism’ that characterizes all primates with large cephalopelvic proportions (if there is any dimorphism at all). Accordingly, it is important to consider both size and shape differences between males and females within each species rather than looking for patterns of dimorphism that characterize all species.

b. Dimorphism in the Birth Canals of Non-Human Primates

Pelvic dimorphism is present across many mammalian taxa regardless of relative neonatal size (Gardner, 1936; Dunmire, 1955; Crelin and Newton, 1969; Chapman et al., 1994; Tague, 2003; Berdnikovs et al., 2007; Schutz et al., 2009a; Schutz et al., 2009b; Wells et al., 2012). Accordingly, previous research has not demonstrated a clear association between dimorphism in the size or shape of the birth canal and obstetric demand across anthropoid primates (Schultz, 1949; Steudel, 1981a; Tague, 1991; 2005). Across primates, females exhibit relatively greater transverse diameters of the pelvic inlet compared to males controlling for overall body size regardless of cephalopelvic proportions (Schultz, 1949; Tague, 2005), and pubis length is also known to be dimorphic in anthropoid taxa, even those with small cephalopelvic proportions (Steudel,

1981a). Furthermore, there does not appear to be one pattern of dimorphism that characterizes all species of primates that have large cephalopelvic proportions (Tague, 1991). Yet, though the presence of dimorphism (whether or not there are any differences between sexes) may not be *only* to obstetric demand, it is possible that the magnitude of dimorphism in birth canal size and shape (how different the sexes appear) is greater among taxa with large cephalopelvic proportions compared to those with small proportions (Ridley, 1995).

The observation of pelvic dimorphism among anthropoids with small cephalopelvic proportions has prompted the hypothesis that factors other than parturition, including potentially overall body size or body size dimorphism, might influence pelvic dimorphism in anthropoid primates (Schultz, 1949; Tague, 1991; 2005). In anthropoid species with high levels of body size dimorphism (even those with small cephalopelvic proportions), females have exceptionally large birth canals (Tague, 2005). Thus, it is possible that divergent selection pressures on body size dimorphism (which may be driven by sexual selection) and pelvic dimorphism (which may be driven by obstetric selection) leads to dissociation between body size dimorphism and pelvic dimorphism (Tague, 2000; 2005; Kurki, 2011). Further, it is possible that the magnitude of dimorphism in birth canal size is affected by *both* body size dimorphism and cephalopelvic proportions, such that species with both large cephalopelvic proportions and high levels of body size dimorphism also have the most dimorphic pelves.

Most previous research addresses dimorphism in the size of the birth canal planes or individual bony elements in primates (Washburn, 1948; Schultz, 1949;

Leutenegger, 1974; Mobb and Wood, 1977; Steudel, 1981a; Ridley, 1995; Tague, 2005) rather than dimorphism in birth canal shape. The little research that does exist on dimorphism in birth canal shape in anthropoids indicates there is not a clear association between dimorphism in birth canal shape and cephalopelvic proportions in primates (Tague, 1991). However, it is possible that previous methods used to quantify shape differences in the planes of the birth canal between males and females (using ratios of mediolateral to anteroposterior diameters of each birth canal plane; Tague, 1991) do not capture birth canal shape differences between the sexes. For instance, both monkeys and apes have significant dimorphism in the transverse diameters of the birth canal, but only monkeys (not apes) also have high levels of dimorphism in the anteroposterior diameters of the inlet (Tague, 1991). Thus, when using a ratio of transverse to mediolateral birth canal dimensions to quantify shape in apes, females have “rounder” birth canals than in males (Schultz, 1949; Tague, 1991) due to dimorphism in only the mediolateral dimensions of the birth canal, while in monkeys, the sexes are not different for birth canal shapes (Schultz, 1949; Tague, 1991) because female monkeys have larger mediolateral *and* dorsoventral dimensions of the birth canal than males (Tague, 1991). Furthermore, using ratios of linear distances to quantify birth canal shape also does not allow examination of how dimorphism in the individual bony elements— ilium ischium, pubis, sacrum – contributes to dimorphism in the size and shape of the birth canal. Because dimorphism in the spatial relationships among the bony elements of the pelvic girdle are what actually cause dimorphism in the size and the shape of the birth canal planes, considering three dimensional birth canal morphology is necessary (Moffett et al., 2013; Lycett and von Cramon-Taubdel, 2013).

Similar to dimorphism in size, it is possible that there is dimorphism in birth canal shape across anthropoid taxa regardless of cephalopelvic proportions, but that the magnitude of dimorphism is greater in species with large proportions. If this is the case, it would be expected that there is little overlap in birth canal shape between males and females in species with large cephalopelvic proportions, but more overlap between sexes in species with small proportions (because there is theoretically low obstetric selection on birth canal form in these females). However, this hypothesis has not been tested across anthropoid primates.

II. HYPOTHESES

The goal of the current study is to determine how obstetric demand and cephalopelvic proportions influence dimorphism in the size and shape of the birth canal across anthropoids. This study tests the following hypotheses:

Hypothesis 1: Dimorphism in birth canal size is due to obstetric selection.

Prediction 1a: In species with large cephalopelvic proportions, females will have larger birth canals overall (quantified as centroid size of birth canal) compared to males controlling for body size, and this will not be the case for species with small proportions.

Prediction 1b: In species with large cephalopelvic proportions, females will have larger circumferences of the inlet, midplane, and outlet compared to males controlling for body size, and this will not be the case in species with small proportions.

Prediction 1c: In species with large cephalopelvic proportions, females will have larger mediolateral and dorsoventral dimensions of the inlet, midplane, and outlet compared to males controlling for body size, and this will not be the case in species with small proportions.

Prediction 1d: If dimorphism in birth canal size is found in species with *both* large and small cephalopelvic proportions, there will be a greater magnitude of dimorphism in birth canal dimensions among species with large cephalopelvic proportions compared with species having small proportions.

Hypothesis 2: Dimorphism in birth canal shape is due to obstetric selection.

Prediction 2a: In species with large cephalopelvic proportions, males and females are dimorphic for the overall shape of the birth canal and this is not true in species with small proportions.

Prediction 2b: In species with large cephalopelvic proportions, females have rounder inlets, midplanes, and outlets compared to males, and this is not true in species with small proportions.

Prediction 2c: If dimorphism in birth canal shape is not restricted to species with large cephalopelvic proportions, there is a greater magnitude of dimorphism (i.e., less shape overlap) in birth canal shape among species with large cephalopelvic proportions compared with species having small proportions.

III. MATERIALS AND METHODS

a. Samples

Species were chosen for this study based on: 1) existing data on cephalopelvic proportions (Schultz, 1949; Leutenegger, 1982; Stoller, 1995) and 2) adequate samples available for shape analysis. Sample size for morphometric comparisons of pelvic dimensions was determined using a power analysis, conducted in R using the package ‘pwr’, of 5 male and 5 female specimens of *H. lar*. Results indicated that sample size should equal at least 12 individuals *per species, per sex* to achieve power of 0.90 for detecting pelvic shape differences between sexes using Student’s t-tests.

Adult male and female pelvises (n=920) from 9 anthropoid species (Table 2.1) constituted the sample for the current study. Skeletal maturity was determined using fusion of the iliac crest and ischial tuberosity. Of the species included in this study, 6 have large cephalopelvic proportions [*Homo sapiens* (n=156), *Hylobates lar* (n=112), *Macaca mulatta* (n=187), *Nasalis larvatus* (n=33), *Papio anubis* (n=21), *Saimiri sciureus* (n=153)] and 3 have small proportions [*Alouatta seniculus* (n=38), *Gorilla gorilla* (n=106), *Pan troglodytes* (n=114)]. This sample comprises a range of cephalopelvic proportions, phylogenetic affinity, overall body size, and body size dimorphism among extant primates. While phylogeny may influence birth canal morphology, samples for too few taxa exist to achieve sufficient power (Blomberg et al., 2003) due to a dearth of information on cephalopelvic proportions among many primates. However, including species with large and small cephalopelvic proportions within hominoids [*Homo sapiens* and *Hylobates lar* (large proportions); *Gorilla gorilla* and *Pan troglodytes* (small proportions)] and platyrrhines [*Saimiri sciureus* (large

proportions) and *Alouatta seniculus* (small proportions)] provided a set of comparisons with which to consider phylogeny and develop hypotheses for robust testing if a broader range of taxa become available. Similarly, locomotor repertoire may be an important factor, but locomotion is completely confounded with phylogeny in anthropoids. Thus, no formal tests considering locomotion were performed.

b. Landmarks

Paired ossa coxae and sacra were articulated with isobutylene-isoprene polymer adhesive mounting putty and rubber bands (Tague, 1991) without compensating for cartilage (Tague, 1986; Grabowski, 2013). 5 bilateral and 5 midline landmarks representing the birth canal are then collected with a Microscribe G2X digitizer. Landmarks (Table 2.2; Figure 2.1) include sacroiliac joint at arcuate line, lateral arcuate line, arcuate line at acetabulum, superior pubic symphysis, and anterior S1 body (inlet); the ischial spine, inferior pubic symphysis, and inferior S1 body (midplane); and the posterior ischial tuberosity, inferior pubic symphysis, and inferior sacrum (outlet) (Figure 2.1). In humans, the dorsal-most point of the midplane is typically measured from the anterior S4 vertebrae (Tague, 1992, Brown, 2007; Kurki, 2007, 2011). However, modal numbers of sacral vertebrae in great apes, *H. lar*, and monkeys are 5, 4, and 3, respectively (Schultz, 1936). Therefore, for this study, the anterior inferior S1 vertebral body was chosen as the posterior landmark for the midplane so that this point could be collected at the same point on all specimens.

Error in digitizing was assessed using repeated measures analysis (Kohn, 1992). One pelvis of *P. troglodytes* (large body size) and one pelvis of *S. sciureus* (small body size) was digitized, and all landmarks were collected on each specimen ten times. For this study, repeated measures are used to quantify landmark repeatability (Kohn, 1995). Repeated measures analysis yielded error averages for all landmarks equal to or less than 0.16 mm for *Pan. troglodytes* and 0.19 mm for *Saimiri sciureus*. These averages were less than 0.002% of centroid size for both specimens, and error was equally distributed across the three axes. This analysis indicated that all landmarks can be collected with high repeatability regardless of the size of specimens.

c. Testing Hypothesis 1

To test the hypothesis that dimorphism in birth canal size is due to large cephalopelvic proportions, centroid size of the birth canal (a measure of overall birth canal size) was calculated as the square root of the sum of the squared distances between all birth canal landmarks and the centroid of the configuration (Bookstein, 1991) for each individual. Centroid size was chosen to represent the size of the entire birth canal. Circumferences of the inlet, midplane, and outlet were quantified following Tague (1991) and secondarily calculated from landmark data following the formulas in Table 2.3 (illustrated in Figure 2.2). Dorsoventral and mediolateral diameters of the inlet, midplane, and outlet were also quantified following Tague (1991), and each linear distance was secondarily calculated from landmark data following the formulas in Table 2.3 (also illustrated in Figure 2.2). The circumferences and mediolateral/anteroposterior dimensions of each plane quantified the size of each plane of the birth canal.

Absolute measures of birth canal size are of limited utility for evaluating sexual dimorphism, because absolute measures are *expected* to be sexually dimorphic in species in which males have much larger body size than females – for example *Gorilla gorilla* and *Nasalis larvatus* (Table 2.1). However, the fact that males have *absolutely* larger measurements in such species does not preclude the possibility of females possessing *relatively* larger birth canals when controlled for body size, which is the question being investigated here. Thus, ratios of birth canal dimensions against body size proxies (see below) were computed in order to compare the size of the birth canal between males and females. Ratios were calculated as (absolute birth canal dimension)/(S1 body breadth) for each birth canal size variable for each individual (Moffett et al., 2013). These ratios represent the relative size (controlling for body size) of each birth canal size variable.

Performing statistical analyses on ratios can lead to spurious results, especially if there is non-isometric scaling among variables (Atchley et al., 1976), and any differences between sexes in relative pelvic size may simply be due to allometric scaling between pelvic size variables and S1 body breadth. Therefore, any measure of body size chosen for the present study should ideally scale isometrically with all measures of birth canal size. The most appropriate measure of body size is body mass (Smith and Jungers, 1997), but individual body mass data does not exist for most specimens included in this study. Previous authors have used the geometric mean of pelvic linear data as a proxy for body size in anthropoids (Steudel, 1981a; Li, 2002), but this measure of body size is inappropriate for the present study because it is not independent of the measures of birth canal size analyzed. This study therefore used one

body size proxy that is independent of the aspects of pelvic form being analyzed here: transverse breadth of the first sacral (S1) vertebral body. S1 body breadth (also called lumbosacral articulation; Jungers, 1988) is strongly correlated with body mass across primates (Jungers, 1988; 1991). It should be noted that previous authors have found that many postcranial skeletal indicators of body size produce inaccurate estimates of body size dimorphism in primates compared to cranial indicators (Plavcan, 2003). However, body mass was unavailable for most specimens included, and many pelvises were not paired with associated crania.

Next it was necessary to assess whether the pelvic size variables examined in this study scale isometrically with S1 body breadth. It is ideal to perform regressions on the smallest subgroups (individual sexes within individual species) because this ensures similar scaling between sexes within individual taxa. However, for some taxa, there was not enough variation in body size within sexes, or even within species – for example, in *Saimiri sciureus* and *Hylobates lar* - to obtain a strong correlation between variables. Therefore, regressions were performed across (a) all taxa included in order to obtain scaling of birth canal dimensions across a wide range of body sizes and (b) within phylogenetic groups (i.e., apes and monkeys) to determine whether scaling patterns are similar across these groups. Regressions were performed only on male specimens in order to determine allometric scaling of birth canal dimensions (used here to mean dimensions of the pelvis that in females contribute the birth canal, as of course males do not have birth canals) when birth is not a factor. Natural logged birth canal dimensions were regressed against natural logged body size proxies using reduced major axis regression (Harvey and Pagel, 1991; Warton et al., 2006; Smith, 2009; but see Hansen

and Bartoszek, 2012) in R using the package ‘lmodel2’. Strength of the relationship between body size proxies and birth canal dimensions was determined using r-squared values. Isometry was determined using 95% confidence intervals, such that confidence intervals which include a slope of 1 are considered isometric.

For pelvic size variables that scale isometrically with S1 body breadth, ratios of these variables with S1 body breadth may be used to compare relative size between males and females. Within each species, birth canal size ratios were statistically compared between males and females within each species using a two-tailed Student’s t-test at $\alpha=0.035$ (see justification for α -level below). If females have relatively larger birth canals than males controlling for overall body size, this should manifest itself as statistically larger ratios (of pelvic size variables divided by S1 body breadth) in females.

For pelvic size variables which scale allometrically with S1 body breadth, ratios may be unreliable. Therefore, within each species, residuals from the male-only taxon-wide regression (i.e., within apes or within monkeys) between each pelvic size variable and S1 body breadth were calculated, and residuals were statistically compared between males and females using Student’s t-tests. If females have relatively large birth canals controlling for body size compared to males, this should manifest itself as larger and more positive residuals from the taxon-wide regression in females, but not in males. Furthermore, if dimorphism in birth canal size is due to large cephalopelvic proportions, residuals should be statistically different in males and females in species with cephalopelvic proportions, but not different in males and females in species with small proportions.

It is possible that dimorphism in birth canal size (i.e., significant differences in birth canal dimensions) is present across taxa regardless of cephalopelvic proportions, but that there is a larger magnitude of dimorphism (greater difference in birth canal size) among species with large cephalopelvic proportions. Therefore, for each birth canal dimension, a dimorphism index was created within each species to facilitate comparison of the magnitude of dimorphism (i.e. the magnitude of difference between males and females with species) among species. Each dimorphism index was calculated as:

$$\text{dimorphism index} = \left[\frac{\text{female mean}}{\text{male mean}} \right] * 100$$

such that the further the value of the dimorphism index is from 1, the larger the difference between males and females for a given birth canal dimension. For each birth canal dimension, dimorphism indices for species were ranked from largest (females larger than males) to smallest (little difference between the sexes) in order to allow comparison of the magnitude of dimorphism in birth canal size.

Hypothesis 1 was considered falsified if within each species having large cephalopelvic proportions (a) females do not exhibit statistically larger centroid sizes of their birth canals compared to males controlling for overall body sizes; (b) females do not exhibit larger circumferences of the pelvic inlet, midplane and outlet than males controlling for overall body sizes; (c) females do not exhibit larger mediolateral or transverse diameters of the pelvic inlet, midplane and outlet than males controlling for overall body size; or (d) there is not a greater magnitude of dimorphism in species with large cephalopelvic proportions compared to species with small proportions.

d. Testing Hypothesis 2

To test the hypothesis that dimorphism in overall birth canal shape is due to large cephalopelvic proportions, it was first necessary to quantify the overall shape of the birth canal (landmarks used to quantify birth canal shapes shown in Figure 2.1) were quantified using 3-dimensional geometric morphometrics. Original landmark data were scaled, translated, and rotated using generalized Procrustes analysis. Principal components analysis (PCA), an eigenanalysis-based tool for ordination, was then employed to compare birth canal shapes within each species. To obtain shape coordinates, all size information is removed by scaling (Zelditch et al., 2004); therefore, principal components scores reflect size-free shape data. All PCAs were conducted using Morphologika 2.5© software. To determine which successive principal components (PCs) significantly contributed to shape variability within each species, scree plots were used to visualize the inflection points of variance explained by successive PCs (Zelditch et al., 2004). For scree plots which did not have an obvious inflection point, PCs which represented more than 10% of total shape variance were included in the analysis, as these components can be said to contribute to biologically meaningful variation (Zelditch et al., 2004).

Discriminant Function Analysis (DFA) was employed to determine whether males and females are significantly different for birth canal shape, quantified as principal components scores of birth canal shape within each species. All Discriminant Function Analyses were performed in R using the package 'MASS'. However, sample

size effects are known to affect error rates in DFA (Lachenbruch, 1968). Power analysis indicated that in order to achieve power of 0.90 for detecting pelvic shape differences between sexes using DFA at effect size of 18 individuals per species per sex. Therefore, this method of determining sex differences in overall birth canal shape could lead to an increased probability of Type II error for species represented by small sample sizes, specifically *Papio anubis* (Female n=5) and *Nasalis larvatus* (Female n=16). Therefore, as an additional strategy to quantify the degree of overlap in birth canal shapes within each species in a manner that is not sensitive to sample size, a polygon was placed around the male shape distribution (which theoretically represents the shape of the structure when there is no obstetric selection) in the principal components plot. Then, the proportion of females that fell within the male distribution was calculated.

In order to determine which Principal Components of birth canal shape males and females separate along, Student's t-tests were performed on raw Principal Component scores between males and females within each species for all PCs that encompass significant shape variation (i.e., >10% of intraspecies shape variation). All t-tests of differences in means between male and female PC scores within species were performed in R. Visualization of shape differences between males and females within each species was facilitated using wireframes created in Morphologika.

While PCA is useful for determining whether there is dimorphism in birth canal shape within species, these techniques do not provide details of which elements of the birth canal actually differ between males and females. Thus, in order to determine precisely which regions of the birth canal differ between males and females, Euclidean Distance Matrix Analysis (EDMA) was used to localize shape differences between

males and females (Lele and Richtmeier, 1991; 1995; 2001; following Brown, 2011). EDMA's FORM analysis allows quantification of the linear distances (for this study, interlandmark distances) which significantly contribute to overall shape differences between samples using a bootstrap approach. Significance of each interlandmark distance was determined using bootstrapped confidence intervals. The FORM procedure also estimates the difference between mean forms (i.e., overall form differences between groups). For differences between mean forms using EDMA's FORM procedure, all p-values <0.035 were considered significant (see justification for α -level below). The FORM procedure was performed on both unscaled data as well as data scaled to each individual's geometric mean (in order to obtain shape information controlling for size; Lele and Richtmeier, 1991; 1995). All FORM analyses were performed in WinEDMA Version 1.0.1 Beta (Cole, 2002).

“Roundness” of the birth canal planes between males and females was also quantified within each species. An index was created following Tague (1991) in which the mediolateral dimension of each birth canal plane (secondarily calculated from landmark data; Figure 2.2; Table 2.3) was divided by the dorsoventral dimension of that plane (secondarily calculated from landmark data; Figure 2.2; Table 2.3) for each individual. Thus, in this ratio, a larger value (close to or exceeding one) indicates a transversely rounder inlet, midplane, or outlet whereas a smaller ratio (less than one) indicates a more ellipsoid plane. Ratios calculated for the shape of the inlet, midplane, and outlet cannot be statistically compared between males and females because there are different allometric scaling relationships for mediolateral and dorsoventral diameters of the birth canal with body size (see Results below and Table 2.5). However,

these ratios do provide information about the relative roundness or ellipsoid-shape of each pelvic plane in females versus males.

The predictions of Hypothesis 2 were considered falsified if in species with large cephalopelvic proportions (a) there is significant overlap in overall birth canal shape between males and females or (b) females do not have rounder birth canal shapes compared to males.

e. Controlling for multiple comparisons

A potential issue with performing a large number of statistical analyses is the increasing probability of false positives, or Type I Errors, with the increasing number of tests. In this study, multiple statistical procedures are performed on related data; therefore, using an α -level of 0.05 would lead to an increased probability to Type I Error. Therefore, in order to control for multiple comparisons in this study, a False Discovery Rate (FDR) procedure (Benjamini and Hochberg, 1995) was conducted on all p-values obtained from this study (i.e., all those obtained in Student's t-tests of absolute and relative birth canal dimensions, DFA, Student's t-tests of PC scores, and EDMA's FORM tests) using the R package 'qvalue' (Storey, 2015). Unlike a Bonferroni correction, FDR is not excessively conservative in which results are considered significant. The FDR procedure indicated that in order to maintain a false discovery rate of 5%, α -level should be set at 0.035. Therefore, unadjusted p-values are reported in the text, but only those p-values less than 0.035 were considered significant.

IV. RESULTS

a. Allometry in Birth Canal Size Variables

Allometric scaling of birth canal dimensions with S1 body breadth is presented in Table 2.4 and Table 2.5. Birth canal centroid size and circumferences of the inlet, midplane, and outlet scale with isometry with S1 body breadth both across all anthropoid taxa and within apes and monkeys (Table 2.4). Therefore, differences between males and females in the ratio of birth canal centroid size and/or circumferences of the inlet, midplane and outlet against S1 body breadth are likely not due to allometric scaling. Within apes and monkeys, mediolateral inlet diameter and dorsoventral inlet diameters also scale isometrically with S1 body breadth (Table 2.5), meaning that any differences between males and females within taxa in either mediolateral or dorsoventral inlet diameter is likely not due to allometry.

Mediolateral midplane diameter scales isometrically with S1 body breadth in monkeys but very slightly negatively allometrically in apes (Table 2.5), which indicates that differences between males and females for relative mediolateral midplane diameter is likely not due to allometric scaling in monkeys or apes with low levels of body size dimorphism (*H. sapiens*, *Hy. lar*, *P. troglodytes*). However, mediolateral midplane diameter might be relatively larger in females than males in ape species with extremely high levels of body size dimorphism (*G. gorilla*) simply due to allometric scaling of mediolateral midplane diameter with S1 body breadth in apes.

Dorsoventral diameters of the midplane scale isometrically with S1 body breadth in apes, but positively allometrically in monkeys (Table 2.5). This indicates that

among apes, any dimorphism in relative dorsoventral midplane diameters is likely not due to allometric scaling. However, in monkey taxa with extremely high levels of body size dimorphism (*N. larvatus* and *P. anubis*), it would be expected that males would be relatively larger than females for dorsoventral midplane diameters, but this should not be the case in monkey taxa with low levels of body size dimorphism (*Macaca mulatta*, *Saimiri sciureus* and *Alouatta seniculus*).

Mediolateral outlet diameter scaled with strong positive allometry in apes but negative allometry in monkeys (Table 2.5). Therefore, it would be expected that among ape taxa which are highly dimorphic in body size, males are relatively larger than females for outlet diameter due to allometric scaling, but this should not be the case in ape taxa with low levels of body size dimorphism. In contrast, in monkey taxa with high levels of body size dimorphism, females should exhibit relatively larger mediolateral outlet diameters compared to males, but this should not be the case in monkey taxa which are less dimorphic in body size.

Dorsoventral outlet diameter scales with very slight negative allometry in apes but strong positive allometry in monkeys (Table 2.5). Based on these scaling relationships, it is expected that in apes with very high levels of body size dimorphism females are relatively larger than males for dorsoventral outlet diameter, but this should not be true in apes with lower levels of body size dimorphism. In monkeys with high levels of body size dimorphism, males should be relatively much larger than females for dorsoventral outlet diameters, but in less body size dimorphic taxa, scaling should not affect dimorphism in dorsoventral outlet diameter.

a. Is dimorphism in birth canal size within species is due to obstetric selection?

This hypothesis first predicts that in species with large cephalopelvic proportions, females will have a larger overall birth canal compared to males controlling for body size, but this will not be true in species with small proportions. The results of this study (Tables 2.6-2.8) do not support this hypothesis. The presence of dimorphism in birth canal centroid size (controlling for body size) is not restricted to species with large cephalopelvic proportions. Across species with large cephalopelvic proportions (*Homo sapiens*, *Hylobates lar*, *Macaca mulatta*, *Nasalis larvatus*, *Papio anubis*, and *Saimiri sciureus*), females do indeed have larger centroid sizes of the birth canal than males controlling for overall body size (all p-values <0.001; Tables 2.6 and 2.8). However, in *Pan troglodytes* (small proportions), females are also relatively larger than males for birth canal centroid size controlling for body size (p<0.001; dimorphism index = 106; Table 2.6). These results are not due to allometric scaling of birth canal centroid size with S1 body breadth, because birth canal centroid size scales isometrically with S1 body breadth across apes and monkeys, and t-tests performed on residuals of the RMA regression between pelvic centroid size and S1 body breadth are identical to the results obtained using ratios (Table 2.8).

Hypothesis 1 also predicts that in species with large cephalopelvic proportions females have relatively larger circumferences of the pelvic inlet, midplane, and outlet than males, but that this is not the case in species with small proportions. This prediction is also not supported because the presence of dimorphism in circumferences of the inlet, midplane, and outlet (controlling for body size) is not restricted to species with large cephalopelvic proportions (Table 2.6). Females are relatively larger than

males (controlling for body size) for the circumferences of the inlet (all p-values <0.001), midplane (all p-values <0.003), and outlet (all p-values <0.006; Table 2.6) in taxa with large cephalopelvic proportions. However, in *Gorilla gorilla* and *Pan troglodytes* (both with small proportions), females are relatively larger than males for pelvic inlet and midplane circumferences (all p-values <0.001), and in *P. troglodytes* females are also relatively larger than males for outlet circumference (p<0.001). Because all birth canal circumferences scale isometrically with S1 body breadth across apes and monkeys, these results are not due to allometric scaling (Table 2.8).

Next, Hypothesis 1 predicts that in species with large cephalopelvic proportions, females have larger mediolateral and dorsoventral dimensions of the inlet, midplane, and outlet compared to males controlling for body size, and this is not the case in species with small proportions. This prediction is also not supported. Dimorphism in the relative mediolateral and dorsoventral diameters of the inlet, midplane, and outlet are not restricted to species with large cephalopelvic proportions (Table 2.7). The transverse diameter of the inlet is relatively larger in females than males (controlling for body size) in *Homo sapiens*, *Hylobates lar*, *Nasalis larvatus*, and *Saimiri sciureus* (all having large cephalopelvic proportions) as well as *Gorilla gorilla* and *Pan troglodytes* (small proportions; Table 2.7). This result is not due to allometric scaling (Table 2.8), because mediolateral inlet diameter scales isometrically with S1 body breadth in apes and monkeys. The transverse diameter of the midplane is also relatively larger in females than males in *H. sapiens*, *Hy. lar*, *N. larvatus*, *S. sciureus*, *G. gorilla*, and *P. troglodytes* (Table 2.7) and results obtained using residuals (Table 2.8) indicate that females have relatively larger transverse midplane diameters than males in *M. mulatta*

and *P. anubis*. The transverse diameter of the outlet (which scales positively allometrically with S1 body breadth in apes and negatively in monkeys; Table 2.5) is relatively larger in females than males in all taxa with large cephalopelvic proportions as well as *P. troglodytes* (small proportions).

The dorsoventral diameters of the inlet and midplane are relatively larger in females than males in all taxa with large proportions (Table 2.8), but also in *P. troglodytes* (small proportions). The dorsoventral diameter of the outlet is relatively larger in females among some taxa with large cephalopelvic proportions (*H. sapiens*, *H. lar*, *M. mulatta*; Table 2.8) as well as in *G. gorilla* and *P. troglodytes* (small proportions).

Even though all species (regardless of cephalopelvic proportions) exhibit some dimorphism in birth canal size, the magnitude of dimorphism in birth canal centroid size and circumferences of the pelvic inlet, midplane, and outlet generally differ between taxa with small and large cephalopelvic proportions (Table 2.9), supporting Hypothesis 1 Prediction 1d. In species with large proportions, there is a high magnitude of dimorphism in birth canal centroid size [dimorphism index ranging from 105 (females slightly larger than males) in *H. lar* and *M. mulatta* to 130 (females much larger than males) in *N. larvatus*; Table 2.9] compared to species with small proportions, in which dimorphism indices are lower (ranging from 100 in *A. seniculus* to 106 in *P. troglodytes*). These results indicate that species with large cephalopelvic proportions do tend to be more dimorphic than those without, though there are exceptions (for example, *P. troglodytes*). Among species with large cephalopelvic proportions, there also tend to be higher dimorphism indices for the relative circumferences of the pelvic

inlet (index range = 108-122), midplane (range = 105-117), and outlet (range = 106-119) compared to species with small proportions for the inlet (range = 100-109), midplane (range = 103-107), and outlet (100-107).

Though females do have relatively larger birth canals than males, in most species (all those studied here except *Alouatta seniculus*), there is a great degree of overlap in birth canal size across most taxa (except for *Nasalis larvatus* and *Papio anubis*; see Appendix A). Thus, differences in birth canal size may not be observable at small sample sizes in many taxa. This is especially important to consider when examining dimorphism in birth canal size in fossil specimens, which will be represented by smaller sample sizes than the species included here.

Though dimorphism in birth canal size is not restricted to species with large cephalopelvic proportions, species with large cephalopelvic proportions do tend to be more dimorphic in birth canal centroid size and circumferences of the inlet, midplane, and outlet than species with small cephalopelvic proportions. So although the data reject the hypothesis that cephalopelvic proportions are the determinant of pelvic dimorphism, they suggest that cephalopelvic proportions influence dimorphism, and result in more dimorphic pelves in taxa with relatively larger neonates.

b. Is dimorphism in birth canal shape within species is due to obstetric selection?

Hypothesis 2 Prediction a posits that males and females will be dimorphic for the overall shape of the birth canal in species with large cephalopelvic proportions but

not in those with small proportions. This hypothesis is not supported by these analyses. Discriminant Function Analysis indicates that in both taxa with large and small cephalopelvic proportions, the sexes differ in the overall shape of the birth canal (Table 2.10) Among all taxa included in this study, males and females significantly separate in shape space along one or more Principal Components (Table 2.11), and EDMA's FORM results likewise indicate that the sexes are significantly different for overall birth canal shape in all species except *A. seniculus* (Table 2.12).

Hypothesis 2 also predicts that in species with large cephalopelvic proportions, females have a “rounder” birth canal compared to the bony equivalent in males, but this is not true in species with small proportions. The data do not support this hypothesis, either (Table 2.13). Only one species with large cephalopelvic proportions (*Hylobates lar*) has females which have rounder pelvic inlets than males, and one species with small cephalopelvic proportions (*Pan troglodytes*) also has females which exhibit rounder inlets compared to males. Females have rounder pelvic midplanes compared to males in all taxa (regardless of cephalopelvic proportions) except for *Saimiri sciureus* (which notably has the largest cephalopelvic proportions). Females do have rounder pelvic outlets than males in all species with large proportions except *Saimiri sciureus*, but in *P. troglodytes* (small proportions) females also have rounder outlets compared to males (Table 2.13).

Finally, Hypothesis 2 predicts that even if there is some shape dimorphism in all taxa, it will be greater species with large cephalopelvic proportions. Data show that there is less overlap between males and females in birth canal shapes among species with large cephalopelvic proportions (ranging from 0% to 39% overlap between sexes

for birth canal form; Table 2.14) compared to species with small proportions (ranging from 38% to 79% overlap between sexes for birth canal form; Table 2.14; Figure 2.3).

Though dimorphism in birth canal form is not restricted to species with large cephalopelvic proportions, the magnitude of dimorphism in birth canal shape is greater among species with large cephalopelvic proportions compared to species with small cephalopelvic proportions.

c. Interspecific Differences in Pattern of Dimorphism

All species included in this study exhibit dimorphism for some aspects of birth canal size and shape, but each species in a slightly different way.

Large Cephalopelvic Proportions

Homo sapiens:

Birth Canal Size: In *H. sapiens*, females are relatively larger than males for relative birth canal centroid size (Table 2.6), and females are absolutely and relatively larger for the circumferences of the inlet, midplane, and outlet (Table 2.6). Females achieve these spacious birth canal planes by having absolutely larger transverse midplane and outlet diameters and dorsoventral inlet and outlet diameters, and females are also relatively larger for the transverse inlet diameter and dorsoventral midplane diameter (Table 2.7).

Birth Canal Shape: *Homo sapiens* males and females exhibit dramatic differences in birth canal shape (Figures 2.4a and 2.4b; Tables 2.10-2.12). Only ten percent of females fall within the male distribution for birth canal form (Figure 2.4a;

Table 2.14). Females have longer and more coronally-oriented pubes, shorter pubic symphyses and sacra, more dorsally-angled caudal sacra and laterally flaring ischial spines and ischial tuberosities, and relatively wider sacra (Figures 2.4a and 2.4b). Males are relatively larger for pubic symphysis length, sacral length, ischial length, and length of the lateral linea terminalis (Figure 2.4b).

Hylobates lar

Birth Canal Size: In *H. lar*, sexes are monomorphic for body size (Table 2.1), but females are absolutely and relatively larger than males for centroid size of the birth canal and circumferences of the inlet, midplane, and outlet (Table 2.7). Females achieve these larger birth canals with absolutely larger transverse and dorsoventral diameters of the inlet, midplane, and outlet (Table 2.7).

Birth Canal Shape: Birth canal shape is unambiguously dimorphic in some dimensions in this species (Figures 2.5a and 2.5b: Tables 2.10-2.12), but there is more overlap in birth canal shapes between sexes in *H. lar* compared to *H. sapiens* – 33% of females fall within the male distribution (Figure 2.5a; Table 2.14). Males have a more rostrocaudally elongated canal due to a higher position of the sacra, longer sacra, longer ischia, and longer pubic symphyses. Females have mediolaterally expanded birth canals as a result of relatively longer pubes and wider sacra (Figure 2.5b).

Macaca mulatta

Birth Canal Size: In contrast to *H. sapiens*, *M. mulatta* has large cephalopelvic proportions but also greater body size dimorphism (Table 2.1), so males are absolutely larger than females for birth canal centroid size and circumferences of the inlet and

midplane (Table 2.6), but relative to body size females have larger birth canal centroid size and circumferences of all three planes (Table 2.6). Females achieve these relatively larger birth canal circumferences by being relatively larger for the mediolateral and dorsoventral diameters of the inlet and outlet (Table 2.7). Midplane diameters are not significantly dimorphic, but are slightly larger in females, contributing to dimorphism in relative midplane circumference.

Birth Canal Shape: Birth canal shape is significantly and dramatically dimorphic in *M. mulatta* (Tables 2.10-2.12; Figures 2.6a and 2.6b). Only ten percent of females fall within the male distribution for birth canal form (Figure 2.6a; Table 2.14). Females exhibit mediolaterally expanded inlets and outlets due to their relatively longer pubes, mediolaterally expanded sacral alae, and laterally flared ischia. Males have a rostrocaudally expanded birth canal due to relatively longer sacra, ischia, and pubic symphyses (Figure 2.6b).

Nasalis larvatus

Birth Canal Size: In *N. larvatus*, males have absolutely larger midplane and outlet circumferences (but not inlet circumferences) than do females (Table 2.6), but females are relatively larger in centroid sizes and all birth canal circumferences (Table 2.6). Females achieve these relatively larger birth canals by having relatively larger mediolateral and dorsoventral diameters of all birth canal planes (Table 2.7).

Birth Canal Shape: Males and females clearly exhibit differences in birth canal shapes (Tables 2.11 – 2.12; Figures 2.7a and 2.7b). Though DFA indicates that there are no significant differences between sexes (Table 2.10), this result is likely due

to small sample size, because there is no overlap between the sexes for birth canal form in this species (Figure 2.7a; Table 2.14). Females have elongated pubic bones (Figures 2.7a and 2.7b). In contrast, males have a much narrower birth canal due to longer and medially-projecting dorsal ischia, and relatively longer pubic symphyses and sacra (Figure 2.7b).

Papio anubis

Birth Canal Size: In this species, males are absolutely larger than females for midplane circumference, but sexes do not differ in any other absolute measure (Table 2.6). However, females are relatively larger for birth canal centroid size and all circumferences (Table 2.6). Females have larger mediolateral and dorsoventral dimensions of the inlet (Table 2.7), and although slightly larger across midplane and outlet these differences between sexes are not significant, possibly due to the small sample size available for this taxon). Still, these differences contribute to dimorphism in relative midplane and outlet circumference (Table 2.6).

Birth Canal Shape: In *P. anubis*, sexes have significant differences in birth canal shape (Tables 2.10-2.12; Figures 2.8a and 2.8b). Though DFA indicates that there are no significant differences between sexes for shape (Table 2.13), this result is likely due to small sample size, because there is no overlap between the sexes for shape in *P. anubis* (Figure 2.8a; Table 2.14). Female *P. anubis* have laterally flaring inferior ischia due to more coronally-oriented inferior pubic rami in females (Figures 2.8a and 2.8b). Conversely, males have absolutely (and relatively) longer pubic symphyses and ischia (Figure 2.8b).

Saimiri sciureus

Birth Canal Size: Females are absolutely (and relatively) larger than males for birth canal centroid size and circumferences of the inlet, midplane, and outlet (Table 2.6). Females achieve these large birth canals by being absolutely and relatively larger for the transverse diameters of the inlet and midplane and all dorsoventral diameters of the inlet, midplane and outlet. Females are also relatively (but not absolutely) larger for the transverse diameter of the outlet (Table 2.7).

Birth Canal Shape: Males and females exhibit dramatic and significant differences in birth canal shapes (Tables 2.10-2.12; Figures 2.9a and 2.9b). Females have relatively shorter and wider sacra, more dorsally-angled inferior sacra, longer pubes, a more inferior position of the inferior and superior pubic rami (Figure 2.9b). Males have relatively longer pubic symphyses, ischia, and sacra compared to females. Compared to other large cephalopelvic proportion species, there is considerable overlap in shape between the sexes in *S. sciureus* (39%, Figure 2.9a; Table 2.14).

Small Cephalopelvic Proportions:

Gorilla gorilla

Birth Canal Size: In *G. gorilla*, a species with high levels of body size dimorphism (Table 2.1), males are absolutely larger than females for birth canal centroid size and circumferences of the inlet, midplane, and outlet (Table 2.6), yet females are relatively larger for all of these variables. Females are relatively larger for the mediolateral dimensions of the inlet and midplane (but not the outlet – possibly due

to allometric scaling; Table 2.5) as well as the dorsoventral diameters of all three pelvic planes (Table 2.7).

Birth Canal Shape: Males and females have significantly different birth canal shapes (Tables 2.10 - 2.12; Figures 2.10a and 2.10b), but there is considerable overlap between the sexes (Figure 2.10a; Table 2.14) such that 38% of females fall within the male distribution for birth canal shape. Females exhibit elongation of their pubes, more inferiorly-projecting superior pubic rami, and rostrocaudally shorter sacra (Figures 2.10a and 2.10b). Males exhibit rostro-caudally expanded sacra and longer pubic symphyses (Figure 2.10b).

Pan troglodytes

Birth Canal Size: In *P. troglodytes*, females are relatively (but not absolutely) larger than males for birth canal centroid size and the circumferences of all three pelvic planes (Table 2.6). Females achieve these large birth canals by having relatively larger transverse and dorsoventral diameters of the pelvic inlet, midplane, and outlet (Table 2.7).

Birth Canal Shape: Overall birth canal shape is significantly dimorphic in *P. troglodytes* (Tables 2.10-2.12; Figures 2.11a and 2.11b), but there is considerable overlap between the sexes (Figure 2.11a; Table 2.14), such that 79% of females fall within the male distribution for birth canal shape. Females have longer and more coronally-oriented pubes, and laterally flaring caudal ischia. Males have rostro-caudally longer sacra, pubic symphyses, and ischia (Figures 2.11a and 2.11b).

Alouatta seniculus

Birth Canal Size: In *A. seniculus*, there are no differences between males and females for relative (controlling for S1 body breadth) birth canal centroid size or circumferences of the inlet, midplane, or outlet (Table 2.6). There are also no statistical differences between sexes for the relative (controlling for S1 body breadth) mediolateral or dorsoventral diameters of any birth canal plane (Table 2.7).

Birth Canal Shape: Dimorphism in birth canal form is less pronounced in *A. seniculus* compared to other taxa (Tables 2.10-2.12; Figures 2.12a and 2.12b). There is considerable overlap between the sexes for birth canal shape (Table 2.14) such that 67% of females fall within the male distribution. Differences in the overall shape of the birth canal between males and females are insignificant (Tables 2.10 and 2.12). However, this species does exhibit a few localized sex differences in birth canal shape. Sexes significantly separate along PC2 (which encompasses 11% of shape variation in this species; Table 2.11), and males have relatively longer sacra and pubic symphyses (Figures 2.12a and 2.12b), and females have a slight anteroposterior expansion of the outlet.

VII. DISCUSSION AND CONCLUSIONS

The results of this study support the hypothesis that birth canal dimorphism in nonhuman anthropoids is not due solely to large cephalopelvic proportions (Schultz, 1949; Steudel, 1981a; Tague, 1991; 2005), because size and shape of the birth canal are dimorphic in species with both large and small cephalopelvic proportions. These results are consistent with the presence of dimorphism in many species of mammals, regardless

of neonate size (Gardner, 1936; Dunmire, 1955; Crelin and Newton, 1969; Chapman et al., 1994; Tague, 2003; Berdnikovs et al., 2007; Schutz et al., 2009a; Schutz et al., 2009b), (Tague, 2003; Schutz et al., 2009a; Schutz et al., 2009b).

The specific aspects contributing to this dimorphism are less clear. It has been hypothesized that dimorphism in relative sacral breadth is due to large cephalopelvic proportions (Moffett et al., 2013). If dimorphism in relative sacral breadth is only found among species with large cephalopelvic proportions, dimorphism in relative sacral breadth could be responsible for the increased magnitude of dimorphism in the birth canal in species with large cephalopelvic proportions. Moffett et al.'s (2013) hypothesis is further examined in Chapter 3. In contrast to sacral breadth, all species in this study are dimorphic in relative pubis length regardless of cephalopelvic proportions (except for *A. seniculus*), and this result is consistent with previous research which have found dimorphism in relative pubis length to be unrelated to cephalopelvic proportions (Steudel, 1981a). It is unlikely that dimorphism in pubis length accounts for the greater magnitude of dimorphism in the birth canals of species with large cephalopelvic proportions.

Previous authors have found that birth canal dimorphism is a correlate of dimorphism in overall body size, such that in species with high levels of body size dimorphism, females exhibit exceptionally large birth canals compared to males (Schultz, 1949; Leutenegger, 1974; Tague, 2005). The results of the present study partially support this hypothesis (Table 5.9). Among species with high levels of body size dimorphism *and* large cephalopelvic proportions (*Nasalis larvatus*, *Papio anubis*), the magnitude of dimorphism in birth canal centroid size (controlling for body size) is

higher than any other taxa (dimorphism indices 130 and 121, respectively). In contrast, *Gorilla gorilla* (which exhibits large body size dimorphism and small cephalopelvic proportions) is minimally dimorphic in relative birth canal centroid size (dimorphism index of 103, the second lowest of all taxa). The combination of large cephalopelvic proportions and high levels of body size dimorphism (rather than *only* high levels of body size dimorphism) produces the highest magnitudes of dimorphism in relative birth canal size. In fact, *Nasalis larvatus* and *Papio anubis* have the least overlap in birth canal size, whereas most other taxa have a higher degree of overlap in birth canal size (see Appendix A). This means that differences in birth canal size may not be observable at small sample sizes in many taxa. In fossils for which we have more than one pelvis, it may be impossible to tell whether there is dimorphism in birth canal size due to small sample size.

Similar to dimorphism in birth canal size, dimorphism in birth canal shape (measured as overlap between males and females in shape space; Table 2.14) is greatest among species with both large cephalopelvic proportions and high body size dimorphism (*Nasalis larvatus*, *Papio anubis*) and lowest in species with small cephalopelvic proportions and low to intermediate body size dimorphism (*Alouatta seniculus*, *Pan troglodytes*). It should be noted that species that give birth to relatively large neonates but are less dimorphic in body size (i.e., *Hylobates lar* and *Macaca mulatta*) tend to have lower levels of dimorphism in birth canal size, more similar to what is seen in taxa with small cephalopelvic proportions (Table 5.9).

In contrast to other taxa, humans have low levels of body size dimorphism but a high magnitude of dimorphism in birth canal size and shape. Humans have the third

highest magnitude of dimorphism in relative birth canal centroid size and relative inlet circumference (Table 2.10) and the highest magnitude of dimorphism in relative circumferences of the midplane and outlet despite exhibiting very low body size dimorphism. Furthermore, the shape of the birth canal is highly dimorphic in humans, and few females (10%) fall within the male shape distribution (Table 2.14). Conversely, in *H. lar* (an ape that also has large cephalopelvic proportions and limited body size dimorphism) there is a low dimorphism index in relative birth canal centroid size and the relative circumferences of the inlet, midplane, and outlet, and there is a larger degree of overlap (33%) between males and females for birth canal form in *H. lar* compared to humans. When compared with *Saimiri sciureus* (a species with even higher cephalopelvic proportions and body size dimorphism levels than humans), *H. sapiens* has a greater magnitude of dimorphism in birth canal centroid size and circumferences of the midplane and outlet (Table 2.10). Further, there is less shape overlap between the sexes in *H. sapiens* than *S. sciureus* (Table 2.14). The degree of pelvic dimorphism in humans cannot be accounted for based only on our large cephalopelvic proportions – otherwise it would be expected that *H. lar* and *S. sciureus* would show a similar magnitude of dimorphism in birth canal size and shape as humans.

Why do humans have birth canals that are more dimorphic than other monomorphic (for body size) taxa with large cephalopelvic proportions? The high degree of dimorphism seen in the human pelvis may be related to the fact that in bipeds there is actually some risk associated with having a wider pelvis, possibly including greater frequency of knee injuries due to a high valgus angle, weakness of pelvic floor muscles and reduced support of pelvic viscera due to a greater distance between the

ischia (Abitbol, 1988), or reduced bipedal locomotor efficiency due to an increased distance between the sacroiliac joints and acetabulae (Washburn, 1950, 1960; Pinkerton, 1973; Zihlman, 1978; Ruff, 1995; Lovejoy, 2005; contra Warrener et al., 2015).

Finally, in anthropoids, females are shown to have larger birth canal centroid sizes than males controlling for body size (all taxa except *A. seniculus* and *G. gorilla*). It is possible that females achieve these bigger birth canals by increasing the size of the entire pelvis, not just the parts of the pelvis which directly participate in the birth canal. Females also have mediolaterally wider inlets (all taxa except *A. seniculus*), midplanes (all taxa except *A. seniculus*, *M. mulatta*, and *P. anubis*), and outlets (all taxa except *A. seniculus*, *P. anubis*, and *G. gorilla*), and it is therefore likely that many aspects of the non-obstetric pelvis, or those parts which do not directly participate in the birth canal (including biacetabular breadth, ischial length and ischial tuberosity breadth, and inferior iliac height) are also dimorphic across primates. The hypothesis that dimorphism in the overall size and mediolateral dimensions of the birth canal correspond to dimorphism in parts of the pelvis which do not directly participate in the birth canal is tested in Chapter 4.

Table 2.1: Numbers of individuals, body mass dimorphism, and cephalopelvic proportions

Species	N		Body mass dimorphism index* (F/M)	Cephalopelvic index [†]
	F	M		
Large Cephalopelvic proportions				
<i>Homo sapiens</i>	73	83	1.14 [§]	1.02 [‡]
<i>Hylobates lar</i>	55	57	1.11	0.94
<i>Macaca mulatta</i>	106	81	1.24	1.00
<i>Nasalis larvatus</i>	16	17	2.08	0.95
<i>Papio anubis</i>	5	16	1.81	0.96
<i>Saimiri sciureus</i>	75	78	1.46	1.21
Small Cephalopelvic Proportions				
<i>Pan troglodytes</i>	77	37	1.30	0.72
<i>Gorilla gorilla</i>	50	56	2.38	0.64
<i>Alouatta seniculus</i>	18	20	1.48	0.81

* Values for body size dimorphism based on body mass values from Smith and Jungers (1997).

[†] Calculated as (neonate head breadth/maternal pelvic inlet transverse diameter). Values for neonate head and maternal inlet from Schultz (1949).

[§] Worldwide average body size dimorphism for humans (Smith and Jungers, 1997).

[‡] The sagittal diameter of the neonate head and transverse breadth of the maternal inlet were used to build this ratio because this is how the human neonate modally engages the inlet.

Sample sizes differ between lumbar and sacral vertebrae because not all specimens included retained both a measurable sacrum and caudal-most lumbar vertebra.

Table 2.2: Birth canal Landmarks

Bilateral Landmarks	Description
(1) SI joint at arcuate line*	Point on ilium where arcuate line intersects the sacroiliac joint
(2) Lateral arcuate line*	Lateral-most point of arcuate on articulated pelvis
(3) Pubis at arcuate line*	Arcuate at right angle to anterior acetabular rim
(4) Ischial spine*	Ischial spine on posterior ischium
(5) Posterior ischial tuberosity*	Posterior-most point on the ischial tuberosity
Midline Landmarks	Description
(6) Inferior pubic symphysis*	Inferior-most point on symphysis at the midline
(7) Superior pubic symphysis*	Superior-most point on symphysis at the midline
(8) Ventral S1body	Ventral-most point on the first vertebral body at midline
(9) Inferior S1 body*	Inferior S1 vertebral body at midline
(10) Inferior sacrum*	Inferior-most point on sacrum at midline

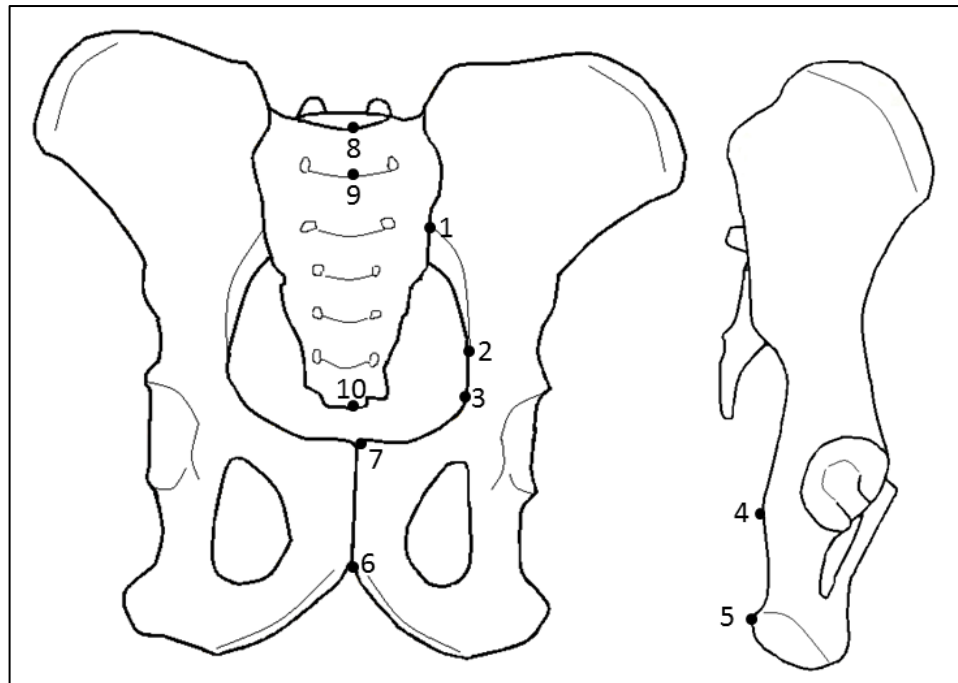


Figure 2.1: Landmarks collected on the birth canal. (1) Sacroiliac joint at arcuate line; (2) Lateral arcuate line (3) Pubis at arcuate line; (4) Ischial spine; (5) posterior ischial tuberosity; (6) inferior pubic symphysis; (7) superior pubic symphysis; (8) ventral S1 body; (9) inferior S1 body; (10) inferior sacrum.

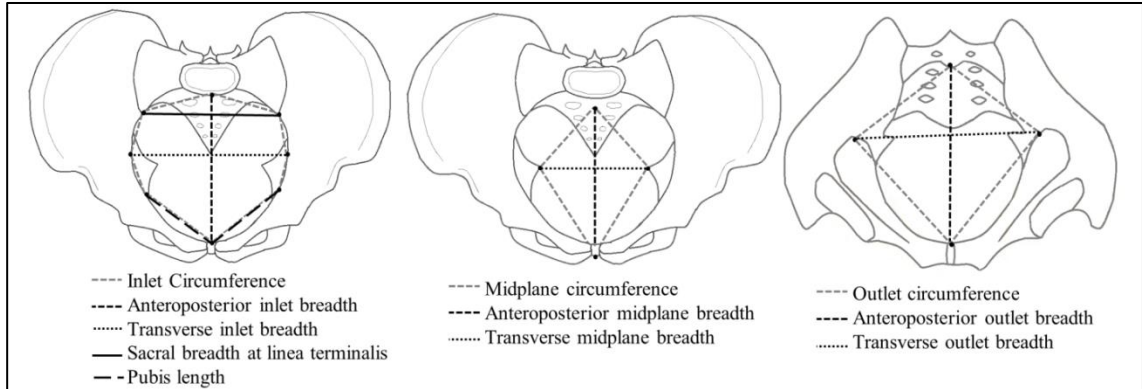


Figure 2.2: Linear distances in the birth canal secondarily calculated from landmark data. For the inlet, circumference is calculated as the sum of the bilateral linear distances between the anterior S1 body and sacroiliac joint at arcuate line, sacroiliac joint at arcuate line and lateral arcuate line and arcuate line at acetabulum, and arcuate line at acetabulum and superior pubic symphysis. Midplane and outlet circumferences are calculated as the bilateral sum of [distance between inferior sacrum and ischial spine + distance between ischial spine and inferior pubic symphysis] and [distance between inferior sacrum and posterior ischial tuberosity + distance between posterior ischial tuberosity and inferior pubic symphysis] respectively, following Tague (1991). Dorsoventral and transverse diameters of the inlet and midplane are calculated following Tague (1991) secondarily from landmark data.

Table 2.3: Birth canal dimension calculations

Dimension	Calculation
Inlet Circumference	Sum of linear distances between landmark 8 and 1; 1 and 2; 2 and 3; 3 and 7 on right and left sides
Midplane Circumference	Sum of linear distances between landmark 9 and 4, and 4 and 6 on right and left sides
Outlet Circumference	Sum of linear distances between landmark 10 and 5, and 5 and 6 on right and left sides
Mediolateral Inlet Diameter	Linear distance between bilateral landmarks 2
Mediolateral Midplane Diameter	Linear distance between bilateral landmarks 4
Mediolateral Outlet Diameter	Linear distance between bilateral landmarks 5
Dorsoventral Inlet Diameter	Linear distance between landmarks 7 and 8
Dorsoventral Midplane Diameter	Linear distance between landmarks 6 and 9
Dorsoventral Outlet Diameter	Linear distance between landmarks 6 and 10

Table 2.4: Reduced major axis regressions of natural logged birth canal size against S1 body breadth

	x S1 Body Breadth			
	r ²	Slope Anthropoids (C.I)	Slope Apes (C.I)	Slope Monkeys (C.I)
Birth Canal Centroid Size	0.88	1.02* (0.99-1.06)	1.02* (0.97-1.05)	0.94* (0.88-1.02)
Inlet Circumference	0.91	1.02* (1.00-1.06)	0.99* (0.95-1.02)	0.95* (0.89-1.01)
Midplane Circumference	0.84	1.05 (1.01-1.09)	1.00* (0.97-1.04)	0.98* (0.90-1.07)
Outlet Circumference	0.88	0.99* (0.95-1.20)	1.08 (1.01-1.11)	0.95* (0.90-1.02)

Regressions were performed on male specimens only.

*Denotes isometry

Table 2.5: Reduced major axis regressions of natural logged birth canal dimensions against logged S1 body breadth *

	x S1 Body Breadth			
	r ²	Slope Anthropoids (C.I)	Slope Apes (C.I)	Slope Monkeys (C.I)
Mediolateral Inlet	0.91	1.09 (1.06-1.12)	1.00* (0.96-1.04)	0.93* (0.87-1.00)
Mediolateral Midplane	0.87	1.08 (1.05-1.12)	0.94 (0.89-0.98)	1.05 (0.97-1.15)
Mediolateral Outlet	0.85	1.16 (1.12-1.21)	1.29 (1.23-1.35)	0.82 (0.77-0.92)
Dorsoventral Inlet	0.81	1.09 (1.04-1.13)	0.98* (0.94-1.02)	1.03* (0.98-1.09)
Dorsoventral Midplane	0.83	1.11 (1.07-1.15)	1.00* (0.96-1.03)	1.18 (1.09-1.26)
Dorsoventral Outlet	0.85	1.07 (1.03-1.11)	0.94 (0.90-0.99)	1.24 (1.14-1.32)

Bold denotes isometry.

*Regressions were performed on male specimens only.

Table 2.6: Student's t-tests for dimorphism in absolute and relative birth canal size

<i>Homo sapiens</i> (Large Cephalopelvic Proportions)				
	F Mean (SD)	M Mean (SD)	p-value	Dimorphism Index [(F/M)*100]
S1 Body Breadth	45.8 (4.1)	50.9 (4.4)	<0.001*	90
Birth Canal Centroid Size	270.1 (13.2)	265.6 (14.0)	0.043	102
/S1 Body Breadth	5.93 (0.47)	5.25 (0.49)	<0.001*	113
Inlet Circumference	383.8 (23.1)	374.7 (24.9)	0.020*	102
/S1Body Breadth	8.43 (0.74)	7.41 (0.77)	<0.001*	114
Midplane Circumference	354.6 (18.8)	337.2 (18.9)	<0.001*	105
/S1Body Breadth	7.79 (0.68)	6.67 (0.64)	<0.001*	117
Outlet Circumference	377.3 (23.6)	351 (22.2)	<0.001*	107
/S1Body Breadth	8.29 (0.77)	6.94 (0.70)	<0.001*	119
<i>Hylobates lar</i> (Large Cephalopelvic Proportions)				
	F Mean (SD)	M Mean (SD)	p-value	Dimorphism Index [(F/M)*100]
S1 Body Breadth	18.9 (1.5)	19.3 (1.7)	0.291	98
Birth Canal Centroid Size	151.4 (6.1)	146.2 (6.4)	<0.001*	104
/S1 Body Breadth	8.02 (0.55)	7.63 (0.53)	<0.001*	105
Inlet Circumference	207.1 (8.92)	194.9 (9.24)	<0.001*	106
/S1Body Breadth	10.98 (0.80)	10.18 (0.77)	<0.001*	108
Midplane Circumference	202.5 (9.9)	196 (10.6)	<0.001*	103
/S1Body Breadth	10.73 (0.78)	10.22 (0.68)	<0.001*	105
Outlet Circumference	200.5 (11.0)	191.7 (10.9)	<0.001*	105
/S1Body Breadth	10.6 (0.81)	10.0 (0.69)	<0.001*	106

Absolute measurements are in millimeters.

*Indicates significance at $\alpha=0.035$.

Table 2.6 (cot'd): Student's t-tests for dimorphism in absolute and relative birth canal size

Macaca mulatta (Large Cephalopelvic Proportions)				
	F Mean (SD)	M Mean (SD)	p-value	Dimorphism Index [(F/M)*100]
S1 Body Breadth	20.9 (1.2)	23.7 (1.6)	<0.001*	88
Birth Canal Centroid Size	142.9 (6.2)	154.3 (7.0)	<0.001*	93
/S1 Body Breadth	6.85 (0.45)	6.53 (0.42)	<0.001*	105
Inlet Circumference	197.0 (11.2)	202.3 (11.5)	<0.001*	97
/S1Body Breadth	9.46 (0.74)	8.56 (0.66)	<0.001*	111
Midplane Circumference	195.0 (12.4)	206.0 (10.3)	<0.001*	95
/S1Body Breadth	9.34 (0.75)	8.72 (0.61)	<0.001*	107
Outlet Circumference	227.0 (13.4)	226.0 (11.1)	0.550	100
/S1Body Breadth	10.9 (0.85)	9.56 (0.63)	<0.001*	114
Nasalis larvatus (Large Cephalopelvic Proportions)				
	F Mean (SD)	M Mean (SD)	p-value	Dimorphism Index [(F/M)*100]
S1 Body Breadth	22.7 (1.0)	29.0 (3.2)	<0.001*	78
Birth Canal Centroid Size	156.1 (10.8)	153.1 (13.5)	0.490	102
/S1 Body Breadth	6.91 (0.64)	5.33 (0.75)	<0.001*	130
Inlet Circumference	200.4 (11.0)	208.7 (13.5)	0.063	96
/S1Body Breadth	8.84 (0.37)	7.25 (0.81)	<0.001*	122
Midplane Circumference	161.8 (14.6)	180.5 (16.3)	0.002*	90
/S1Body Breadth	7.13 (0.50)	6.27 (0.78)	<0.001*	114
Outlet Circumference	201.6 (15.2)	231.3 (12.9)	<0.001*	87
/S1Body Breadth	8.89 (0.54)	8.03 (0.81)	0.001*	111

Absolute measurements are in millimeters.

*Indicates significance at $\alpha=0.035$.

Table 2.6 (cot'd): Student's t-tests for dimorphism in absolute and relative birth canal size

<i>Papio anubis</i> (Large Cephalopelvic Proportions)				
	F Mean (SD)	M Mean (SD)	p-value	Dimorphism Index [(F/M)*100]
S1 Body Breadth	27.1 (2.2)	32.4 (1.9)	<0.001*	84
Birth Canal Centroid Size	199.6 (12.3)	197.4 (12.5)	0.739	101
/S1 Body Breadth	7.41 (0.71)	6.12 (0.54)	<0.001*	121
Inlet Circumference	252.3 (17.9)	269.4 (15.4)	0.105	94
/S1Body Breadth	9.33 (0.34)	8.33 (0.37)	<0.001*	112
Midplane Circumference	243.7 (10.9)	259.4 (13.8)	0.028*	94
/S1Body Breadth	9.03 (0.42)	8.03 (0.41)	0.003*	112
Outlet Circumference	287.5 (15.2)	300.1 (20.7)	0.176	96
/S1Body Breadth	10.65 (0.66)	9.28 (0.57)	0.006*	115
<i>Saimiri sciureus</i> (Large Cephalopelvic Proportions)				
	F Mean (SD)	M Mean (SD)	p-value	Dimorphism Index [(F/M)*100]
S1 Body Breadth	10.0 (0.6)	10.4 (0.7)	<0.001*	96
Birth Canal Centroid Size	65.7 (3.1)	62.3 (3.7)	<0.001*	105
/S1 Body Breadth	6.62 (0.42)	6.01 (0.37)	<0.001*	110
Inlet Circumference	94.9 (4.3)	82.9 (5.8)	<0.001*	114
/S1Body Breadth	9.56 (0.66)	7.99 (0.59)	<0.001*	120
Midplane Circumference	85.6 (6.6)	77.8 (6.9)	<0.001*	110
/S1Body Breadth	8.61 (0.70)	7.49 (0.60)	<0.001*	115
Outlet Circumference	96.3 (5.9)	90.4 (7.0)	<0.001*	107
/S1Body Breadth	9.70 (0.79)	8.72 (0.70)	<0.001*	111

Absolute measurements are in millimeters.

*Indicates significance at $\alpha=0.035$.

Table 2.6 (cot'd): Student's t-tests for dimorphism in absolute and relative birth canal size

Gorilla gorilla (Small Cephalopelvic Proportions)				
	F Mean (SD)	M Mean (SD)	p-value	Dimorphism Index [(F/M)*100]
S1 Body Breadth	41.3 (3.9)	48.8 (5.3)	<0.001*	85
Birth Canal Centroid Size	333.9 (21.5)	381.9 (18.3)	<0.001*	87
/S1 Body Breadth	8.12 (0.64)	7.89 (0.69)	0.072	103
Inlet Circumference	447.9 (33.3)	494.7 (28.1)	<0.001*	91
/S1Body Breadth	10.89 (0.92)	10.21 (0.90)	<0.001*	107
Midplane Circumference	451.7 (31.8)	500.2 (29.7)	<0.001*	90
/S1Body Breadth	10.99 (0.89)	10.32 (0.92)	<0.001*	106
Outlet Circumference	461.1 (38.3)	521.1 (37.0)	<0.001*	88
/S1Body Breadth	11.23 (1.21)	10.79 (1.32)	0.073	104
Pan troglodytes (Small Cephalopelvic Proportions)				
	F Mean (SD)	M Mean (SD)	p-value	Dimorphism Index [(F/M)*100]
S1 Body Breadth	34.5 (3.3)	36.1 (3.0)	0.013*	96
Birth Canal Centroid Size	292.1 (14.6)	287.6 (11.5)	0.103	102
/S1 Body Breadth	8.53 (0.77)	8.01 (0.76)	0.001*	106
Inlet Circumference	380.3 (22.7)	365.4 (17.9)	<0.001*	104
/S1Body Breadth	11.10 (1.06)	10.17 (1.05)	<0.001*	109
Midplane Circumference	399.4 (23.3)	389.7 (17.2)	0.016*	102
/S1Body Breadth	11.65 (0.96)	10.85 (1.05)	<0.001*	107
Outlet Circumference	413.0 (28.2)	402.7 (25.0)	0.066	103
/S1Body Breadth	12.06 (1.20)	11.27 (1.11)	<0.001*	107

Absolute measurements are in millimeters.

*Indicates significance at $\alpha=0.035$.

Table 2.6 (cot'd): Student's t-tests for dimorphism in absolute and relative birth canal size

<i>Alouatta seniculus</i> (Small Cephalopelvic Proportions)				
	F Mean (SD)	M Mean (SD)	p-value	Dimorphism Index [(F/M)*100]
S1 Body Breadth	34.3 (2.9)	36.2 (2.9)	0.044	95
Birth Canal Centroid Size	135.8 (8.0)	144.0 (10.5)	0.015*	94
/S1 Body Breadth	3.97 (0.24)	3.98 (0.18)	0.949	100
Inlet Circumference	191.7 (11.8)	202.6 (14.9)	0.165	95
/S1Body Breadth	5.61 (0.31)	5.60 (0.27)	0.988	100
Midplane Circumference	160.1 (11.7)	164.9 (17.4)	0.325	97
/S1Body Breadth	4.68 (0.27)	4.55 (0.39)	0.265	103
Outlet Circumference	202.7 (13.3)	213.7 (16.6)	0.030*	95
/S1Body Breadth	5.93 (0.40)	5.90 (0.29)	0.818	100

Absolute measurements are in millimeters.

*Indicates significance at $\alpha=0.035$.

Table 2.7: Student's t-tests for dimorphism in absolute and relative birth canal dimensions

	<i>Homo sapiens</i>				<i>Hylobates lar</i>			
	F Mean	M Mean	p-value	Dimorphism Index [(F/M)*100]	F Mean	M Mean	p-value	Dimorphism Index [(F/M)*100]
Transverse Inlet Diameter /S1Body Breadth	125.1	122.6	0.108	102	57.3	53.5	<0.001*	107
	2.75	2.42	<0.001*	114	3.04	2.79	<0.001*	109
Transverse Midplane Diameter /S1Body Breadth	104.9	87.6	<0.001*	120	49.4	45.5	<0.001*	109
	2.31	1.73	<0.001*	134	2.62	2.37	<0.001*	111
Transverse Outlet Diameter /S1Body Breadth	134.7	120.9	<0.001*	111	54.9	50.1	<0.001*	110
	2.96	2.39	<0.001*	124	2.91	2.61	<0.001*	111
Dorsoventral Inlet Diameter /S1Body Breadth	114.3	108.2	<0.001*	106	79.0	75.7	<0.001*	104
	2.51	2.14	<0.001*	117	4.19	3.95	<0.001*	106
Dorsoventral Midplane Diameter /S1Body Breadth	128.6	127.0	0.289	101	83.4	81.2	0.019*	103
	2.82	2.51	<0.001*	112	4.42	4.24	0.004*	104
Dorsoventral Outlet Diameter /S1Body Breadth	121.8	113.7	<0.001*	107	69.8	67.3	0.005*	104
	2.68	2.25	<0.001*	119	3.70	3.51	<0.001*	105
	<i>Macaca mulatta</i>				<i>Nasalis larvatus</i>			
	F Mean	M Mean	p-value	Dimorphism Index [(F/M)*100]	F Mean	M Mean	p-value	Dimorphism Index [(F/M)*100]
Transverse Inlet Diameter /S1Body Breadth	50.2	52.1	0.003*	96	54.7	60.7	<0.001*	90
	2.41	2.20	<0.001*	110	2.41	2.11	<0.001*	114
Transverse Midplane Diameter /S1Body Breadth	43.3	47.2	<0.001*	92	43.8	40.2	0.034*	109
	2.07	2.00	0.045	104	1.93	1.40	<0.001*	138
Transverse Outlet Diameter /S1Body Breadth	51.6	51.5	0.863	100	42.0	37.1	0.008*	113
	2.47	2.18	<0.001*	113	1.85	1.29	<0.001*	143
Dorsoventral Inlet Diameter /S1Body Breadth	67.3	68.9	0.012*	98	70.9	71.1	0.929	100
	3.23	2.91	<0.001*	111	3.12	2.47	<0.001*	126
Dorsoventral Midplane Diameter /S1Body Breadth	77.3	86.5	<0.001*	89	74.8	88.7	<0.001*	84
	3.71	3.66	0.244	101	3.30	3.08	0.039	107
Dorsoventral Outlet Diameter /S1Body Breadth	73.8	79.9	<0.001*	92	67.9	80.2	<0.001*	85
	3.54	3.38	<0.001*	105	2.99	2.79	0.030*	107

*Indicates males and females exhibit statistical differences at $\alpha=0.035$.

Table 2.7 (cot'd): Student's t-tests for dimorphism in absolute and relative birth canal dimensions

	<i>Papio anubis</i>				<i>Saimiri sciureus</i>			
	F Mean	M Mean	p-value	Dimorphism Index [(F/M)*100]	F Mean	M Mean	p-value	Dimorphism Index [(F/M)*100]
Transverse Inlet Diameter	72.0	79.8	0.016*	90	25.1	22.8	<0.001*	110
/S1Body Breadth	2.67	2.46	0.001*	109	2.53	2.20	<0.001*	115
Transverse Midplane Diameter	53.0	52.8	0.935	100	18.5	17.2	<0.001*	108
/S1Body Breadth	1.97	1.63	0.062	121	1.86	1.65	<0.001*	113
Transverse Outlet Diameter	77.7	75.5	0.692	103	25.4	24.6	0.085	103
/S1Body Breadth	2.89	2.33	0.063	124	2.56	2.37	<0.001*	108
Dorsoventral Inlet Diameter	85.3	83.9	0.697	102	29.8	25.9	<0.001*	115
/S1Body Breadth	3.15	2.60	<0.001*	121	3.00	2.50	<0.001*	120
Dorsoventral Midplane Diameter	98.7	111.6	<0.001*	88	30.9	27.7	<0.001*	112
/S1Body Breadth	3.66	3.45	0.099	106	3.11	2.67	<0.001*	116
Dorsoventral Outlet Diameter	93.0	105.1	<0.001*	88	27.7	24.3	<0.001*	114
/S1Body Breadth	3.45	3.24	0.130	106	2.79	2.35	<0.001*	119
	<i>Gorilla gorilla</i>				<i>Pan troglodytes</i>			
	F Mean	M Mean	p-value	Dimorphism Index [(F/M)*100]	F Mean	M Mean	p-value	Dimorphism Index [(F/M)*100]
Transverse Inlet Diameter	123.9	137.4	<0.001*	90	106.0	97.1	<0.001*	109
/S1Body Breadth	3.02	2.84	0.002*	106	3.09	2.70	<0.001*	114
Transverse Midplane Diameter	102.3	107.1	0.024*	96	90.2	81.5	<0.001*	111
/S1Body Breadth	2.49	2.22	<0.001*	112	2.63	2.27	<0.001*	116
Transverse Outlet Diameter	141.7	164.2	<0.001*	86	129.6	123.7	0.021*	105
/S1Body Breadth	3.45	3.40	0.540	101	3.79	3.44	<0.001*	110
Dorsoventral Inlet Diameter	172.2	190.0	<0.001*	91	144.4	142.6	0.376	101
/S1Body Breadth	4.19	3.92	0.002*	107	4.22	3.97	0.015*	106
Dorsoventral Midplane Diameter	183.4	206.9	<0.001*	89	156.8	156.2	0.770	100
/S1Body Breadth	4.46	4.27	0.014*	104	4.58	4.35	0.020*	105
Dorsoventral Outlet Diameter	150.1	160.8	<0.001*	93	129.9	126.3	0.117	103
/S1Body Breadth	3.65	3.33	<0.001*	110	3.78	3.51	<0.001*	108

*Indicates males and females exhibit statistical differences at $\alpha=0.035$.

Table 2.7 (cont'd): Student's t-tests for dimorphism in absolute and relative birth canal dimensions

	<i>Alouatta seniculus</i>			
	F Mean	M Mean	p-value	Dimorphism Index [(F/M)*100]
Transverse Inlet Diameter	48.9	51.2	0.175	96
/S1Body Breadth	2.88	2.85	0.742	101
Transverse Midplane Diameter	42.0	42.7	0.674	98
/S1Body Breadth	2.48	2.37	0.210	105
Transverse Outlet Diameter	54.3	58.1	0.084	93
/S1Body Breadth	3.20	3.22	0.855	99
Dorsoventral Inlet Diameter	70.1	73.5	0.045	95
/S1Body Breadth	4.14	4.10	0.777	101
Dorsoventral Midplane Diameter	71.7	74.9	0.882	96
/S1Body Breadth	4.23	4.17	0.584	101
Dorsoventral Outlet Diameter	66.4	68.5	0.254	97
/S1Body Breadth	3.91	3.82	0.314	102

*Indicates males and females exhibit statistical differences at $\alpha=0.035$.

Table 2.8: Student's t-test results for differences between males and females in residuals from Reduced Major Axis regressions of pelvic size variables with S1 body breadth

<i>Birth Canal Centroid Size</i>			
Large Cephalopelvic Proportions	<i>Mean Female Residual</i>	<i>Mean Male Residual</i>	<i>p-value (larger sex)</i>
<i>Homo sapiens</i>	-0.15	-0.26	<0.001* (f)
<i>Hylobates lar</i>	2.15	-0.03	<0.001* (f)
<i>Macaca mulatta</i>	0.16	0.12	<0.001* (f)
<i>Nasalis larvatus</i>	0.17	-7.34	<0.001* (f)
<i>Papio anubis</i>	0.25	0.08	<0.001* (f)
<i>Saimiri sciureus</i>	0.09	-0.01	<0.001* (f)
Small Cephalopelvic Proportions			
<i>Gorilla gorilla</i>	0.15	0.14	0.703
<i>Pan troglodytes</i>	0.17	0.11	<0.001* (f)
<i>Alouatta seniculus</i>	-0.35	-0.35	0.756
<i>Inlet Circumference</i>			
Large Cephalopelvic Proportions	<i>Mean Female Residual</i>	<i>Mean Male Residual</i>	<i>p-value (larger sex)</i>
<i>Homo sapiens</i>	-0.03	-0.14	<0.001* (f)
<i>Hylobates lar</i>	0.09	0.02	<0.001* (f)
<i>Macaca mulatta</i>	0.19	0.09	<0.001* (f)
<i>Nasalis larvatus</i>	0.12	-0.07	<0.001* (f)
<i>Papio anubis</i>	0.18	0.08	<0.001* (f)
<i>Saimiri sciureus</i>	0.15	-0.02	<0.001* (f)
Small Cephalopelvic Proportions			
<i>Gorilla gorilla</i>	0.21	0.17	0.009* (f)
<i>Pan troglodytes</i>	0.19	0.12	<0.001* (f)
<i>Alouatta seniculus</i>	-0.31	-0.31	0.911
<i>Midplane Circumference</i>			
Large Cephalopelvic Proportions	<i>Mean Female Residual</i>	<i>Mean Male Residual</i>	<i>p-value (larger sex)</i>
<i>Homo sapiens</i>	-0.1	-0.24	<0.001* (f)
<i>Hylobates lar</i>	0.07	0.02	<0.001* (f)
<i>Macaca mulatta</i>	0.22	0.16	<0.001* (f)
<i>Nasalis larvatus</i>	-0.05	-0.17	0.001* (f)
<i>Papio anubis</i>	0.2	0.08	<0.001* (f)
<i>Saimiri sciureus</i>	0.13	-0.01	<0.001* (f)
Small Cephalopelvic Proportions			
<i>Gorilla gorilla</i>	0.22	0.19	0.015* (f)
<i>Pan troglodytes</i>	0.25	0.19	<0.001* (f)
<i>Alouatta seniculus</i>	-0.46	-0.48	0.261
<i>Outlet Circumference</i>			
Large Cephalopelvic Proportions	<i>Mean Female Residual</i>	<i>Mean Male Residual</i>	<i>p-value (larger sex)</i>
<i>Homo sapiens</i>	-0.06	-0.22	<0.001* (f)
<i>Hylobates lar</i>	0.09	0.04	<0.001* (f)
<i>Macaca mulatta</i>	0.25	0.12	<0.001* (f)
<i>Nasalis larvatus</i>	0.05	-0.04	0.003* (f)
<i>Papio anubis</i>	0.24	0.11	<0.001* (f)
<i>Saimiri sciureus</i>	0.09	-0.01	<0.001* (f)
Small Cephalopelvic Proportions			
<i>Gorilla gorilla</i>	0.23	0.21	0.261
<i>Pan troglodytes</i>	0.28	0.22	<0.001* (f)
<i>Alouatta seniculus</i>	-0.33	-0.34	0.969

Table 2.8 (cot'd): Student's t-test results for differences between males and females in residuals from Reduced Major Axis regressions of pelvic size variables with SI body breadth

<i>Transverse Inlet Diameter</i>			
Large Cephalopelvic Proportions	<i>Mean Female Residual</i>	<i>Mean Male Residual</i>	<i>p-value (larger sex)</i>
<i>Homo sapiens</i>	0.03	-0.08	<0.001* (f)
<i>Hylobates lar</i>	0.07	-0.01	<0.001* (f)
<i>Macaca mulatta</i>	0.16	0.08	<0.001* (f)
<i>Nasalis larvatus</i>	0.17	0.05	<0.001* (f)
<i>Papio anubis</i>	0.28	0.22	0.031* (f)
<i>Saimiri sciureus</i>	0.16	0.02	<0.001* (f)
Small Cephalopelvic Proportions			
<i>Gorilla gorilla</i>	0.11	0.07	0.007* (f)
<i>Pan troglodytes</i>	0.13	0.01	<0.001* (f)
<i>Alouatta seniculus</i>	-0.33	-0.34	0.758
<i>Transverse Midplane Diameter</i>			
Large Cephalopelvic Proportions	<i>Mean Female Residual</i>	<i>Mean Male Residual</i>	<i>p-value (larger sex)</i>
<i>Homo sapiens</i>	0.12	-0.08	<0.001* (f)
<i>Hylobates lar</i>	0.11	0.05	0.015* (f)
<i>Macaca mulatta</i>	0.21	0.17	0.026* (f)
<i>Nasalis larvatus</i>	0.14	-0.21	<0.001* (f)
<i>Papio anubis</i>	0.15	-0.05	0.009* (f)
<i>Saimiri sciureus</i>	0.14	0.02	<0.001* (f)
Small Cephalopelvic Proportions			
<i>Gorilla gorilla</i>	0.12	0.19	0.026* (m)
<i>Pan troglodytes</i>	0.26	0.14	0.039
<i>Alouatta seniculus</i>	-0.33	-0.38	0.078
<i>Transverse Outlet Diameter</i>			
Large Cephalopelvic Proportions	<i>Mean Female Residual</i>	<i>Mean Male Residual</i>	<i>p-value (larger sex)</i>
<i>Homo sapiens</i>	0.05	-0.18	<0.001* (f)
<i>Hylobates lar</i>	0.13	0.02	<0.001* (f)
<i>Macaca mulatta</i>	0.18	0.07	<0.001* (f)
<i>Nasalis larvatus</i>	-0.09	-0.42	<0.001* (f)
<i>Papio anubis</i>	0.38	0.19	0.025* (f)
<i>Saimiri sciureus</i>	0.1	0.03	<0.001* (f)
Small Cephalopelvic Proportions			
<i>Gorilla gorilla</i>	0.21	0.18	0.193
<i>Pan troglodytes</i>	0.35	0.22	<0.001* (f)
<i>Alouatta seniculus</i>	-0.18	-0.16	0.564
<i>Dorsoventral Inlet Diameter</i>			
Large Cephalopelvic Proportions	<i>Mean Female Residual</i>	<i>Mean Male Residual</i>	<i>p-value (larger sex)</i>
<i>Homo sapiens</i>	-0.2	-0.34	<0.001* (f)
<i>Hylobates lar</i>	0.16	0.1	<0.001* (f)
<i>Macaca mulatta</i>	0.22	0.11	<0.001* (f)
<i>Nasalis larvatus</i>	0.19	-0.06	<0.001* (f)
<i>Papio anubis</i>	0.19	-0.01	<0.001* (f)
<i>Saimiri sciureus</i>	0.17	-0.02	<0.001* (f)
Small Cephalopelvic Proportions			
<i>Gorilla gorilla</i>	0.3	0.26	0.048
<i>Pan troglodytes</i>	0.27	0.21	0.015* (f)
<i>Alouatta seniculus</i>	-0.25	-0.26	0.687

Table 2.8 (cot'd): Student's t-test results for differences between males and females in residuals from Reduced Major Axis regressions of pelvic size variables with SI body breadth

Dorsoventral Midplane Diameter			
Large Cephalopelvic Proportions	Mean Female Residual	Mean Male Residual	p-value (larger sex)
<i>Homo sapiens</i>	-0.19	-0.28	<0.001* (f)
<i>Hylobates lar</i>	0.10	0.06	0.002* (f)
<i>Macaca mulatta</i>	0.20	0.17	0.008* (f)
<i>Nasalis larvatus</i>	0.07	-0.04	0.004* (f)
<i>Papio anubis</i>	0.15	0.06	0.009* (f)
<i>Saimiri sciureus</i>	0.15	-0.01	<0.001* (f)
Small Cephalopelvic Proportions			
<i>Gorilla gorilla</i>	0.25	0.24	0.349
<i>Pan troglodytes</i>	0.24	0.20	0.018* (f)
<i>Alouatta seniculus</i>	-0.45	-0.48	0.392
Dorsoventral Outlet Diameter			
Large Cephalopelvic Proportions	Mean Female Residual	Mean Male Residual	p-value (larger sex)
<i>Homo sapiens</i>	-0.05	-0.20	<0.001* (f)
<i>Hylobates lar</i>	0.09	0.04	<0.001* (f)
<i>Macaca mulatta</i>	0.20	0.16	0.007* (f)
<i>Nasalis larvatus</i>	-0.03	-0.02	0.875
<i>Papio anubis</i>	0.08	0.06	0.645
<i>Saimiri sciureus</i>	0.06	0.05	0.763
Small Cephalopelvic Proportions			
<i>Gorilla gorilla</i>	0.24	0.18	0.009* (f)
<i>Pan troglodytes</i>	0.24	0.18	0.002* (f)
<i>Alouatta seniculus</i>	-0.48	-0.52	0.089

Table 2.9: Dimorphism Index Ranks

Species	Dimorphism Index for relative birth canal centroid size*	Cephalopelvic Proportions
<i>Nasalis larvatus</i>	130	large
<i>Papio anubis</i>	121	large
<i>Homo sapiens</i>	117	large
<i>Saimiri sciureus</i>	110	large
<i>Pan troglodytes</i>	106	small
<i>Hylobates lar</i>	105	large
<i>Macaca mulatta</i>	105	large
<i>Gorilla gorilla</i>	103	small
<i>Alouatta seniculus</i>	100	small

Species	dimorphism index for relative inlet circumference*	Cephalopelvic Proportions
<i>Nasalis larvatus</i>	122	large
<i>Saimiri sciureus</i>	120	large
<i>Homo sapiens</i>	114	large
<i>Papio anubis</i>	112	large
<i>Macaca mulatta</i>	111	large
<i>Pan troglodytes</i>	109	small
<i>Hylobates lar</i>	108	large
<i>Gorilla gorilla</i>	107	small
<i>Alouatta seniculus</i>	100	small

Species	dimorphism index for relative midplane circumference*	Cephalopelvic Proportions
<i>Homo sapiens</i>	117	large
<i>Saimiri sciureus</i>	115	large
<i>Nasalis larvatus</i>	114	large
<i>Papio anubis</i>	112	large
<i>Macaca mulatta</i>	107	large
<i>Pan troglodytes</i>	107	small
<i>Gorilla gorilla</i>	106	small
<i>Hylobates lar</i>	105	large
<i>Alouatta seniculus</i>	103	small

Species	dimorphism index for relative outlet circumference*	Cephalopelvic Proportions
<i>Homo sapiens</i>	119	large
<i>Papio anubis</i>	115	large
<i>Macaca mulatta</i>	114	large
<i>Nasalis larvatus</i>	111	large
<i>Saimiri sciureus</i>	111	large
<i>Pan troglodytes</i>	107	small
<i>Hylobates lar</i>	106	large
<i>Gorilla gorilla</i>	104	small
<i>Alouatta seniculus</i>	100	small

*Calculated as $\{[(\text{female mean})/(\text{male mean})]*100\}$.

Table 2.9 (cot'd): Dimorphism Index Ranks

Species	dimorphism index for relative mediolateral diameter of the inlet*	Cephalopelvic Proportions
<i>Saimiri sciureus</i>	115	large
<i>Homo sapiens</i>	114	large
<i>Nasalis larvatus</i>	114	large
<i>Pan troglodytes</i>	114	small
<i>Macaca mulatta</i>	110	large
<i>Hylobates lar</i>	109	large
<i>Papio anubis</i>	109	large
<i>Gorilla gorilla</i>	106	small
<i>Alouatta seniculus</i>	101	small

Species	dimorphism index for relative mediolateral diameter of the midplane*	Cephalopelvic Proportions
<i>Nasalis larvatus</i>	138	large
<i>Homo sapiens</i>	134	large
<i>Papio anubis</i>	121	large
<i>Pan troglodytes</i>	116	small
<i>Saimiri sciureus</i>	113	large
<i>Gorilla gorilla</i>	112	small
<i>Hylobates lar</i>	111	large
<i>Alouatta seniculus</i>	105	small
<i>Macaca mulatta</i>	104	large

Species	dimorphism index for relative mediolateral diameter of the outlet*	Cephalopelvic Proportions
<i>Nasalis larvatus</i>	143	large
<i>Homo sapiens</i>	124	large
<i>Papio anubis</i>	124	large
<i>Macaca mulatta</i>	113	large
<i>Hylobates lar</i>	111	large
<i>Pan troglodytes</i>	110	small
<i>Saimiri sciureus</i>	108	large
<i>Gorilla gorilla</i>	101	small
<i>Alouatta seniculus</i>	99	small

Species	dimorphism index for relative dorsoventral diameter of the inlet*	Cephalopelvic Proportions
<i>Nasalis larvatus</i>	126	large
<i>Papio anubis</i>	121	large
<i>Saimiri sciureus</i>	120	large
<i>Homo sapiens</i>	117	large
<i>Macaca mulatta</i>	111	large
<i>Gorilla gorilla</i>	107	small
<i>Hylobates lar</i>	106	large
<i>Pan troglodytes</i>	106	small
<i>Alouatta seniculus</i>	101	small

*Calculated as $\{[(\text{female mean})/(\text{male mean})]*100\}$.

Table 2.9 (cot'd): Dimorphism Index Ranks

Species	dimorphism index for relative dorsoventral diameter of the midplane*	Cephalopelvic Proportions
<i>Saimiri sciureus</i>	116	large
<i>Homo sapiens</i>	112	large
<i>Nasalis larvatus</i>	107	large
<i>Papio anubis</i>	106	large
<i>Pan troglodytes</i>	105	small
<i>Gorilla gorilla</i>	104	small
<i>Hylobates lar</i>	104	large
<i>Alouatta seniculus</i>	101	small
<i>Macaca mulatta</i>	101	large

Species	dimorphism index for relative dorsoventral diameter of the outlet*	Cephalopelvic Proportions
<i>Saimiri sciureus</i>	119	large
<i>Homo sapiens</i>	119	large
<i>Gorilla gorilla</i>	110	small
<i>Pan troglodytes</i>	108	small
<i>Nasalis larvatus</i>	107	large
<i>Papio anubis</i>	106	large
<i>Hylobates lar</i>	105	large
<i>Macaca mulatta</i>	105	large
<i>Alouatta seniculus</i>	102	small

*Calculated as $\{[(\text{female mean})/(\text{male mean})]*100\}$.

Table 2.10: Results for Discriminant function analyses of the influence of sex on intraspecies principal components scores for birth canal shape

Large Cephalopelvic Proportions	Procrustes Distance	Mahalanobis Distance	p-value
<i>Homo sapiens</i>	0.0919	4.896	<0.0001*
<i>Hylobates lar</i>	0.0402	3.156	<0.0001*
<i>Macaca mulatta</i>	0.1086	5.378	<0.0001*
<i>Nasalis larvatus</i>	0.1057	19.592	0.4145
<i>Papio anubis</i>	0.0847	5.588	0.9023
<i>Saimiri sciureus</i>	0.0842	5.561	<0.0001*

Small Cephalopelvic Proportions	Procrustes Distance	Mahalanobis Distance	p-value
<i>Alouatta seniculus</i>	0.0316	4.470	0.9871
<i>Gorilla gorilla</i>	0.0641	4.923	<0.0001*
<i>Pan troglodytes</i>	0.0435	2.578	<0.0001*

*Indicates males and females exhibit statistical differences in overall birth canal form at $\alpha=0.035$.

Table 2.11: Student's t-tests for dimorphism in birth canal shape along each Principal Component‡

Large Proportions	p-value for PC1	Variation explained	p-value for PC2	Variation explained	p-value for PC3	Variation explained
<i>Homo sapiens</i>	<0.001*	30%	0.029*	14%	0.227	11%
<i>Hylobates lar</i>	<0.001*	25%	<0.001*	12%	0.049	10%
<i>Macaca mulatta</i>	<0.001*	38%	0.255	12%	0.074	11%
<i>Nasalis larvatus</i>	<0.001*	36%	0.005*	24%	0.328	11%
<i>Papio anubis</i>	0.002*	32%	0.191	19%	0.097	12%
<i>Saimiri sciureus</i>	0.001*	28%	<0.001*	19%	<0.001*	13%
Small Proportions	p-value for PC1	Variation explained	p-value for PC2	Variation explained	p-value for PC3	Variation explained
<i>Alouatta seniculus</i>	0.818	34%	0.026*	11%	0.535	10%
<i>Gorilla gorilla</i>	<0.001*	23%	<0.001*	18%	<0.001*	11%
<i>Pan troglodytes</i>	<0.001*	22%	0.036	14%	0.136	11%

‡Birth canal shape defined as individuals' Principal Components scores of PCAs of intraspecies birth canal landmark data.

*Indicates males and females exhibit statistical differences in principal components scores (significant differences quantified using Student's t-tests) at $\alpha=0.035$.

Table 2.12: Euclidean Distance Matrix Analyses FORM test of male and female differences in overall birth canal shape within species

	birth canal form (unscaled)	birth canal form (scaled to geometric mean)
Large Cephalopelvic Proportions	p-value	p-value
<i>Homo sapiens</i>	<0.001*	<0.001*
<i>Hylobates lar</i>	0.007*	0.003*
<i>Macaca mulatta</i>	<0.001*	<0.001*
<i>Nasalis larvatus</i>	<0.001*	<0.001*
<i>Papio anubis</i>	0.009*	0.014*
<i>Saimiri sciureus</i>	<0.001*	<0.001*
Small Cephalopelvic Proportions	p-value	p-value
<i>Alouatta seniculus</i>	0.337	0.332
<i>Gorilla gorilla</i>	<0.001*	<0.001*
<i>Pan troglodytes</i>	0.006*	0.007*

*Indicates males and females exhibit statistical differences in overall birth canal form at $\alpha=0.035$.

Table 2.13: Shape of the pelvic planes in female and male anthropoids*

	Inlet shape		Midplane Shape		Outlet Shape	
	F	M	F	M	F	M
Large Proportions						
<i>Homo sapiens</i>	1.10	1.14	0.82	0.69	1.11	1.07
<i>Hylobates lar</i>	0.73	0.71	0.59	0.56	0.79	0.75
<i>Macaca mulatta</i>	0.75	0.76	0.56	0.55	0.70	0.65
<i>Nasalis larvatus</i>	0.77	0.86	0.59	0.45	0.62	0.46
<i>Papio anubis</i>	0.85	0.95	0.54	0.47	0.84	0.72
<i>Saimiri sciureus</i>	0.85	0.88	0.60	0.62	0.92	1.02
Small Proportions						
<i>Gorilla gorilla</i>	0.72	0.73	0.56	0.52	0.95	1.03
<i>Pan troglodytes</i>	0.74	0.69	0.58	0.53	1.00	0.99
<i>Alouatta seniculus</i>	0.70	0.70	0.59	0.57	0.82	0.85

*Measured as $\{(\text{mediolateral dimension of pelvic plane})/(\text{anteroposterior dimension of pelvic plane})\}$.

Table 2.14: Shape overlap between sexes*

Large Proportions	Percent of Females in Male Shape Space
<i>Homo sapiens</i>	10%
<i>Hylobates lar</i>	33%
<i>Macaca mulatta</i>	10%
<i>Nasalis larvatus</i>	0%
<i>Papio anubis</i>	0%
<i>Saimiri sciureus</i>	39%
Small Proportions	Percent of Females in Male Shape Space
<i>Gorilla gorilla</i>	38%
<i>Pan troglodytes</i>	79%
<i>Alouatta seniculus</i>	67%

*Calculated as the percentage of females falling within the male distribution along PC1 and PC2 in an interspecies Principal Components Analysis.

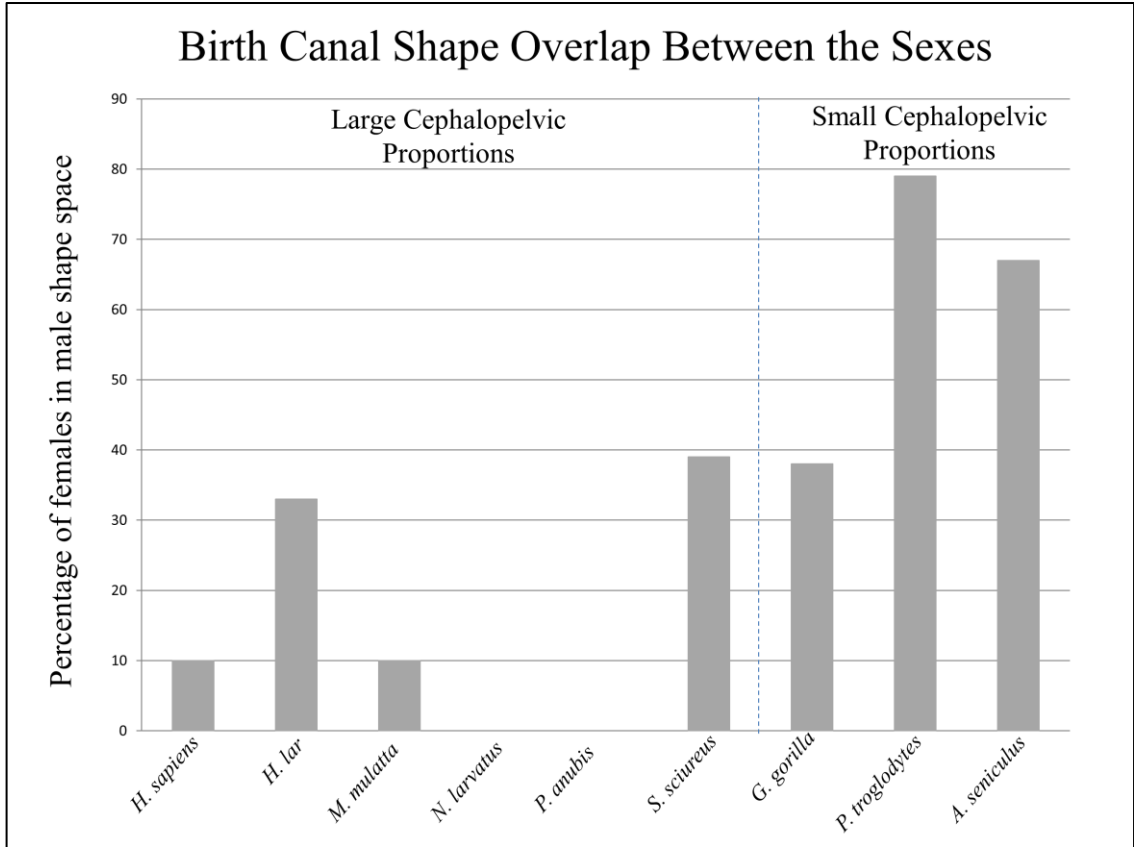


Figure 2.3: Birth canal shape overlap between the sexes, calculated as the percentage of females falling within the male distribution along PC1 and PC2 in an interspecies Principal Components Analysis.

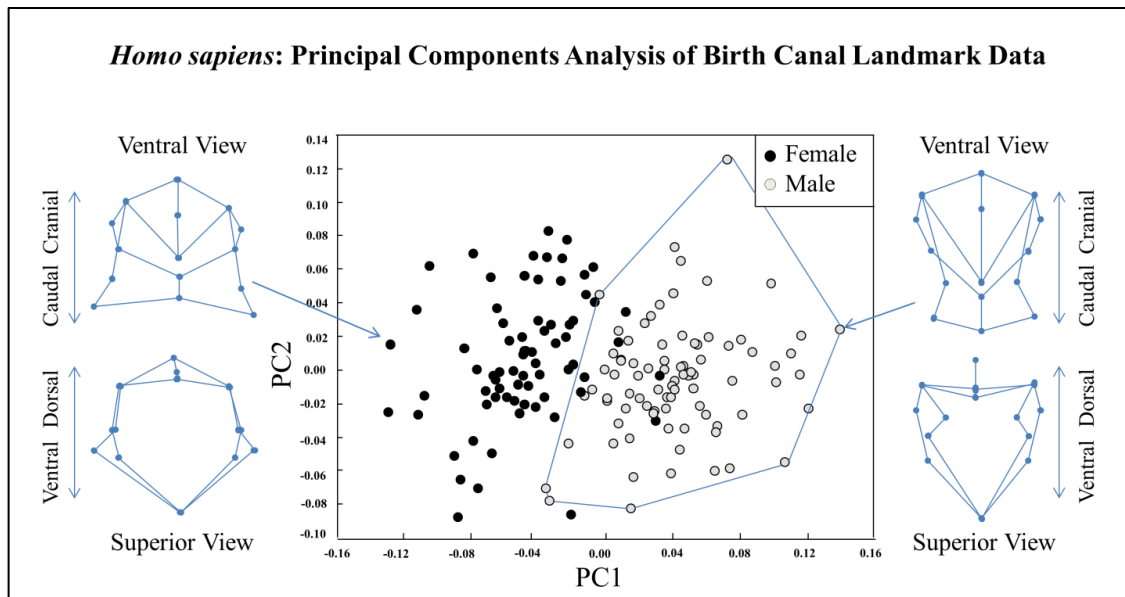


Figure 2.4a: Principal components analysis of birth canal shape in *Homo sapiens*. Note the diverging distributions of males and females along Axis 1.

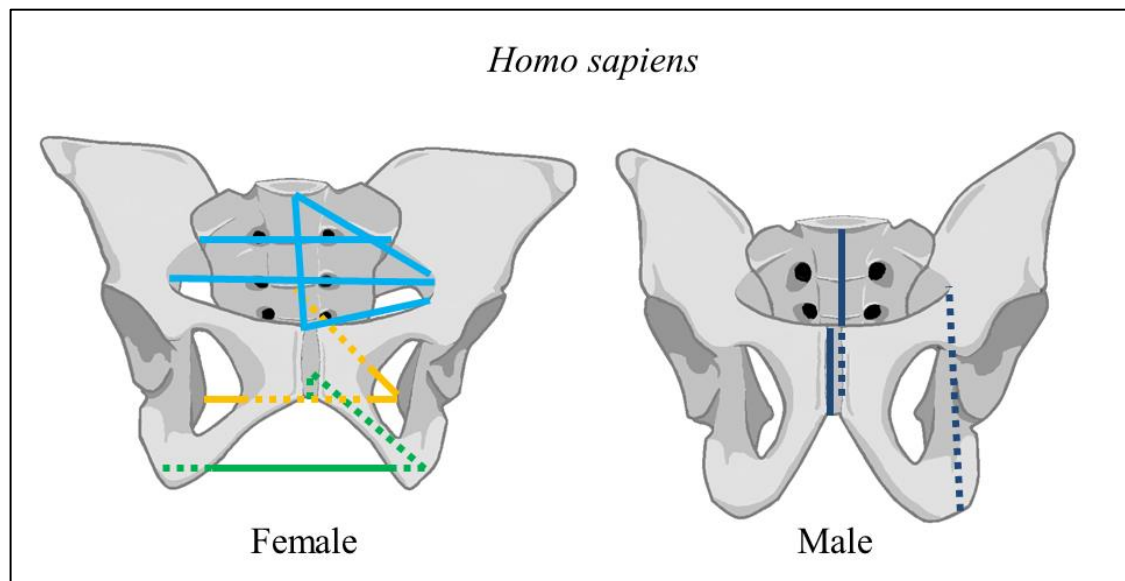


Figure 2.4b: Results of FORM procedure to obtain dimorphic linear distances in the pelvis of *Homo sapiens* when pelvis are scaled to each individual's geometric mean (body size proxy). Light blue represents linear distances which are greater in females than males in the inlet, yellow represents distances which are greater in females than males in the midplane, and green represents linear distances which are greater in females than males in the outlet. Dark blue represents linear distances which are relatively greater in males compared to females. Only non-overlapping distances are included.

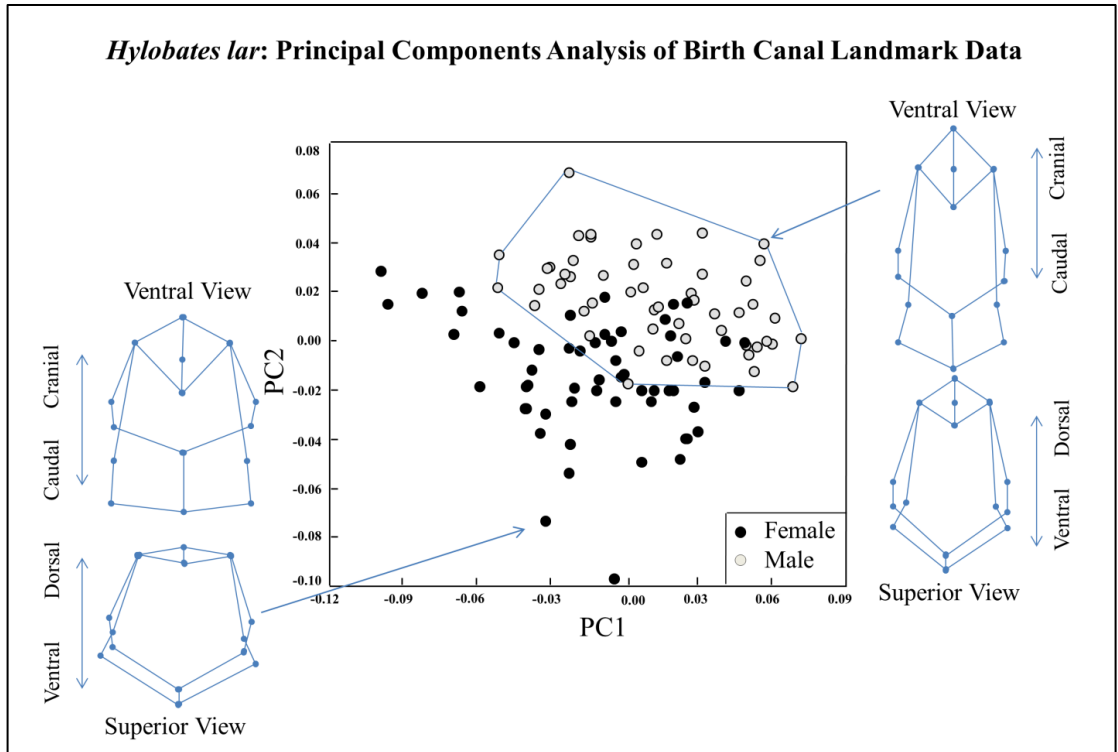


Figure 2.5a: Principal components analysis of birth canal shape in *Hylobates lar*. Note the diverging distributions of males and females along Axis 1 and Axis 2.

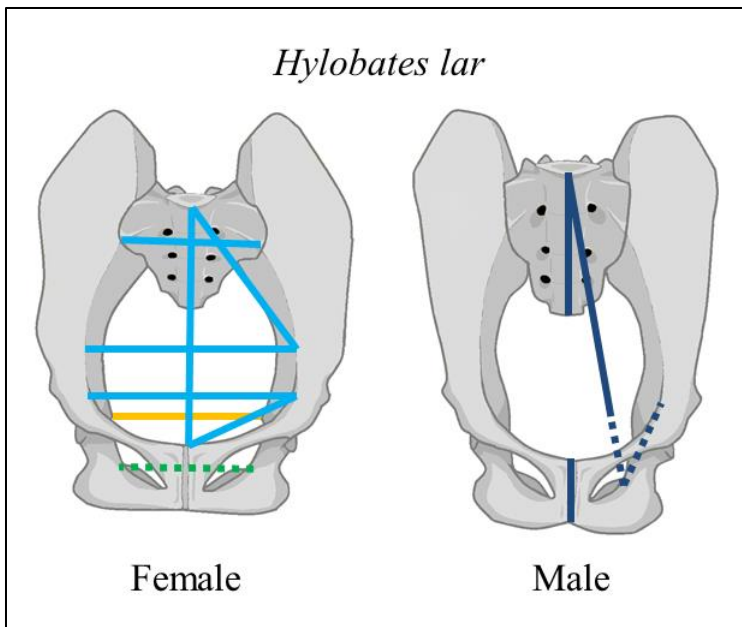


Figure 2.5b: Results of FORM procedure to obtain dimorphic linear distances in the pelvis of *Hylobates lar* when pelvis are scaled to each individual's geometric mean. Light blue represents distances which are greater in females than males in the inlet, yellow represents distances which are greater in females in the midplane, and green represents distances which are greater in females in the outlet. Dark blue represents linear distances which are relatively greater in males. Only non-overlapping distances are included.

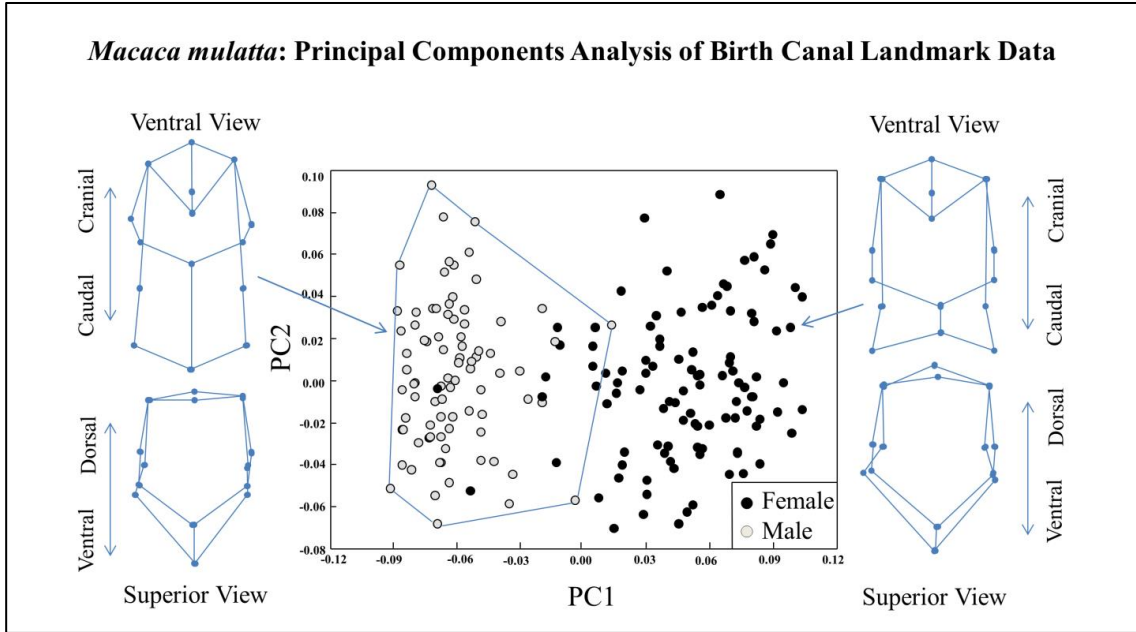


Figure 2.6a: Principal components analysis of birth canal shape in *Macaca mulatta*. Note the diverging distributions of males and females along Axis 1.

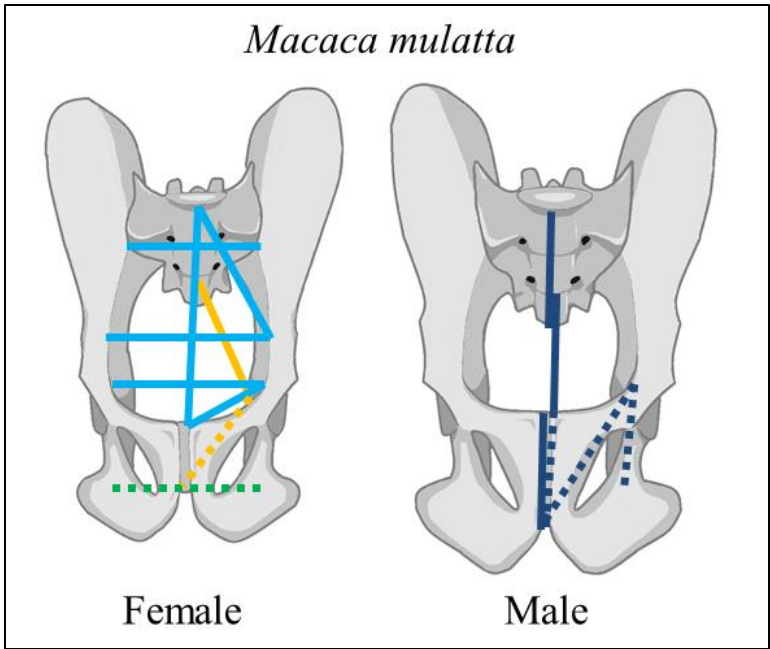


Figure 2.6b: Graphical representation of results of Euclidean Distance Matrix Analysis's FORM procedure to obtain dimorphic linear distances in the pelvis of *Macaca mulatta* when pelves are scaled to each individual's geometric mean. Light blue represents distances which are greater in females than males in the inlet, yellow represents distances which are greater in females in the midplane, and green represents distances which are greater in females in the outlet. Dark blue represents linear distances which are relatively greater in males. Only non-overlapping distances are included.

greater in females in the outlet. Dark blue represents linear distances which are relatively greater in males. Only non-overlapping distances are included.

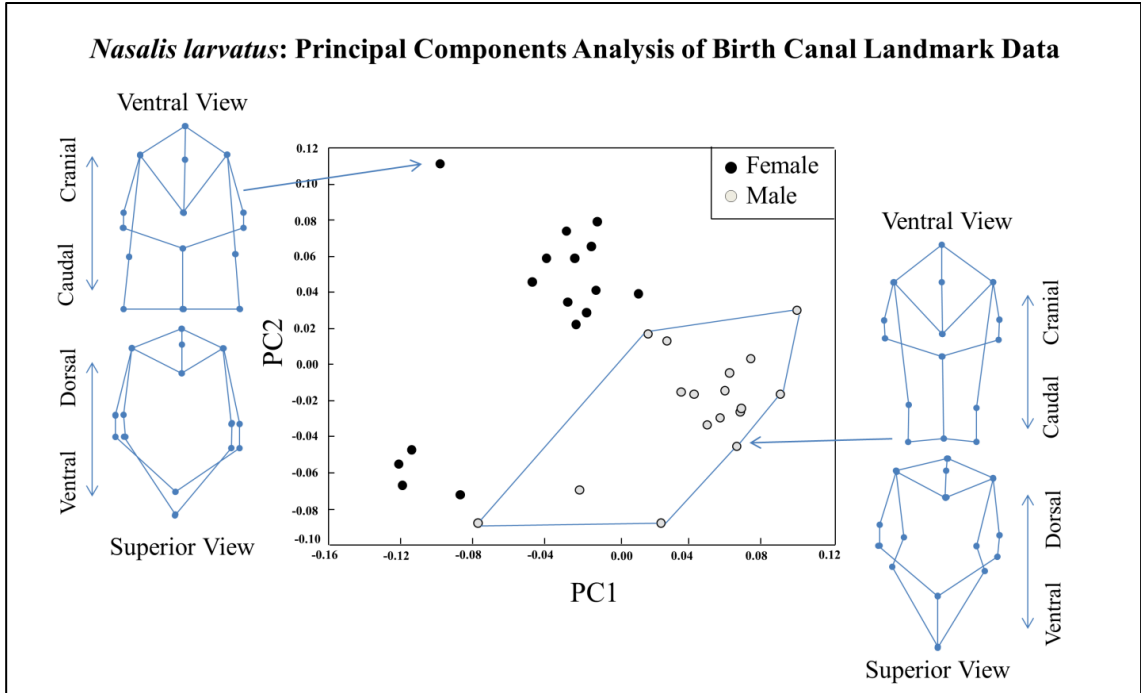


Figure 2.7a: Principal components analysis of birth canal shape in *Nasalis larvatus*. Note the diverging distributions of males and females along Axis 1 and Axis 2.

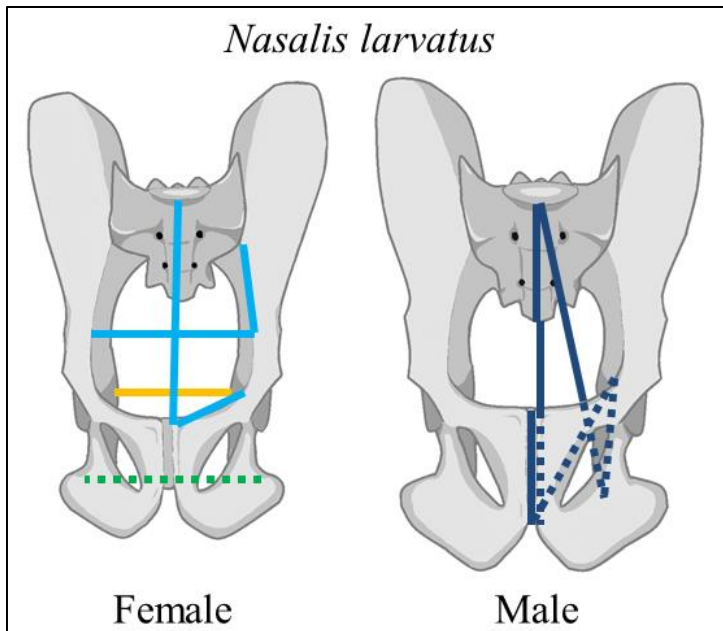


Figure 2.7b: Results of FORM procedure to obtain dimorphic linear distances in the pelvis of *Nasalis larvatus* when pelvis are scaled to each individual's geometric mean. Light blue represents distances which are greater in females than males in the inlet, yellow represents distances which are greater in females in the midplane, and green represents distances which are greater in females in the outlet. Dark blue represents linear

distances which are relatively greater in males. Only non-overlapping distances are included.

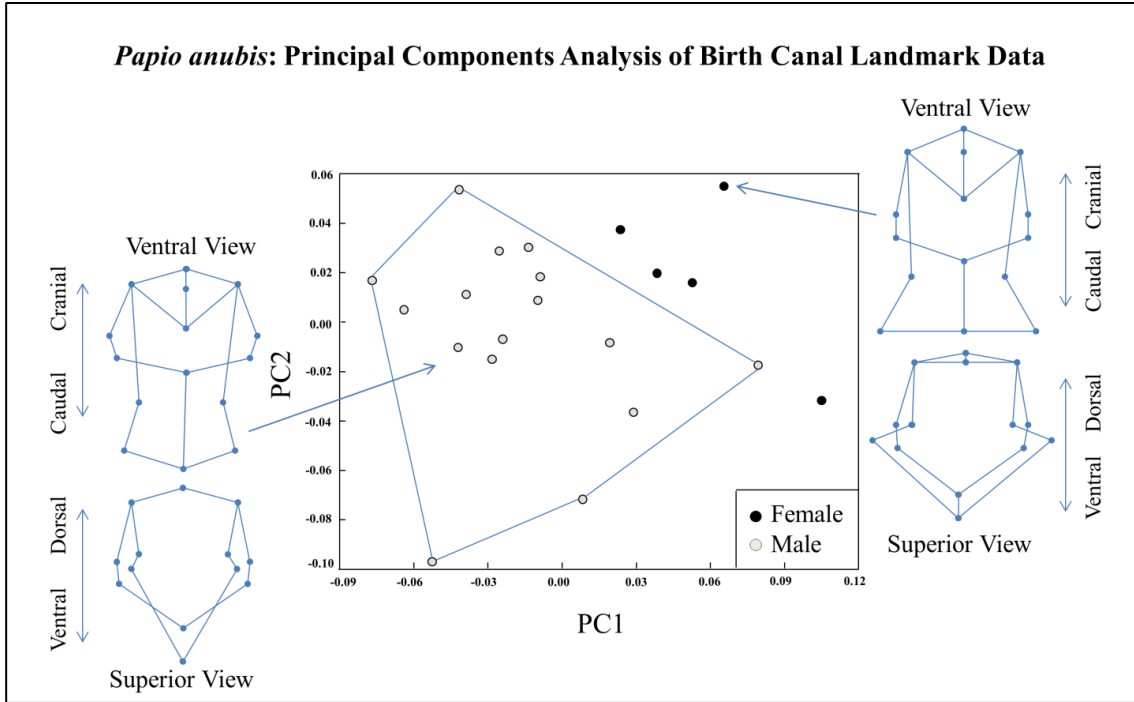


Figure 2.8a: Principal components analysis of birth canal shape in *Papio anubis*. Note the diverging distributions of males and females along Axis 1.

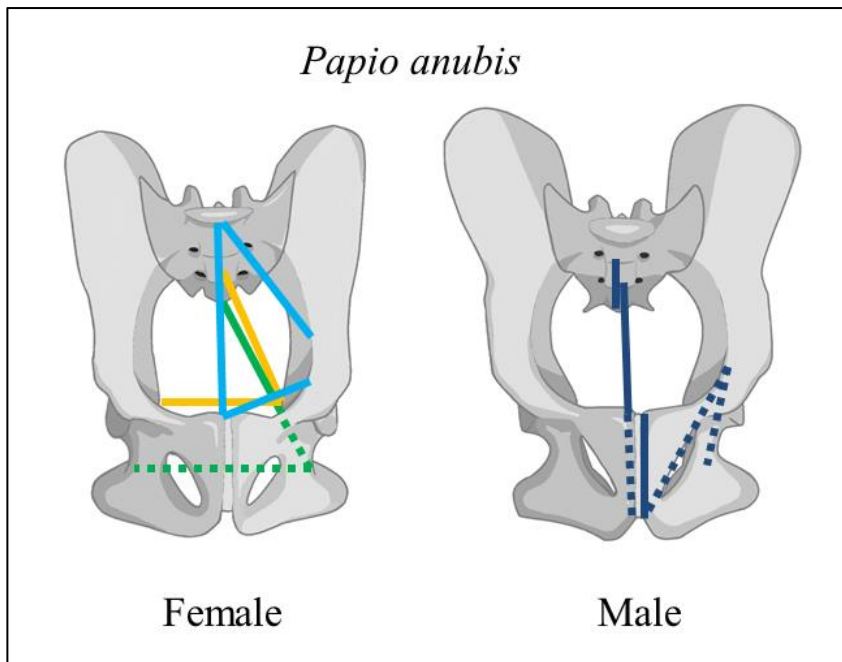


Figure 2.8b: Results of FORM procedure to obtain dimorphic distances in the pelvis of *Papio anubis* when pelves are scaled to geometric mean. Light blue represents distances which are greater in females than males in the inlet, yellow represents distances which are greater in females in the midplane, and green represents distances greater in females in the outlet. Dark blue represents linear distances greater in males. Only non-overlapping distances are included.

Only non-overlapping distances are included.

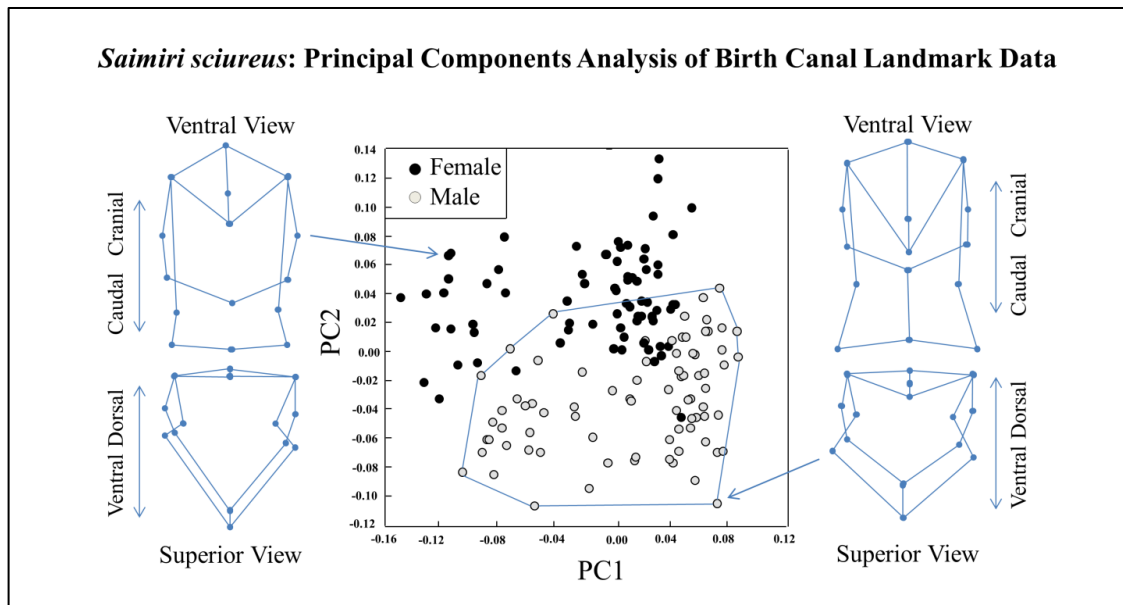


Figure 2.9a: Principal components analysis of birth canal shape in *Saimiri sciureus*. Note the diverging distributions of males and females along Axis 1 and Axis 2.

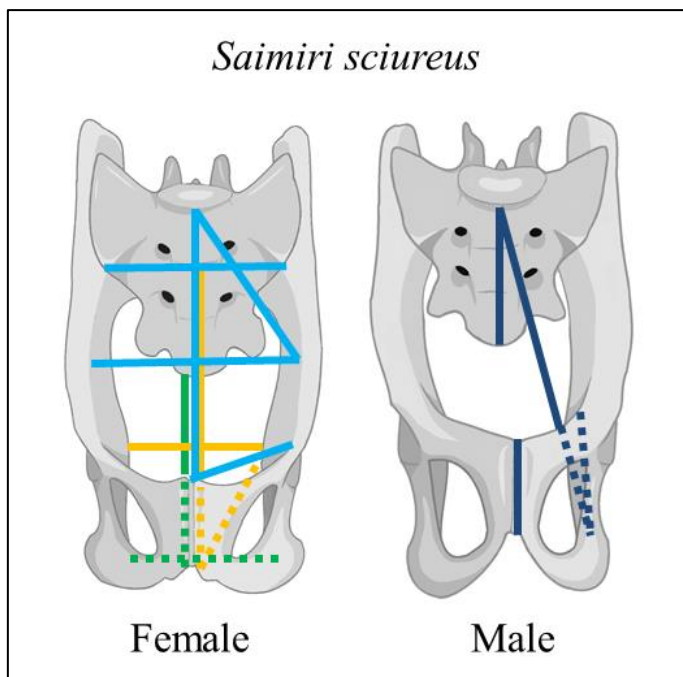


Figure 2.9b: Graphical representation of results of Euclidean Distance Matrix Analysis's FORM procedure to obtain dimorphic distances in the pelvis of *Saimiri sciureus* when pelves are scaled to geometric mean. Light blue represents distances which are greater in females than males in the inlet, yellow represents distances which are greater in females in the midplane, and green represents distances greater in females in the outlet. Dark blue represents linear

distances relatively greater in males than females. Only non-overlapping distances are included.

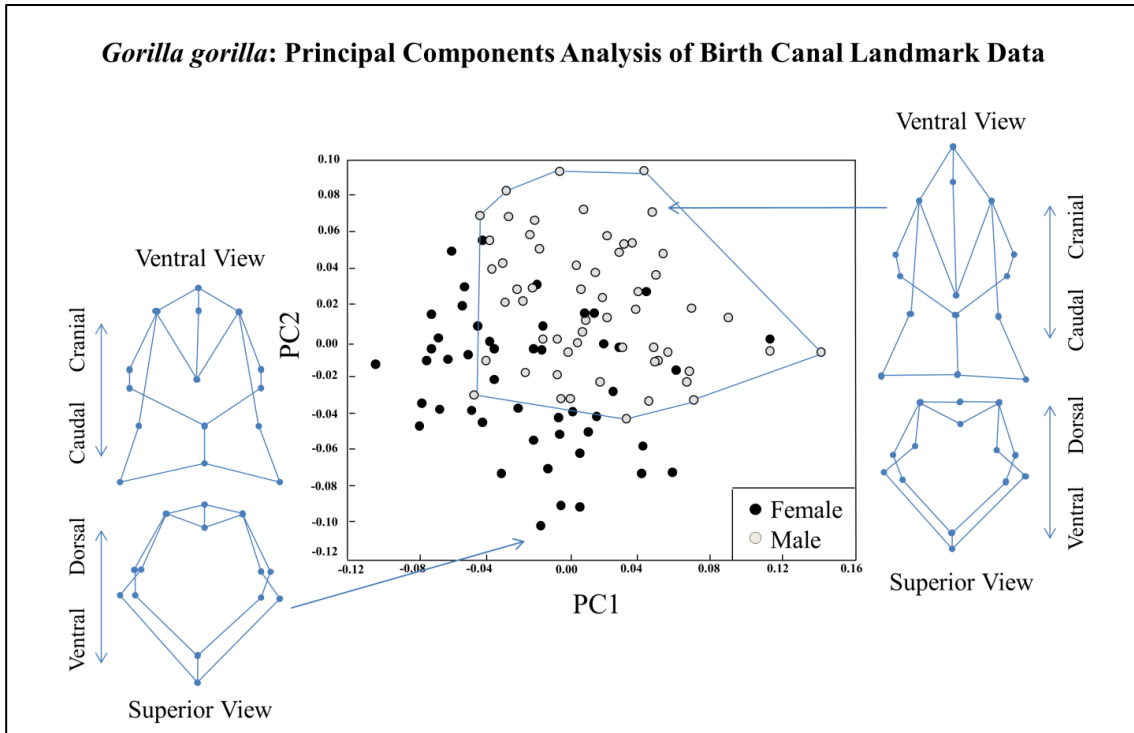


Figure 2.10a: Principal components analysis of birth canal shape in *Gorilla gorilla*. Note the diverging distributions of males and females along Axis 1 and Axis 2.

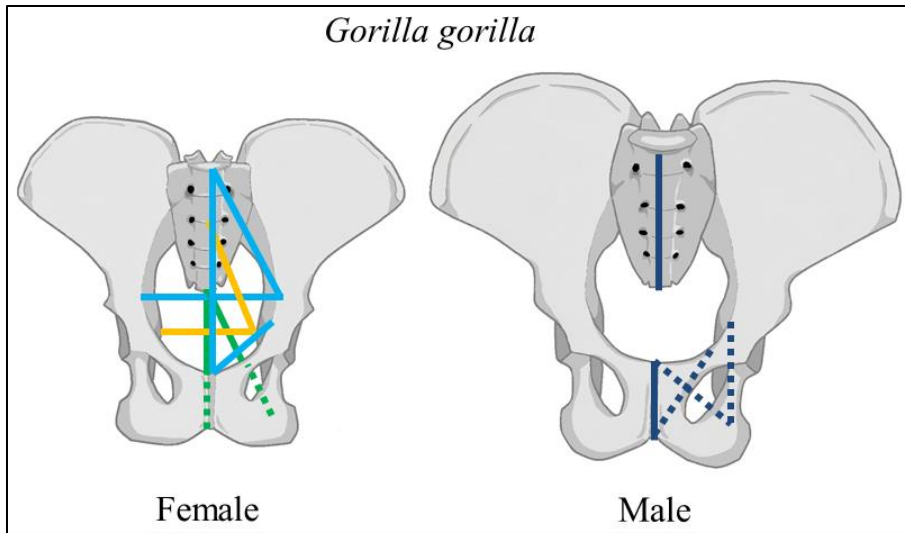


Figure 2.10b: Results of FORM procedure to obtain dimorphic distances in the pelvis of *Gorilla gorilla* when pelvises are scaled to geometric mean. Light blue represents distances greater in females than males in the inlet,

yellow represents distances greater in females in the midplane, and green represents distances greater in females in the outlet. Dark blue represents linear distances relatively greater in males. Only non-overlapping distances are included.

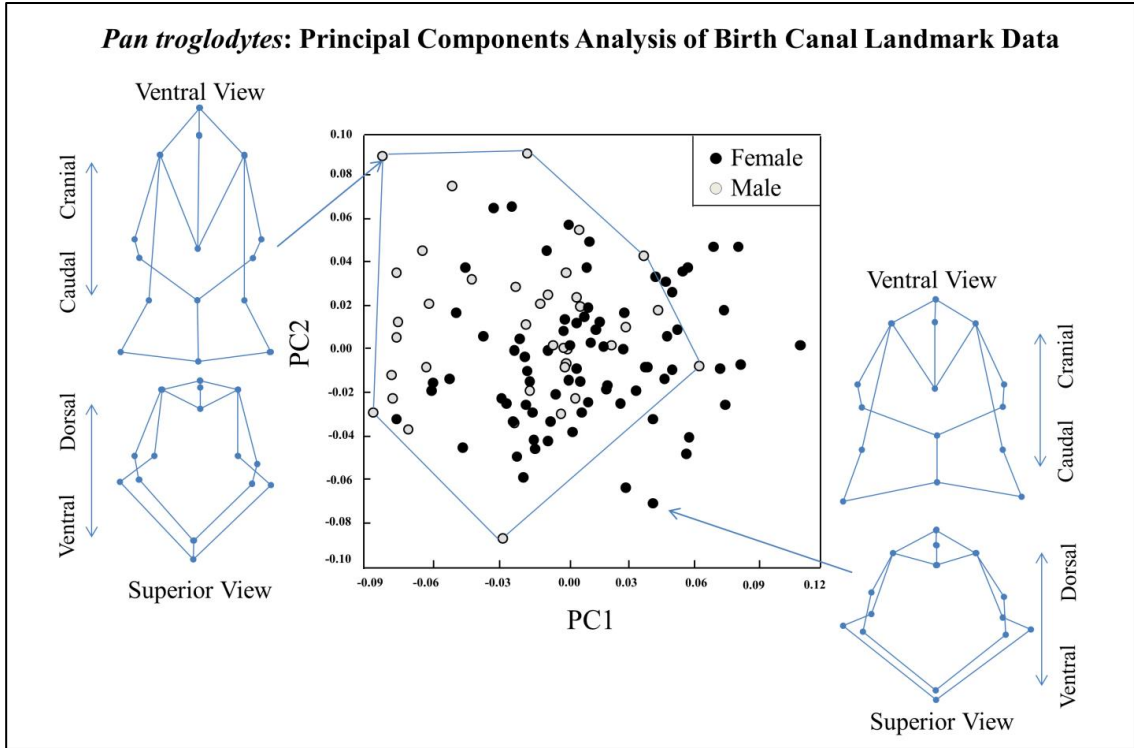


Figure 2.11a: Principal components analysis of birth canal shape in *Pan troglodytes*. Note lack of diverging distributions of males and females.

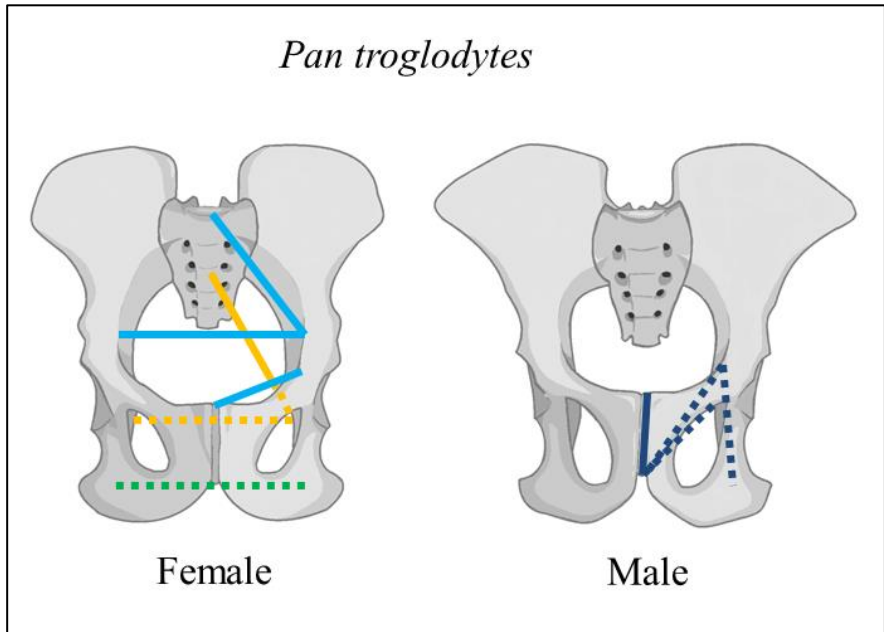


Figure 2.11b: Results of FORM procedure in *Pan troglodytes* when pelves are scaled to geometric mean. Light blue represents distances greater in females than males in the inlet, yellow represents distances greater in females in the midplane, and green represents distances greater in females in the outlet. Dark blue represents distances relatively greater in males. Only non-overlapping distances are included.

in females in the midplane, and green represents distances greater in females in the outlet. Dark blue represents distances relatively greater in males. Only non-overlapping distances are included.

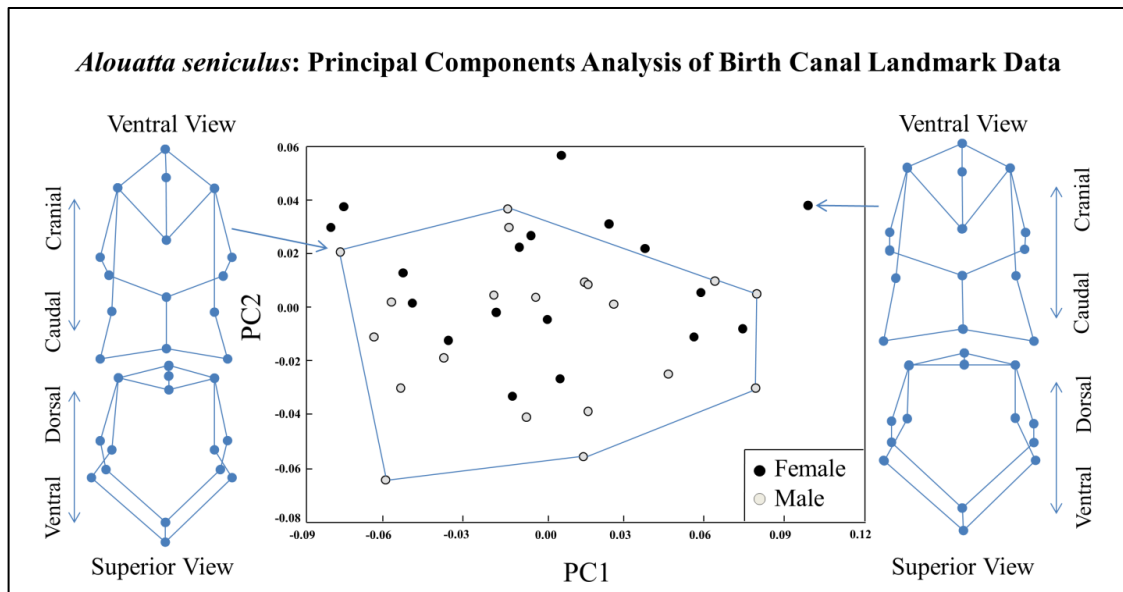


Figure 2.12a: Principal components analysis of birth canal shape in *Alouatta seniculus*. Note lack of diverging distributions of males and females.

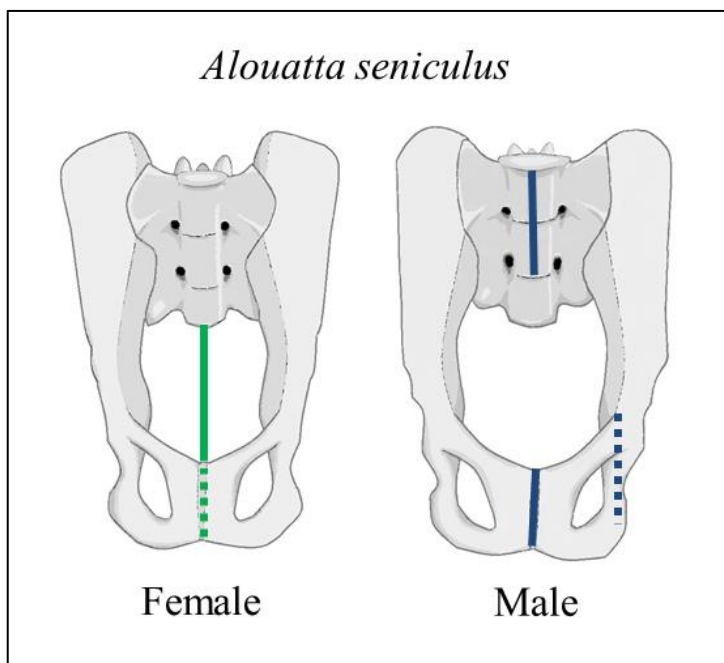


Figure 2.12b: Results of FORM procedure in *Alouatta seniculus* when pelves are scaled to geometric mean. Light blue represents distances greater in females than males in the inlet, yellow represents distances greater in females in the midplane, and green represents distances greater in females in the outlet. Dark blue represents distances relatively greater in males. Only non-overlapping distances are included.

CHAPTER 3: DIMORPHISM IN RELATIVE SACRAL BREADTH AMONG CATARRHINE PRIMATES

I. BACKGROUND

Chapter 2 of this study finds that the magnitude of dimorphism in birth canal size and shape is generally greater among species with large cephalopelvic proportions compared to species with small cephalopelvic proportions, leading to the hypothesis that the greater magnitude of dimorphism in the birth canals of species with large cephalopelvic proportions may be due to the presence of dimorphism in the breadth of the sacrum among taxa with large proportions. The sacrum contributes to the size and shape of the inlet, midplane, and outlet of the bony pelvis and thus represents a potentially important target for obstetric selection. However, very few studies of sacral sexual dimorphism in non-human primates have been conducted (Tague, 1991; Tague, 1992). Consequently, little is currently known about either the existence of sexual dimorphism in the sacrum of extant non-human primates, or what factors may lead to dimorphic sacral morphology, if present. Moreover, such a limited understanding of primate sacral sexual dimorphism constrains interpretation of fossil hominin sacral morphology (Robinson, 1972; Leutenegger, 1977; Berge et al., 1984; Rosenberg, 1986; Tague and Lovejoy, 1986; Tague, 1991). This is unfortunate given the number of well-preserved sacra in the hominin fossil record, including Stw 431 and Sts 14 (*Australopithecus africanus*), A.L. 288-1 (*A. afarensis*), MH 2 (*A. sediba*), BSN49/P27

(*Homo erectus*), SH 1 (*H. heidelbergensis*) and the Kebara 2 Neandertal (Leutenegger, 1977; Johanson et al., 1982; Rak and Arensburg, 1987; Arsuaga et al., 1999; Toussaint et al., 2003; Simpson et al., 2008; Bonmatí et al., 2010; Kibii et al., 2011).

a. Dimorphism in the human sacrum

Hominin sacral morphology is often interpreted in light of both locomotor and obstetric adaptations (Waterman, 1929; Robinson, 1972; Abitbol, 1987a; Ward, 2002) due to the fact that humans are both bipedal and have notoriously large cephalopelvic proportions (large size of the neonate head compared to the dimensions of the pelvic planes). Accordingly, both males and females in the genus *Homo* are widely argued to be under selection for reduced dimensions of the pelvic planes in order to facilitate efficient bipedal locomotion (Washburn, 1950, 1960; Pinkerton, 1973; McHenry, 1975; Zihlman, 1978). However, human females, unlike their male counterparts, are believed to be simultaneously under selection to maintain an obstetrically sufficient bony pelvis, and it is this “obstetric dilemma” in females which has typically been viewed as a primary factor driving dimorphic pelvic morphology in humans (Berge et al., 1984; Tague and Lovejoy, 1986; Abitbol, 1987b; Hager, 1989; Rosenberg, 1992; Abitbol, 1996; Rosenberg and Trevathan, 2002; but see Dunsworth et al., 2012; Wells et al., 2012). Although it is currently unclear at what point during hominin evolution neonatal encephalization initiated increased cephalopelvic proportions, it has previously been suggested that cephalopelvic proportions similar to modern humans may have evolved as early as *Homo erectus* (Walker and Ruff, 1993; Ruff, 1995; Simpson et al., 2008; but see DeSilva, 2011) and were almost certainly present among *H. heidelbergensis*,

Neandertals, and early *H. sapiens* (Arsuaga et al., 1999; Ponce de León et al., 2008; Franciscus, 2009; Weaver and Hublin, 2009; see also Rosenberg et al., 2006).

Given the important evolutionary implications of pelvic morphology, it is perhaps unsurprising that sexual dimorphism in the human sacrum has long garnered anthropological interest, as the first sacral (S1) vertebra comprises the posterior border of the pelvic inlet (Paterson, 1893; Derry, 1912; Trotter, 1926; Fawcett, 1938; Flander, 1978; Kimura, 1982; Tague, 2007; Benazzi et al., 2009). Interestingly, however, it is not overall width of the sacrum which exhibits sexual dimorphism in humans (Flander, 1978; Tague, 1992). Rather, it is the relative contributions to the overall width of the sacrum by the alae and S1 vertebral body that exhibits sexual dimorphism in humans, with the alae constituting a greater proportion of overall breadth in females compared to males (Fawcett, 1938; Flander, 1978; Tague, 2007; Benazzi et al., 2009). Indeed, breadth of the S1 alae is one of the most highly dimorphic measurements of the human pelvis (Tague, 1992; 2007). Breadth of the S1 alae is also positively correlated with pelvic inlet breadth (Tague, 2007), suggesting the relative lateral expansion of the sacral alae among human females likely reflects functional differences between male and female pelvis (see also Flander and Corruccini, 1980), with expanded sacral alae in females likely a response to heightened obstetric demands (Tague, 2007).

b. Dimorphism in the sacra of other primates

It remains unexplored whether any anthropoid taxa besides humans exhibit dimorphism in sacral breadth controlling for body size, but it is possible that obstetric

demand influences dimorphism in relative sacral breadth in non-human primates, as obstetric demand is thought to result in the sexually dimorphic sacra of humans (Fawcett, 1938; Flander, 1978; Tague, 2007; Benazzi et al., 2009). Humans are not the only primates with large cephalopelvic proportions (Table 1; Schultz, 1949; Stoller 1995), and it is possible that these other primate species with large cephalopelvic proportions also exhibit dimorphism in the breadth of the sacral alae (with females exhibiting wider sacra than males controlling for overall body size). If obstetric demand is the only factor which influences dimorphism in the breadth of the sacrum, it would be predicted that species with small cephalopelvic proportions are not dimorphic in sacral breadth.

However, obstetric demand is not the only factor which could lead to dimorphism in sacral breadth. While many researchers relate dimorphism in features such as the ischo-pubic index of primates primarily to cephalopelvic proportions (Leutenegger, 1974; Mobb and Wood, 1977; Wood and Chamberlain, 1986; Ridley, 1995), others link pelvic dimorphism in primates chiefly to overall body size dimorphism (Steudel, 1981, 1984; Tague, 2005). Pelvic dimorphism may be greater among species that are highly dimorphic in body size compared to species that are monomorphic in body size (Schultz, 1949; Tague, 1991; 2005; see also Chapter 2), and this could indicate a non-isometric relationship between pelvic shape and body size within highly dimorphic species. Any disparities between male and female pelvic morphology could be due to allometry (Steudel, 1981) biomechanical differences between the sexes (Steudel, 1981, 1984) or hormonally-driven modification of the male pelvis beyond the “default” morphology of the female (Tague, 2005).

Finally, it is possible that the presence of dimorphism in sacral breadth in anthropoids is due to a complex interplay of body size dimorphism, obstetric demand, and phylogeny (Schultz, 1949; Tague, 1991; 2005). Schultz (1949) specifically relates pelvic sexual dimorphism among monkeys and humans to obstetric factors, but argues body size dimorphism to be the primary influence on pelvic dimorphism among the other apes, including gibbons (which have large cephalopelvic proportions). Similarly, Chapter 2 of the current study finds that dimorphism in the size and shape of the birth canal exists across anthropoid taxa, but that the magnitude of dimorphism in birth canal size and shape is greatest among species with both large cephalopelvic proportions and high levels of body size dimorphism. Clearly, both cephalopelvic proportions and body size dimorphism influence dimorphism in the birth canals of primates (Schultz, 1949; Leutenegger, 1974), and it is possible that both of these factors can lead to dimorphism in sacral breadth in anthropoid taxa.

Although sacral breadth relative to S1 vertebral body breadth is known to be dimorphic in humans (Fawcett, 1938; Flander, 1978; Tague, 2007), to the authors' best knowledge, no research has been conducted examining dimorphism in this ratio among non-human primates. Therefore, an inter-specific evaluation of dimorphism in this ratio would clarify the relationships among pelvic dimorphism, relative neonate size, and body size dimorphism in primates.

Specifically, the existence of sexual dimorphism in the relative breadth of the human sacrum leads to two important questions about sexual dimorphism of the sacrum in non-human primates:

- 1) Is sexual dimorphism in breadth of the sacrum relative to S1 vertebral body breadth present in non-human primates?
- 2) If present in non-human primates, is sexual dimorphism in this ratio related specifically to obstetrics, body size dimorphism, or a combination of these factors?

The purpose of the present study is first to determine whether sexual dimorphism of the sacrum exists in other anthropoid species, and second, to test hypotheses related to obstetrics, body size dimorphism, and relative sacral breadth in humans and non-human primates.

II. MATERIALS AND METHODS

a. Samples

For this study, measurements of lumbar and sacral vertebrae were collected on a total of 266 primate specimens, encompassing *Homo sapiens* (n=71), *Hylobates lar* (n=69), *Gorilla gorilla* (n=44), *Pan troglodytes* (n=27), *Nasalis larvatus* (n=27), *Pongo pygmaeus* (n=15), and *Pan paniscus* (n=13). This sample differs from the sample from Chapter 1 because it was necessary to take measurements on lumbar vertebrae for this study (see below). All specimens of non-human primates were obtained from wild populations. In order to ensure that only adult specimens were included, measurements were only taken on specimens in which the apophyses of the iliac crest and ischial tuberosity are fused. Furthermore, all specimens were free of obvious pathology, and only specimens with modal numbers of lumbar and sacral vertebrae (Schultz and Straus,

1945) were included. Sampled taxa were chosen to encompass a wide spectrum of body size dimorphism known to exist in living primates as well as a range of relative neonate head dimensions to adult female pelvic inlet size combinations (Table 3.1; Figure 3.1). This sample consists primarily of hominoid taxa, with *Nasalis larvatus* representing the only non-hominoid species. While the inclusion of a cercopithecine species in an otherwise hominoid-only sample presents an obvious phylogenetic confound, the inclusion of *N. larvatus* was integral to determining the influence of cephalopelvic proportions and body size dimorphism within primates, as this species is characterized by both large body size dimorphism and large cephalopelvic proportions, a combination which does not exist among living hominoids. Moreover, inclusion of this species also allowed comparisons of sacral sexual dimorphism between hominoids and non-hominoids.

Specimens of *Hylobates lar*, *Pongo pygmaeus*, *Gorilla gorilla*, and *Pan troglodytes*, as well as specimens of *Homo sapiens* at the University of Iowa-Stanford Collection (all collected by Elizabeth A. Moffett) were included. Specimens of *Pan paniscus* collected at the Royal Museum of Central Africa, additional specimens of *H. lar* at the Museum of Comparative Zoology; *G. gorilla*, *P. pygmaeus*, and *P. troglodytes* at the Cleveland Museum of Natural History; and *G. gorilla*, *N. larvatus*, *P. pygmaeus*, and *P. troglodytes* at American Museum of Natural History (all collected by Carol V. Ward; Table 3.1) were also included. Sample size was determined as the maximum number of possible individuals of each species at these institutions. Interobserver error for each measurement was assessed using technical error of measurement (Perini et al., 2005) as described by Moffett et al. (2013) on one specimen of *Homo sapiens* and one

specimen of *Pan troglodytes*. For the *H. sapiens* specimen, the absolute and relative (in parentheses) technical errors were as follows: lumbar vertebral body breadth = 0.383 (0.8%), lumbar bi-transverse breadth = 0.138 (0.2%), S1 vertebral body breadth = 0.594 (1.4%), and sacral breadth at linea terminalis = 0.981 (1.1%). For the *P. troglodytes* specimen, the absolute and relative (in parentheses) technical errors of measurement for lumbar vertebral body breadth, lumbar bi-transverse breadth, S1 vertebral body breadth, and sacral breadth at linea terminalis were 0.071 (0.2%), 0.263 (0.4%), 0.167 (0.4%), and 0.501 (0.8%) respectively. The low values for intraobserver technical error indicate a high level of repeatability for each observer.

Finally, sampled taxa were divided into four categories based on distinct combinations of body size dimorphism and cephalopelvic proportions (summarized in Table 3.1). The assignment of taxa to specific cephalopelvic categories was based on previous studies of cephalopelvic proportions in the taxa included here (Schultz, 1949; Smith and Jungers, 1997). While an obvious method for assigning taxa to body size dimorphism categories would be to simply employ body mass dimorphism, previous authors (Gordon, 2006; Plavcan, 2012) have noted that there is not a uniform correspondence between body mass and skeletal dimorphism. Accordingly, categorization based on body size dimorphism was based on both previously published values for body mass dimorphism (Smith and Jungers, 1992) *and* one indicator of skeletal dimorphism (Table 3.1; Figure 3.1a), namely the index of dimorphism in caudal-most lumbar vertebral body width, as size of the caudal-most lumbar vertebral body is known to be highly correlated with body mass in anthropoid primates (Nakatsukasa and Hirose, 2003). This lumbar dimorphism index based on linear

measurements was cubed [(male mean lumbar vertebral body breadth/female mean lumbar vertebral body breadth)³] to permit direct comparisons with the body mass dimorphism index. Based on these cephalopelvic proportion and body size dimorphism data (Figure 3.1b), each species was assigned to one of the four following categories:

Category A (minimal to moderate body size dimorphism and large

cephalopelvic proportions): This category is represented by two species,

Homo sapiens and *Hylobates lar*. Both species exhibit low levels of body size dimorphism (i.e., have a male/female body mass index falling between 1.00-1.30) such that they are generally considered to be either monomorphic (*H. lar*) or minimally dimorphic (*H. sapiens*) in body size (Smith and Jungers, 1997). The lumbar vertebral body breadth dimorphism index also indicates that these species are minimally skeletally dimorphic (1.06 in *H. lar* and 1.23 in *H. sapiens*). Moreover, these two species have large cephalopelvic proportions with neonates that occupy over 90% of the transverse diameter of the pelvic inlet at the time of birth (Schultz, 1949).

Category B (minimal to moderate body size dimorphism and small

cephalopelvic proportions): This category encompasses the species *Pan*

troglodytes and *Pan paniscus*. These two species exhibit both low body size dimorphism (male/female body mass index 1.30 or lower), a low index of lumbar vertebral body breadth dimorphism (1.12 and 1.00, respectively) and relatively small neonate size, with the neonatal head reaching only 72% of the transverse diameter of the maternal pelvic inlet at term (Schultz, 1949; Smith and Jungers, 1997).

Category C (large body size dimorphism and large cephalopelvic

proportions): This category is composed of a single species: *Nasalis larvatus*.

This species has extremely high levels of body size dimorphism, with adult males having over twice the body mass of females (Smith and Jungers, 1997), and the lumbar vertebral body dimorphism index of this species (1.87) indicates that males are substantially larger than females for this skeletal measure.

Additionally, this species gives birth to relatively large neonates, with the breadth of the full-term neonate head occupying 95% the diameter of the maternal pelvic inlet (Schultz, 1949).

Category D (large body size dimorphism and small cephalopelvic

proportions): Category D is represented by two species, *Gorilla gorilla* and *Pongo pygmaeus*. These species are characterized by high levels of body size dimorphism in which adult male body mass is typically over twice that of adult females (Smith and Jungers, 1997). The lumbar vertebral body breadth index further indicates that *P. pygmaeus* and *G. gorilla* are highly dimorphic, with index values of 1.69 and 1.91, respectively. Moreover, these species give birth to relatively small neonates, with the transverse diameter of the neonate head at term reaching less than 75% the diameter of the pelvic inlet (Schultz, 1949).

b. Methods

Two measurements of the sacrum (Figure 3.2) were collected on each specimen:

- 1) S1 vertebral body width and 2) sacral breadth at linea terminalis. Most previous

studies (e.g., (Fawcett, 1938; Flander, 1978; Tague, 2007) have measured maximum breadth of the sacrum (i.e., the widest distance across the sacral alae). However, in the present study, breadth of the sacrum was specifically measured at linea terminalis because this measurement quantifies the contribution of the sacrum to the posterior portion of the pelvic inlet and is thus a more obstetrically-relevant measurement. In order to collect sacral breadth at linea terminalis, the sacrum and os coxae were articulated using the method described by Tague (1992; 2007), and the linear distance was taken between the sacroiliac joints on the anterior sacrum at the level of linea terminalis (Figure 3.2a).

In order to evaluate whether potential sexual dimorphism in the sacrum simply reflects a more systematic expression of body size dimorphism in primates, two measurements of the caudal-most lumbar vertebrae were also collected on each specimen (Figure 3.2b): lumbar vertebral body width and bi-transverse process breadth. The caudal-most lumbar vertebra was specifically chosen because this vertebra has previously been shown to be highly correlated with body size in primates (Nakatsukasa and Hirose, 2003), and permits similar measurements to those taken on the sacrum (i.e., overall and vertebral body breadths) to be assessed on an adjacent vertebral element that is not directly affected by obstetric demands (although lumbar bi-transverse breadth and sacral breadth at linea terminalis are likely functionally integrated for non-obstetric reasons).

Absolute measures of sacral or lumbar vertebrae are of limited utility for evaluating sexual dimorphism, however, as absolute measures of sacral breadth at linea terminalis or bi-transverse process breadth of the lumbar vertebra are *expected* to be

sexually dimorphic in species in which males have much larger body size than females. However, the fact that males have *absolutely* wider measurements in such species does not preclude the possibility of females possessing *relatively* wider sacra or lumbar vertebra when controlled for vertebral body size, which is the question being investigated here. Thus, two ratios were computed:

$$(1) \text{ Relative Sacral Breadth} = \frac{\text{sacral breadth at linea terminalis}}{\text{S1 vertebral body width}}$$

$$(2) \text{ Relative Lumbar Breadth} = \frac{\text{lumbar bi-transverse breadth}}{\text{lumbar vertebral body width}}$$

In these ratios, the overall breadth of each vertebra (i.e., breadth of the sacrum at linea terminalis or bi-transverse process breadth of the lumbar vertebra) was divided by the breadth of the corresponding vertebral body width, and the values thus represent the relative contribution of the alae or transverse processes to the overall breadth of the vertebral element. Because all relationships investigated here were isometric (see below), these ratios create a measure of relative vertebral breadth that was independent of the absolute size of the vertebral element, allowing comparisons within species that have large sexual body size dimorphism (e.g., *Pongo pygmaeus*) and between species that are largely divergent in body size (e.g., *Gorilla gorilla* versus *Hylobates lar*).

In order to verify isometric scaling in the ratios employed in the study, natural log-transformed values of lumbar bi-transverse process breadth and sacral breadth at linea terminalis were regressed on their respective natural log-transformed vertebral body widths using reduced major axis regression (Table 3.2). Slope values for sacral and lumbar regressions across all species both showed some deviation from isometry, with the sacrum exhibiting slight positive allometry (slope = 1.111, 95% Confidence

Interval = 1.072-1.150) and lumbar vertebrae exhibiting slight negative allometry (slope = 0.939, 95% CI = 0.897-0.981). However, in both cases these deviations could be attributed to the undue influence of specific outlying species rather than a consistent allometric trend across primates. For the sacrum, it is apparent that humans, which exhibit exceptionally wide sacral alae compared to other primate species (Abitbol, 1987a; Lovejoy, 2005), are driving the allometric result, as removal of this species results in an isometric slope (slope = 0.984, CI = 0.943-1.024) across all other primate species. Conversely, allometry in the lumbar vertebrae is clearly driven by the morphology of the only cercopithecine and palmigrade quadruped in the sample, *Nasalis larvatus*, with isometry characterizing all other species (slope = 0.969, CI = 0.928-1.010). These results suggest that structural proportions between the vertebral body and alae/costal processes are generally maintained in primates regardless of size, indicating that the use of natural log-transformed ratios in this study is appropriate for species-specific between-sex comparisons.

Due to unequal sample sizes between sexes within species, and potential issues regarding homogeneity of variances between species, randomization tests on natural log-transformed ratios were carried out on a per-species basis to test for differences in relative sacral and lumbar breadths between males and females in each species. Ratios are natural log-transformed because ratios frequently exhibit non-normal distributions (Atchley et al., 1976). Randomization tests are permutation tests which identify how likely the obtained group differences could be obtained by chance (Good, 1994; Edgington, 1995), and are commonly used when examining differences between groups with small sample sizes, as sample size is irrelevant to the validity of the test statistic

(Ninness et al., 2002). For each test, the p-value was determined analytically via randomization using 100,000 Monte Carlo simulations (Roff, 2006), with a significance level of $\alpha = 0.05$. Subsequently, the four previously described cephalopelvic proportions to body size dimorphism categories were employed to test a set of four specific hypotheses regarding sexual dimorphism in relative sacral breadth among primates (Table 3.3).

Hypothesis 1: Sexual dimorphism in relative sacral breadth does not exist in non-human catarrhines.

Prediction 1a: This hypothesis predicts that no species included in this study should exhibit dimorphism in relative sacral breadth.

Hypothesis 2: Sexual dimorphism in relative sacral breadth is *exclusively* due to body size dimorphism.

Prediction 2a: This hypothesis postulates that dimorphism in relative sacral breadth should exist in both Categories C and D (large body size dimorphism) but should not exist in Categories A and B (minimal body size dimorphism).

Hypothesis 3: Sexual dimorphism in relative sacral breadth is *exclusively* related to cephalopelvic proportions.

Prediction 3a: This hypothesis anticipates that dimorphism in relative sacral breadth should exist in both Categories A and C (relatively large neonates), but should not exist in Categories B and D (relatively small neonates).

Hypothesis 4: Sexual dimorphism in relative sacral breadth is *not exclusively* due to either body size dimorphism level or cephalopelvic proportions.

Prediction 4a: This hypothesis posits that sexual dimorphism in relative sacral breadth cannot be conclusively related to just body size dimorphism level or cephalopelvic proportions (see above). Accordingly, this hypothesis would suggest that sexual dimorphism in relative sacral breadth is related to either a combination of both body size dimorphism level and cephalopelvic proportions, and/or phylogeny.

Criteria used to reject each hypothesis are summarized in Table 3.3. In order to test Hypothesis 1 (lack of dimorphism in relative sacral breadth in non-human species), distributions of male and female relative sacral breadth values are first evaluated for statistical differences in each species. The presence of statistically significant sexual dimorphism in one or more of the six non-human species was taken as grounds for rejection of Hypothesis 1, which was subsequently followed by simultaneous testing of Hypothesis 2 and Hypothesis 3. Rejection of Hypothesis 2 (dimorphism in relative sacral breadth exclusively due to body size dimorphism) requires that statistically significant levels of sexual dimorphism in relative sacral breadth be found in any species in Categories A or B (minimal body size dimorphism). Grounds for rejection of Hypothesis 3 (dimorphism in relative sacral breadth exclusively due to cephalopelvic proportions) included the presence of statistically significant levels of dimorphism in relative sacral breadth in any species in Categories B or D (relatively small neonates). Rejection of both Hypothesis 2 and Hypothesis 3 would result in the adoption of Hypothesis 4 (dimorphism in relative sacral breadth due to a combination of body size

dimorphism and cephalopelvic proportions and/or to phylogeny) as a null hypothesis for future research.

Finally, to determine whether potential dimorphism in relative sacral breadth is due to differences in sacral breadth at linea terminalis relative to S1 vertebral breadth or vice versa, the absolute breadth of the S1 vertebral body and sacral breadth at linea terminalis were evaluated for sexual dimorphism using randomization tests of differences in means. Specifically, among any species found to exhibit sexual dimorphism in relative sacral breadth, the relationship between S1 vertebral breadth and sacral breadth at linea terminalis was examined to determine if all sexually dimorphic species shared a common morphological pattern or whether dimorphism could be attributed to multiple sacral morphologies. Again, due to sample size considerations, the p-values were determined via randomization using 100,000 Monte Carlo simulations.

III. RESULTS

Results for this study are summarized in Tables 3.4 and 3.5. Samples in Category A, encompassing *Hylobates lar* ($p < 0.001$) and *H. sapiens* ($p < 0.001$); Category C, including the single species *N. larvatus* ($p = 0.019$); and a single species in Category D, *Gorilla gorilla* ($p < 0.001$), are found to have statistically significant levels of sexual dimorphism in relative sacral breadth (Table 3.5). Due to the fact that sexual dimorphism in relative sacral breadth is identified in multiple primate species in this study, Hypothesis 1 (non-existence of sexual dimorphism in relative sacral breadth) is rejected.

Because sexual dimorphism in relative sacral breadth is found to exist in minimally dimorphic species (Category A), predictions based upon Hypothesis 2 (dimorphism in relative sacral breadth exclusively related to body size dimorphism) are not substantiated, and this hypothesis was accordingly rejected. Additionally, Hypothesis 3 (dimorphism in relative sacral breadth related exclusively to relative neonate size) is rejected, as *Gorilla gorilla*, which has small cephalopelvic proportions, is also found to be dimorphic for relative sacral breadth. Moreover, in all species found to be dimorphic for relative sacral breadth, including gorillas, females are found to have statistically larger relative sacral breadth values than males (Table 3.5). As sexual dimorphism in relative sacral breadth is not found to be related exclusively to body size dimorphism (Hypothesis 2) or cephalopelvic proportions (Hypothesis 3) in this study, Hypothesis 4 (sexual dimorphism in relative sacral breadth is *not exclusively* due to either body size dimorphism level or cephalopelvic proportions) cannot be rejected.

Nasalis larvatus is the only species with statistically significant levels of sexual dimorphism in both relative sacral breadth *and* relative lumbar breadth ($p=0.033$). In contrast, the other three species found to be dimorphic for relative sacral breadth (*Homo sapiens*, *Hylobates lar*, and *Gorilla gorilla*) are not dimorphic for relative lumbar breadth ($p=0.695$, $p=0.290$, and $p=0.588$ respectively).

For the four species dimorphic for relative sacral breadth, dimorphism in absolute breadth of S1 and sacral breadth at linea terminalis is further evaluated (Table 3.4). *Homo sapiens* is found not to be dimorphic for sacral breadth at linea terminalis but is dimorphic for S1 vertebral body width ($p < 0.001$) with males possessing significantly larger S1 vertebral bodies than females. In contrast, *Hylobates lar* is not

found to be dimorphic for S1 vertebral body width but is significantly sexually dimorphic for sacral breadth at linea terminalis ($p < 0.001$), with female gibbons being larger than males for this variable. *Nasalis larvatus* is significantly dimorphic for both breadth of S1 ($p < 0.001$) and sacral breadth at linea terminalis ($p < 0.001$) with males absolutely larger than females in both measurements. Similarly, *Gorilla gorilla* is also significantly dimorphic for both breadth of S1 ($p < 0.001$) and sacral breadth at linea terminalis ($p = 0.001$).

IV. DISCUSSION AND CONCLUSIONS

In this study, four species - *Homo sapiens*, *Hylobates lar*, *Nasalis larvatus* and *Gorilla gorilla* - are found to be sexually dimorphic in relative sacral breadth (Figure 3.3). These four species exhibit variability in overall body size dimorphism ranging from monomorphic to highly dimorphic. Of these, *H. sapiens*, *H. lar*, and *N. larvatus* have large cephalopelvic proportions, whereas *G. gorilla* has small cephalopelvic proportions. In contrast, *Pongo pygmaeus*, *Pan troglodytes*, and *Pan paniscus*, are not statistically sexually dimorphic for relative sacral breadth. The results of this study therefore indicate that sexual dimorphism in relative sacral breadth does indeed exist in some species of non-human primates, and that, at least among catarrhines, dimorphism in relative sacral breadth is not exclusively related to either cephalopelvic proportions or to body size dimorphism. However, because all of the species with large cephalopelvic proportions included in this study (*H. sapiens*, *H. lar*, and *N. larvatus*) exhibit dimorphism in relative sacral breadth, the results of this study do broadly suggest that,

among species with large cephalopelvic proportions, there is selective pressure on females to possess relatively broader sacral alae than their male counterparts.

A more detailed inspection of the data reveals that the relationship between overall sacral breadth, S1 vertebral body breadth, and length of the alae varies considerably among *Homo sapiens*, *Hylobates lar*, *Nasalis larvatus*, and *Gorilla gorilla*. Results indicate that sacral breadth at linea terminalis is not sexually dimorphic in *H. sapiens*, whereas breadth of the S1 vertebral body is significantly dimorphic, with human females possessing absolutely narrower vertebral bodies than males. These findings are in accordance with previous research (Fawcett, 1938; Flander, 1978; Tague, 2007; Benazzi et al., 2009), and since these results show that human females have narrower S1 vertebral bodies, but similar overall sacral widths, it is clear that relatively wide sacral alae in human females serves to produce a disproportionately wide sacrum relative to a small vertebral body. As S1 vertebral body size closely tracks overall body size in humans (McHenry, 1992), females among *H. sapiens* possess relatively, but not absolutely, wider sacra than males when body size is taken into account. Conversely, *H. lar* is significantly dimorphic for sacral breadth at linea terminalis, but not S1 vertebral body breadth. Thus, for gibbons, elongated sacral alae actually produce an absolutely wider sacral breadth in females compared to males, despite the similarity in vertebral body size between the sexes (Figure 3.3). Consequently, while some authors (Schultz, 1949; Steudel, 1981; Tague, 2005) have argued the pelvis of *H. lar* to be monomorphic, these results support the findings of Leutenegger (1974) and Ridley (1995) who found features of the gibbon pelvis, such as the ischio-pubic index, to be moderately dimorphic.

The remaining two dimorphic species, *Nasalis larvatus* and *Gorilla gorilla*, are each found to be sexually dimorphic for both sacral breadth at linea terminalis and S1 vertebral body breadth, with males exhibiting absolutely larger values for both measurements (Table 3.4). However, comparisons of the relative magnitude of differences in the two measurements indicate that, despite their larger absolute size, males of both species exhibit disproportionately narrower alae relative to their vertebral bodies when compared to those of females. As a result, male *N. larvatus* possess sacra that are, on average, only 14% wider than those of females, despite possessing S1 vertebral bodies 20% larger than their female counterparts. This trend is even more pronounced among *G. gorilla*, in which males have S1 vertebral bodies 21% larger than those of females but sacra that are on average only 7% wider than females.

The finding of sexual dimorphism in relative sacral breadth in *Gorilla gorilla* is particularly interesting in the context of this study, as, opposed to *Homo sapiens*, *Hylobates lar*, and *Nasalis larvatus*, this species represents the only taxon in which dimorphism in relative sacral breadth was found in conjunction with small cephalopelvic proportions. Thus, given these small cephalopelvic proportions, it appears unlikely that dimorphism in relative sacral breadth in *G. gorilla* is related to obstetric demands placed on females. Consequently, this raises the possibility that sacral dimorphism among gorillas may be primarily attributable to selection on males for relatively narrower sacra, rather than relatively broader sacra in females. While it is possible that potential selection on relative sacral breadth among *G. gorilla* males could be related to large body size dimorphism alone, this appears unlikely considering that *Pongo pygmaeus*, which is also characterized by large male body size, does not exhibit

dimorphism in relative sacral breadth. Alternatively, previous authors have related both narrower sacra (Abitbol, 1987a; Lovejoy, 2005) and greater lumbar entrapment (Lovejoy et al., 2009a; Lovejoy et al., 2009b) in apes compared to hominins to locomotor demands. Accordingly, relatively narrow sacra in gorilla males may be related to unique locomotor pressures faced by large male gorillas during terrestrial knuckle-walking (compared to smaller female gorillas and chimpanzees), or to decreased frequency of suspensory postures among *G. gorilla* males compared to females (Remis, 1995). Thus, the results of the current study highlight the need to more fully understand selection on male pelvic morphology, especially among species in which males and females are largely divergent in body size and/or exhibit slight differences in locomotor patterns.

In contrast to gorillas, in which sexual dimorphism in relative sacral breadth appears predominantly related to body size dimorphism, in *Nasalis larvatus*, dimorphism in relative sacral breadth is found in association with both large body size dimorphism and large cephalopelvic proportions. Thus, while the presence of large cephalopelvic dimensions in *N. larvatus* suggests at least one evolutionary pressure exerted on female sacral morphology (especially given the demonstrated changes to female sacra in other primate species with similarly large cephalopelvic dimensions), the possibility that large body size dimorphism may have also affected male sacral morphology (as in gorillas), leads to the possibility that dimorphism in relative sacral breadth in *N. larvatus* may be the result of divergent selective pressures placed on male and female sacral morphology in this species. In other words, obstetric demands may have placed a selective pressure on females of this species for relatively broader sacra,

while, simultaneously, factors related to increased body size (locomotor demands, etc.) may have selected for relatively narrower sacra in males. Similar arguments for the appearance of sexual dimorphism through divergent selective pressures on males and females have previously been made for other features among primates, including body mass and canine tooth size (Plavcan, 2011). However, further examination of dimorphism in relative sacral breadth among other cercopithecines is needed to more definitively determine the underlying factors driving sexual dimorphism in relative sacral breadth in *N. larvatus*.

Interestingly, *Nasalis larvatus* is also unusual in that it is the only species in this study to display dimorphism in relative lumbar breadth, with females being significantly larger than males. While the reason for sexual dimorphism in relative lumbar breadth among *N. larvatus* is unclear, it is plausible that either phylogeny or locomotion plays a role in shaping this lumbar morphology, as *N. larvatus* represents the only cercopithecine species in the sample, as well as the only species which employs a palmigrade/plantigrade quadrupedal locomotor pattern. Alternatively, it is also possible that dimorphism in relative lumbar breadth represents a transition to the dimorphic sacral morphology in the vertebral column of this species; however, it should be noted that neither *Gorilla gorilla*, *Hylobates lar*, nor *Homo sapiens*, which also display sexual dimorphism in relative sacral breadth, exhibit sexual dimorphism in relative lumbar breadth. Nonetheless, further research is needed to identify the underlying mechanisms which produce sexually dimorphic lumbar morphology of this species.

Wide sacral alae in females of catarrhine species with large cephalopelvic proportions is most likely related to maintaining obstetrically sufficient pelvic inlet

dimensions. Although the relationship between relative sacral breadth and transverse breadth of the inlet was not directly evaluated in this study, Tague (2007) has previously demonstrated a positive correlation between breadth of the S1 alae and pelvic inlet breadth in humans. Accordingly, given that the biparietal (transverse) diameter of the neonate head is the most obstetrically constrained dimension in non-human primates (Schultz, 1949; Leutenegger, 1974), it appears reasonable to suggest that the relatively wide alae among *Hylobates lar* and *Nasalis larvatus* females also serves to expand the transverse diameter of the pelvic inlet in these species with large cephalopelvic proportions. In *H. sapiens*, *H. lar*, and *N. larvatus*, females have relatively (controlling for S1 body breadth) wider pelvic inlets compared to males (and in *H. lar*, females have absolutely wider pelvic inlets compared to males; see Chapter 2), and dimorphism in the breadth of the sacral alae contributes to dimorphism in inlet breadth in these species. Females also possess relatively wider sacra than males in *G. gorilla*, though this is presumably unrelated to obstetrics, and in this species females also possess relatively wider pelvic inlets than males (see Chapter 2). Though males and females are not dimorphic for relative sacral breadth in *P. troglodytes*, this species does exhibit dimorphism in transverse inlet diameter controlling for S1 body breadth (see Chapter 2). Therefore, dimorphism in inlet breadth in *P. troglodytes* is not due to dimorphism in relative sacral breadth, but rather is likely due to dimorphism in pubis length in this species (see Chapter 2).

In addition to providing novel insights into sexual dimorphism in living primates, the results of the present study may have implications for making behavioral inferences about fossil anthropoids, including hominins. While it is generally accepted

that australopiths were characterized by considerably greater levels of body size dimorphism than exhibited by modern humans (McHenry, 1991, 1992; Richmond and Jugers, 1995; Lockwood et al., 1996), the relative size of australopith neonates, and thus obstetric constraints, have been the subject of debate (Tague and Lovejoy, 1986; DeSilva, 2011). Tague (2007) has previously assessed sexual dimorphism in australopith sacra, finding that two sacra hypothesized to belong to females, A.L. 288-1 (*Australopithecus afarensis*) and Sts 14 (*Australopithecus africanus*), possessed relatively longer sacral alae than the putatively male Stw 431 (*A. africanus*) sacrum (for information on these sex attributions see Leutenegger, 1977; Johanson et al., 1982; Tague and Lovejoy, 1998; Toussaint et al., 2003; but see Häusler and Schmid, 1995). However, Tague (2007) contended that the australopith sacrum is not, in fact, dimorphic, as he regarded this sexually dimorphic result as either a statistical artifact of small sample size or due to the possible subadult status of Stw 431 (Berge and Gommery, 1999), and thus that the sacrum of australopiths “was not associated with obstetric imperatives”. However, the results of the current study suggest that, even if australopiths were characterized by sexual dimorphism in relative sacral breadth, this dimorphism may not necessarily be indicative of large cephalopelvic proportions. While potential dimorphism in relative sacra breadth among australopiths could be influenced by selection for relatively broader sacral alae among females related to obstetrics (as in *Homo sapiens*, *Hylobates lar* and probably *Nasalis larvatus*), given that australopiths were likely characterized by a large degree of body size dimorphism (McHenry, 1991, 1992; Richmond and Jugers, 1995; Lockwood et al., 1996), it is also possible that dimorphism in relative sacral breadth could be driven by selection on male australopith

sacra due to factors related to overall body size (as appears likely for *Gorilla gorilla*). Consequently, should further fossil discoveries corroborate dimorphism in sacral morphology among australopiths, the present study indicates that there is no reason to assume *a priori* that such dimorphism is predominantly female-driven, or exclusively related to obstetric demand.

Because this study includes only catarrhine species, future research should address whether platyrrhine species with large cephalopelvic proportions, such as *Saimiri sciureus* and *Ateles geoffroyi* (Schultz, 1949; Bowden et al., 1967; Hopf, 1967), similarly exhibit sexual dimorphism in relative sacral breadth. Future studies of sexual dimorphism in relative sacral breadth should also attempt to include larger sample sizes for *Pan paniscus* and *Pongo pygmaeus*, as this study included only limited samples of each of these species. Moreover, future studies including a more diverse sample of cercopithecine primates would likely further elucidate the roles of cephalopelvic proportions and body size dimorphism on sacral morphology among catarrhines.

The results of this study indicate that obstetric selection (quantified as cephalopelvic proportions) may be related to dimorphism in relative sacral breadth among species with large cephalopelvic proportions. Together with the results of Chapter 2 (which suggest that cephalopelvic proportions do influence the magnitude of dimorphism in the size and shape of the birth canal), these results indicate that obstetric selection plays an important role in modifying the morphology of the birth canal in females compared to the bony equivalent in males. However, it is unknown whether differences in birth canal morphology between males and females translates into dimorphism in other parts of the pelvis (i.e., parts of the pelvis which do not directly

participate in the birth canal). Therefore, Chapter 4 of the present study examines whether dimorphism in the size and shape of the birth canal is related to dimorphism in the size and shape of the non-obstetric pelvis in anthropoids.

Table 3.1: Sampled taxa

Species	n		n		Body mass dimorphism index*	Lumbar body dimorphism index [‡]	Cephalo-pelvic index [†]	Body size dimorphism to cephalopelvic category ⁺
	Lumbar		Sacral					
	F	M	F	M	(M/F)			
<i>Homo sapiens</i> ¹	41	30	18	25	1.14 [§]	1.23	1.02 [‡]	A
<i>Hylobates lar</i> ²	27	38	29	40	1.11	1.06	0.94	A
<i>Pan paniscus</i> ³	4	2	6	7	1.36	1.00	0.72	B
<i>Pan troglodytes</i> ^{2,4,5}	13	10	13	14	1.30	1.12	0.72	B
<i>Nasalis larvatus</i> ^{2,5}	15	12	15	11	2.08	1.86	0.95	C
<i>Gorilla gorilla</i> ^{2,4,5}	21	20	21	23	2.38	1.91	0.64	D
<i>Pongo pygmaeus</i> ^{2,4,5,6}	7	7	7	8	2.19	1.69	0.73	D

1, University of Iowa-Stanford Collection; 2, Museum of Comparative Zoology; 3, Royal Museum of Central Africa; 4, Cleveland Museum of Natural History; 5, American Museum of Natural History; 6, National Museum of Natural History.

* Values for body size dimorphism based on body mass values from Smith and Jungers (1997).

[‡] Values for lumbar vertebral body dimorphism index are based on the values for average male lumbar vertebral body width divided by the average female lumbar vertebral body width obtained in this study and are calculated as [(male mean lumbar vertebral body breadth/female mean lumbar vertebral body breadth)³].

[†] Calculated as (neonate head breadth/maternal pelvic inlet transverse diameter). Values for neonate head and maternal inlet from Schultz (1949).

⁺ Categories defined as: (A) minimal body size dimorphism and large cephalopelvic proportions; (B) minimal body size dimorphism and small cephalopelvic proportions; (C) large body size dimorphism and large cephalopelvic proportions; (D) large body size dimorphism and small cephalopelvic proportions.

[§] Worldwide average body size dimorphism for humans (Smith and Jungers, 1997).

[‡] The sagittal diameter of the neonate head and transverse breadth of the maternal inlet are used to build this ratio because this is how the human neonate modally engages the inlet.

Sample sizes differ between lumbar and sacral vertebrae because not all specimens included retained both a measurable sacrum and caudal-most lumbar vertebra.

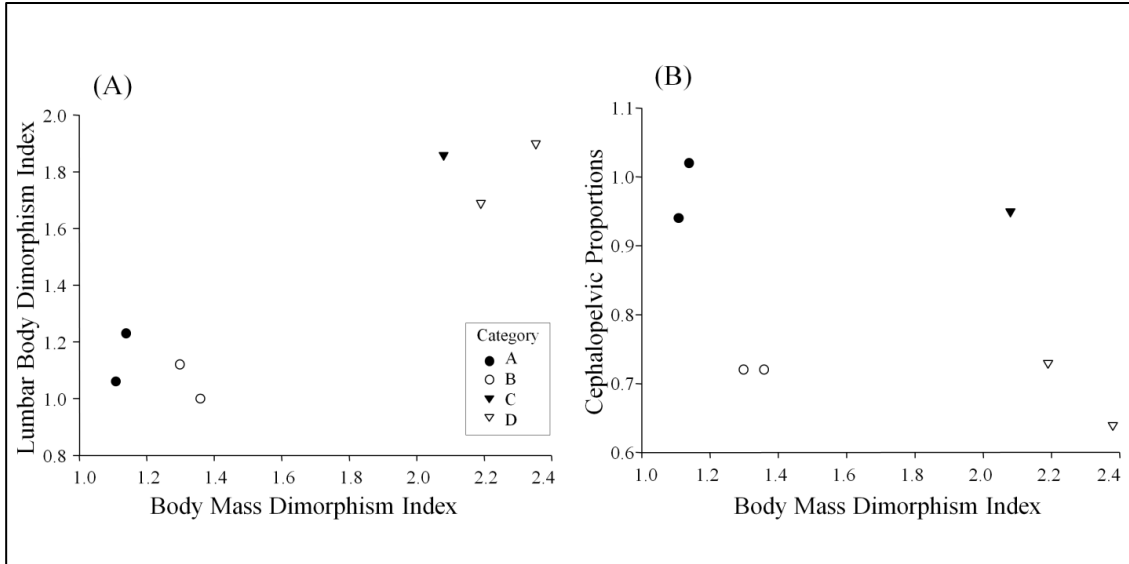


Figure 3.1: Scatter plots of (A) body mass dimorphism index versus lumbar vertebral body dimorphism index and (B) body mass dimorphism index versus cephalopelvic proportions. Categories defined as: A, minimal body size dimorphism and large cephalopelvic proportions (includes *Homo sapiens* and *Hylobates lar*); B, minimal body size dimorphism and small cephalopelvic proportions (*Pan troglodytes* and *Pan paniscus*); C, large body size dimorphism and large cephalopelvic proportions (*Nasalis larvatus*); D, large body size dimorphism and small cephalopelvic proportions (*Gorilla gorilla* and *Pongo pygmaeus*).

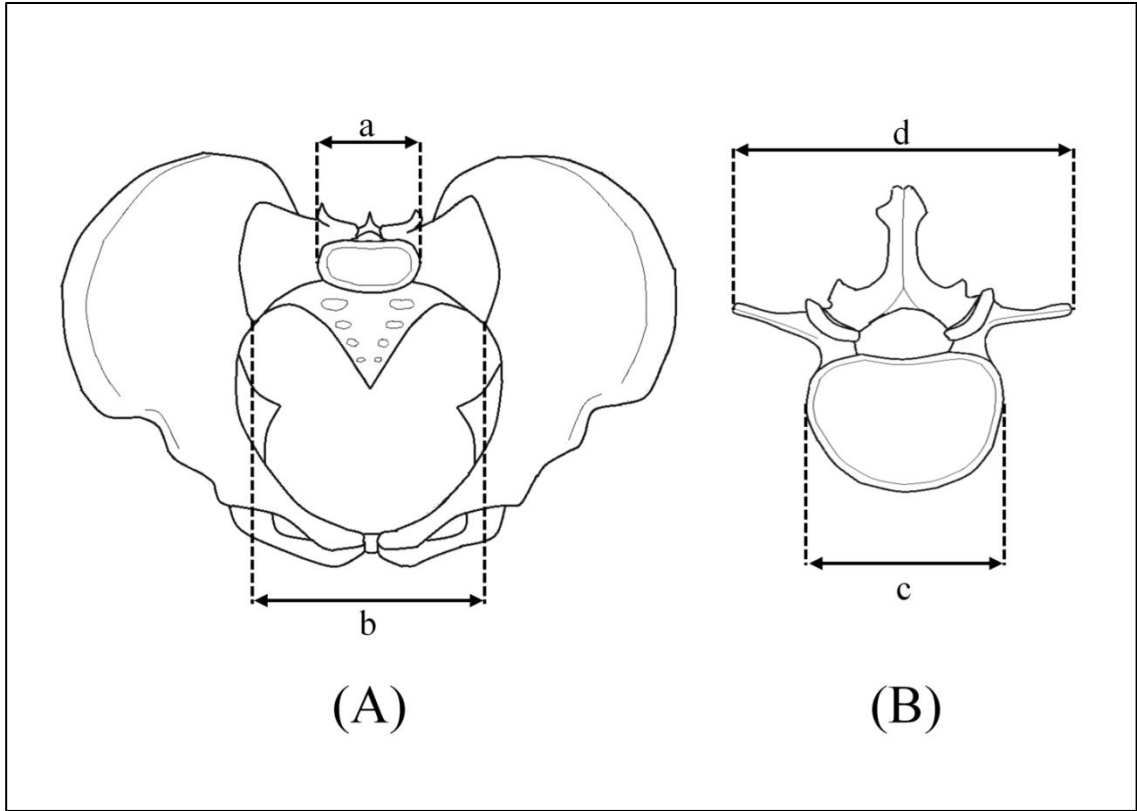


Figure 3.2: Measurements of the (A) sacrum and (B) lumbar vertebra. Linear measurements are: a) S1 vertebral body width; b) sacral breadth at linea terminalis; c) caudal-most lumbar vertebral body width; and d) caudal-most lumbar bi-transverse process breadth.

Table 3.2: Isometry test results

In S1 body breadth vs. In sacral breadth at linea terminalis				
Group	N	Slope	95% CI	R²
All species	265	1.111	1.072-1.150	0.9154
All females	133	1.154	1.098-1.209	0.9226
All males	132	1.072	1.025-1.119	0.9366
All hominoids	239	1.100	1.059-1.141	0.9145
All hominoid females	118	1.128	1.068-1.189	0.9155
All hominoid males	121	1.066	1.018-1.113	0.9398
All non-humans	194	0.984*	0.943-1.024	0.9159
All non-human females	92	0.992*	0.934-1.050	0.9222
All non-human males	102	0.985*	0.933-1.037	0.9293
In lumbar body breadth vs. In lumbar bi-costal breadth				
Group	N	Slope	95% CI	R²
All species	220	0.939	0.897-0.981	0.8855
All females	105	0.904	0.837-0.971	0.8577
All males	115	0.963*	0.907-1.019	0.9025
All hominoids	193	0.969*	0.928-1.010	0.9110
All hominoid females	90	0.958*	0.892-1.023	0.8958
All hominoid males	103	0.974*	0.920-1.029	0.9195
All non-humans	177	0.846	0.799-0.892	0.8630
All non-human females	87	0.800	0.727-0.873	0.8211
All non-human males	90	0.875	0.814-0.937	0.8900

*Confidence interval includes isometry.

Table 3.3: Hypotheses and predictions outlined in text

Hypothesis:	Predictions:	Criteria for Rejection:
H₁: Dimorphism in relative sacral breadth not present	No dimorphism in relative sacral breadth in non-human species	Any non-human species with dimorphism in relative sacral breadth
H₂: Dimorphism in relative sacral breadth due to body size dimorphism	Dimorphism in relative sacral breadth exclusively in species with moderate to high body size dimorphism	Any minimally dimorphic species having dimorphism in relative sacral breadth
H₃: Dimorphism in relative sacral breadth due to cephalopelvic proportions	Dimorphism in relative sacral breadth exclusively in species with large cephalopelvic proportions	Any species with small cephalopelvic proportions having dimorphism in relative sacral breadth
H₄: Sexual dimorphism in relative sacral breadth not exclusively related to body size dimorphism or cephalopelvic proportions	Sexual dimorphism in relative sacral breadth related to a combination of both body size dimorphism level and cephalopelvic proportions, and/or to phylogeny	Dimorphism in relative sacral breadth exclusively related either to body size dimorphism or to cephalopelvic proportions

Table 3.4: Randomization tests (2-tailed) for sexual dimorphism in vertebral measurements

S1 vertebral body width					
Species	Female		Male		p-value
	Mean	S.D.	Mean	S.D.	
<i>H. sapiens</i>	47.59	4.86	52.84	5.34	<0.001*
<i>H. lar</i>	19.50	1.28	19.86	1.25	0.238
<i>P. paniscus</i>	31.69	2.12	31.45	2.08	0.849
<i>P. troglodytes</i>	34.50	3.58	35.79	3.87	0.377
<i>N. larvatus</i>	23.19	1.17	28.91	2.52	<0.001*
<i>G. gorilla</i>	41.85	3.75	50.98	3.64	<0.001*
<i>P. pygmaeus</i>	35.57	5.03	39.04	3.79	0.150

Sacral breadth at linea terminalis					
	Female		Male		p-value
	Mean	S.D.	Mean	S.D.	
<i>H. sapiens</i>	108.68	6.70	107.13	6.55	0.335
<i>H. lar</i>	38.40	2.75	35.36	2.06	< 0.001*
<i>P. paniscus</i>	61.45	5.80	60.87	5.30	0.823
<i>P. troglodytes</i>	64.75	5.73	63.45	6.73	0.594
<i>N. larvatus</i>	41.92	2.72	48.89	2.98	< 0.001*
<i>G. gorilla</i>	78.99	6.79	86.63	7.28	0.001*
<i>P. pygmaeus</i>	74.14	9.91	78.12	2.14	0.297

Lumbar vertebral body width					
	Female		Male		p-value
	Mean	S.D.	Mean	S.D.	
<i>H. sapiens</i>	50.77	4.29	54.48	4.60	0.011*
<i>H. lar</i>	20.43	1.07	20.87	1.09	0.115
<i>P. paniscus</i>	31.04	0.54	31.05	2.06	0.939
<i>P. troglodytes</i>	36.47	2.50	38.17	3.84	0.207
<i>N. larvatus</i>	23.30	1.22	28.72	1.84	<0.001*
<i>G. gorilla</i>	44.87	3.81	56.26	3.71	<0.001*
<i>P. pygmaeus</i>	37.38	5.20	44.40	1.99	0.011*

Lumbar bi-transverse process breadth					
	Female		Male		p-value
	Mean	S.D.	Mean	S.D.	
<i>H. sapiens</i>	86.40	6.53	93.84	7.64	0.002*
<i>H. lar</i>	34.14	2.38	34.17	2.75	0.968
<i>P. paniscus</i>	47.20	4.09	56.98	10.25	0.171
<i>P. troglodytes</i>	56.04	5.52	55.86	7.31	0.945
<i>N. larvatus</i>	46.51	3.41	54.75	4.46	<0.001*
<i>G. gorilla</i>	62.68	7.32	77.26	8.74	<0.001*
<i>P. pygmaeus</i>	60.98	9.82	73.22	7.06	0.017*

*Denotes significance at $\alpha=0.05$.

Table 3.5: Randomization test results for sexual dimorphism in relative sacral and relative lumbar breadths*

Species	Category*	Mean relative sacral breadth		p-value [†]	Mean relative lumbar breadth		p-value [†]
		F	M		F	M	
		<i>H. sapiens</i>	A		2.27	2.02	
<i>H. lar</i>	A	1.97	1.78	<0.001*	1.67	1.65	0.290
<i>P. paniscus</i>	B	1.93	1.96	0.991	1.52	1.83	0.135
<i>P. troglodytes</i>	B	1.90	1.93	0.221	1.54	1.49	0.266
<i>N. larvatus</i>	C	1.81	1.70	0.019*	2.00	1.91	0.033
<i>G. gorilla</i>	D	2.07	1.87	<0.001*	1.40	1.37	0.588
<i>P. pygmaeus</i>	D	2.03	2.02	0.442	1.63	1.66	0.831

*Denotes significance at $\alpha=0.05$.

*Categories defined as: (A) minimal body size dimorphism and large cephalopelvic proportions; (B) minimal body size dimorphism and small cephalopelvic proportions; (C) large body size dimorphism and large cephalopelvic proportions; (D) large body size dimorphism and small cephalopelvic proportions.

[†] While raw values for relative sacral breadth are shown in the table, p-values are calculated using natural-logged values for relative sacral breadth and relative lumbar breadth.

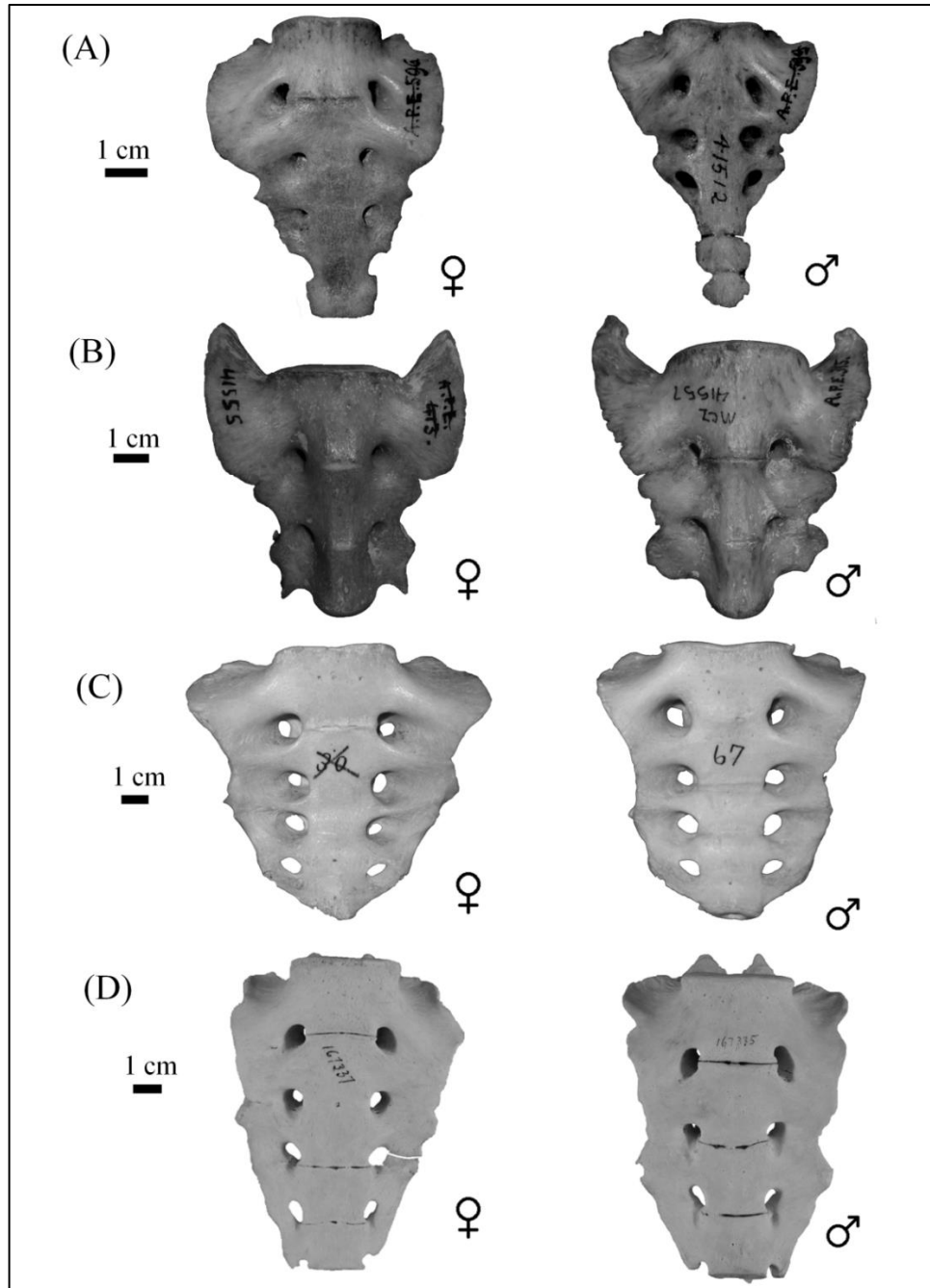


Figure 3.3: Anterior views of male and female sacra of: (a) *Hylobates lar*; (b) *Nasalis larvatus*; (c) *Homo sapiens*; (d) *Gorilla gorilla*. Note the relative lengthening of the sacral alae among females compared to males. Specimens depicted are: 41512 and 41523 (*H. lar*; Harvard Museum of Comparative Zoology); 41555 and 41557 (*N. larvatus*; Harvard Museum of Comparative Zoology); MU 30 and 67 (*H. sapiens*; University of Missouri Anatomy Osteology Collection); 167335 and 167337 (*G. gorilla*; American Museum of Natural History; gorilla photos courtesy of Gabrielle Russo).

CHAPTER 4: DIMORPHISM IN NON-OBSTETRIC PELVIC MORPHOLOGY IN ANTHROPOIDS

I. BACKGROUND:

Dimorphism in the size and shape of the parts of the pelvis that form the bony birth canal (hereafter referred to as the birth canal) is nearly ubiquitous in anthropoid primates (see Chapter 2; see also Schultz, 1949; Leutenegger, 1974; Steudel, 1981a; Tague, 1991; Ridley, 1995; Tague, 2005). Females have birth canals that are relatively larger (measured as centroid size of the birth canal and circumferences of the inlet, midplane, and outlet) compared to males controlling for body size. However, female birth canals are not just isometrically scaled up versions of those of males - their birth canals are also relatively wider, but not necessarily dorsoventrally expanded, meaning females tend to have rounder birth canals compared to those of males (see Chapter 2) due to a wider sacrum and longer pubis. Species with large cephalopelvic proportions (relatively large neonates) are especially dimorphic (Chapter 2; see also Ridley, 1995).

Dimorphism in birth canal size and shape means that there also must be size and/or shape dimorphism in parts of the pelvis not directly related to birth, termed here the “non-obstetric pelvis”. There are three ways that dimorphism in birth canal morphology might manifest itself in other parts of the pelvis.

First, in most species (all except for *Alouatta seniculus*; Chapter 2), females have relatively larger birth canals than males. So, it is possible that the non-obstetric parts of female pelves are also larger than those of males, but that the shapes of their non-obstetric pelves remain the same. This would result in both (a) overall non-obstetric pelvic size (centroid size) being larger in females controlling for body size and (b) all or most linear distances of the non-obstetric pelvis being proportionately larger in females compared to males with no shape differences between sexes. This effect should be greatest in species with large cephalopelvic proportions, as they have more dimorphic birth canal size than those with small proportions (see Chapter 2). If this is the case, non-obstetric pelvic size dimorphism would be comparable to obstetric dimorphism.

A second option not mutually exclusive to the first scenario is that pelvic shape might differ between sexes. Females not only have larger birth canals than males, they also have relatively wider inlets, midplanes and/or outlets (all except *A. seniculus*) compared to rostrocaudal (dorsoventral) diameters. This effect is greatest in species with large cephalopelvic proportions. Therefore, the second possibility is that females have non-obstetric pelves that are mediolaterally wider than those of males, but that rostrocaudal dimensions of the non-obstetric pelvis are similar. If so, biacetabular and biiliac breadths should be wider in females (Ruff and Hayes, 1983; Ruff, 1987, 1995; Lovejoy, 2005), but rostrocaudal dimensions of the pelvis (e.g., the distance between the superior ilium and inferior ischium) should be similar controlling for body size. This effect would be especially pronounced in species with large cephalopelvic proportions (see Chapter 2). It is also possible that there is some shape dimorphism in the non-obstetric pelvis that is unrelated to birth canal dimorphism, especially in species with

high levels of body size dimorphism in which there may be slight differences in locomotor repertoire or ecological niches between sexes (see also Steudel, 1981b; Moffett et al., 2013).

The existence of dimorphism in the birth canals of non-human primates presents an opportunity to test (a) the hypothesis that dimorphism in the size and shape of the non-obstetric pelvis is the result of dimorphism in the birth canal, and (b) the hypothesis that obstetric selection (measured as cephalopelvic proportions) affects dimorphism in non-obstetric pelvic morphology. If dimorphism in the non-obstetric pelvis is a direct result of dimorphism in birth canal size and/or shape, this would increase the information that can be gleaned from fossil pelvises about sex, birth canal morphology, and tradeoffs between locomotor and obstetric selection, especially in pelvises that are fragmentary or do not preserve a complete birth canal.

II. HYPOTHESES

The purpose of the current study is to determine the patterns of dimorphism in the shape and size of the non-obstetric pelvis across anthropoid primates, and to determine whether the magnitude of dimorphism in non-obstetric pelvic size and shape is influenced by cephalopelvic proportions. This study tests the following hypotheses:

Hypothesis 1: Dimorphism in the size of the non-obstetric pelvis reflects dimorphism in birth canal size.

Prediction 1a: In species that have dimorphism in birth canal centroid size controlling for body size (all taxa except *Alouatta seniculus* and

Gorilla gorilla), females will also have larger non-obstetric pelvic centroid sizes than males controlling for body size.

Prediction 1b: Species with large cephalopelvic proportions will have a higher magnitude of dimorphism in relative pelvic size compared to species with small proportions.

Hypothesis 2: Dimorphism in the 3D shape of the non-obstetric pelvis reflects dimorphism in the shape of the birth canal.

Prediction 2a: In species that exhibit dimorphism in birth canal shape (all taxa except *A. seniculus*), there is dimorphism in non-obstetric pelvic shape, such that females have more laterally flaring ischia and inferior ilia relative to the midline, wider biiliac breadth, and wider biacetabular breadths.

Prediction 2b: The magnitude of dimorphism in pelvic shape is greater among taxa with large cephalopelvic proportions than in taxa with small proportions.

III. MATERIALS AND METHODS

a. Samples

Samples chosen for the current study were outlined in Chapter 2. This sample comprises a range of cephalopelvic proportions, phylogenetic affinity, locomotor adaptations, and body size dimorphism among extant anthropoid primates.

Phylogeny may influence pelvic morphology, but samples for too few taxa are available to achieve sufficient power (Blomberg et al., 2003) using formal phylogenetic analyses. However, including species with large and small cephalopelvic proportions within hominoids [*Homo sapiens* and *Hylobates lar* (large proportions); *Gorilla gorilla* and *Pan troglodytes* (small proportions)] and platyrrhines [*Saimiri sciureus* (large proportions) and *Alouatta seniculus* (small proportions)] provides a set of comparisons with which to informally consider phylogeny. Similarly, locomotor repertoire may be an important factor, but locomotion is completely confounded with phylogeny in anthropoids. Thus, no formal tests considering locomotion are performed.

b. Landmarks

Methods for articulating paired ossa coxae and sacra were outlined in Chapter 2. Landmarks representing the non-obstetric pelvis (Figure 4.1 and described in Table 4.1) included posterior inferior iliac spine, posterior superior iliac spine, superior iliac crest, anterior superior iliac spine, superior acetabulum, inferior acetabulum, acetabulum center, posterior acetabulum, posterior ischial neck, posterior ischial tuberosity, lateral ischial ramus, lateral ischial tuberosity, inferior pubic ramus, inferior pubic symphysis, superior pubic symphysis. Landmark error was assessed using repeated measures (Kohn et al., 1995) as described in Chapter 2. Error averages for all landmarks is less than 0.002% of centroid size, and error is equally distributed across all axes, indicating that all landmarks can be collected with high repeatability.

c. Testing Hypothesis 1

Hypothesis 1 predicts that dimorphism in non-obstetric pelvic *size* is due to dimorphism in birth canal size. Overall pelvic size was quantified as non-obstetric pelvic centroid size, which was calculated as the square root of the sum of the squared distances between all non-obstetric landmarks (Figure 4.1; Table 4.2) and the centroid of the configuration (Bookstein, 1991) for each individual.

Testing hypotheses about relative pelvic size between sexes requires consideration of body size and allometric scaling of pelvic size with body size. As in Chapter 2, transverse breadth of the first sacral (S1) vertebral body was chosen as a proxy for body size because it is strongly correlated with body mass across primates (Jungers, 1988; 1991). Scaling of non-obstetric dimensions was evaluated following methods described in Chapter 2. Within monkeys, pelvic centroid size scales isometrically (95% confidence interval (CI) = 0.90-1.04; Table 4.2), but in apes pelvic centroid size scales with slight negative allometry (CI = 0.82-0.98; Table 4.2). Therefore, it was deemed inappropriate to use ratios of non-obstetric pelvic measurements to S1 body breadth to compare relative pelvic size between males and females within apes, as any dimorphism in these ratios could simply reflect allometric scaling. Instead, analysis of residuals was used, as described below.

Diagonal (RMA) residuals were calculated for each individual from the male-only (within apes or within monkeys) regression. For each species, the mean residual of males was compared with that for females for each species using Student's t-tests at $\alpha = 0.028$ (justification for α -level discussed below) to assess the presence of dimorphism.

In order to control for Type I Error in this study, a False Discovery Rate (FDR) procedure (Benjamini and Hochberg, 1995) as described in Chapter 2 was performed on all raw p-values (i.e., all those obtained in Student's t-tests of absolute and relative pelvic dimensions, residuals, DFA, Student's t-tests of PC scores, and EDMA's FORM tests). The FDR procedure indicated that in order to maintain a false discovery rate of 5%, α -level should be set at 0.028. Therefore, unadjusted p-values are reported in the text, but only those p-values less than 0.028 were considered significant.

Hypothesis 1 also predicts that species with large cephalopelvic proportions will have a higher magnitude of dimorphism in relative pelvic size compared to species with small proportions. The magnitude of dimorphism within each species was calculated as [(mean female residual)-(mean male residual)]. The larger the resulting number, the higher the magnitude of dimorphism between sexes. A more positive number indicates that females were relatively larger than males (i.e., females have larger residuals), while a more negative number indicates that males were relatively larger.

Hypothesis 1 Prediction 1a was considered rejected if all species which have dimorphism in birth canal centroid size (all except *Alouatta seniculus*) do not also exhibit dimorphism in non-obstetric pelvic centroid size. Further, prediction b was considered falsified if species with large cephalopelvic proportions did not have a higher degree of dimorphism in non-obstetric pelvic centroid size compared to species with small proportions.

d. Testing Hypothesis 2

Hypothesis 2 Prediction 2a predicts that the existence of dimorphism in the 3D shape of the non-obstetric pelvis is due to dimorphism in birth canal shape. To quantify shape, principal components analysis (PCA) was employed as described in Chapter 2. Landmarks representing the non-obstetric pelvis (Figure 4.1, Table 4.1) were scaled, translated, and rotated using generalized Procrustes analysis and subjected to tangent space projection. All PCAs were conducted using Morphologika 2.5© software. Methods for determination of which successive principal components (PCs) significantly contributed to shape variability within each species were described in Chapter 2.

To further quantify the degree of overlap in non-obstetric pelvic shapes within each species, a polygon was placed around the male shape distribution (which theoretically represents the shape of the pelvis when there is no obstetric selection) in the principal components plot. Then, the proportion of females that fell within the male distribution was calculated (see also Chapter 2).

Non-obstetric pelvic shape dimorphism for each species was assessed using Student's t-tests performed on raw principal component scores. PC scores of each sex were compared within species for all PCs that encompass significant shape variation (i.e., >10% of intraspecies shape variation) as described in Chapter 2 at $\alpha=0.028$ (see justification for α -level above). Visualization of shape differences between males and females within each species was facilitated using wireframes.

Euclidean Distance Matrix Analysis's (EDMA) FORM procedure was used to localize shape differences between males and females as described in Chapter 2.

Significance of each interlandmark distance was determined using bootstrapped confidence intervals as described in Chapter 2. The FORM procedure also allowed an estimation of the difference between mean forms (i.e., overall form differences between groups). For differences between mean forms using EDMA's FORM procedure, all p-values <0.028 were considered significant (see justification for α -level above). The FORM procedure was performed on both unscaled data as well as data scaled to each individual's geometric mean (in order to obtain shape information controlling for size).

Hypothesis 2 Prediction 2a was considered rejected if taxa which exhibit dimorphism in 3D birth canal shape (all except *Alouatta seniculus*) did not also exhibit dimorphism in the shape of the non-obstetric pelves such that females have mediolaterally broader pelves (wider biiliac and biacetabular breadths and more laterally flaring ischia) compared to males. Further, Prediction 2b was also rejected if species with large cephalopelvic proportions did not also have a greater magnitude of dimorphism in non-obstetric pelvic shape compared to species with small proportions.

IV. RESULTS

a. Dimorphism in Non-Obstetric Pelvic Size

Hypothesis 1 (prediction a) posits that species which have dimorphism in birth canal centroid size (all except *Alouatta seniculus*) also have dimorphism in the size of the non-obstetric pelvis. This prediction is supported, because females in all species in this study except for *Alouatta seniculus* have larger pelves than males controlling for body size (Table 4.3).

Hypothesis 1 also predicts that the magnitude of dimorphism in non-obstetric pelvic size is greater among species with large cephalopelvic proportions compared to those with small proportions. This prediction is also supported because species with large cephalopelvic proportions do tend to have a higher magnitude of dimorphism in non-obstetric pelvic size than those with small proportions. The magnitudes of dimorphism in species with large cephalopelvic proportions range from 0.25 to 0.02, (with the mean for all larger proportion taxa being 0.10, and females larger than males in all taxa; Table 4.3) while the range for species with small proportions is 0.05-0.01 (with the mean for small proportion taxa being 0.04; Table 4.3). However, it should also be noted that there is a great deal of overlap in non-obstetric pelvic size between males and females in most taxa except *Nasalis larvatus* and *Papio anubis* (See Appendix A).

b. Dimorphism in Non-Obstetric Pelvic Shape

Hypothesis 2 (prediction a) predicts that species which have dimorphism in the shape of the birth canal (all except *Alouatta seniculus*) also have dimorphism in the shape of the non-obstetric pelvis. This prediction is supported. Non-obstetric pelvic shape is significantly dimorphic in all taxa except *A. seniculus* and *Papio anubis* (Table 4.7). This result for *P. anubis* might be related to small female sample size, however, because only 25% of females fall into male shape space (Table 4.5).

Hypothesis 2 prediction b posits that if non-obstetric pelvic shape dimorphism is found in taxa with large and small cephalopelvic proportions, the magnitude of dimorphism should be higher in species with large proportions. This prediction is supported. The magnitude of dimorphism in 3D pelvic shape (Table 4.5, Figure 4.2)

tends to be much higher in taxa with large cephalopelvic proportions (in which the percentage of females falling in male shape space ranges from 6% to 60%) compared to taxa with small proportions (in which the percentage of females falling in male shape space ranges from 50% to 78%).

All taxa except *A. seniculus* do exhibit shape dimorphism (i.e., female pelves are not just isometrically scaled up versions of those of males). Generally, females are larger for dimensions that increase the mediolateral dimensions of the pelvis, whereas males are larger for rostrocaudal dimensions (Figures 4.3-4.11). Among most species, females are relatively larger than males for biacetabular breadth (all species except *M. mulatta* and *A. seniculus*) and length of the caudal pubic ramus (all taxa). In contrast, males are relatively larger than females for relative ischial length (all taxa except *P. anubis*), and pubic symphysis height (all species).

For the ilium, upper ilium height (distance between dorsal caudal and dorsal rostral iliac spines) is relatively larger in males in all taxa except *P. anubis* and *A. seniculus*, but the lower ilium is relatively longer in females among all taxa except *A. seniculus* (Figures 4.3-4.11). This result is likely due to the fact that the upper ilium is spatially separated from the birth canal (so it is not subject to obstetric selection), but the lower ilium laterally bounds the pelvic inlet and midplane, so any increase in length should increase the circumference of the birth canal.

Biiliac breadth is statistically similar between sexes controlling for S1 body breadth in all taxa except for *Nasalis larvatus*. This linear distance is also strongly positively allometric with body size in anthropoids (Lewton, 2015), so it is possible that there may be sex differences in biiliac breadth when allometry is taken into account.

This is the case (Table 4.3). Analysis of residuals of biiliac breadth against S1 body breadth indicate that when allometric scaling is taken into account, females have relatively wider biiliac breadth than males (all taxa except *Nasalis larvatus*, *Pan troglodytes*, and *Alouatta seniculus*).

In *Pan troglodytes* and *Gorilla gorilla*, males have a relatively wider ilium breadth (but not biiliac breadth) than females (Figures 4.9-4.10), but this is not the case in any monkey taxa or in humans (Figures 4.3-4.11). It is possible that in these taxa, males do have wider ilia, but that they are slightly more coronally-oriented so that relative biiliac breadth is statistically similar between sexes. A potential explanation for the observation of dimorphism in relative iliac breadth in *G. gorilla* and *P. troglodytes* is that both of these are suspensory taxa with moderate (*Pan*) to high (*Gorilla*) levels of body size dimorphism. A relatively broader ilium in males creates more area for the attachment of latissimus dorsi, which attaches to the upper crest of the ilium (Waterman, 1929). Therefore, a broader ilium in males could be advantageous for suspensory locomotion at such large body sizes. In contrast, in most monkeys the iliac blades are narrow (Waterman, 1929) and laterally facing (Ward, 1993), which might suggest that iliac breadth (or just body breadth) is more constrained in monkeys than in large bodied apes.

VIII. DISCUSSION AND CONCLUSIONS

Some level of dimorphism in non-obstetric pelvic size and shape exists across most anthropoids, just as is seen in birth canal (see Chapter 2). This is also seen across

many mammalian taxa, including mice (Gardner, 1936; Schutz et al., 2009a), bats (Crelin and Newton, 1969), foxes (Schutz et al., 2009b), opossums (Tague, 2003), and lorises (Leutenegger, 1973). Thus, it is clear that dimorphism in pelvic size and shape is not relegated to just the birth canal, and dimorphism is not just found in species that give birth to relatively large neonates. Moreover, this may be an ancestral character for primates, or indeed for mammals.

The *presence* of pelvic dimorphism even outside the birth canal cannot be taken as evidence that a species has rigorous obstetric selection or large cephalopelvic proportions. Yet, it is clear that there is an effect of relative neonate size on the *magnitude* of dimorphism in pelvic size across anthropoids, even outside the birth canal. Taxa with large cephalopelvic proportions are more dimorphic in non-obstetric pelvic size and shape than species with small proportions, as they are in the parts of the pelvis contributing to the birth canal (see Chapter 2). The magnitude non-obstetric size and shape dimorphism generally corresponds to the magnitude of dimorphism birth canal size and shape. Those taxa that have a high degree of overlap in birth canal size and shape also have a high degree of overlap in non-obstetric pelvic size and shape (see also Appendix A).

Though females do have relatively larger pelves than males, in most species (all those studied here except *Alouatta seniculus*), there is a great degree of overlap in non-obstetric pelvic size across most taxa (except for *Nasalis larvatus* and *Papio anubis*; see Appendix A). Thus, differences in non-obstetric pelvic size may not be observable at small sample sizes in many taxa. This is especially important to consider when

examining dimorphism in pelvic size in fossil specimens, which will be represented by smaller sample sizes than the species included here.

Though females do have statistically larger non-obstetric pelvic size than males in most taxa, female pelves are not just isometrically larger versions of male pelves. Females tend to have wider pelves, but not rostrocaudally taller pelves than those of males. Biacetabular distance, which is immediately adjacent to the midplane of the birth canal, is dimorphic among most taxa included here (except *A. seniculus* and *Macaca mulatta*). Notably, relative midplane breadth is also not dimorphic in either *A. seniculus* or *M. mulatta*. Therefore, these results indicate that dimorphism in biacetabular breadth is a result of dimorphism in the breadth of the pelvic midplane. It has been hypothesized that increased biacetabular distance could be energetically costly in bipeds because it will increase the abductor forces required to prevent hip drop during bipedal locomotion when there is not a concurrent increase in femoral neck length (Ruff, 1995). It is reasonable to assume that increased biacetabular breadth would increase the distance between the origin (gluteal plane of ilium; Waterman, 1929) and insertions (greater trochanter of femur) of these muscles. This distance would be further increased by a relatively larger lower iliac height in females (see further discussion below). It is possible that increasing this distance could be biomechanically disadvantageous in non-human primates – the lesser gluteal muscles aid in maintaining squatting or upright sitting postures in most primates (Waterman, 1929). Increasing the distance between the center of mass and the attachment of the lesser gluteals will increase their required effort to maintain these postures. Therefore, a wider biacetabular breadth may be

energetically costly for females among non-human primates. Further research is needed to examine this hypothesis.

Biiliac breadth is strongly positively allometric in primates (Lewton, 2015), so it is unsurprising that females (smaller body size) do not have relatively wider biiliac breadth than males (larger body size) controlling for body size. However, females do have relatively wider biiliac breadth than males when controlling for allometric scaling (Table 4.3). However, this result does indicate that the ischiopubis is disproportionately wider in females than males compared to the upper ilium, which remains statistically similar in breadth between sexes controlling for body size. It is possible that this result also reflects the fact that the upper ilium is spatially separated from the birth canal in primates, so a drastic increase in biiliac breadth in females would not provide a direct obstetric advantage. In contrast, increasing the breadth of the ischiopubis directly affects the size and shape of the birth canal.

Lower iliac height is relatively larger in females than males among all species included here except *Alouatta seniculus* and *Papio anubis*. This longer lower iliac height in females compared to males is in accordance with the fact that females also have larger circumferences of the inlet, midplane, and outlet among most species - increasing lower iliac height necessarily increases the distance between the sacroiliac joints, acetabulae, and ischia. Further, increasing inferior iliac height also lengthens the distance between the iliac fossae (origins for the gluteus medius and minimus) and the hip joint. A decreased inferior iliac height in bipeds is thought to help combat hip drop during single-leg stance (Lovejoy, 2005; Lovejoy and McCollum, 2010), so increasing this distance could impact this function in human females. In all primates (not just

humans) lower iliac height is also a rough measurement of the power arm of the gluteal muscles for movement about the hip joint (Waterman, 1929). Additionally, it has been argued that a short iliac breadth is selectively advantageous, especially in primates that have high forces being transmitted through this region of the pelvis (e.g., in leaping primates and in bipeds; Morbeck, 1976; Fleagle, 1978), because a short lower iliac height could decrease the torque produced when the weight of the upper trunk is opposed by upward forces from the lower limb contacting substrate at the acetabulum (Steudel, 1981b). Therefore, dimorphism in lower iliac height among humans and non-human primates may be related to the fact that a short lower iliac height (in males) is advantageous from a locomotor standpoint, but a long lower iliac height (in females) is advantageous for birth.

The fact that dimorphism in lower iliac height is (a) concurrent with dimorphism in birth canal size and (b) found in nearly all primates included here (except *Alouatta seniculus*) holds promise for interpretation of pelvic dimorphism and sex in fossils, even when the birth canal may not be preserved (which is typically the case). Though only a few fossil hominin pelvises preserve a complete or nearly complete birth canal – A.L. 288-1 (*Au. afarensis*; Johansen et al., 1982), BSN49 (probably *Homo erectus*; Simpson et al., 2008), Kebara 2 (Neandertal; Rak and Arensburg, 1987) – the lower ilium is preserved in many specimens, including Sts 14 (*Au. africanus*), MH2 (*Au. sediba*), KNM-ER 3228 and 5881 (early *Homo*; Rose, 1984; Ward et al., 2015); KNM-WT 15000 (*Homo erectus*; Brown et al., 1985) and Tabun 1 and Qafzeh 9 (both Neandertal). Unlike the upper ilium and pubis, the region between the auricular surface of the ilium and the acetabulum is frequently preserved in fossil hominins because this area is

typically quite robust. Because dimorphism in lower ilium height is associated with dimorphism in birth canal size, lower ilium height may be instrumental in increasing the amount of information known about birth canal size in early hominins.

Because dimorphism in the non-obstetric pelvis – including the lower ilium and ischiopubis - appears to be correlated with dimorphism in the birth canal, this implies that the birth canal and non-obstetric pelvis may not be completely independent, though the rostral ilium could be less integrated with other aspects of the pelvis (since this area does not increase in breadth in females to the same extent the ischiopubis does). This decreased integration of some parts of the non-obstetric pelvis with the birth canal could be reflected in how modular the primate pelvis is. This hypothesis is tested in Chapter 5. Further, both the results of this chapter as well as Chapter 2 indicate that pelvic dimorphism is most pronounced in taxa with large cephalopelvic proportions, and this indicates that obstetric selection might maintain these high pelvic dimorphism levels through selection on female pelvic form. This should result in tighter pelvic integration in females than males, especially in species with large cephalopelvic proportions - a hypothesis that is also tested in Chapter 5.

Table 4.1: False Pelvis Landmarks

Bilateral Landmarks	Description
(1) Posterior inferior iliac spine	Posterior-most point of the posterior inferior iliac spine
(2) Posterior superior iliac spine	Posterior-most point of the posterior superior iliac spine
(3) Superior iliac crest	Superior-most point on the iliac crest
(4) Anterior superior iliac spine	Lateral-most point on the anterior superior iliac spine
(5) Superior acetabulum	Point on superior rim of acetabulum in the same plane as anterior inferior iliac spine
(6) Inferior acetabulum	Point on inferior rim of acetabulum in the same plane as ischial ramus
(7) Acetabulum center	Point in the acetabulum at the center of the lunate surface
(8) Posterior acetabulum	Rim of the acetabulum in the same plane as landmarks 7 and 9
(9) Posterior ischial neck	Point on the posterior ischium in the same plane as landmarks 8 and 9
(10) Posterior ischial tuberosity	Posterior-most point on the ischial tuberosity
(11) Lateral ischial ramus	Deepest point along the ischial ramus inferior to the acetabulum
(12) Lateral ischial tuberosity	Lateral-most projection of the ischial tuberosity
(13) Inferior pubic ramus	Point between ischial ramus and inferior pubic ramus in same plane as lateral obturator foramen
Midline Landmarks	Description
(14) Inferior pubic symphysis*	Inferior-most point on symphysis at the midline
(15) Superior pubic symphysis*	Superior-most point on symphysis at the midline

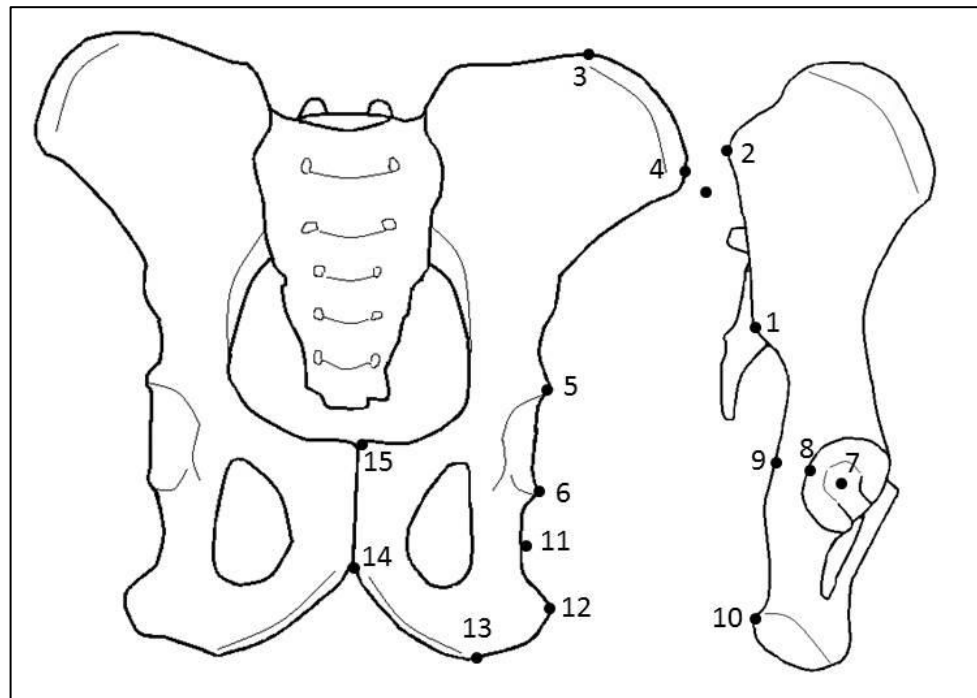


Figure 4.1: Landmarks of the false pelvis: (1) posterior inferior iliac spine; (2) posterior superior iliac spine; (3) superior iliac crest; (4) anterior superior iliac spine; (5) superior acetabulum; (6) inferior acetabulum; (7) acetabulum center; (8) posterior acetabulum; (9) posterior ischial neck; (10) posterior ischial tuberosity; (11) lateral ischial ramus; (12) lateral ischial tuberosity; (13) inferior pubic ramus; (14) inferior pubic symphysis; (15) superior pubic symphysis.

Table 4.2: Reduced major axis regressions of natural logged non-obstetric pelvis dimensions against logged S1 body breadth *

	r ²	x S1 Body Breadth		
		Slope	Slope	Slope
		Anthropoids	Apes	Monkeys
		(C.I)	(C.I)	(C.I)
Pelvic Centroid Size	0.94	1.04* (1.00-1.07)	0.90 (0.82-0.98)	0.97* (0.90-1.04)

*Denotes isometry.

Table 4.3: Dimorphism in non-obstetric pelvic size; Student's t-Tests on residuals

	Pelvic Centroid Size			
	F Mean Residual	M Mean Residual	p-value (sex with more positive mean residual)	Magnitude of Dimorphism [(mean female residual)- (mean male residual)]
Large Cephalopelvic Proportions				
<i>Homo sapiens</i>	-0.13	-0.21	<0.001* (f)	0.08
<i>Hylobates lar</i>	0.07	0.03	0.010* (f)	0.04
<i>Macaca mulatta</i>	0.14	0.12	0.008* (f)	0.02
<i>Nasalis larvatus</i>	0.18	-0.07	<0.001* (f)	0.25
<i>Papio anubis</i>	0.23	0.06	0.002* (f)	0.17
<i>Saimiri sciureus</i>	0.04	-0.02	<0.001* (f)	0.06
Small Cephalopelvic Proportions				
<i>Gorilla gorilla</i>	0.15	0.10	0.024* (f)	0.05
<i>Pan troglodytes</i>	0.18	0.13	0.005* (f)	0.05
<i>Alouatta seniculus</i>	-0.45	-0.44	0.453	0.01
	Iliac Breadth			
	F Mean Residual	M Mean Residual	p-value (sex with more positive mean residual)	Magnitude of Dimorphism [(mean female residual)- (mean male residual)]
Large Cephalopelvic Proportions				
<i>Homo sapiens</i>	-0.23	-0.30	0.005* (f)	0.07
<i>Hylobates lar</i>	0.12	0.05	0.008* (f)	0.07
<i>Macaca mulatta</i>	0.19	0.11	<0.001* (f)	0.08
<i>Nasalis larvatus</i>	0.26	0.17	0.034	0.09
<i>Papio anubis</i>	0.26	0.14	0.006* (f)	0.12
<i>Saimiri sciureus</i>	0.03	-0.01	0.025* (f)	0.04
Small Cephalopelvic Proportions				
<i>Gorilla gorilla</i>	0.29	0.17	0.003* (f)	0.12
<i>Pan troglodytes</i>	0.26	0.23	0.081	0.03
<i>Alouatta seniculus</i>	-0.62	-0.64	0.435	-0.02

* Denotes significance at $\alpha=0.028$.

Table 4.4: Magnitude of Dimorphism Ranks for the Non-Obstetric Pelvis

Species	Magnitude of Dimorphism in Residual Pelvic Centroid Size*	Cephalopelvic Proportions
<i>Nasalis larvatus</i>	0.25	large
<i>Papio anubis</i>	0.17	large
<i>Homo sapiens</i>	0.08	large
<i>Saimiri sciureus</i>	0.06	large
<i>Gorilla gorilla</i>	0.05	small
<i>Pan troglodytes</i>	0.05	small
<i>Hylobates lar</i>	0.04	large
<i>Macaca mulatta</i>	0.02	large
<i>Alouatta seniculus</i>	0.01	small

*Calculated as {(female mean residual) – (male mean residual)}.

Table 4.5: Shape overlap between sexes*

Large Proportions	Percent of Females in Male Shape Space
<i>Homo sapiens</i>	23%
<i>Hylobates lar</i>	60%
<i>Macaca mulatta</i>	9%
<i>Nasalis larvatus</i>	6%
<i>Papio anubis</i>	25%
<i>Saimiri sciureus</i>	12%
Small Proportions	Percent of Females in Male Shape Space
<i>Gorilla gorilla</i>	50%
<i>Pan troglodytes</i>	78%
<i>Alouatta seniculus</i>	67%

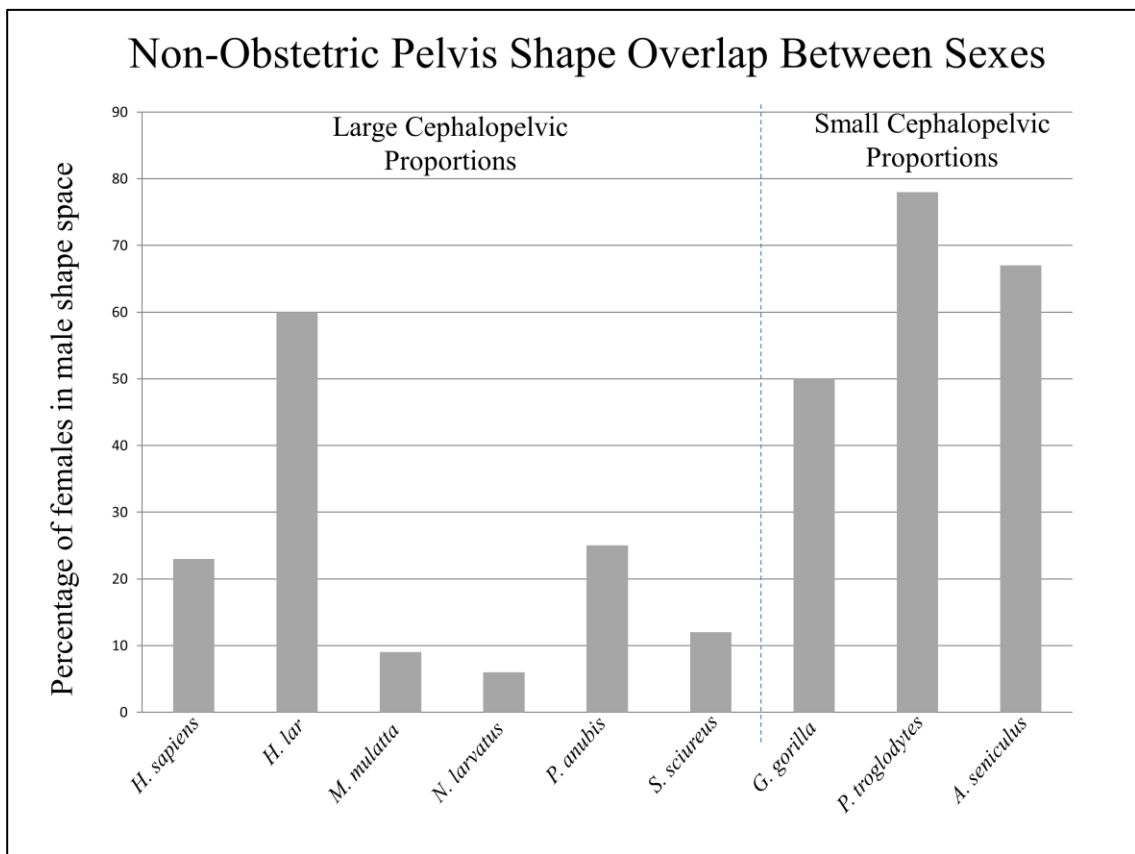


Figure 4.2: Overlap between sexes in 3-D non-obstetric pelvis shape.

Table 4.6: Student's t-tests for dimorphism in birth canal shape‡

	p-value for PC1	Variation explained	p-value for PC2	Variation explained	p-value for PC3	Variation explained
Large Proportions						
<i>Homo sapiens</i>	2.20E-16*	26.7%	2.72E-08*	15.0%	6.01E-03*	9.1%
<i>Hylobates lar</i>	1.85E-07*	23.0%	2.53E-02*	9.9%	2.19E-03*	8.7%
<i>Macaca mulatta</i>	2.20E-16*	24.1%	4.19E-03*	13.6%	9.61E-04*	8.9%
<i>Nasalis larvatus</i>	1.27E-09*	27.6%	3.98E-01	15.2%	1.91E-01	11.9%
<i>Papio anubis</i>	3.53E-02	20.5%	1.61E-01	16.9%	4.29E-01	11.8%
<i>Saimiri sciureus</i>	1.52E-10*	21.7%	2.20E-16*	12.6%	2.88E-01	8.3%
Small Proportions						
<i>Alouatta seniculus</i>	4.43E-02	23.2%	9.24E-01	14.9%	5.07E-01	10.2%
<i>Gorilla gorilla</i>	6.06E-01	18.2%	8.52E-08*	11.8%	2.17E-06*	10.3%
<i>Pan troglodytes</i>	2.45E-03	16.7%	9.30E-04*	13.2%	2.83E-02	9.2%

*Denotes significance at $\alpha=0.028$.

Table 4.7: Euclidean Distance Matrix Analyses of male and female differences in overall non-obstetric pelvis shape within species

	Non-Obstetric Pelvis (unscaled)	Non-Obstetric Pelvis (scaled to geometric mean)
	p-value	p-value
Large Cephalopelvic Proportions		
<i>Homo sapiens</i>	<0.001*	<0.001*
<i>Hylobates lar</i>	0.007*	0.003*
<i>Macaca mulatta</i>	<0.001*	<0.001*
<i>Nasalis larvatus</i>	<0.001*	<0.001*
<i>Papio anubis</i>	0.029	0.032
<i>Saimiri sciureus</i>	<0.001*	<0.001*
Small Cephalopelvic Proportions		
<i>Alouatta seniculus</i>	0.566	0.568
<i>Gorilla gorilla</i>	<0.001*	<0.001*
<i>Pan troglodytes</i>	0.017*	0.018*

*Denotes significance at $\alpha=0.028$.

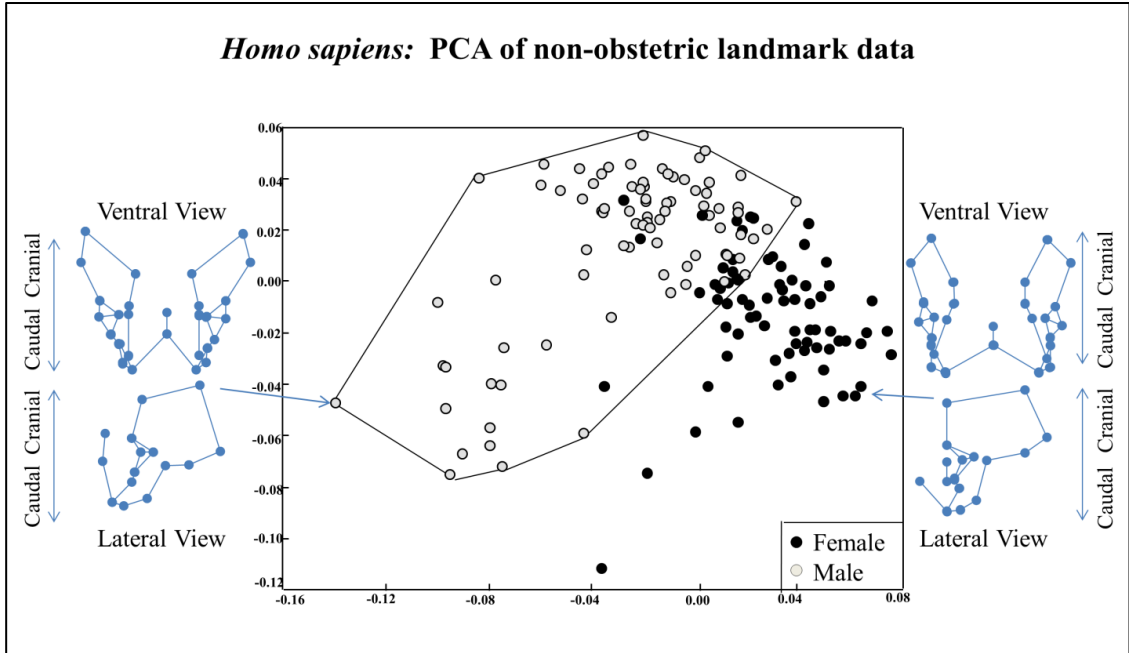


Figure 4.3a: Shape analysis for the false pelvis of *Homo sapiens*. (a) Principal components analysis of false pelvis landmark data. Note the separate clustering of males and females along the X-axis (PC1).

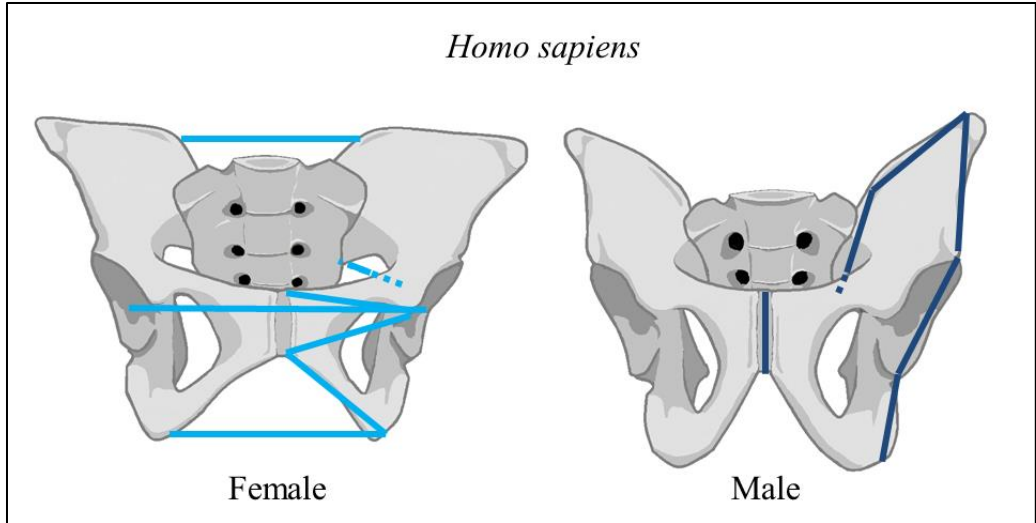


Figure 4.3b: FORM procedure results to obtain dimorphic linear distances in the pelvis of *Homo sapiens* when pelvises are scaled to each individual's geometric mean (body size proxy). Light blue represents linear distances which are greater in females than males. Dark blue represents linear distances which are relatively greater in males compared to females. Only non-overlapping distances are included.

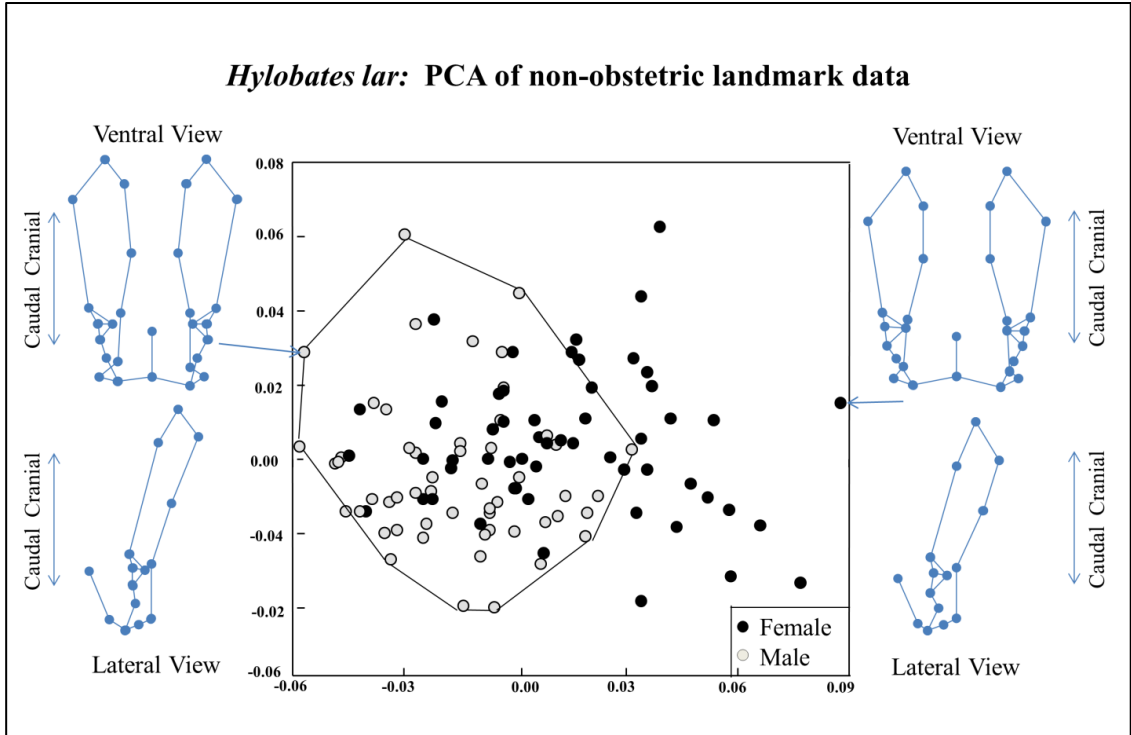


Figure 4.4a: Shape analysis for the false pelvis of *Hylobates lar*. (a) Principal components analysis of false pelvis landmark data.

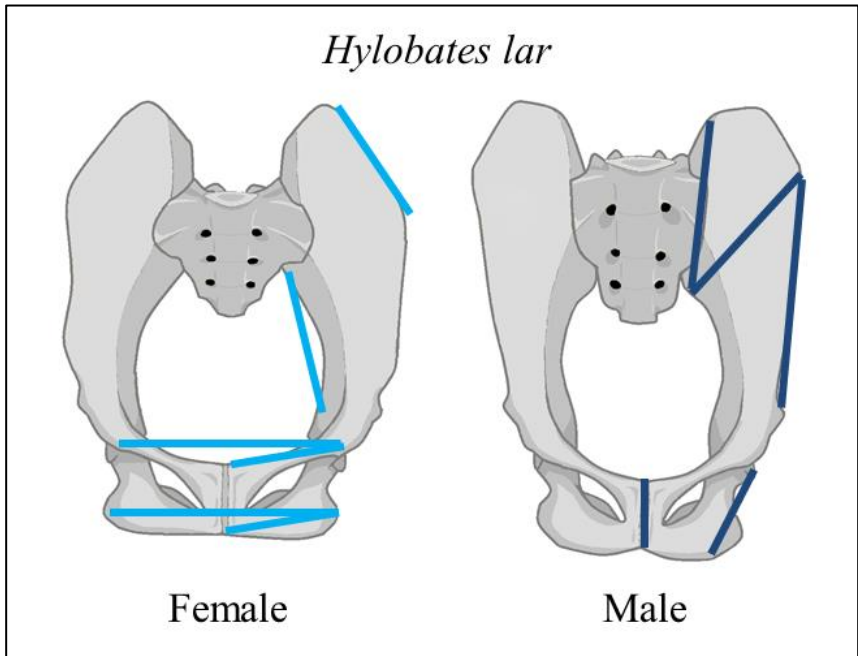


Figure 4.4b: FORM procedure results to obtain dimorphic linear distances in the pelvis of *Hylobates lar* when pelvises are scaled to each individual's geometric mean (body size proxy). Light blue represents linear distances which are greater in

females than males. Dark blue represents linear distances which are relatively greater in males compared to females. Only non-overlapping distances are included.

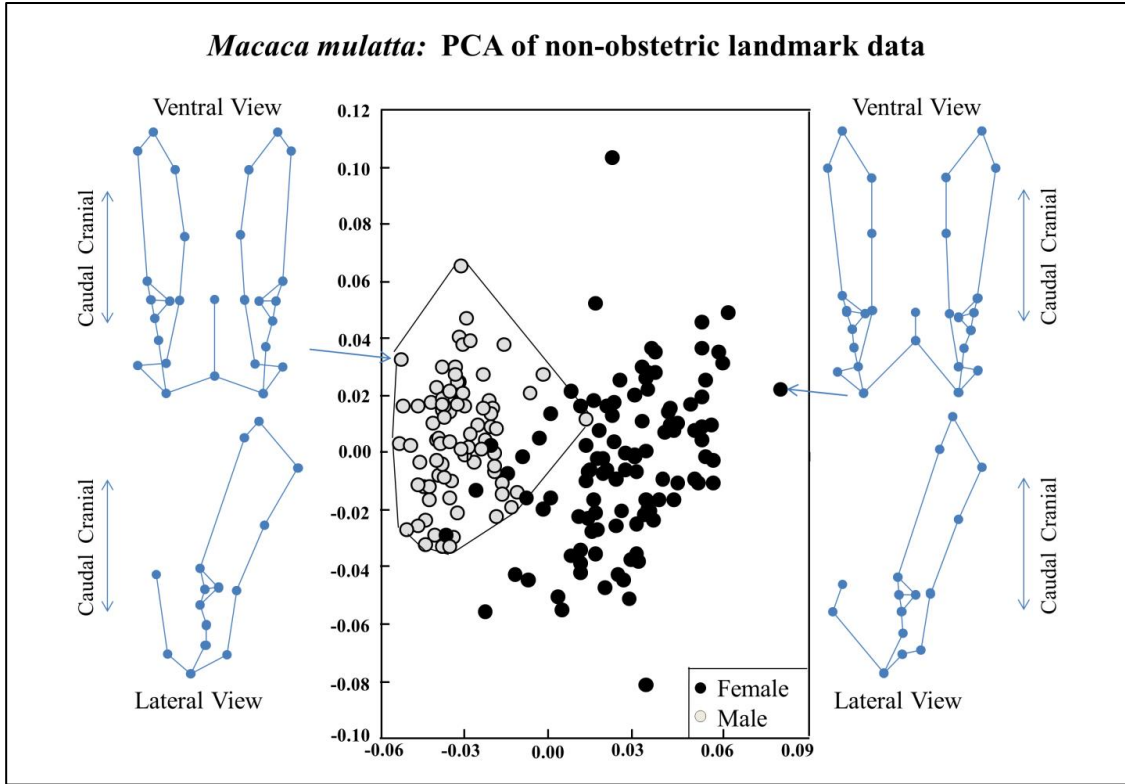


Figure 4.5a: Shape analysis for the false pelvis of *Macaca mulatta*. (a) Principal components analysis of false pelvis landmark data. Note the separate clustering of males and females along the X-axis (PC1).

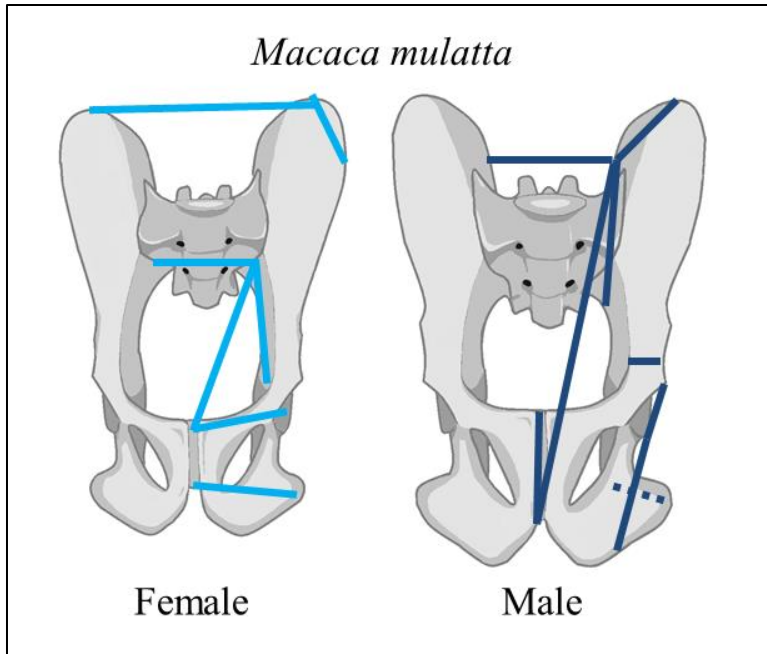


Figure 4.5b: FORM procedure results to obtain dimorphic linear distances in the pelvis of *Macaca mulatta* when pelvises are scaled to each individual's geometric mean (body size proxy). Light blue represents linear distances which are greater in females than males. Dark blue represents linear distances which are relatively greater in males compared to females. Only non-

overlapping distances are included.

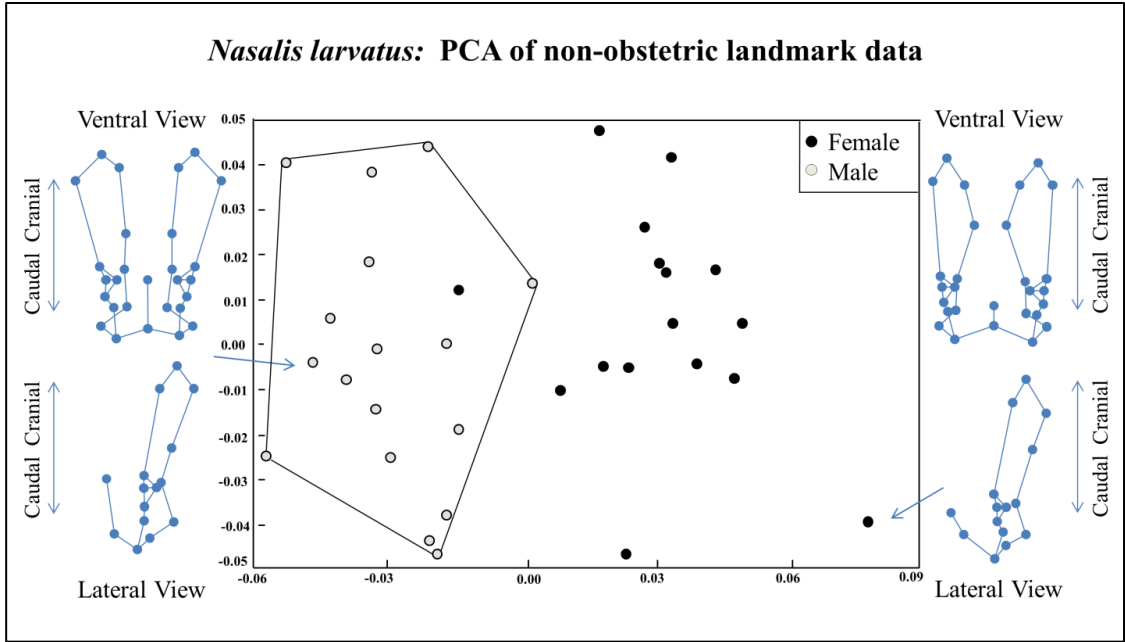


Figure 4.6a: Shape analysis for the false pelvis of *Nasalis larvatus*. (a) Principal components analysis of false pelvis landmark data. Note the separate clustering of males and females along the X-axis (PC1).

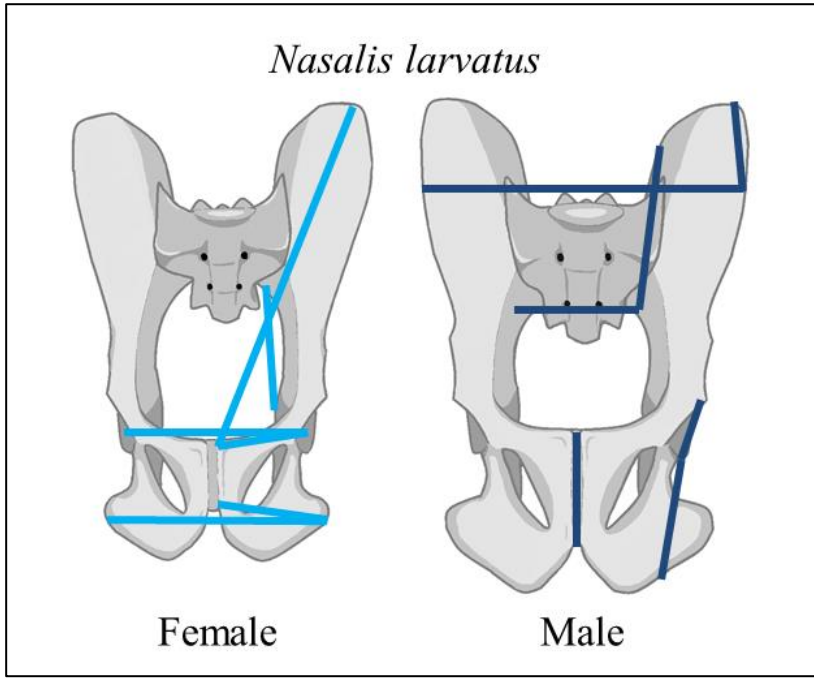


Figure 4.6b: FORM procedure results to obtain dimorphic linear distances in the pelvis of *Nasalis larvatus* when pelves are scaled to each individual's geometric mean (body size proxy). Light blue represents linear distances which are greater in females than males. Dark blue represents linear distances which are relatively greater in

males compared to females. Only non-overlapping distances are included.

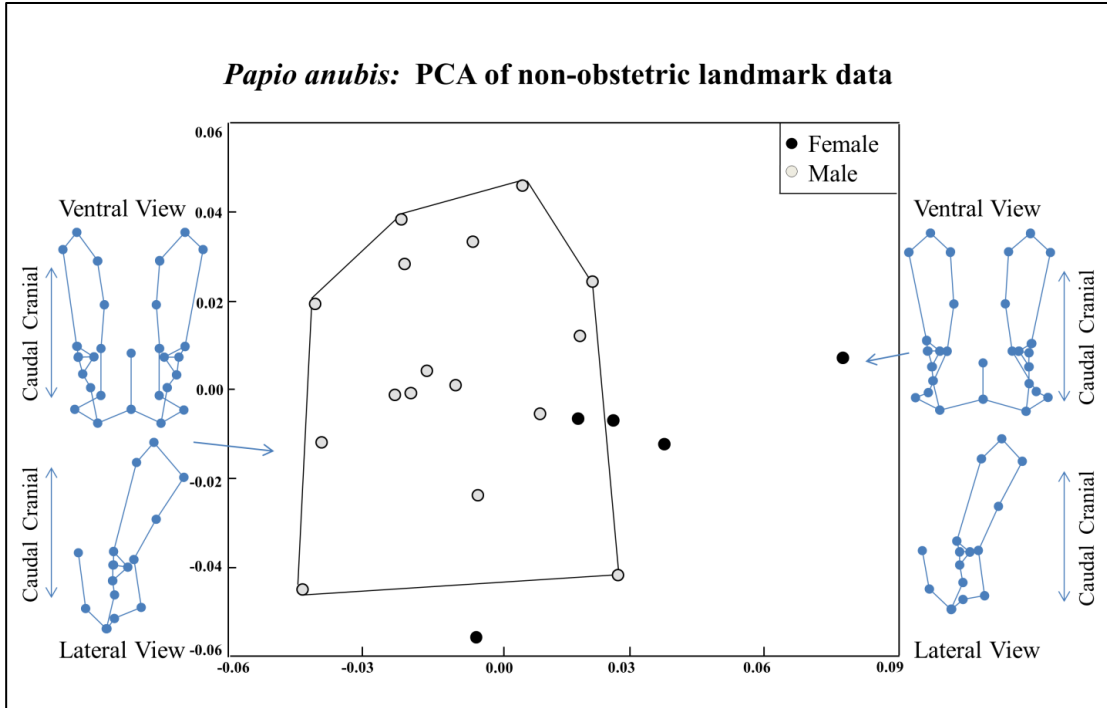


Figure 4.7a: Shape analysis for the false pelvis of *Papio anubis*. (a) Principal components analysis of false pelvis landmark data. Note the separate clustering of males and females along the X-axis (PC1).

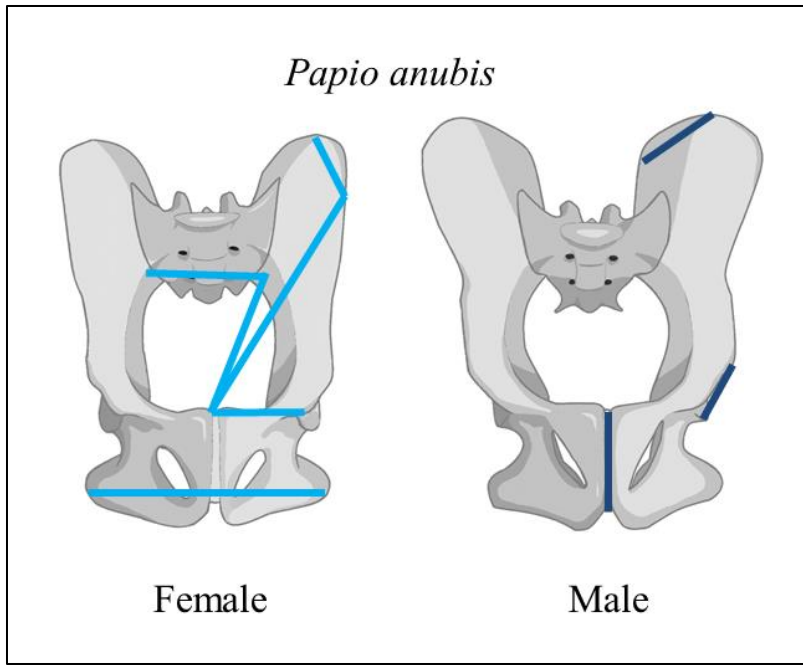


Figure 4.7b: FORM procedure results to obtain dimorphic linear distances in the pelvis of *Papio anubis* when pelvis are scaled to each individual's geometric mean (body size proxy). Light blue represents linear distances which are greater in females than males. Dark blue represents linear distances which are relatively greater in males compared to females. Only non-overlapping distances are included.

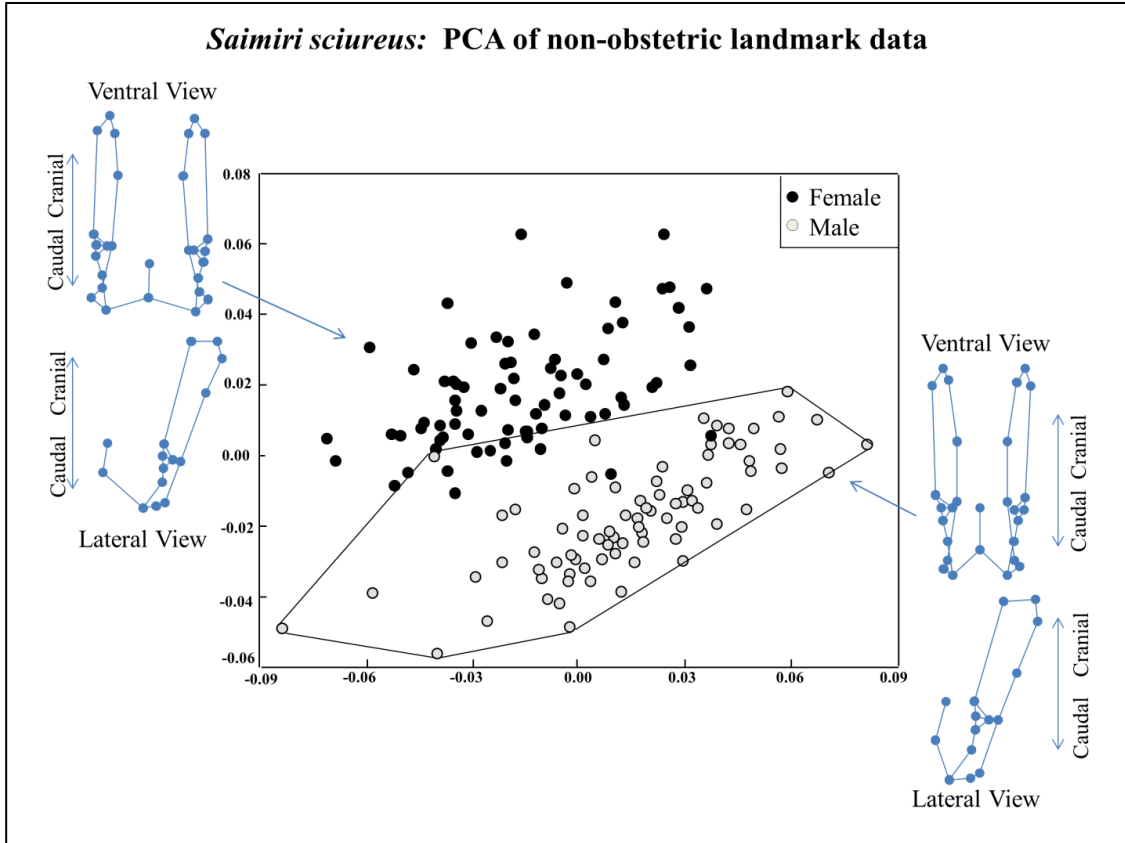


Figure 4.8a: Shape analysis for the false pelvis of *Saimiri sciureus*. (a) Principal components analysis of false pelvis landmark data. Note the separate clustering of males and females along PC1 and PC2.

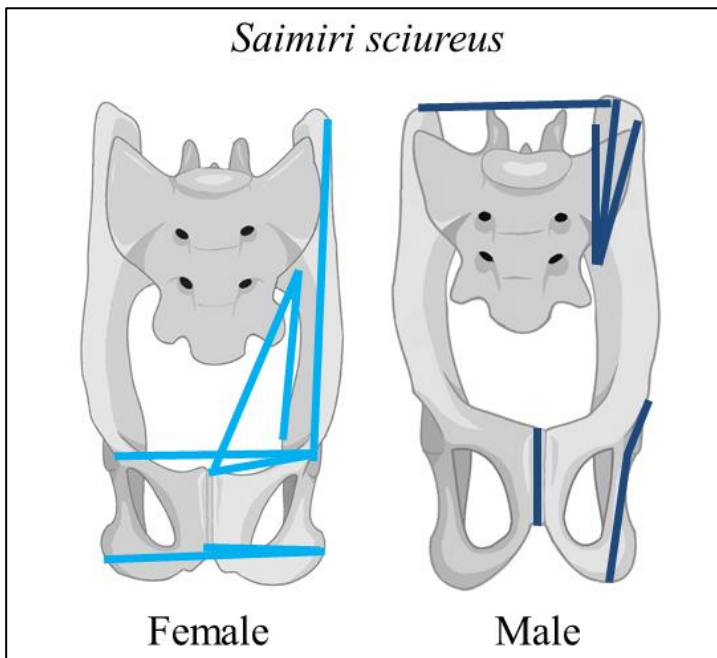


Figure 4.8b: FORM procedure results to obtain dimorphic linear distances in the pelvis of *Saimiri sciureus* when pelvis are scaled to each individual's geometric mean (body size proxy). Light blue represents linear distances which are greater in females than males. Dark blue represents linear distances which are relatively greater in males compared to females. Only non-overlapping distances are included.

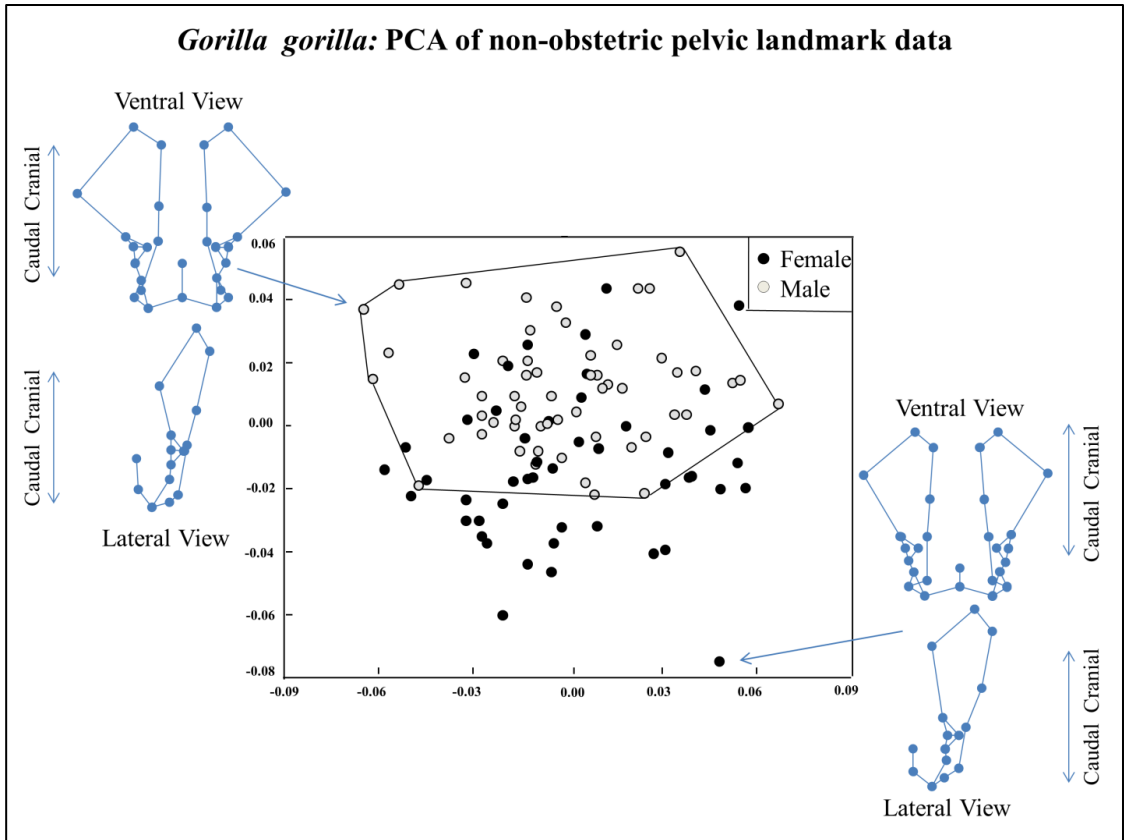


Figure 4.9a: Shape analyses for the false pelvis of *Gorilla gorilla*. (a) Principal components analysis of false pelvis landmark data. Note the lack of clustering of males and females along PC1 and PC2.

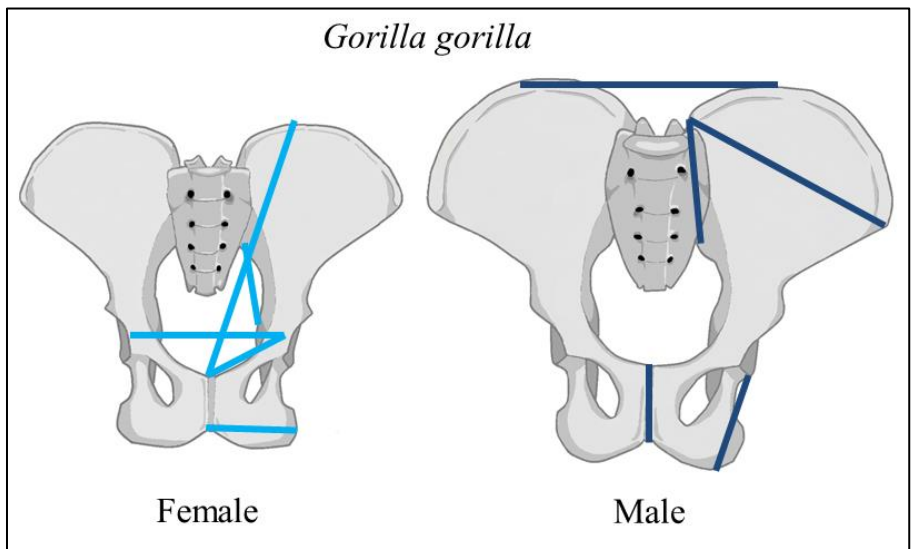


Figure 4.9b: FORM procedure results in *Gorilla gorilla* when pelves are scaled to geometric mean. Light blue represents distances relatively greater in females. Dark

blue represents distances which are relatively greater in males. Only non-overlapping distances are included.

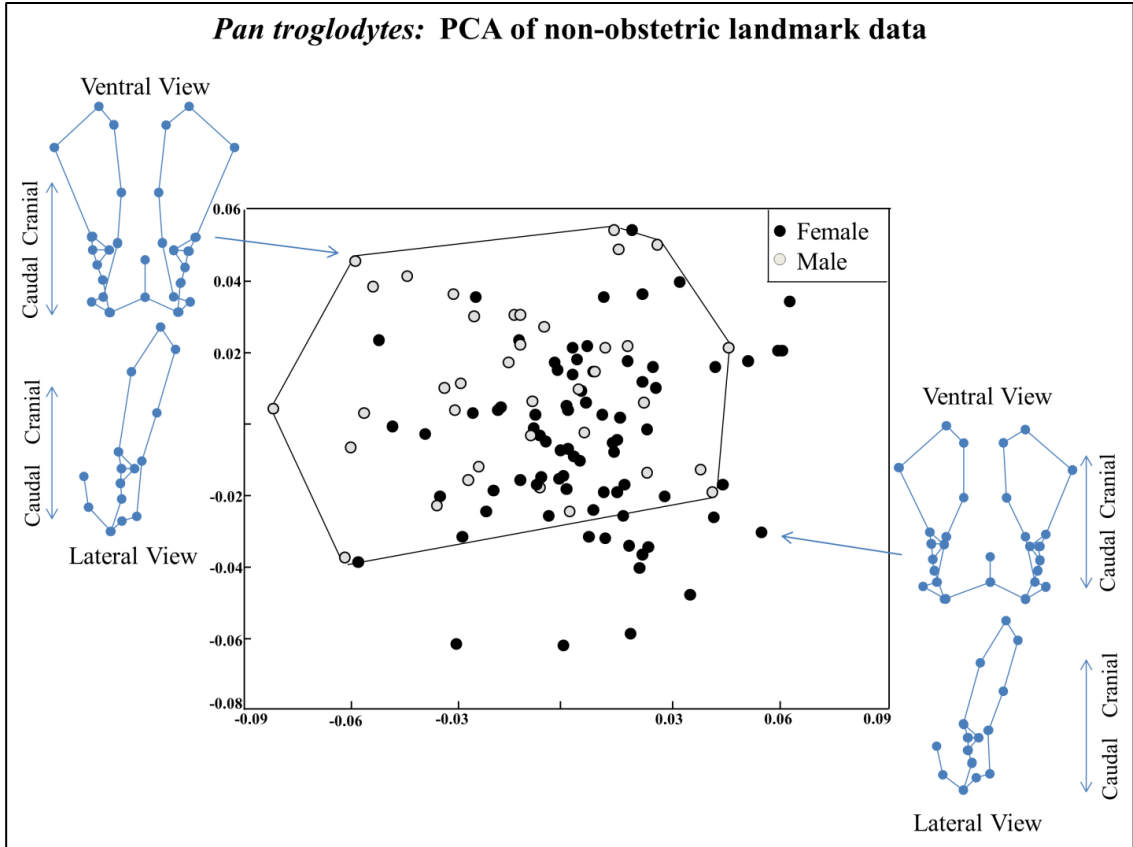


Figure 4.10a: Shape analyses for the false pelvis of *Pan troglodytes*. (a) Principal components analysis of false pelvis landmark data. Note the clustering of males and females along PC1 and PC2.

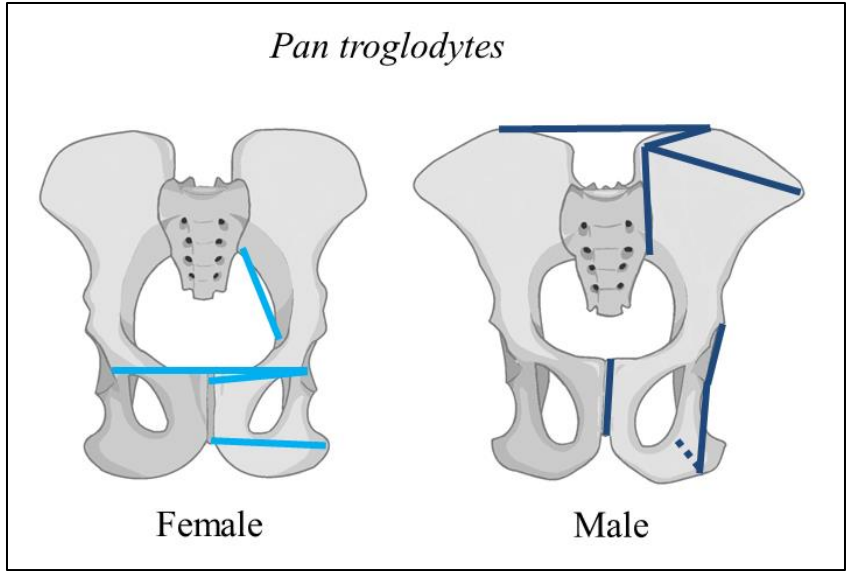


Figure 4.10b: FORM procedure results in *Pan troglodytes* when pelvis are scaled to geometric mean. Light blue represents distances which are relatively greater in females. Dark blue represents distances which are relatively greater in males.

Only non-overlapping distances are included.

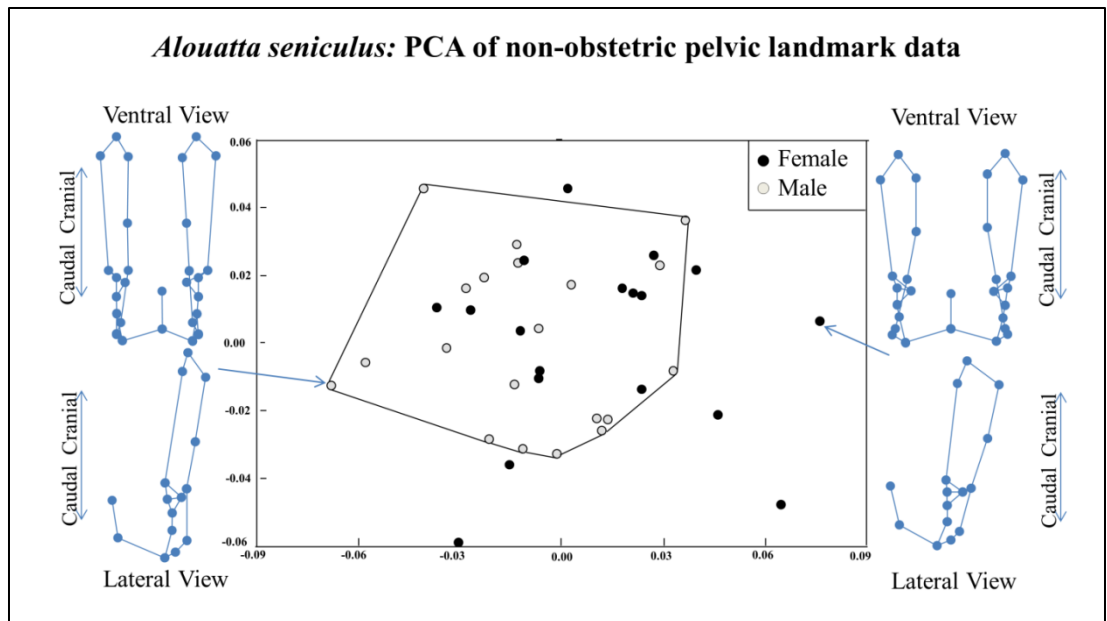


Figure 4.11a: Shape analyses for the false pelvis of *Alouatta seniculus*. (a) Principal components analysis of false pelvis landmark data. Note the lack of clustering of males and females along PC1 and PC2.

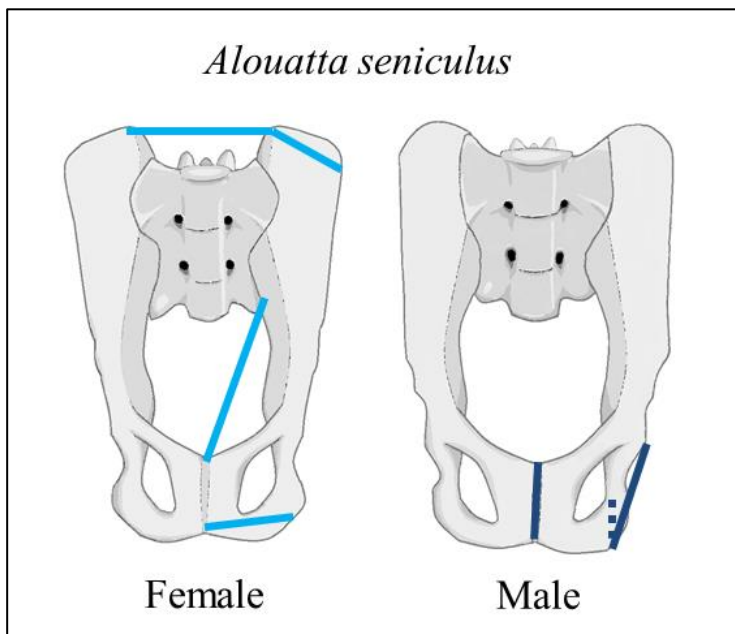


Figure 4.11b: FORM procedure results in *Alouatta seniculus* when pelvis are scaled to geometric mean. Light blue represents distances which are relatively greater in females. Dark blue represents distances which are relatively greater in males. Only non-overlapping distances are included.

CHAPTER 5: INTEGRATION IN THE ANTHROPOID BIRTH CANAL AND NON-OBSTETRIC PELVIS

I. BACKGROUND

Morphological integration, covariation between phenotypic characters (Olsen and Miller, 1958; Chernoff and Magwene, 1999), is influenced by natural selection (Cheverud, 1981). Obstetric (birth-related) selection, which immediately affects maternal and offspring fitness, should affect morphological integration in primate pelves (Grabowski et al., 2011; Lewton, 2012; Grabowski, 2013) because all primates give birth through the bony birth canal. There is a range of cephalopelvic proportions (the fit between maternal birth canal and neonatal head) across anthropoids (Shultz, 1949; Leutenegger, 1970; Stoller, 1995), and primates that give birth to relatively large neonates are under more rigorous obstetric selection than individuals from taxa which give birth to relatively small neonates (Schultz, 1949; Leutenegger, 1970; Stoller, 1995). Consequently, there is more dimorphism in the pelves of primates that give birth to relatively large neonates compared to those that give birth to relatively small ones (See chapters 2-4) – birth canal size and shape is highly dimorphic in these species, and some parts of the non-obstetric pelvis (including biacetabular breadth and lower iliac height) are as well. This indicates that obstetric selection could also affect which parts of the pelvis are integrated (e.g., dimensions of the birth canal) as well as the degree to which they are integrated. The variation in cephalopelvic proportions in anthropoids

provides an opportunity to quantify the effects of obstetric selection on pelvic integration.

Selection for obstetric sufficiency may shape pelvic integration in primates in several ways. First, such selection could determine how the pelvis is divided up into separate modules. (i.e., areas which have strong integration within themselves but low integration between themselves and other such modules; Klingenberg, 2008). Second, obstetric selection could determine how tightly morphologies covary (the *magnitude* of integration) within these individual modules. Third, obstetric selection could determine the patterns of integration (which specific parts strongly covary) within these separate modules. It should be noted that these phenomena are not mutually exclusive, and it is possible for obstetric selection to shape integration in all of these ways simultaneously. Moreover, the modular organization of the pelvis by definition results from the patterns and magnitudes of integration within modules.

A “module” is a unit or number of units of a phenotype which: 1) collectively serve a primary functional role; 2) are integrated; and 3) are somewhat independent (uncorrelated) of other such units (Cheverud, 1988, 1996; Wagner, 1996; Klingenberg, 2008). If only some parts of the pelvis are subject to selection for obstetric selection (e.g., the birth canal; see Chapter 2), whereas other parts of the pelvis are not under direct selection for birth (e.g., the non-obstetric pelvis; see Chapter 4) this could lead to the formation of separate pelvic modules (Grabowski et al., 2011; Lewton, 2012), or it could lead to a reorganization of existing modules into a new modular pattern. Results from Chapters 2 and 4 indicate that while obstetric selection does influence the size and shape of the birth canal, such selection only affects isolated parts of the non-obstetric

pelvis (including biacetabular breadth and lower iliac height), indicating that selection on the non-obstetric pelvis might be somewhat (but not entirely) independent from the birth canal. Indeed, some previous research has indicated that the ischiopubis (which participates heavily in the birth canal) may be in a separate module than the upper ilium (Lewton, 2012), and this could indicate that the birth canal and non-obstetric pelvis may be separate modules in primates.

Previous research has indicated that humans, who have large cephalopelvic proportions and more difficult birth compared to other apes (Schultz, 1949), also have reduced covariation between the birth canal and non-obstetric pelvis compared to other apes (Grabowski, 2013). If the formation of these separate modules (i.e., birth canal and non-obstetric pelvis) in humans (compared to other great apes) is only the result of obstetric demand, other primates with large cephalopelvic proportions (e.g., small-bodied monkeys) should also exhibit low covariation between the birth canal and non-obstetric pelvis. However, this should not be the case in species with small cephalopelvic proportions, which theoretically do not have antagonistic selection pressures on the birth canal and non-obstetric pelvis. Obstetric selection should decrease the covariation between the birth canal and non-obstetric pelvis such that these are separate modules in taxa with large cephalopelvic proportions.

Selection for obstetric sufficiency may also influence how strongly traits covary (the *magnitude* of integration) within each of these hypothesized modules (birth canal and non-obstetric pelvis). It might be expected that taxa which give birth to relatively large neonates should have the strongest covariation between linear distances of the birth canal, because there should be strong stabilizing selection on birth canal size and

shape in these species. Indeed, humans have higher magnitudes of integration in the birth canal compared to other apes (Grabowski et al., 2011), but it is unknown whether this is also the case in other species with large cephalopelvic proportions.

Similarly, taxa with large cephalopelvic proportions might also be expected to have higher magnitudes of integration between linear distances in the non-obstetric pelvis. Chapter 4 demonstrates that selection for obstetric sufficiency increases biacetabular breadth and lower iliac height (distance between the acetabulum and sacroiliac joints) because increasing these linear distances increases birth canal size. Any variation in linear distances of the non-obstetric pelvis could thus affect the size of the birth canal (see Chapter 4). Therefore, it might be expected that species with large cephalopelvic proportions have higher magnitudes of integration among linear distances of the non-obstetric pelvis.

Additionally, in species with large cephalopelvic proportions, it might be expected that females should have higher magnitudes of integration within the birth canal and non-obstetric pelvis compared to males (because females are under direct selection for obstetric sufficiency, but males are not). In contrast, in taxa that give birth to relatively small neonates, females should not have higher magnitudes of integration than males because these females are not subject to rigorous obstetric selection. This would also help to explain why there is a high magnitude of dimorphism in the birth canals and non-obstetric pelvises of anthropoids with large cephalopelvic proportions (see Chapters 2-4) – higher integration in females would constrain female pelvic morphology compared to that of males. In summary, in species with large cephalopelvic proportions, females should have greater magnitudes of integration in the birth canal

and in the non-obstetric pelvis compared to males, but this should not be the case in species with small cephalopelvic proportions.

A final way that obstetric selection could influence pelvic integration is by modifying the *patterns* of integration (which traits strongly covary within modules) in the birth canals and non-obstetric pelvises of anthropoids. However, patterns of morphological integration in the primate skeleton tend to be conserved (Cheverud, 1996; Ackerman and Cheverud, 2000; Marroig and Cheverud, 2001). Therefore, it would be unlikely that obstetric selection modifies integration patterns within the birth canal or non-obstetric pelvis, but it is still possible. For example, it could be the case that taxa with large cephalopelvic proportions have strong integration between the mediolateral dimensions and circumferences of the pelvic inlet, midplane, and outlet (which are under strong stabilizing selection for obstetric sufficiency; see Chapter 2) but weaker integration between the rostrocaudal dimensions of the birth canal, which are under less stringent selection for obstetric sufficiency (see Chapter 2). However, this pattern would not be expected to be shared with taxa with small cephalopelvic proportions, because these smaller proportioned taxa are not subject to the same obstetric selection pressures.

Similar to what was proposed for magnitudes of integration, it might be expected that patterns of integration within modules could differ between males and females within large cephalopelvic proportion taxa (such that the sexes have different integration patterns due to obstetric selection on females), but again this would be unlikely considering that integration patterns within modules tend to remain conserved

in primates (Cheverud, 1996; Ackerman and Cheverud, 2000; Marroig and Cheverud, 2001).

The goal of this study is to quantify the effects of cephalopelvic proportions on pelvic modularity, as well as to test whether obstetric demand influences the magnitudes or patterns of integration within these hypothesized modules - the birth canal or non-obstetric pelvis - of anthropoid primates. This chapter tests the following hypotheses:

II. HYPOTHESES

Hypothesis 1: (Table 5.1) The birth canal and non-obstetric pelvis represent two separate modules.

Prediction 1a: Large cephalopelvic proportions result in low covariation between the birth canal and non-obstetric pelvis. Species with large cephalopelvic proportions will exhibit high covariation within those modules but low covariation between separate modules. However, this pattern will not be apparent in species with small cephalopelvic proportions.

Hypothesis 2: (Table 5.1) Large cephalopelvic proportions result in higher *magnitudes* of integration within the birth canal.

Prediction 2a: Primates with large cephalopelvic proportions will exhibit greater magnitudes of integration (i.e., greater covariance

between linear distances) in the birth canal, due to obstetric selection maintaining pelvic morphology, compared to species with small cephalopelvic proportions.

Prediction 2b: In species with large cephalopelvic proportions females will have a greater magnitudes of integration in the birth canal compared to males, but this will not be true in species with small proportions.

Hypothesis 3: (Table 5.1) Large cephalopelvic proportions result in higher *magnitudes* of integration within the non-obstetric pelvis (because selection for birth sufficiency might also select for strong covariation between specific morphologies of the non-obstetric pelvis).

Prediction 3a: Primates with large cephalopelvic proportions will exhibit greater magnitudes of integration (i.e., greater covariance between linear distances) in the non-obstetric pelvis compared to species with small cephalopelvic proportions.

Prediction 3b: If prediction 3a is not supported, in species with large cephalopelvic proportions females will have greater magnitudes of integration in the non-obstetric pelvis compared to males, but in species with small cephalopelvic proportions females will not have higher integration than males.

Hypothesis 4: (Table 5.1) Large cephalopelvic proportions are not associated with specific *patterns* of integration in the birth canal.

Prediction 4a: All species share similar patterns of integration in the birth canal regardless of cephalopelvic proportions.

Prediction 4b: Within species, males and females will have similar patterns of integration within the birth canal.

Hypothesis 5: (Table 5.1) Large cephalopelvic proportions are not associated with specific *patterns* of integration in the non-obstetric pelvis.

Prediction 5a: All species share similar patterns of integration in the non-obstetric pelvis regardless of cephalopelvic proportions.

Prediction 5b: Within species, males and females will have similar patterns of integration within the non-obstetric pelvis.

III. MATERIALS AND METHODS

a. Samples

Previous studies have determined that integration analyses require 40-60 individuals per species per sex for sufficient power to determine differences in integration between samples (Cheverud, 1988; Grabowski et al., 2011; Grabowski, 2013). Sufficiently large samples existed for six taxa (see also Chapter 2, Table 2.1), including four with large cephalopelvic proportions [*Homo sapiens* (n=156), *Hylobates lar* (n=112), *Macaca mulatta* (n=187), *Saimiri sciureus* (n=153)], and two with small proportions [*Gorilla gorilla* (n=106) and *Pan troglodytes* (n=114)]. Cephalopelvic

proportions for species included in the present study have been presented previously (Chapter 2).

It is likely that phylogeny may influence pelvic integration, but the small number of taxa included in this study preclude formal phylogenetic testing - though techniques are available, statistical analysis would have low power to detect phylogenetic signal in the small number of taxa included (Blomberg et al. 2003). However, the sample in the present study included apes (*Homo*, *Hylobates*, *Gorilla*, *Pan*), as well as a species of Old World Monkey (*Macaca mulatta*) and a species of New World Monkey (*Saimiri sciureus*). Furthermore, this sample comprised the largest sample sizes currently in existence worldwide for most taxa represented. Moreover, the sample included large sample sizes of both monkeys and hominoids, as well as increased sample sizes of individual monkey taxa compared to previous studies (Lewton, 2012; Grabowski, 2013).

b. Data

Three-dimensional landmark data collected on the pelves of adult male and female pelves (collection techniques presented in Chapter 2), were used for these analyses (Figure 5.1, Table 5.1). All statistical procedures were performed on unilateral landmarks in these integration analyses in order to avoid spurious findings of increased magnitudes of integration due to high covariation among bilaterally-distributed landmarks (Chapters 2 and 4 included bilateral landmarks).

For some integration analyses it was necessary to use linear distances within the birth canal and within the non-obstetric pelvis to determine the magnitude and pattern of integration. Therefore, in addition to using landmark data from the birth canal and non-obstetric pelvis, linear distances which reflect important obstetric or biomechanically-relevant dimensions in the pelvis (as described in Chapters 2 and 4) were also included. These distances were derived from 3D landmark data (Figures 5.2 and 5.3). Linear distances for the birth canal (n=8; Figure 5.2) include the anteroposterior and mediolateral dimensions of the pelvic inlet, midplane, and outlet, as well as sacral breadth at linea terminalis and pubis length. Linear distances chosen to represent the non-obstetric pelvis (n=7; Figure 5.3) included inferior (lower) iliac height, superior (upper) iliac height, iliac breadth, iliac neck thickness, ischial length, ischial tuberosity breadth, and biacetabular breadth.

c. Testing Hypothesis 1

The first hypothesis (Table 5.1) predicts that the birth canal and non-obstetric pelvis represent two separate modules. Modularity testing of 3D landmarks (Klingenberg, 2009) was used to test this hypothesis. Modularity testing uses the R_V coefficient (a measure of covariation between the sets of landmarks in separate modules) to test modularity statistically, with significance of each modularity test determined using a permutation test of randomly-generated modules (10,000 permutations). For each species, the R_V coefficient for the hypothesized modules (i.e., the birth canal and non-obstetric pelvis) was compared to the distribution of R_V

coefficients derived for all randomly-generated modules. If the R_V coefficient for the hypothesized modules was smaller than 95% of other randomly-generated modules, the test was considered significant (*i.e.*, that there is low correlation between modules). A significant result for modularity testing indicated that the partitioning of hypothesized modules (birth canal and non-obstetric pelvis) was supported (and that there was low correlation between modules). All modularity tests were conducted in MorphoJ (Klingenberg, 2009). This study included a much larger number of specimens for individual taxa and similar numbers of landmarks ($n=22$) compared to a previous study of pelvic modularity (Lewton, 2012; 17 landmarks), which indicated that the power should be relatively high for the current analyses for detecting covariation between hypothesized modules.

If the birth canal and non-obstetric pelvis do, in fact, represent two modules that can respond separately to selection pressures, results for modularity testing should indicate a significant result supporting the presence of these two hypothesized modules.

d. Testing Hypothesis 2

Prediction 2a (Table 5.1) is that primates with large cephalopelvic proportions will exhibit an increased *magnitude* of integration in the birth canal compared to species with small cephalopelvic proportions. Therefore, in order to test this hypothesis, the magnitude of integration among linear birth canal dimensions was first calculated (Figure 5.2).

Covariance matrices for birth canal linear metric data were calculated using R. In order to be able to compare statistics calculated using multiple covariance matrices, these matrices must be standardized; here, covariance matrices were standardized by the individual linear distance means within the matrices (Houle, 1992; Hansen and Houle, 2008) prior to further analysis. In order to control for the confounding effects of geographic variation within taxa the residual covariance from MANOVAs were used, with linear distances as the dependent variables and either (a) racial origin (for humans; either black or white) or (b) subspecies designation or country of origin (if known for non-human taxa) as the dependent variables (Young et al. 2010; Grabowski, 2011; Middleton, 2015). Covariances were then pooled across populations. Similarly, differences between sexes within a single population could affect measures of integration (Marroig et al., 2009). Therefore, in all analyses that compare integration between taxa, residual covariances from MANOVAs (this time with sex as the independent variable) were pooled across sexes.

To quantify the magnitude of birth canal integration within each species, the variance of each covariation matrix's eigenvalues – i.e., eigenanalysis (Cheverud, 1983; Wagner, 1984; Cheverud, 1989) - was employed to quantify the overall level of integration within each species. The rationale for employing eigenanalysis in this context is that when linear distances strongly covary with one another, the majority of the variation resides in the first dimension of a principal components analysis, which increases the variance of the eigenvalues of the first eigenvector (Wagner, 1984; Cheverud et al., 1989; Villmoare et al., 2011; Lewton, 2012). This means that species that have high magnitudes of integration (covariation) between birth canal linear

distances exhibit high eigenvalue variances of the first eigenvector (VE), whereas taxa with low levels of integration between linear distances exhibit low VE values.

VE values are not directly comparable between samples (Pavlicev, 2009). Therefore, for each species, the original covariation matrix was bootstrapped 1000 times to create a bootstrapped sample of VE values, and the bootstrapped VE values were standardized by the maximum possible eigenvalue variance of each matrix (standardized VE) (Pavlicev, 2009). Standardized VE values were then compared between separate samples in a pairwise fashion using a bootstrap resampling method (Manly, 1997) following Lewton (2012) and Scott (2010). Statistical significance of each interspecific pairwise comparison was assessed using a difference of means test following Lewton (2012) and Scott (2010). Each specific pairwise comparison revealed whether species have statistically different magnitudes of integration within the birth canal. All eigenanalysis-based integration analyses were performed in R using the “boot” package (Ripley, 2016). The number of linear distances included for the birth canal ($n=8$) was very low compared to the number of individuals represented by each species (minimum $n=106$), and this indicates that the power for all eigenanalysis-based integration analyses should be high (Cheverud, 1988).

The hypothesis that magnitude of integration in the birth canal will be greater in species with large cephalopelvic proportions compared to species with small proportions was considered to be falsified if species having large cephalopelvic proportions did not have statistically greater mean integration (and statistically greater standardized VE values) in the birth canal compared to species with small cephalopelvic proportions.

Prediction 2b posits that among species with large cephalopelvic proportions, females will have a higher magnitude of integration within the birth canal compared to males, but this will not be the case in species with small cephalopelvic proportions. In order to test this hypothesis, standardized eigenvalue variance (Standardized VE; see description above) was calculated for each sex within each species for (a) linear distances of the birth canal and (b) linear distances of the non-obstetric pelvis and then compared between sexes using a bootstrap resampling method (Manly, 1997). For each sex, the original covariation matrix was bootstrapped 1000 times, and standardized VE was calculated from the bootstrapped sample. Statistical significance of each between sex comparison was assessed using a difference of means test following Lewton (2012) and Scott (2010). Each specific pairwise comparison demonstrated whether sexes shared different magnitudes of integration within the birth canal. All eigenanalysis-based integration analyses were performed in R using the “boot” package (Ripley, 2016).

The hypothesis that females in species with large cephalopelvic proportions have higher magnitudes of integration in the birth canal and non-obstetric pelvis compared to males was rejected if females of species with large cephalopelvic proportions do not have statistically greater magnitudes of integration in the birth canal and non-obstetric pelvis than males.

e. Testing Hypothesis 3

Prediction 3a (Table 5.1) is that primates with large cephalopelvic proportions will exhibit an increased *magnitude* of integration in the non-obstetric pelvis compared to species with small cephalopelvic proportions. Covariance matrices for linear metric data contributing to the non-obstetric pelvis (Figure 5.3) were calculated, and matrices were standardized (Houle, 1992; Hansen and Houle, 2008) following the procedures described above (d. Testing Hypothesis 2). As previously described for the birth canal, pooled covariances from MANOVAs were used to control for the confounding effects of geographic variation and sex.

To quantify the magnitude of non-obstetric pelvis integration within each species, eigenanalysis (Cheverud, 1983; Wagner, 1984; Cheverud, 1989) was employed as described above. In order to be able to directly compare the magnitude of integration (VE) among species, VEs of each species-specific covariation matrix were standardized (standardized VE; Pavlicev, 2009) as described above, and then standardized VE was compared across all species in a pairwise fashion using a bootstrap resampling method (Manly, 1997). Statistical significance of each interspecific pairwise comparison was assessed using a difference of means test as described above. The number of linear distances included for the non-obstetric pelvis ($n=7$) was very low compared to the number of individuals represented by each species (minimum $n=106$), and this indicates that the power of all eigenanalysis-based integration analyses should be high (Cheverud, 1988).

The hypothesis that magnitude of integration in the non-obstetric pelvis will be greater in species with large cephalopelvic proportions compared to species with small proportions was considered to be falsified if species having large cephalopelvic

proportions did not have statistically greater mean integration (and statistically greater standardized VE values) in the non-obstetric pelvis compared to species with small cephalopelvic proportions.

Prediction 3b further predicts that among species with large cephalopelvic proportions, females will have a higher magnitude of integration within the non-obstetric pelvis compared to males, but this will not be the case in species with small cephalopelvic proportions. In order to test this hypothesis, standardized eigenvalue variance (Standardized VE; see description above) was calculated for each sex within each species for linear distances of the non-obstetric pelvis and then compared between sexes using a bootstrap resampling method (Manly, 1997), as described above. Statistical significance of each between sex comparison was assessed using a difference of means test.

The hypothesis that females in species with large cephalopelvic proportions have higher magnitudes of integration in the non-obstetric pelvis compared to males was rejected if females of species with large cephalopelvic proportions do not have statistically greater magnitudes of integration in the non-obstetric pelvis than males.

f. Testing Hypothesis 4

Prediction 4a (Table 5.1) states that all species will exhibit similar *patterns of* integration within the birth canals. In order to test this hypothesis, Mantel tests of matrix similarity (Mantel, 1967) were used to compare integration patterns in the birth canal between species pairs. Mantel tests quantified the correlation between two matrices

using a permutation approach with the null hypothesis that two matrices are completely unrelated. Thus, a significant positive result ($p < 0.025$ as indicated by the False Discovery Rate procedure; see section g below for justification for this alpha level) indicated that two matrices are not statistically significantly different, and that two species share a similar overall pattern of integration. Power for these Mantel tests is high due to the large sample sizes collected for this study (Dietz, 1983).

Mantel tests of matrix similarity, which quantify whether there are statistical differences in the pattern of integration between species, do not allow interpretation of *how* these patterns of integration actually differ between groups (if integration patterns do differ). However, these statistics did provide information about *whether* patterns of pelvic integration differ between groups, which provided a set of hypotheses to test further in the future using bootstrap-based methods (Cole, 2002) to localize the sites where these patterns of integration differ.

Prediction 4b posits that the *patterns* of integration in the birth canal are similar between sexes. Mantel tests of matrix similarity, as outlined above, were used to test whether males and females within each species differed in their overall patterns of integration in the birth canal.

g. Testing Hypothesis 5

Prediction 5a (Table 5.1) posits that all species will exhibit a similar *pattern* of integration within the non-obstetric pelvis. In order to test this hypothesis, Mantel tests (Mantel, 1967) of matrix similarity were used to compare integration patterns in the

birth canal between species pairs as described above. Power for these Mantel tests should be relatively high due to the large sample sizes collected for this study (Dietz, 1983).

Prediction 5b posits that the *patterns* of integration in the non-obstetric pelvis are similar between sexes. Mantel tests of matrix similarity were used to test this hypothesis.

h. Controlling for Multiple Comparisons

In order to control for Type I Error in this study, a False Discovery Rate (FDR) procedure (Benjamini and Hochberg, 1995) as described in Chapter 2 was performed on all raw p-values. The FDR procedure indicates that in order to maintain a false discovery rate of 5%, α -level should be set at 0.025. Therefore, unadjusted p-values are reported in the text, but only those p-values less than 0.025 are considered significant.

i. Limitations

The statistics used here to quantify differences in the pattern of integration among species and between sexes (i.e., Mantel Tests of matrix similarity) did not allow interpretation of specifically how and where these patterns of integration actually differ between groups. Therefore, future research should aim to quantify the precise differences in patterns of integration between sexes and between species using bootstrap-based methods (Cole, 2002).

The samples used here were not ideal for controlling for phylogeny, as there are only six taxa represented. However, these are the only taxa in existence with large enough sample sizes to perform integration analyses for which there are also data on cephalopelvic proportions, which is key to these analyses. Therefore, future studies should seek to quantify cephalopelvic proportions in larger numbers of taxa, as this will allow further comparison of integration patterns as well as formal phylogenetic comparisons.

IV. RESULTS

a. Hypothesis 1: Are the Birth Canal and Non-Obstetric Pelvis Separate Modules?

Hypothesis 1 predicts that the birth canal and non-obstetric pelvis represent two separate modules within the pelvis, and that this should be most apparent in species with large cephalopelvic proportions. This hypothesis can be rejected (Table 5.1). Modularity testing (Table 5.4) does indicate that the birth canal and non-obstetric pelvis are separate modules in two of the four taxa with large cephalopelvic proportions - *Homo sapiens* ($p = 0.0005$; Table 5.4) and *Macaca mulatta* ($p = 0.0096$; Table 5.4). Support was not found for these being separate modules in any other species ($p > 0.025$ in all cases). It is possible that sample size affects the outcome of the observed results because positive results were obtained for the two taxa with the largest sample sizes (*H. sapiens* $n=156$; *M. mulatta* $n=187$), but these are similar sample sizes to other taxa for which positive results were not obtained (e.g., *Saimiri sciureus*, $n=153$). Therefore,

these results do not appear to be sample size dependent. Thus, the results of this study indicate that the birth canal and non-obstetric pelvis are separate modules in *H. sapiens* and *M. mulatta*, but not in other included taxa. Because low covariation between the birth canal and non-obstetric pelvis characterizes only two species with large cephalopelvic proportions, the hypothesis that large cephalopelvic proportions influence pelvic modularity (Hypothesis 1; Table 5.1) is not supported.

b. Hypothesis 2: Do cephalopelvic proportions influence the *magnitude* of integration in the birth canal?

Prediction 2a posits that primates with large cephalopelvic proportions exhibit an increased *magnitude* of integration in the birth canal compared to species having small cephalopelvic proportions. Prediction 2a is not supported (Tables 5.5 and 5.6). Overall, species with large cephalopelvic proportions do not have statistically higher magnitudes of integration in the birth canal than species with small proportions (Table 5.6). Though *Hylobates lar* (large proportions) does have the highest magnitude of integration in the birth canal (Standardized VE = 0.10; Table 5.5), *Gorilla gorilla* (small proportions) has a higher magnitude of integration than *Homo sapiens* and *Macaca mulatta* (0.0838 in *Gorilla* vs. 0.0787 in both *Homo* and 0.0625 in *Macaca*; Table 5.5). These results do not appear to be due to sample size discrepancies, because two taxa which have low magnitudes of integration *H. sapiens* and *M. mulatta* also have the highest sample sizes. Thus, taxa with large proportions do not have greater magnitudes

of integration in the birth canal compared to small proportion species (Prediction 2a not supported).

However, if we look within species, cephalopelvic proportions do appear to increase the magnitude of integration in females compared to males (Table 5.7), supporting Prediction 2b. Across species with large cephalopelvic proportions except for *Macaca mulatta*, females have higher magnitudes of integration (i.e., higher standardized VE values; Table 5.7) in the birth canal than males (all p-values <0.025). This result for *M. mulatta* could be related to the fact that this sample comes from a population living in a non-native environment that may exhibit reduced genetic variability compared to wild specimens, which could affect integration in this sample (see further discussion below). This is not true for either species with small cephalopelvic proportions - in *Gorilla gorilla*, there is no difference between the sexes in the magnitude of integration in birth canal linear distances (p=0.672), while in *Pan troglodytes*, males actually have greater birth canal integration than females (p=0.002).

Because large cephalopelvic proportions are found to be related to higher magnitudes of integration in female birth canals compared to those of males in 3 of 4 species with large cephalopelvic proportions (and neither species with small proportions), Hypothesis 2 cannot be rejected.

c. Hypothesis 3: Do cephalopelvic proportions influence *magnitudes of integration in the non-obstetric pelvis*?

Hypothesis 3, Prediction 3a predicts that species with large cephalopelvic proportions will have higher magnitudes of integration in the non-obstetric pelvis than species with small proportions. This prediction is supported, because taxa with large cephalopelvic proportions (with the exception of *Macaca mulatta*) do have statistically higher magnitudes of integration (Range of 0.0599-0.0759; Table 5.9) (standardized VE) in the non-obstetric pelvis compared to all taxa with small proportions (both < 0.0595; Table 5.8 and 5.9).

Prediction 3b further predicts that females among species with large cephalopelvic proportions will have greater magnitudes of integration in the non-obstetric pelvis compared to males, but this will not be the case in species with small proportions. This prediction is also supported in 3 of 4 species with large cephalopelvic proportions (Table 5.10). Within all species with large cephalopelvic proportions except *Homo sapiens*, females do have higher magnitudes of integration compared to males (all p-values <0.002; Table 5.10), but this is not the case in either species with small cephalopelvic proportions. The fact that in humans, males have statistically higher magnitudes of non-obstetric pelvic integration could reflect the fact that human female non-obstetric pelvic form is frequently argued to represent a tradeoff between obstetric and locomotor functions, whereas that of males represents selection for locomotion only, because bipeds are under selection for reduced biacetabular breadth and lower iliac height (Washburn, 1960; Pinkerton, 1973; Zihlman, 1978; Ruff, 1995), but reduction of these distances is obstetrically dangerous (Rosenberg, 1992; Ruff, 1995; Rosenberg, 2002).

d. Hypothesis 4: Do cephalopelvic proportions influence *patterns of integration in the birth canal*?

Prediction 4a predicts all species share similar patterns of integration in the birth canal regardless of cephalopelvic proportions. This prediction is supported because the results of pairwise Mantel tests of matrix similarity (Table 5.11) indicate that integration patterns in the birth canal are similar among all anthropoid species included ($p < 0.001$ in all cases). Differences in cephalopelvic proportions across taxa do not appear to influence differences in birth canal integration patterns across species.

Similarly, males and females have similar patterns of integration in the birth canal among all taxa included (Table 5.12).

Based on the results of this study, Hypothesis 4 cannot be rejected (Table 5.1).

e. Hypothesis 5: Do cephalopelvic proportions influence *patterns of integration in the non-obstetric pelvis*?

Prediction 5a posits that primates have similar patterns of integration in the non-obstetric pelvis regardless of cephalopelvic proportions. This prediction is not supported (Table 5.13), because all primates do not share one pattern of integration (Table 5.13). However, patterns of integration do not appear to be associated with cephalopelvic proportions. *Homo sapiens* share similar integration patterns in the non-obstetric pelvis with *Saimiri sciureus* ($p = 0.010$; large proportions) and *Gorilla gorilla* ($p = 0.10$; small proportions; Table 5.13). *Gorilla gorilla* and *Pan troglodytes* (both small proportions)

also share similar patterns of integration ($p < 0.001$). *Hylobates lar* and *Saimiri sciureus* (both large proportions) do share a similar pattern of integration ($p < 0.001$) in the non-obstetric pelvis, but this pattern is not shared with other species with large cephalopelvic proportions. *Macaca mulatta* does not share a pattern of integration with any other taxon.

Predictions 5b predicts that sexes share similar patterns of integration in the non-obstetric pelvis. This was the case for most species, but not for *Macaca mulatta* (large cephalopelvic proportions) and *Pan troglodytes* (small proportions). These sex differences in the *patterns* of integration in the non-obstetric pelvis do not appear to be influenced by cephalopelvic proportions (Table 5.14).

Based on the results of this study, Hypothesis 5 cannot be rejected (Table 5.1) because although there are some differences among taxa in integration patterns, these patterns do not appear to be related to cephalopelvic proportions.

V. DISCUSSION AND CONCLUSIONS

The hypothesis that the birth canal and non-obstetric pelvis are separate modules across anthropoids was rejected for all taxa besides *Homo sapiens* and *Macaca mulatta*. This result for *H. sapiens* is consistent with previous research (Grabowski, 2013), which found humans to have less covariation between the birth canal and other pelvic traits compared to apes. There are two possibilities that may explain this increased modularity in human pelvis. First, this result could reflect the fact that the birth canal and non-obstetric pelvis are hypothesized to be under antagonistic pressures of selection for

obstetric sufficiency and selection for bipedal locomotion (termed the “obstetric dilemma”; Washburn, 1960; Pinkerton, 1973; Zihlman, 1978; Ruff, 1995; Lovejoy, 2005). This is also consistent with the fact that in *H. sapiens*, females have statistically greater mean integration (higher covariation) between linear distances of the birth canal, but males have greater integration than females in non-obstetric pelvic traits, a pattern not seen in any other species. If increased modularity in humans is the result of antagonistic selection pressures, it is likely that selection for obstetric sufficiency has increased covariation between linear distances in the birth canals of females (because any variation in birth canal shape could lead to cephalopelvic disproportion), but this selection pressure for birth in females simultaneously reduced integration between non-obstetric linear distances in females compared to males, who are only under direct selection for bipedal locomotion and visceral support. In this scenario, decreased covariation between the birth canal and non-obstetric pelvis is the result of increasing cephalopelvic proportions in bipedal hominins.

An alternative possibility is that greater modularity between the birth canal and non-obstetric pelvis characterized early hominins (who likely had smaller cephalopelvic proportions than modern humans; Tague and Lovejoy, 1986; Desilva, 2011) due to the adoption of a novel form of locomotion (bipedalism). Covariation between linear distances in the hominin pelvis was decreased during the transition to bipedal locomotion, and this increased pelvic modularity in hominins allowed our pelvises to more easily adapt for successful birth as neonatal brain size increased later in our lineage (see also Grabowski et al., 2011). In this second scenario, the increased modularity of hominin pelvises is the result of selection for bipedalism, and this increased

modularity was the coopted for birth once neonatal (and adult) brain size began to increase.

Like humans, there is less covariation between the birth canal and non-obstetric pelvis in *Macaca mulatta*, but the reasons for this result are less apparent, and is likely different from the reasons that humans have increased modularity. The sample of *M. mulatta* used for this study came from a free-ranging, provisioned population from Caya Santiago, Puerto Rico (a non-native environment for this taxon, which consists of descendants of individuals transferred from India in 1938). The increased modularity seen in this sample of *M. mulatta* could be related to the fact that this population was recently removed from their natural environment and is in the process of adapting to this novel location. Alternatively, since this population of macaques is descended from a small group that was brought from India, it is possible that this population is descended from a small group that had reduced covariation between the birth canal and non-obstetric pelvis, and this group went through a genetic bottleneck event when transferred. This bottleneck hypothesis for the Cayo Santiago macaques has been supported by genetic data (Buettner-Janusch et al., 1974; Buettner-Janusch and Sockol, 1977; Duggleby et al., 1986; Kanthaswamy et al., 2016). Future research should examine the difference between pelvic modularity in this sample as compared to wild *M. mulatta* specimens.

It is also possible that there is a common explanation for increased modularity in both *Homo sapiens* and *Macaca mulatta*. Both humans and *M. mulatta* have very wide species ranges. In fact, *M. mulatta* has the largest species range of any extant non-human primate, with the species inhabiting a large region that spans both warm tropical

and cold high altitude environments (Pocock, 1932; Miller, 1933). Greater phenotypic plasticity and lower genetic and developmental constraints are thought to contribute to success in novel environments (the adaptive plasticity hypothesis; Agrawal, 2001; Kawecki, 2008). Greater modularity in the pelves of these two species could reflect selection for reduced covariation due to genetic factors, and consequently greater plasticity, in these species. It should be noted that besides humans and *M. mulatta*, all other species included in this study exhibit smaller species ranges – *Hylobates lar* is restricted to southeast Asia (Brandon-Jones et al., 2004); *Saimiri sciureus* is primarily restricted to tropical regions of the Amazon basin (Boubli et al., 2008); *Gorilla gorilla* and *Pan troglodytes* are both restricted to equatorial regions of western Africa.

Unlike covariation between modules (modularity), the magnitudes of integration within both the birth canal and non-obstetric pelvis are clearly influenced by selection for obstetric sufficiency within species. Among taxa included in this study that give birth to relatively large neonates, females tend to have higher magnitudes of integration in the birth canal (all species except *M. mulatta*) and non-obstetric pelvis (all species except *H. sapiens*) than males. This is not true in species with small cephalopelvic proportions. It is possible that this result is influenced by phylogeny - the two species included with small proportions are closely phylogenetically related (*Gorilla gorilla* and *Pan troglodytes*). Yet, *Pan troglodytes* is more closely related to *Homo sapiens*, so it appears that phylogeny does not influence sex differences in the magnitudes of integration to the extent of cephalopelvic proportions.

Thus, the results of this study do suggest that sex differences in the magnitude of integration in the birth canal and non-obstetric pelvis (such that females have greater

integration than males) is related to large cephalopelvic proportions (Tables 5.7 and 5.10). This result is not unexpected, because females are under direct selection for obstetric sufficiency, whereas males are not. Therefore, variation in birth canal or non-obstetric size or shape will have more immediate selective consequences in females who give birth to relatively large neonates. Furthermore, this increased magnitude of integration in females compared to males (but only in species with large cephalopelvic proportions) also helps to explain why these species also maintain high levels of dimorphism in birth canal and non-obstetric pelvic form (see Chapters 2- 4). In species with large proportions, female pelvic form is more constrained compared to that of males, but this is not true in species with small proportions, which is consistent with the fact that there is typically more overlap between male and female pelvic morphology in smaller proportioned taxa (see Chapters 2 and 4).

Finally, the patterns of integration (which specific traits strongly covary) in the birth canal and non-obstetric pelvis do not appear to be influenced by cephalopelvic proportions at all (Tables 5.11- 5.14). This result is consistent with previous research which finds *patterns* of morphological integration in the skeleton tend to be more conserved across primates than *magnitudes* of integration (Cheverud, 1996; Ackerman and Cheverud, 2000; Marroig and Cheverud, 2001). Indeed, patterns of integration in the birth canal (Tables 5.11) are shared among all taxa included in this study (and between sexes in all taxa; Table 5.12). This could reflect that fact that there is strong stabilizing selection on the pattern of birth canal integration in primates because it is vital that the shapes of the birth canal planes covary in a certain way – any variation in birth canal shapes could be selectively disadvantageous for birth, even in taxa with

small cephalopelvic proportions (because a birth canal shape that is highly atypical could also affect birth in these species). Additionally, it is possible that this shared pattern of integration is an ancestral character for anthropoids (or mammals). Future research should further test this hypothesis by comparing primate birth canal integration patterns to those of other mammalian taxa.

Table 5.1: Hypotheses and predictions

Hypothesis <i>Prediction</i>	Results	
H1: The birth canal and non-obstetric pelvis represent two separate modules <i>1a:</i> In species with large CP, there will be low covariance between the birth canal and non-obstetric pelvis, but this will not be the case in taxa with small CP	Reject <i>Not supported</i>	[Table 5.4]
H2: Large cephalopelvic proportions produce high magnitudes of integration in the birth canal <i>2a:</i> Primates with large CP will exhibit a greater <i>magnitude</i> of integration in the birth canal than species with small CP <i>2b:</i> In species with large CP, females will exhibit a greater <i>magnitude</i> of integration in the birth canal than males, but this will not be the case in taxa with small CP	Cannot Reject <i>Not Supported</i> <i>Supported</i>	[Table 5.5] [Table 5.7]
H3: Large cephalopelvic proportions produce high magnitudes of integration in the non-obstetric pelvis <i>3a:</i> Primates with large CP will exhibit a greater <i>magnitude</i> of integration in the non-obstetric pelvis than species with small CP <i>3b:</i> In species with large CP, females will exhibit a greater <i>magnitude</i> of integration in the non-obstetric pelvis than males, but this will not be the case in taxa with small CP	Cannot Reject <i>Supported</i> <i>Supported</i>	[Table 5.8] [Table 5.10]
H4: Large cephalopelvic proportions do not produce specific <i>patterns</i> of integration in the birth canal <i>4a:</i> All species share similar patterns of integration in the birth canal regardless of cephalopelvic proportions <i>4b:</i> Within species, males and females will have similar patterns of integration within the birth canal	Cannot Reject <i>Supported</i> <i>Supported</i>	[Table 5.11] [Table 5.12]
H5: Large cephalopelvic proportions do not produce specific <i>patterns</i> of integration in the non-obstetric pelvis <i>5a:</i> All species share similar patterns of integration in the non-obstetric pelvis regardless of cephalopelvic proportions <i>5b:</i> Within species, males and females will have similar patterns of integration within the non-obstetric pelvis	Cannot Reject <i>Not Supported</i> <i>Supported</i>	[Table 5.13] [Table 5.14]

*Cephalopelvic Proportions (CP)

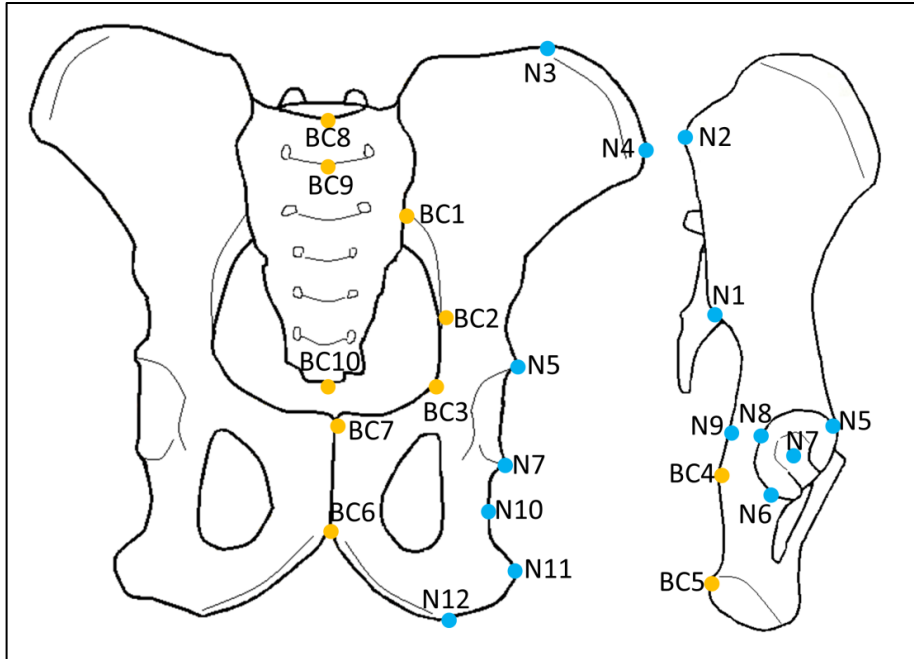


Figure 5.1: Landmarks of the birth canal (orange) and non-obstetric pelvis (blue). Landmark descriptions are listed in Table 5.1.

Table 5.2: Landmarks of the Birth Canal

Birth Canal Landmarks	Description
(BC1) SI joint at arcuate line	Point on ilium where arcuate line intersects the sacroiliac joint
(BC2) Lateral arcuate line	Lateral-most point of arcuate on articulated pelvis
(BC3) Pubis at arcuate line	Arcuate at right angle to anterior acetabular rim
(BC4) Ischial spine	Ischial spine on posterior ischium
(BC5) Posterior ischial tuberosity	Posterior-most point on the ischial tuberosity
(BC6) Inferior pubic symphysis	Inferior-most point on symphysis at the midline
(BC7) Superior pubic symphysis	Superior-most point on symphysis at the midline
(BC8) Ventral S1body	Ventral-most point on the first vertebral body at midline
(BC9) Inferior S1 body	Inferior S1 vertebral body at midline
(BC10) Inferior sacrum	Inferior-most point on sacrum at midline

Table 5.3: Landmarks of the non-obstetric pelvis

Non-Obstetric Landmarks	Description
(N1) Posterior inferior iliac spine	Posterior-most point of the posterior inferior iliac spine
(N2) Posterior superior iliac spine	Posterior-most point of the posterior superior iliac spine
(N3) Superior iliac crest	Superior-most point on the iliac crest
(N4) Anterior superior iliac spine	Lateral-most point on the anterior superior iliac spine
(N5) Superior acetabulum	Point on superior rim of acetabulum in the same plane as anterior inferior iliac spine
(N6) Inferior acetabulum	Point on inferior rim of acetabulum in the same plane as ischial ramus
(N7) Acetabulum center	Point in the acetabulum at the center of the lunatic surface
(N8) Posterior acetabulum	Rim of the acetabulum in the same plane as landmarks 7 and 9
(N9) Posterior ischial neck	Point on the posterior ischium in the same plane as landmarks 7 and 9
(N10) Lateral ischial ramus	Deepest point along the ischial ramus inferior to the acetabulum
(N11) Lateral ischial tuberosity	Lateral-most projection of the ischial tuberosity
(N12) Inferior pubic ramus	Point between ischial and inferior pubic rami in at lateral edge of obturator foramen

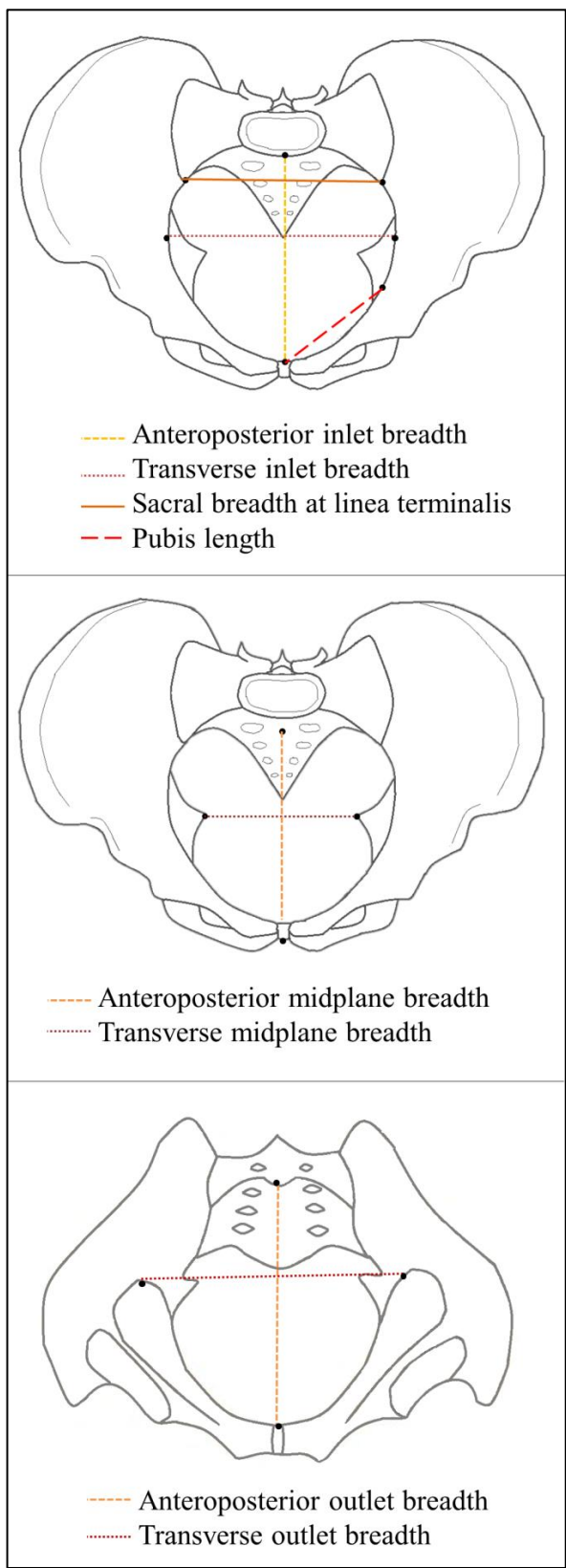


Figure 5.2: Linear distances of the birth canal.

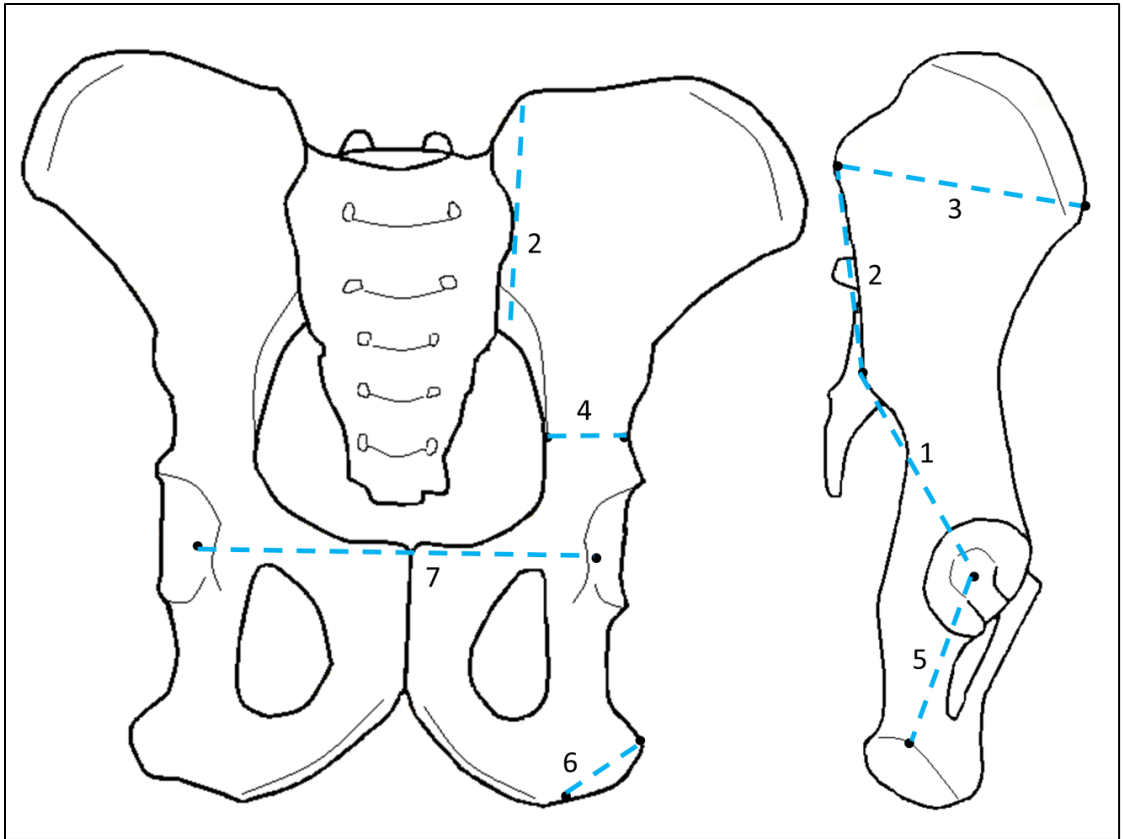


Figure 5.3: Linear distances of the non-obstetric pelvis: (1) inferior iliac height; (2) superior iliac height; (3) iliac breadth; (4) iliac neck breadth; (5) ischial length; (6) ischial tuberosity breadth; (7) biacetabular breadth.

Table 5.4: Hypothesis 1 - Modularity testing for birth canal and non-obstetric pelvis

Large Cephalopelvic Proportions	Modularity Testing R_V coefficient	Proportion of R_V coefficients < R_V coefficient of hypothesized modules§
<i>Homo sapiens</i>	0.2919	0.0005*
<i>Hylobates lar</i>	0.4798	0.2909
<i>Macaca mulatta</i>	0.3417	0.0096*
<i>Saimiri sciureus</i>	0.5519	0.8594
Small Cephalopelvic Proportions		
<i>Gorilla gorilla</i>	0.1893	0.4364
<i>Pan troglodytes</i>	0.4001	0.2765

§Indicates the proportion of R_V coefficients (of 10,000) for randomly-generated modules are less than the R_V coefficient for the hypothesized modules (birth canal and non-obstetric pelvis).

*A significant result indicates that <5% of randomly-generated modules have lower R_V coefficients than the hypothesized modules, thus a low proportion supports the hypothesis that there is support for the two hypothesized modules (*i.e.*, birth canal and non-obstetric pelvis).

Table 5.5: Hypothesis 2 - Magnitudes of integration in birth canal linear distances across species of anthropoids

	Species-Wide Standardized VE†
Large Cephalopelvic Proportions	
<i>Homo sapiens</i>	0.0787
<i>Hylobates lar</i>	0.0932
<i>Macaca mulatta</i>	0.0625
<i>Saimiri sciureus</i>	0.0910
Small Cephalopelvic Proportions	
<i>Gorilla gorilla</i>	0.0838
<i>Pan troglodytes</i>	0.0609

† the Variance of the Eigenvalues (VE; the measure of integration between linear distances of the birth canal used for this study) standardized by the maximum eigenvalue variance for each taxon. Standardized VE can be directly compared between taxa.

Table 5.6: Hypothesis 2 - Difference of means tests for difference in integration magnitudes (Standardized VE) between taxa for birth canal distances

<i>Homo</i>	<i>Hylobates</i>	<i>Macaca</i>	<i>Saimiri</i>	<i>Gorilla</i>	<i>Pan</i>	
-	<0.001*	<0.001*	<0.001*	0.023*	<0.001*	<i>Homo</i>
	-	<0.001*	0.056	0.019*	<0.001*	<i>Hylobates</i>
		-	<0.001*	<0.001*	0.521	<i>Macaca</i>
			-	0.010*	<0.001*	<i>Saimiri</i>
				-	<0.001*	<i>Gorilla</i>
					-	<i>Pan</i>

*Indicates significant difference between species for birth canal linear distances at $\alpha=0.025$

Table 5.7: Hypothesis 2 - Differences in the magnitudes of integration in birth canal linear distances between males and females across anthropoids

	Female Standardized VE	Male Standardized VE	p-value (sex with higher integration)
Large Cephalopelvic Proportions			
<i>Homo sapiens</i>	0.0820	0.0722	0.002* (f)
<i>Hylobates lar</i>	0.0941	0.0866	0.024* (f)
<i>Macaca mulatta</i>	0.0632	0.0647	0.835
<i>Saimiri sciureus</i>	0.0912	0.0835	0.004* (f)
Small Cephalopelvic Proportions			
<i>Gorilla gorilla</i>	0.0818	0.0830	0.672
<i>Pan troglodytes</i>	0.0558	0.0652	0.002* (m)

*Indicates significant difference between sexes for integration in birth canal linear distances at $\alpha=0.025$.

Table 5.8: Hypothesis 3 - Magnitudes of integration in non-obstetric pelvic linear distances across species of anthropoids

	Species-Wide Standardized VE†
Large Cephalopelvic Proportions	
<i>Homo sapiens</i>	0.0664
<i>Hylobates lar</i>	0.0678
<i>Macaca mulatta</i>	0.0599
<i>Saimiri sciureus</i>	0.0759
Small Cephalopelvic Proportions	
<i>Gorilla gorilla</i>	0.0582
<i>Pan troglodytes</i>	0.0595

† the Variance of the Eigenvalues (the measure of integration used for this study) standardized by the maximum eigenvalue variance for each taxon. Standardized VE can be directly compared between taxa.

Table 5.9: Hypothesis 3 - Similarity in integration magnitudes between taxa for non-obstetric pelvic distances

<i>Homo</i>	<i>Hylobates</i>	<i>Macaca</i>	<i>Saimiri</i>	<i>Gorilla</i>	<i>Pan</i>	
-	0.476	0.039	0.009*	0.004*	0.005*	<i>Homo</i>
	-	0.002*	<0.001*	0.002*	0.007*	<i>Hylobates</i>
		-	<0.001*	0.530	0.878	<i>Macaca</i>
			-	<0.001*	<0.001*	<i>Saimiri</i>
				-	0.709	<i>Gorilla</i>
					-	<i>Pan</i>

*Indicates significant difference between species for birth canal linear distances at $\alpha=0.025$

Table 5.10: Hypothesis 3 - Differences in the magnitudes of integration in non-obstetric pelvic linear distances between males and females across anthropoids

	Female Standardized VE	Male Standardized VE	p-value (sex with higher integration)
Large Cephalopelvic Proportions			
<i>Homo sapiens</i>	0.0535	0.0750	<0.001* (m)
<i>Hylobates lar</i>	0.0646	0.0522	<0.001* (f)
<i>Macaca mulatta</i>	0.0797	0.0625	0.002* (f)
<i>Saimiri sciureus</i>	0.0929	0.0737	<0.001* (f)
Small Cephalopelvic Proportions			
<i>Gorilla gorilla</i>	0.0667	0.0597	0.028
<i>Pan troglodytes</i>	0.0582	0.0745	<0.001* (m)

*Indicates significant difference between sexes for integration in non-obstetric pelvic linear distances at $\alpha=0.025$.

Table 5.11: Hypothesis 4 – Mantel tests of similarity in interspecies integration patterns between birth canal traits

<i>Homo</i>	<i>Hylobates</i>	<i>Macaca</i>	<i>Saimiri</i>	<i>Gorilla</i>	<i>Pan</i>	
-	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<i>Homo</i>
	-	<0.001*	<0.001*	<0.001*	<0.001*	<i>Hylobates</i>
		-	<0.001*	<0.001*	<0.001*	<i>Macaca</i>
			-	0.002*	<0.001*	<i>Saimiri</i>
				-	<0.001*	<i>Gorilla</i>
					-	<i>Pan</i>

*Indicates a significant result at $\alpha=0.025$. Significance indicates rejection of the null hypothesis – that there is no association between matrix pairs – and therefore indicates that two species share a similar integration pattern.

Table 5.12: Hypothesis 4 - Similarity in birth canal integration patterns between males and females

Large Cephalopelvic Proportions	Mantel Test of Matrix Similarity‡
<i>Homo sapiens</i>	<0.001*
<i>Hylobates lar</i>	<0.001*
<i>Macaca mulatta</i>	<0.001*
<i>Saimiri sciureus</i>	<0.001*
Small Cephalopelvic Proportions	Mantel Test of Matrix Similarity‡
<i>Gorilla gorilla</i>	<0.001*
<i>Pan troglodytes</i>	<0.001*

*Indicates a significant result at $\alpha=0.025$.

‡ Significance of a Mantel test indicates rejection of the null hypothesis – that there is no association between matrix pairs – and therefore indicates that two groups share a similar integration pattern.

Table 5.13: Hypothesis 5 - Mantel tests of similarity in integration patterns between non-obstetric pelvic traits

<i>Homo</i>	<i>Hylobates</i>	<i>Macaca</i>	<i>Saimiri</i>	<i>Gorilla</i>	<i>Pan</i>	
-	0.037	0.233	0.010*	0.010*	0.042	<i>Homo</i>
	-	0.052	<0.001*	0.099	0.100	<i>Hylobates</i>
		-	0.171	0.121	0.096	<i>Macaca</i>
			-	0.090	0.117	<i>Saimiri</i>
				-	<0.001*	<i>Gorilla</i>
					-	<i>Pan</i>

*Indicates a significant result at $\alpha=0.025$. Significance indicates rejection of the null hypothesis – that there is no association between matrix pairs – and therefore indicates that two species share a similar integration pattern.

Table 5.14: Hypothesis 5 - Similarity in non-obstetric integration patterns between males and females

Large Cephalopelvic Proportions	Mantel Test of Matrix Similarity‡
<i>Homo sapiens</i>	0.008*
<i>Hylobates lar</i>	0.005*
<i>Macaca mulatta</i>	0.119
<i>Saimiri sciureus</i>	0.003*
Small Cephalopelvic Proportions	Mantel Test of Matrix Similarity‡
<i>Gorilla gorilla</i>	0.018*
<i>Pan troglodytes</i>	0.031

*Indicates a significant result at $\alpha=0.025$.

‡ Significance of a Mantel test indicates rejection of the null hypothesis – that there is no association between matrix pairs – and therefore indicates that two groups share a similar integration pattern.

CHAPTER 6: SUMMARY AND FUTURE DIRECTIONS

The goal of this dissertation is to ascertain the relationship between obstetric demand, measured here as cephalopelvic proportions, and pelvic dimorphism and morphological integration across anthropoid primates.

The first study (Chapter 2) examines dimorphism in birth canal morphology in anthropoids. Dimorphism is found in the size and shape of the birth canal among all species included except for *Alouatta seniculus*, but taxa with large cephalopelvic proportions are especially dimorphic. The results of this study indicate that the *presence* of dimorphism in the birth canals of primates cannot be attributed to large cephalopelvic proportions because birth canal dimorphism is pervasive across anthropoid taxa regardless of cephalopelvic proportions. In all species except *A. seniculus*, females have relatively larger birth canals than males, but female birth canals are not isometrically larger - female birth canals tend to be relatively mediolaterally wider, but not necessarily relatively larger in the anteroposterior dimensions, and females also have relatively longer pubes (all taxa except *A. seniculus*), which contributes to mediolateral widening of the birth canal planes.

An important implication is that birth canal dimorphism may be a shared feature of most primate taxa. Indeed, dimorphic pubis and birth canal morphology has also been observed in other eutherian mammals (including rodents, bats, and foxes; Gardner, 1936; Dunmire, 1955; Crelin and Newton, 1969; Leutenegger and Kelly, 1977;

Chapman et al., 1994; Berdnikovs et al., 2007; Schutz et al., 2009a; Schutz et al., 2009b) as well as in metatherians (the opossum; Tague, 2003), which have small cephalopelvic proportions. In all of these taxa, females have relatively longer pubis length than males, and increasing pubis length necessarily increases birth canal size in females. Sex differences in pubis length could be a shared feature of a number of mammalian taxa (or a shared feature of mammals), but further research is needed to test this hypothesis. Sex differences in relative pubis length and mediolateral dimensions of the birth canal may therefore be especially useful for inferring biological sex from fossil pelves.

Sex hormones likely play a strong role in the determination of adult dimorphism patterns in mammals (Gardner, 1936; Dunmire, 1955; Tague, 1995). Previous researchers have hypothesized that pelvic dimorphism may be attributable to differences between the sexes in the presence of either testosterone (Tague, 1995) and/or estrogen (Gardner, 1936) during development. Further, dramatic sex differences in the pelvis begin to develop during early adolescence in most primates that have been studied previously (Li, 2002). The results of this study suggest that these developmental pathways are likely shared across most species of primates regardless of cephalopelvic proportions, because most taxa have some level of pelvic dimorphism in adults. Future research should consider the role of sex hormones on birth canal form across primates during ontogeny.

Importantly, this study shows that the *magnitude* of dimorphism in birth canal size and shape is, in fact, related to cephalopelvic proportions. Species with large cephalopelvic proportions, which are presumably under increased obstetric selection

compared to species with small proportions, tend to be more dimorphic than small proportion taxa. Furthermore, species with both high levels of body size dimorphism *and* large cephalopelvic proportions tend to have the most dimorphic birth canals. Previous researchers have noted that primates with high levels of body size dimorphism also have high levels of pelvic dimorphism (Schultz, 1949; Leutenegger, 1973; Tague, 1995; 2005). The reasons for this are twofold. First, secondary sex differences (including both body size dimorphism and pelvic dimorphism) in primates are thought to be influenced by sex hormone levels during ontogeny (Tague, 1995; Li, 2002; Tague, 2005), so species with high levels of body size dimorphism should also be expected have heightened levels of pelvic dimorphism (Schultz, 1949; Tague, 1995; 2005). Second, in taxa with high levels of body size dimorphism, small-bodied females are at an obstetric disadvantage (a) because they have small pelves and (b) because neonatal body size is negatively allometric with maternal body size, meaning they have relatively large neonates (Leutenegger, 1982). Therefore, obstetric selection in these small-bodied females is very high, resulting in females with very large birth canals controlling for body size compared to those of males.

The second study (Chapter 3) examines whether dimorphism in sacral breadth is due to large cephalopelvic proportions. Dimorphism in sacral breadth relative to S1 body breadth is present among all species having large cephalopelvic proportions as well as *Gorilla gorilla* (which has small cephalopelvic proportions), but this may be due to males exhibiting relatively narrow sacra controlling for S1 body breadth in *G. gorilla* (see Chapter 3). No other species having small cephalopelvic proportions exhibit dimorphism in sacral breadth relative to S1 body breadth. This result helps to explain

why taxa with large cephalopelvic proportions also have high magnitudes of dimorphism in birth canal size and shape compared to those with small proportions. The sacrum makes up the posterior border of the pelvic inlet, midplane, and outlet, and increasing sacral breadth necessarily increases the distance between the posterior ilia and ischia and increases the mediolateral breadth (and therefore the circumference) of the birth canal in females. If sacral breadth is significantly dimorphic in species with large cephalopelvic proportions, mediolateral dimensions and circumferences of the birth canal would be expected to be highly dimorphic in these taxa as well, which is exactly what is observed in Chapter 2.

Although the sacrum is often ignored in studies of pelvic form, the results from this dissertation indicate that fossil sacra may provide important information regarding the evolution of cephalopelvic proportions across hominins in taxa for which we have sacra for male and female individuals. There are a number of well-preserved hominin fossil sacra (Leutenegger, 1977; Johanson et al., 1982; Rak and Arensburg, 1987; Arsuaga et al., 1999; Toussaint et al., 2003; Simpson et al., 2008; Bonmatí et al., 2010; Kibii et al., 2011). Tague (2007) has measured relative sacral breadth in three fossil sacra attributed to *Australopithecus*: A.L. 288-1 (*A. afarensis*, typically considered to be female; Johanson and Edey, 1981; Tague and Lovejoy, 1986; but see Häusler and Schmid, 1995), Sts 14 (*A. africanus*, typically considered female; Howell, 1978; but see Robinson, 1972), and Stw 431 (*A. africanus*, typically considered male; Toussaint et al., 2003). Tague's indices of relative sacral breadth in these specimens indicate that the two female specimens do have relatively wider sacra than males, but it is possible that this finding is due to small sample size (Tague, 2007). However, if we assume that these

individuals are representative of the mean sacral morphology for *Australopithecus*, the index of dimorphism in *Australopithecus* is similar to that seen in *Homo sapiens*, *Hylobates lar*, and *Gorilla gorilla*. There are two possible interpretations of this finding: (1) *Australopithecus* was characterized by large cephalopelvic proportions, or (2) high levels of body size dimorphism in *Australopithecus* (McHenry, 1991; Richmond and Jungers, 1995; Gordon and Green, 2008; but see Reno et al., 2003) influenced sacral dimorphism in this taxon, similar to what we find in *G. gorilla*. It is unlikely that *Australopithecus* was characterized by large cephalopelvic proportions similar to those in humans (Leutenegger, 1972; but see Berge et al., 1984), although cephalopelvic proportions would almost certainly have been larger than those in *Pan* or *Gorilla* (Berge et al., 1984; Tague and Lovejoy, 1986). Therefore, the most reasonable interpretation of high levels of dimorphism in relative sacral breadth in *Australopithecus* (if this is not an artifact of small sample size) is that this taxon was characterized by high levels of body size dimorphism, and similar to *Gorilla gorilla*, there may have been slight differences in locomotor function between males and females owing to these body size differences (Stern and Susman, 1983). Data do not exist for relative sacral breadth in other fossil hominins. Thus, future research should aim to reconstruct the evolution of cephalopelvic proportions across fossil hominins using sacral morphology.

Dimorphism in sacral breadth and birth canal morphology influences dimorphism in the non-obstetric pelvis. The third study of this thesis (Chapter 4) finds that shape and size differences in the non-obstetric pelvis are apparent in all species included with the exception of *Alouatta seniculus* (as would be expected based on the results for the presence of birth canal dimorphism in primates). As with the birth canal,

the *presence* of dimorphism in non-obstetric pelvic size and shape is not indicative of large cephalopelvic proportions. Yet, similar to what was found in the birth canal, species with large cephalopelvic proportions are especially dimorphic for non-obstetric pelvic shape and size, such that there is a greater magnitude of dimorphism in pelvic size and less overlap in pelvic shape in these taxa. Generally, the magnitude of dimorphism in the non-obstetric pelvis is a corollary of the magnitude of dimorphism in the birth canal.

Size and shape differences in the non-obstetric pelvis are similar across most taxa, and the parts of the non-obstetric pelvis that are adjacent to the birth canal - the inferior ilium and ischiopubis - are the most dimorphic. Females have relatively wider (but not rostrocaudally larger) ischiopubic regions than males, and females have relatively wider biacetabular breadth in all species except *A. seniculus* and *M. mulatta*. Lower iliac height (distance between sacroiliac and acetabulum) is relatively larger in females than males in all species except *A. seniculus*. However, primates exhibit little dimorphism in the rostral ilium, which is spatially separated from the birth canal in most species. Relative biiliac breadth is not dimorphic controlling for body size in any species (although it is dimorphic for most taxa when allometric scaling is considered). Collectively, these results show that the inferior ilium (which includes the linea arcuata, lateral boundary of the pelvic inlet) and ischiopubis (which bounds the pelvic inlet, midplane, and outlet) tend to be very dimorphic in anthropoids, such that these areas are relatively wider in females than males. This is in contrast to the upper ilium, which does not become relatively wider in females due to strong positive allometric scaling of biiliac breadth (Lewton, 2015). The fact that biiliac breadth is not dramatically wider in

females does not pose an obstetric disadvantage, because this area is spatially separated from the birth canal.

Chapters 2-4 of this thesis establish that species with large cephalopelvic proportions are highly dimorphic for birth canal, sacral, and non-obstetric pelvic morphology, and it is clear that obstetric selection plays a role in constraining female pelvic form in these species. This does not appear to be the case in species with small cephalopelvic proportions, which tend to have less dimorphism in their birth canals, sacra, and non-obstetric pelvis. Therefore, the final study of this thesis (Chapter 5) tests the hypothesis that large cephalopelvic proportions increase the magnitude of integration (covariation) in the birth canal and non-obstetric pelvis. In species with large cephalopelvic proportions, females have higher magnitudes of covariation (more integration) between linear distances of the birth canal (all species except *M. mulatta*) and between linear distances of the non-obstetric pelvis (all species except *H. sapiens*) compared to males. This is not the case in species with small cephalopelvic proportions. This result indicates that there is strong selection on females in species with large cephalopelvic proportions to maintain an obstetrically-sufficient pelvis, and this strong selection maintains high levels of integration between pelvic morphologies in these females. This is not the case in females in taxa with small proportions. This is the first study to examine and establish a difference in the magnitudes of integration in male and female anthropoid pelvis. This study shows that there is a demonstrable effect of obstetric demand on pelvic integration in females in taxa with large cephalopelvic proportions.

There are two species included in this thesis that are unusual compared to other taxa – the first is *Alouatta seniculus*, which is nearly monomorphic in pelvic morphology (not found in any other taxa included), and this consistent with previous research (Leutenegger, 1970). *Alouatta* it is the only known monkey which exhibits small cephalopelvic proportions (hypothesized to be due to decreased cranial capacity in this species; Leutenegger, 1970). It is possible that this decrease in cephalopelvic proportions in *Alouatta* compared to other monkeys dramatically reduced obstetric selection in this taxon. Reduced obstetric selection allows female pelvises to respond to other selective regimes (for example, locomotion or thermoregulation), producing more “male-like” pelvises in females. Alternatively, it is possible that pelvic monomorphism in *Alouatta* is due to growth rates in males. It is hypothesized that male *Alouatta* experience a longer skeletal growth period and faster growth rate during ontogeny than females (Ravosa and Ross, 1994), and this longer, faster growth rate in males could also lead to reduced pelvic dimorphism by increasing pelvic size and breadth in male pelvises to be similar to that of females.

The second species which is unusual is *Homo sapiens*. Humans have more dimorphic pelvises than would be predicted based on our cephalopelvic proportions or body size dimorphism levels alone (see Chapters 2 and 4), and, notably, humans are the only bipedal primates included. In humans, the birth canal and non-obstetric pelvis are hypothesized to be under antagonistic pressures of selection for obstetric sufficiency and selection for bipedal locomotion (termed the “obstetric dilemma”; Washburn, 1960; Pinkerton, 1973; Zihlman, 1978; Ruff, 1995; Lovejoy, 2005). A larger, wider birth canal is beneficial for birth, but a wider biacetabular distance is thought to be

energetically costly in bipeds because it increases the abductor forces required to prevent hip drop (Washburn, 1950, 1960; Pinkerton, 1973; Zihlman, 1978; Ruff, 1995; Lovejoy, 2005; but see Warrener et al., 2015). A wider birth canal also increases the distance between the ischial spines, possibly compromising the function of the pelvic diaphragm in pelvic visceral support in bipeds (Abitbol, 1988), and it increases valgus angle, which could lead to increased incidence of knee injuries (see Warrener et al., 2015). These antagonistic selection pressures between obstetric and locomotor functions are also reflected in the morphological integration in the pelvis – humans have more modular pelvises (less covariation between the birth canal and non-obstetric pelvis) compared to most other primates (Chapter 5; see also Grabowski et al., 2011). This allows for differential selection on the morphology of the birth canals and the non-obstetric pelvises in humans – while the birth canal is more tightly integrated in human females (who give birth), the non-obstetric pelvis displays higher magnitudes of integration in human males (who are only under selection for bipedal locomotion and thermoregulatory imperatives). No other species shows this pattern of having females with higher integration in the birth canal and males with higher integration in the non-obstetric pelvis. Based on the results of this study it appears reasonable to suggest that selection for obstetric demand and selection for bipedal locomotion are at odds in our species (Washburn, 1960; Rosenberg, 1992; Ruff, 1995; Rosenberg and Trevathan, 1996), resulting in both (a) a high magnitude of dimorphism in human pelvises and (b) a lesser degree of covariation between the birth canal and non-obstetric pelvis.

The results of this study have implications for sexing fossil anthropoid pelvises. In previous studies, patterns of dimorphism in modern humans have been used as the basis

to determine sex in fossil hominins (Tague and Lovejoy, 1986; Hager, 1989; Häusler and Schmid, 1995; Tague and Lovejoy, 1998; Simpson et al., 2008; Bonmatí et al., 2010). Hager (1989) noted one obvious problem with doing this. Modern humans have extremely dimorphic pelves (Turner, 1885; Caldwell and Moloy, 1933; Greulich, 1938; Young and Ince, 1940; Coleman, 1969; Krogman and Işcan, 1986; Hager, 1989; Tague, 1989, 1992; Walrath, 1997; Correia et al., 2005; Kurki, 2007; Brown, 2011; Kurki, 2011), and using modern human dimorphism patterns to sex fossils presumes that extinct hominins had similar patterns and magnitudes of pelvic dimorphism as modern humans. Ideally, any pelvic characters that are used to assign sex to fossils should be good indicators of sex in most anthropoid taxa, or at least most hominoids, not just in humans. This thesis establishes a number of pelvic traits which are dimorphic in nearly all anthropoids included (controlling for body size). These include pubis length, mediolateral diameter of the pelvic inlet, biacetabular breadth, and lower iliac height. These linear distances tend to be relatively longer in females than males in anthropoid species regardless of cephalopelvic proportions, so these distances are appropriate for use as sex discriminators in extinct species, even those with small cephalopelvic proportions. Notably, pubis length and inferior iliac height can be measured on pelves that do not preserve a complete birth canal, and lower iliac height (distance between sacroiliac and hip joint) is often preserved in fragmentary fossil hominin pelves (see Rose, 1984; Brown et al., 1985; Simpson et al., 2008; Kibii et al., 2011; Ward et al., 2015).

In humans, difficult and prolonged birth (due to large cephalopelvic proportions and neonatal rotation) is a hallmark of our species, while other great apes have small

cephalopelvic proportions and relatively quick births (Schultz, 1949; Washburn, 1960; Lindberg, 1982; Rosenberg, 1996). In addition, the appearance of large cephalopelvic proportions and a prolonged birth process in hominins is linked to increased birth and postpartum assistance to mothers (which requires increased cooperation between individuals; Trevathan, 1996; Rosenberg and Trevathan, 2002), increased infant dependency (due to neonates being born with less brain development complete compared to other apes; Martin, 1983; DeSilva and Lesnik, 2008; DeSilva, 2011), and increased alloparenting in hominins compared to non-human primates (Hrdy, 2007; 2009). It has therefore been a critical point of research in the past several decades to reconstruct and ascertain cephalopelvic proportions and birth-related behavior in fossil hominins (Tague and Lovejoy, 1986; Rosenberg, 1992; Häusler and Schmid, 1995; Ruff, 1995; Rosenberg and Trevathan, 1996; Trevathan, 1996; Rosenberg and Trevathan, 2002; Coqueugniot et al., 2004; DeSilva and Lesnik, 2008; Ponce de León et al., 2008; Franciscus, 2009; Weaver and Hublin, 2009; DeSilva, 2011). Cephalopelvic proportions and birth-related selection are often inferred in hominins from dimorphism in pelvic morphology (Zihlman, 1978; Berge et al., 1984; Tague and Lovejoy, 1986; Rak and Arensburg, 1987; Hager, 1989; Arsuaga et al., 1999; Simpson et al., 2008; Bonmatí et al., 2010; Ruff, 2010), but results from this dissertation indicate that the *presence* of dimorphism in the birth canal and non-obstetric pelvic morphology (see Chapters 2 and 3) is insufficient to indicate that a species has large cephalopelvic proportions. Indeed, most species of anthropoids included in these studies exhibit some dimorphism in pelvic morphology regardless of cephalopelvic proportions. Therefore,

any indicators of large cephalopelvic proportions in fossils should also be shared by (and be exclusive to) extant taxa with large cephalopelvic proportions.

Based on the results of this thesis, it would be expected that any anthropoid species with large cephalopelvic proportions would be characterized by: (1) dimorphism in relative sacral breadth; (2) high magnitudes of dimorphism in the size and shape of the birth canal; and (3) high magnitudes of dimorphism in biacetabular breadth and lower iliac height. Moreover, in species with large cephalopelvic proportions females should have greater magnitudes of birth canal integration than males (see Chapter 5), although this would be nearly impossible to detect in fossils due to small sample sizes.

Finally, there were two limitations of this thesis that should be addressed with future research. First, there is limited data on cephalopelvic proportions across anthropoids. Future research should quantify cephalopelvic proportions in a larger number of taxa using ultrasound or radiography. Second, this study quantified obstetric demand as bony constraints between the neonatal head and maternal pelvis, but it is possible that there are other factors – including wide neonatal shoulders (Trevathan and Rosenberg, 2000) and soft tissue constraints (including pelvic floor musculature, pelvic ligament deformation, or neonatal cranial deformation due to fontanelles) – which influence the magnitude of obstetric demand in many taxa. Addressing these limitations will create a more complete picture of how obstetric demand correlates with pelvic form in female primates.

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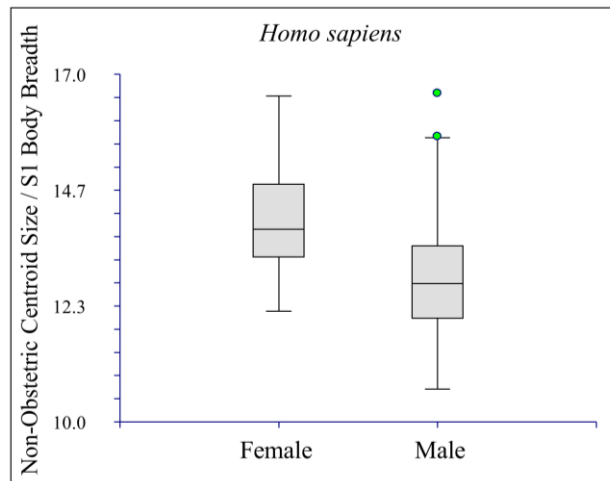
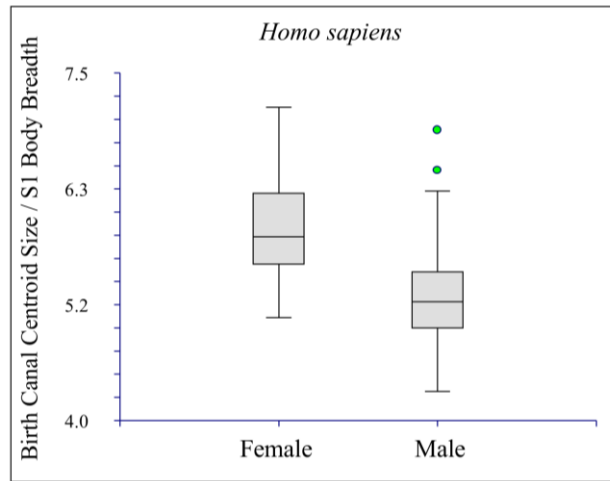
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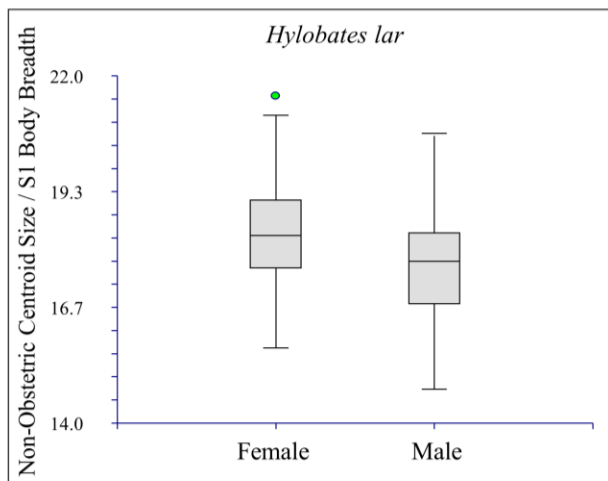
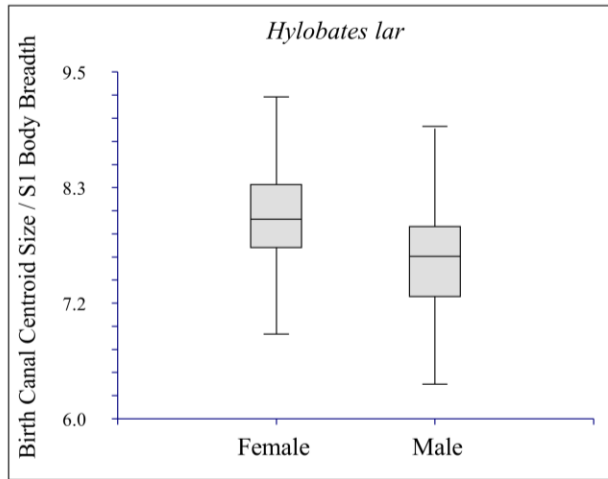
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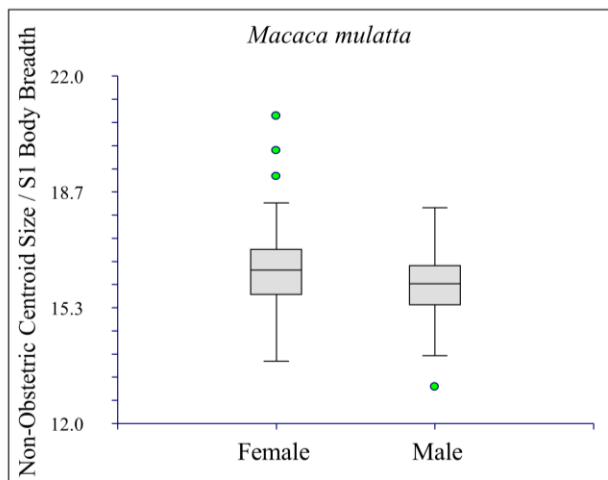
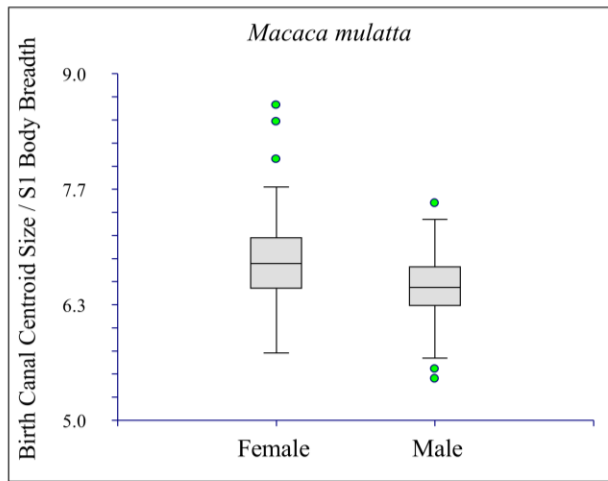
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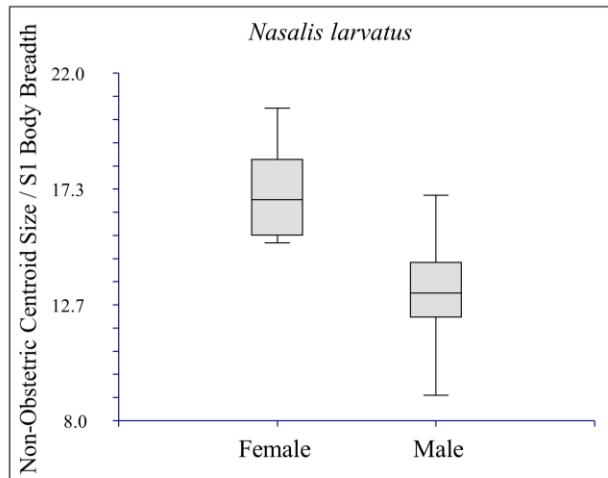
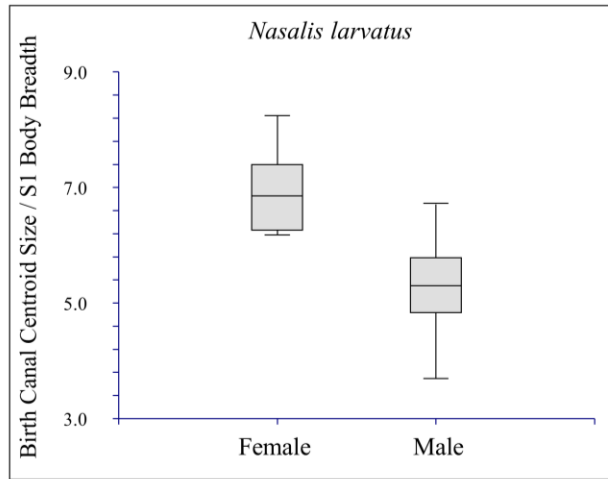
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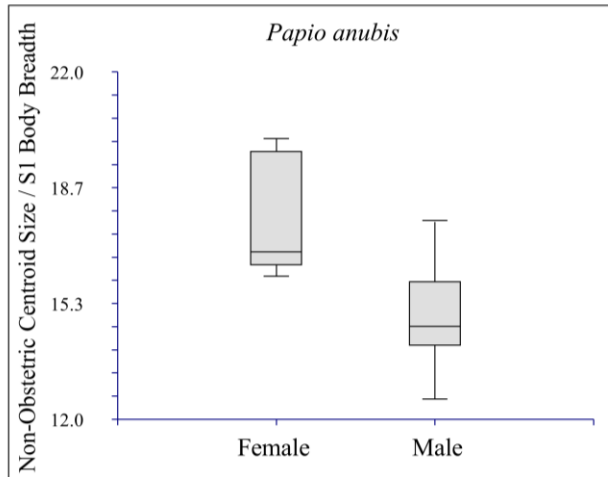
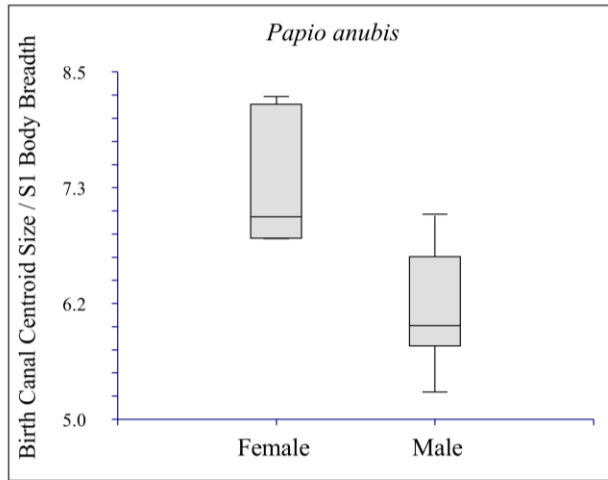
APPENDIX A

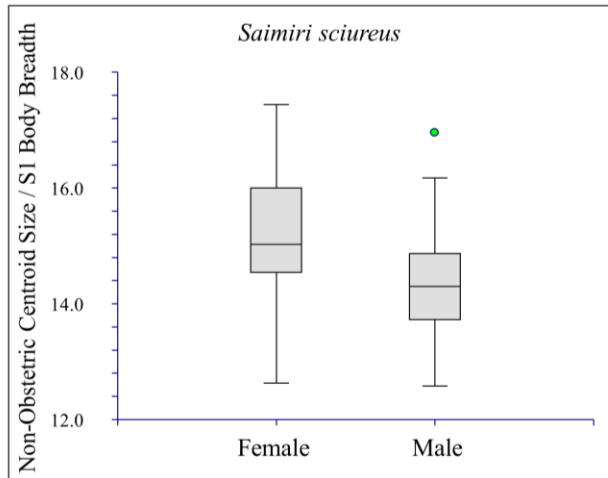
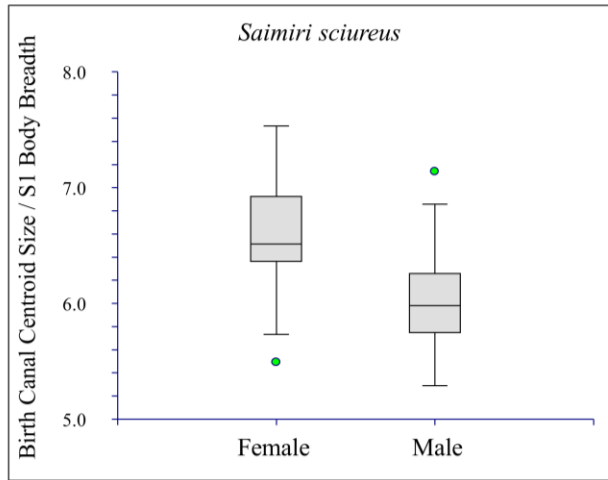


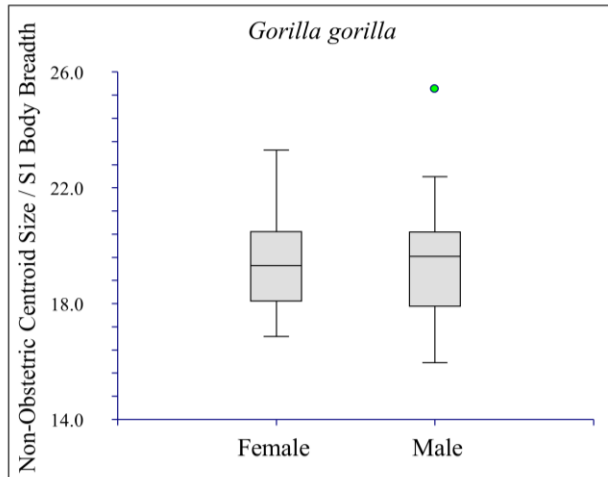
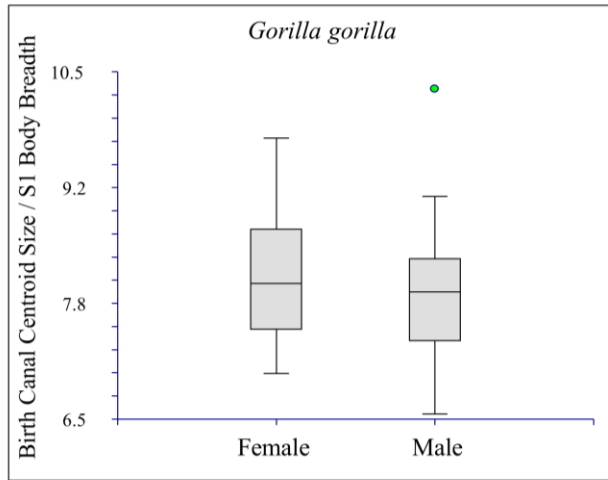


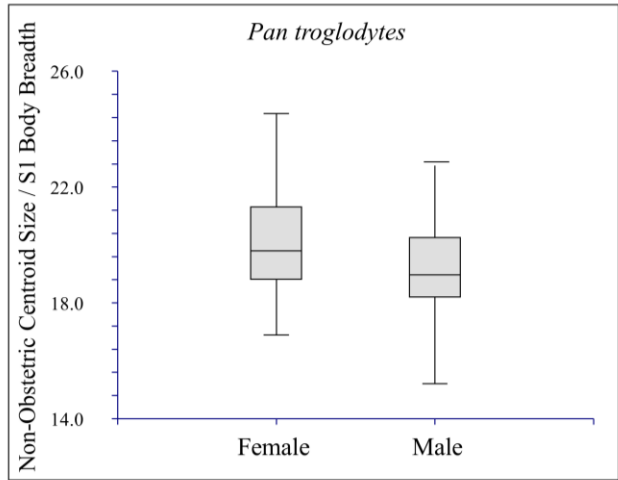
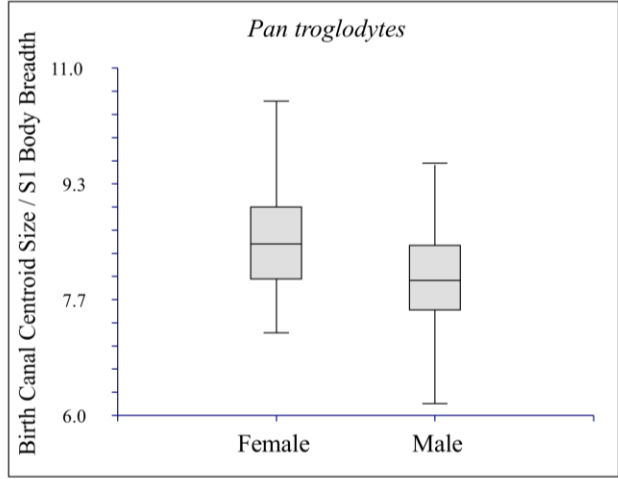


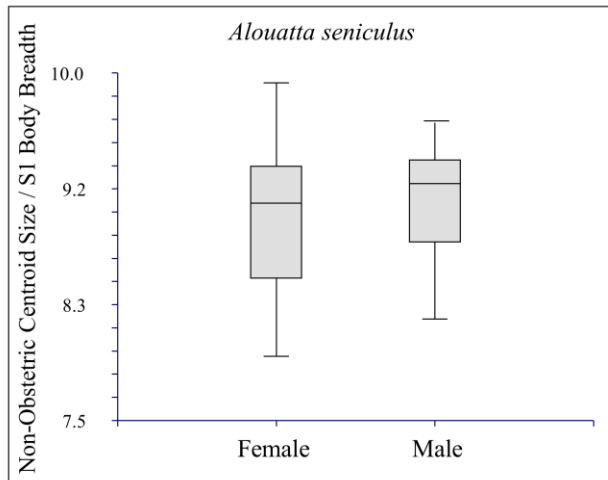
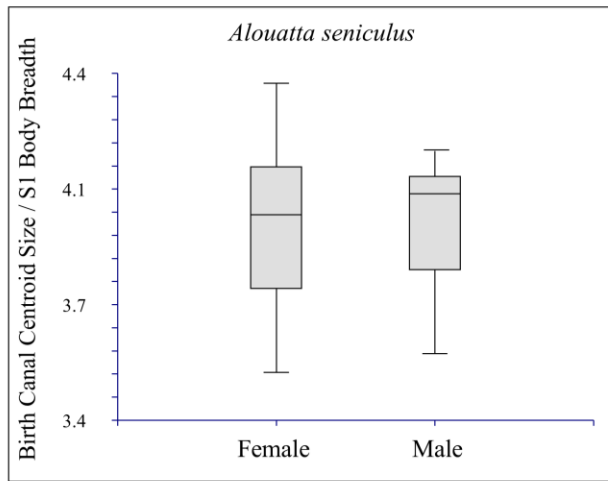












VITA

Elizabeth Moffett attended Louisiana State University for her Bachelors degree in Anthropology, and it was there that she discovered an interest in osteology and pelvic dimorphism. She attended the University of Missouri for her doctoral degree. During her time in the MU Department of Pathology and Anatomical Sciences, she participated in paleontological fieldwork in Kanapoi, Kenya, and traveled to Europe and Puerto Rico for data collection. She also discovered an interest in gross anatomy and functional morphology in graduate school. These experiences have shaped her early career.