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OBSTETRIC LOAD AND THE EVOLUTION OF HUMAN LUMBOPELVIC SEXUAL DIMORPHISM

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OBSTETRIC LOAD AND THE EVOLUTION OF HUMAN LUMBOPELVIC SEXUAL DIMORPHISM

by

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for my parents, Clifford and Phyllis Whitcome

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Obstetric Load and the Evolution of Human Lumbopelvic Sexual Dimorphism

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Despite significant advances in our understanding of parturitional selection factors, we know little about the impact of reproductive load on the hominin skeleton. During human pregnancy, maternal shape and mass distribution change as abdominal muscles stretch and separate to accommodate fetal growth. One important biomechanical consequence of these shape changes is an anterior shift in location of the maternal center of mass that generates strong bending moments about the hip.

It is argued that positional adjustments in lumbar lordosis and anterior sagittal pelvic tilt during pregnancy ensure upper body stability by maintaining the maternal center of mass in a biomechanically efficient position relative to the hip joints (Bullock et al., 1987; Dumas et al., 1995; Franklin and Conner-Kerr, 1998; Foti et al., 2000). While these adjustments may be favorable for upper body control, they redistribute forces through the spinal column, shifting load onto dorsal vertebral structures that are less heavily loaded under nonparous conditions, subjecting the neural arch to increasing compressive and shearing loads. This study tests the prediction that sexual dimorphism in the human lumbopelvic region reflects female adaptive resistance to biomechanical failure resulting from obstetric load-induced acute lumbar lordosis.

Results demonstrate that as fetal load approaches half of its expected term mass, gravid women begin to alter their posture and gait by increasing lumbar lordosis and anterior pelvic tilt. When experimentally constrained from positional adjustment, maternal center of mass anteriorly translates 3.2 cm. However, when gravid women self-select their stance positions, the center of mass remains stationary, translating less than 0.5 cm during pregnancy, suggesting that adjustments in lordosis and pelvic tilt mediate the biomechanical instability of obstetric load. Female vertebrae are dorsally wedged at lumbar levels L3, L4 and L5. At these lordotic levels, females have relatively large and oblique zygapophyseal facets. Conversely, lordotic wedging in human males is less extensive along the column, occurring at lumbar levels L4 and L5. Human lumbopelvic sexual dimorphism is consistent with the spinal loading patterns of the gravid analyses, indicating that unique features of female lumbar vertebrae are adapted to resist structural risks of bipedal obstetric load.

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Chapter 1: Introduction

This dissertation research investigates the functional relevance of sexual dimorphism in osteological features of the human lumbopelvic complex. It departs from previous work in its novel focus on postural and locomotor biomechanics of obstetric load. Specifically, the study hypothesizes that aspects of the female lumbopelvic complex represent unique adaptations to structural risks associated with bipedality, incurred under conditions of fetal load. This hypothesis differs from the current view that lumbopelvic shape sexual dimorphism is functionally related to parturitional adaptation alone (Tague and Lovejoy, 1986; Rosenberg 1992; Tague, 1992).

Through an integrated approach of comparative morphology and positional and gait kinematics, this study investigates both postural and locomotor challenges experienced by the gravid modern human female and explores their relevance in the evolution of hominin bipedality. The experimental kinematic approach tests hypotheses on weight redistribution and loading of the human female pelvis during pregnancy, while the comparative morphometric approach places these results into a broader phylogenetic and evolutionary context.

The study focuses on four critical questions: 1) To what extent does sexual dimorphism of the lumbopelvic complex in humans differ from that of other extant primates? 2) Do kinematic adjustments in lumbar lordosis and sagittal pelvic tilt during human pregnancy mediate risk associated with obstetric spinal loading? 3) Which aspects of human lumbopelvic sexual dimorphism are associated with fetal load? and 4) To what extent is sexual dimorphism in the human lumbopelvic complex an evolutionary solution to the bipedal challenge of hominin fetal load?

FETAL LOAD AND ORTHOGRADY

Among all primates during pregnancy, maternal shape and mass distribution change as abdominal muscles stretch and separate to accommodate fetal growth (Abitbol, 1996; Gilleard et al., 1996). One important biomechanical consequence of these shape changes in orthograde primates, those that frequently maintain an upright position, is an anterior shift in location of the maternal center of mass (COM). As COM translates farther from the supporting joints and body support base, bending moments increase about the hip, reducing upper body stability (Dumas et al., 1995; Jensen et al., 1996). Habitual bipedalism, the human form of orthogrady, makes this a persistent challenge for reproductively active females.

It is argued that during human pregnancy positional adjustments in lumbar lordosis and anterior sagittal pelvic tilt ensure upper body stability by maintaining the maternal COM in a biomechanically efficient position (Bullock et al., 1987; Dumas et al., 1995; Franklin and Conner-Kerr, 1998; Foti et al., 2000). In the absence of kinematic adjustments, gravitational force draws the upper body anteriorly downward inducing torque about the hips (Ortengren and Andersson, 1977). In this gravid biomechanical context, resistance to hip moments requires sustained muscle contraction, an effort which is energetically costly and potentially injurious. While favorable for upper body control, positional changes in lumbar lordosis and pelvic tilt are also problematic in that they redistribute proportional loading through the vertebral column, adding stress to structures that are less heavily loaded under nonparous conditions.

BIOMECHANICS OF HUMAN SPINAL LOADING

Human spinal loading is particularly complex due to the secondary vertebral curve of the lumbar segment. This unique human lordosis becomes morphologically defined during the developmental period of toddler transition from quadrupedal crawling to bipedal walking. Lumbar lordosis positions the center of mass in vertical alignment over the biacetabular axis, functioning as a stabilization mechanism of the upper body. As a result of both static morphology, largely the vertebral body wedging of the lower lumbar region, and dynamic movements of sagittal flexion and extension along the entire lumbar vertebral column, loading proportions of the vertebral bodies and the neural arch components differ at various levels of the lumbar spine (Pal and Routal, 1987). The load-bearing capacity of lumbar vertebral bodies is relatively high, afforded by both large centrum endplate size and approximate transverse orientation of the centrum articular surfaces. As a result of bipedal lumbar lordosis the magnitude of loading through the human neural arch zygapophyses is nearly 25% of the total static spinal load (Adams and Hutton, 1980; Louis, 1985). Dynamic increase in lordosis immediately intensifies loading force through the zygapophyses (Davis, 1961).

Compared to earlier hominins and relative to body size, modern humans present large centrum endplates, particularly of the lower lumbar region (Rose, 1975; Shapiro, 1993a). Based on estimated body size, the centrum surface area of australopithecine lumbar vertebrae was relatively small compared to modern humans (Shapiro, 1993a; Sanders, 1998). Yet, relative to modern humans, australopithecines appear to have had large lumbar zygapophyses and massive sacral superior facets (Sanders, 1998). Vertebral proportions in the *Australopithecus* specimens A.L. 288-1 and Sts-14 led Sanders (1998) to propose that australopithecines may have evolved a derived biomechanical channel for lumbar spinal loading, one characterized by a higher percentage of compressive force transmitted through the dorsal vertebral components. If, as is generally accepted, these two early hominin specimens were female (Robinson, 1972; Tague and Lovejoy, 1986; Wood and Quinney, 1996), the observed robusticity of their dorsal pillar facets may exemplify a broad sex-specific morphology related to fetal load in all hominins. Recovery of additional fossil vertebrae is needed to increase the likelihood of multi-sex sampling before biomechanical predictions of fetal load adaptation in early bipeds can be properly tested. Should results of this analysis support the study hypotheses, the question of agreement in morphology and sex assignment in A.L. 288-1 and Sts-14 will be worth pursuing as more fossil material becomes available.

In some respects, the preserved morphology of the lumbar vertebral column of KNM-WT 15000 (*Homo ergaster*), a presumed male, is similar to that of earlier australopithecines, i.e., relatively small centra and robust dorsal pillar elements (Latimer and Ward, 1993; Sanders, 1995), which may argue against the above hypothesis. However, the juvenile status of the Nariokotome specimen precludes direct comparison with adult human morphology as any observed similarity in the youthful KNM-WT 15000 and adult modern human female may derive from errant projection of one taxon's ontogenetic phase on that of another.

HUMAN PELVIC SEXUAL DIMORPHISM

Pelvic shape is arguably the most recognizable difference in the bony anatomy of human males and females. The pelvic aperture of adult females is relatively broad mediolaterally, the subpubic angle more obtuse than that of males and the ischiopubic ramis arced (Washburn, 1948; Phenice, 1969; Ubelaker and Volk, 2002). Cephalopelvic proportions between the human neonate and the adult female, respectively, provide the basis for our current understanding of human pelvic sexual dimorphism, as many investigators have concluded that the human female pelvis is derived as a result of parturitional selection pressure favoring a maternal birth canal sufficiently spacious for delivery of a relatively large brained or large bodied fetus (e.g., Berge et al., 1984; Tague and Lovejoy, 1986; Abitbol, 1987, 1996; Rosenberg, 1988, 1992; Hager, 1989, 1996; Ruff, 1995; Walrath and Glantz, 1996; Trevathan and Rosenberg, 2001).

Human parturition begins with the cephalic sagittal axis of the fetus aligned mediolaterally at the inlet of the maternal pelvis. The fetal head and body then rotate in order to navigate the pelvic midplane which is broadest anteroposteriorly and circumscribed by bony walls of the ilia, pubic symphysis and sacrum. Navigation of the birth canal in early hominins is thought to have proceeded nonrotationally, with the broad sagittal axis of the neonate head aligned mediolaterally, without reorientation through the pelvic midplane (Tague and Lovejoy, 1986; Rosenberg, 1992). The leading hypothesis for emergence of the rotational birth mechanism emphasizes an encephalization event of rapid increase in average absolute and relative adult cranial capacity in late Middle Pleistocene *Homo* (Begun and Walker, 1993; Rightmire, 1990; Trinkaus and Wolpoff, 1992; Ruff et al., 1997; but see Kappelman, 1996). From adult cranial expansion an increase in fetal cranial capacity is inferred, driving shape change in pelvic birth canal (Ruff, 1995). The rotational mechanism in modern humans further argued for the unique nature of human parturitional obstetrics and the large degree of human pelvic sexual dimorphism.

However, not all data support the rotational conclusion. Berge et al. (1984) in their study of australopithecine pelvic shape concluded that given chimpanzee-like fetal skull proportions a rotational mechanism similar to that of modern humans would have characterized australopithecine birth. Stoller (1995) provided parturitional radiographic observation of fetal rotation in both *Saimiri* and *Papio,* demonstrating that rotational descent by the human fetus is not unique among primates. While our study of pelvic sexual dimorphism has pivoted on the parturition stage of primate reproductive success, there remain points of disagreement and uncertainty as to the selection pressures driving pelvic sex differences in modern humans. Clearly, the anatomical and functional complexity of the lumbopelvic complex continues to challenge our copious and best efforts.

It is important to stress that our current understanding of human pelvic sexual dimorphism is ultimately limited in scope by overlooking the broader stresses of reproductive load and narrowly focusing on sexual dimorphism in pelvic morphology directly related to the birthing event. The obstetric demands of parturition clearly impact pelvic form, yet they are mechanistically limited to localized interactions between the fetal body and the maternal true pelvis. Because pregnancy exerts marked, recurrent biomechanical stress on the postural and locomotor skeleton, reproductive factors other than the immediate mechanisms of birth are likely to have influenced the evolution of human lumbopelvic morphology, particularly given the unique spinal loading patterns associated with bipedal lumbar lordosis. For in their collective role as a functional complex, lumbar vertebrae and pelvic elements provide support and flexibility required for posture and locomotion, the biomechanical environment of which changes during pregnancy.

HUMAN LUMBAR VERTEBRAL SEXUAL DIMORPHISM

Studies of sexual dimorphism in human lumbar vertebrae have been largely descriptive (Cunningham, 1889; Derry, 1912; Trotter, 1929; Danforth, 1930; Odgers, 1933; Bornstein and Peterson, 1966; DeBeer Kaufman, 1974; Knussman and Finke, 1980). Where functional inferences were drawn, investigators concluded that lumbar vertebral morphology in females accommodates their relatively large lumbosacral angle, a feature of the pelvis spatially relevant to parturition (Derry, 1912; Tague, 1992).

Recent work on sexual dimorphism in the human lumbar vertebral column demonstrates that females present relatively smaller centrum surface areas than males, suggesting they carry a greater proportion of their spinal load dorsally (Whitcome, 1999, 2000). Additional research is needed to assess the biomechanical signals of the zygapophyseal areas and entire neural arch anatomy along the lumbosacral spine. Identification of the differential distribution of load between the vertebral bodies and zygapophyses is currently based on size of gross structures and relative surface areas of joints (Pal and Routal, 1991; Shapiro, 1993b), yet these features alone do not fully account for load trajectory and magnitude. Furthermore, previous comparative works quantified only lumbar regions with the modal count of five vertebrae. Because there is variation in the total number of human lumbar vertebrae, from as few as four to as many as six (Latimer and Ward, 1993), further study is needed on sex differences in modern humans whose lumbar columns are nonmodal in number, particularly the extra-modal number of six lumbar vertebrae, which appears to be the modal lumbar number in australopithecines (Robinson, 1972; Sanders, 1998; Tobias, 1998; but see Haeusler et al., 2002). Because lumbar and sacral vertebrae provide the main load-bearing capacity of the human axial skeleton, any skeletal adaptation to the stresses of obstetric load is likely to be evident among them.

HUMAN REPRODUCTIVE BIOMECHANICS

The developing fetus and its placenta alter maternal body proportions and mass distribution (Jensen et al., 1996). From these shape changes an anterior shift in the maternal center of mass is expected (Mittlemark et al., 1991; Abitbol, 1996a, 1996b). The relative position of the body center of mass holds implications for the kinematics of pregnant gait (Stokes et al., 1989). Therefore, any analysis of the effect of obstetric load effect on posture and locomotion should take into account the possible translation of center of mass during pregnancy. Investigated together as in this study, center of mass position and human posture and gait adjustments during pregnancy will inform our understanding of the biomechanical conditions inherent in bipedal obstetric load.

Using these techniques, changes in lumbar lordosis and pelvic tilt during pregnancy can be biomechanically assessed in the context of Pal and Routal's two-pillar model of spinal force transmission (Pal and Routal, 1986, 1987). The model demonstrates that distributional change in the magnitude of compressive force between the ventral pillar of vertebral bodies and the dorsal pillar of the neural arch components is due to dynamic changes in spinal curvature. Angular excursions of the intervertebral and lumbosacral joints within the sagittal plane kinematically alter lumbar lordosis. Both spinal extension and pelvic anterior rotation may augment the lumbar curve.

Kinematic change in lumbar lordosis occurs during pregnancy. A survey of previous studies shows a lack of consensus as to the direction of lordotic change. While Bullock et al. (1987) and Franklin and Conner-Kerr (1998) reported an angular increase of 7 degrees in human lumbar lordosis from early pregnancy through end stage of the third trimester, reduction in lumbar lordosis during pregnancy has also been documented (Snijders et al., 1976; Foti et al., 2000). The latter studies tested only one stage of pregnancy, two weeks prior to partum. In targeting a narrow window in what is within humans a lengthy reproductive process, the full influence of fetal load on maternal positional biomechanics remains undetermined. The inference of Foti et al., (2000) was established indirectly from data that showed a decrease in maternal stature. The interpretation is not conclusive as height loss during pregnancy may result from change in postural factors other than lumbar lordosis.

The human pattern of spinal loading during pregnancy will be better understood from new research closely tracking a large number of women within a longitudinal framework directly testing the location of COM and angles of lordosis and pelvic tilt, one designed to document multiple stages of increasing fetal load.

IMPLICATIONS OF PRIMATE ORTHOGRADY

While lumbar lordosis is unique to hominins and functionally linked to bipedalism, a range of orthograde behaviors among other primates generates similar compressive loadings (Rose, 1975; Shapiro, 1993a, 1995: Johnson and Shapiro, 1998; Shapiro and Simons, 2002). Therefore, evolutionary adaptations to orthograde fetal load may not be limited to bipeds, and comparative investigation of other primates in orthograde and pronograde contexts are a necessary adjunct to test the functional role of lumbopelvic morphology in managing fetal load.

Specifically, this study hypothesizes that sexual dimorphism in the human lumbopelvic region reflects female adaptive resistance to biomechanical failure resulting from fetal load-induced acute lumbar lordosis. If as predicted, human fetal load kinematically increases lumbar lordosis, the bony structures supported in the vertebral column’s dorsal pillar are subject to increased risk of structural failure. Biomechanical failures, such as spondylolysis and spondylolythesis are correlated with relative increase in lordotic acuity which exposes the neural arch to both increasing compressive and increasing shearing loads (Bogduk, 1999). Since the hominin evolutionary skeleton has been repetitively loaded in this fashion, adaptations to fetal load are expected in dorsal pillar structures of the female vertebral column.

Although the biomechanical consequences of lumbar lordosis are likely to result in a pattern of lumbopelvic sexual dimorphism unique to bipeds, generalized orthogrady absent of lumbar lordosis may result in some measure of sexual dimorphism. Because the lumbar transverse processes of orthograde primates project dorsally and are related to maintaining orthograde postures by resisting ventral flexion of the trunk (Shapiro, 1993b, 1995; Ward, 1993; Sanders and Bodenbender, 1994, Johnson and Shapiro, 1998), transverse processes of orthograde females may be more dorsally oriented and relatively larger than those of the males. While the presence of lumbopelvic sexual dimorphism is predicted in nonhuman orthograde primates, without lumbar lordosis non bipedal orthograde females are likely to present ventral pillar structures relatively larger than those of males, in accordance with kyphotic postural support of obstetric load, a contrasting pattern to that expected in bipeds.

OBSTETRIC LOAD: NEW HYPOTHESIS FOR HUMAN LUMBOPELVIC SEXUAL DIMORPHISM

Any persistent interpretation of sexual dimorphism in lumbar and sacral vertebrae as compliant to the pelvis obscures the possibility that vertebrae perform a more immediate functional role in trunk biomechanics. As a framework for interpreting the scope of human lumbopelvic sexual dimorphism, our current parturition-centered conclusions are limited in focusing exclusively on pelvic morphology directly related to the birthing event, thereby overlooking the attendant stresses of reproductive load. Although pregnancy is intermittent, the duration and recurrence of fetal load exert marked stress on the postural and locomotor skeleton, holding implications not only for modern humans, but for earlier bipeds, and therefore, our reconstruction of hominin evolution.

SIGNIFICANCE OF THE STUDY

The major hypothesis introduced in this study proposes that aspects of the human lumbopelvic complex represent unique female adaptations to structural risks associated with bipedality under conditions of fetal load. Despite significant advances in our understanding of parturitional selection factors, we still know very little about the impact of reproductive load on the hominin skeleton. Identification of sexually dimorphic features in the human lumbopelvic complex that are not fundamentally linked to parturition will broaden our evolutionary perspective by introducing the notion that female morphology is not singly driven by childbirth events but is more complexly impacted by a suite of reproductive demands. Adaptations of this nature are likely to have had a more basal influence on the hominin lineage than previously inferred. If fetal load generates sex-specific lumbopelvic loading in humans, it is possible that early hominin adaptations similar to those in modern female lumbopelvic morphology arose in association with orthograde and fetal load prior to the encephalization events that introduced fetal head and body size selection for a larger maternal birth canal.

The relevance of this study is perhaps best exemplified by women whose pregnancies are accompanied by fatigue and discomfort of the lower back. By and large gravid women manage obstetric load well, likely due to the mechanisms this study aims to identify. That bipedal obstetric load can lead to compromised posture and locomotion (e.g., Moore et al., 1990; Ostgaard, 1993; Dumas et al., 1995) highlights the potential vulnerability of the lumbopelvic complex in mediating obstetric load and provides support for the recognition that, in addition to pelvic canal dimensions, morphology of the lumbar and sacral vertebrae is also key to female reproductive success. The adult female lumbopelvic complex is subject to strong selection pressures, applied not only at parturition, the terminal event of pregnancy, but also throughout pregnancy, the protracted period of increasing fetal mass.

ORGANIZATION SUMMARY

Following this introductory Chapter 1, Chapter 2 investigates the impact of obstetric load on the kinematics of human female positional behavior. Posture and locomotor data were collected from nineteen women across six successive periods during pregnancy and a period postpartum to determine location of total body center of mass and segmental position angles to better understand mechanisms of posture and gait under conditions of fetal load and the relevancy of these interactions to hominin bipedal evolution. Chapter 3 investigates the human lumbopelvic complex to identify the presence of sexual dimorphism in features associated with upper body control. In addition to a sample drawn from individuals of modal lumbar vertebral number, two samples were included that represent variation in lumbar vertebral count as a means to further investigate the biomechanics of upper body load on longer and shorter lordotic columns. The former is particularly relevant to the question of early hominin adaptation as australopithecines appear to have had lumbar column length equal to the extra-modal variant in modern humans. Chapter 4 examines lumbopelvic traits in a broad comparative sample of nonhuman primates to determine whether sexual dimorphism differs according to positional orientation. The comparative analysis provides context in which to interpret human sexual dimorphism as consistent with that of other primates, particularly the orthograde taxa or alternatively as a unique phenomenon among primates. The concluding Chapter 5 is a synthesis of the kinematic and morphometric results and a discussion of the evolutionary implications of bipedal obstetric load.

References

Abitbol M. 1987. Obstetrics and posture in pelvic anatomy. J Hum Evol 16*:*243-256.

Abitbol M. 1996a. The shape of the female pelvis: contributing factors. J Rep Med 41:242-250.

Abitbol M. 1996b. Birth and human evolution: anatomical and obstetrical mechanics in primates. Westport, Conn: Bergin and Garvey.

Adams MA, Hutton WC. 1983. The mechanical function of lumbar apophyseal joints. Spine 8:327-330.

Begun D, Walker A. 1993. The endocast. In: Walker A, Leakey R, editors. The Nariokotome *Homo erectus* skeleton. Cambridge, MA:Harvard University Press. p 326-358.

Berge C, Orban-Segebarth R, Schmid P. 1984. Obstetric interpretation of the australopithecine pelvic cavity. J Hum Evol 13:573-587.

Bogduk N. 1999. Clinical anatomy of the lumbar spine and sacrum. Churchill Livingston: New York.

Bornstein P, Peterson R. 1966. Numerical variation of the presacral vertebral column in three population groups in North America. Am J Phys Anthropol 25:139-146.

Bullock J, Jull G, Bullock M.1987. The relationship of low back pain to postural changes during pregnancy. Aust J Phys 33:10-17.

Cunningham D. 1889. The proportion of bone and cartilage in the lumbar section of the vertebral column of the ape and several races of men. J Anat 24:117-126.

Danforth CH. 1930. Numerical variation and homologies in vertebrae. Am J Phys Anthropol 14:463-481.

Davis PR. 1961. Human lower lumbar vertebrae: some mechanical and osteological considerations. J Anat 95:337-344.

DeBeer Kaufmann P. 1974. Variation in the number of presacral vertebrae in Bantu-speaking South African Negroes. Am J Phys Anthropol 40:369-374.

Derry DE. 1912. The influence of sex on the position and composition of the human sacrum. J Anat Physiol 46:184-192.

Dumas GA, Reid JG, Griffin MP, McGrath MJ. 1995. Exercise, posture, and back pain during pregnancy. Clin Biom 10(2):98-105.

Foti T, Davids J, Bagley A. 2000. A biomechanical analysis of gait during pregnancy. J Bone Joint Surg 82A:625-632.

Franklin M, Conner-Kerr T. 1998. An analysis of posture and back pain in the first and third trimesters of pregnancy. J Ortho Sports Phys Ther 28:133-138.

Gilleard D, Brown W, Brown JM. 1996. Structure and function of the abdominal muscles in primigravid subjects during pregnancy and the immediate postbirth period. Phys Ther 76: 750-762.

Haeusler, M., Martelli, S., Boeni, T., 2002. Vertebrae numbers of the early hominid lumbar spine. J Hum Evol 43, 621-643.

Hager LD. 1989. The evolution of sex differences in the hominid bony pelvis. Ph.D. dissertation, University of California at Berkeley, Berkeley, California.

Hager LD. 1996. Sex differences in the sciatic notch of great apes and modern humans. Am J Phys Anthropol 99:287-300.

Jensen R, Doucet S, Treitz T. 1996. Changes in segment mass and mass distribution during pregnancy. J Bio 29:251-256.

Kappelman, J. 1996. The evolution of body mass and relative brain size in fossil hominids. J Hum Evol 30:243-276.

Knussman R, Finke E. 1980. Studies on the sex-specificity of the human spinal profile. J Hum Evol 9:615-620.

Johnson SE, Shapiro LJ. 1998. Positional behavior and vertebral morphology in atelines and cebines. Am J Phys Anthropol 105:333-354.

Latimer B, Ward C. 1993. The thoracic and lumbar vertebrae. In: Walker A, Leakey REF, editors. The Nariokotome *Homo Erectus* Skeleton. Cambridge: Harvard University Press p 266-293.

Louis R. 1985. Spinal stability as defined by the three-column spine concept. Anat Clin 7:33-42.

Mittlemark R, Wiswell R, Drinkwater B. 1991. Exercise in pregnancy. Baltimore: Williams and Wilkins.

Moore K, Dumas GA, Reid, JG. 1990. Postural changes with pregnancy and their relationship with low back pain. Clin Bio 5:169-174.

Odgers P. 1933. The lumbar and lumbosacral diarthrodial joints. J Anat 67:301-317.

Ortengren R, Andersson G. 1977. Electromyographic studies of trunk muscles with special reference to the anatomy of the lumbar spine. Spine 2:44-52.

Ostgaard HC, Andersson GBJ, Schultz AB, Miller JAA. 1993. Influence of some biomechanical factors on low-back pain in pregnancy. Spine 18:61-65.

Pal GP, Routal RV. 1986. A study of weight transmission through the cervical and upper thoracic regions of the vertebral column in man. J Anat 148:245-261.

Pal GP, Routal RV. 1987. Transmission of weight through the lower thoracic and lumbar regions of the vertebral column in man. J Anat 152:93-105.

Pal GP, Routal RV. 1991. Relationship between the articular surface-area of a bone and the magnitude of stress passing through it. Anat Rec 230:570-574.

Phenice TW. 1969. A newly developed visual method of sexing in the *Os pubis.* Am J Phys Anthropol 30:297-301.

Rightmire GP. 1990. Variation in early *Homo* from eastern Africa. Am J Phys Anthropol 81:286-286.

Robinson J. 1972. Early Hominid Posture and Locomotion. Chicago: The University of Chicago Press.

Rose MD. 1975. Functional proportions of primate lumbar vertebral bodies. J Hum Evol 4:21-38.

Rosenberg KR. 1988. The functional significance of Neanderthal pubic length. Cur Anthropol 29: 595-607.

Rosenberg KR. 1992. The evolution of modern human childbirth. Yrbk Phys Anthropol 35:89-124.

Ruff CB. 1995. Biomechanics of the hip and birth in early *Homo*. Am J Phys Anthropol 98:527-574.

Ruff CB, Trinkaus E, Holliday TW. 1997. Body mass and encephalization in Pleistocene *Homo*. Nature 387:173-176.

Sanders WJ. 1995. Function, allometry, and evolution of the australopithecine lower precaudal spine. PhD dissertation, New York University.

Sanders WJ. 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. J Hum Evol 34:249-302.

Sanders WJ, Bodenbender BE. 1994. Morphometric analysis of lumbar vertebra UMP 67-28: Implications for spinal function and phylogeny of the Miocene Moroto Hominoid. J Hum Evol 26:203-237.

Shapiro LJ. 1993a. Evaluation of "unique" aspects of human vertebral bodies and pedicles with a consideration of *Australopithecus africanus.* J Hum Evol 25:433-470.

Shapiro LJ. 1993b. Functional morphology of the vertebral column on primates. In: Gebo DL, editor. Postcranial Adaptation in Nonhuman Primates. DeKalb: Northern Illinois University Press p 121-149.

Shapiro LJ, Simons CVM. 2002. Functional aspects of strepsirrhine lumbar vertebral bodies and spinous processes. J Hum Evol 42:753-783.

Snijders C, Seroo J, Snijders J, Hoedt H. 1976. Changes in form of the spine as a consequence of pregnancy. Digest of the 11th International Conference on Medical and Biological Engineering 1:670-671.

Stokes V, Andersson C, Forssberg H. 1989. Rotational and translational movement features of the pelvis and thorax during adult human locomotion. J Biom 22:43-50.

Stoller M. 1995. The obstetric pelvis and mechanism of labor in nonhuman primates. PhD dissertation, University of Chicago, Chicago, Illinois.

Tague RG. 1992. Sexual dimorphism in the human bony pelvis with a consideration of the Neanderthal pelvis from Kebara Cave, Israel. Am J Phys Anthropol 88:1-21.

Tague RG, Lovejoy CO. 1986. The obstetric pelvis of AL 288-1 (Lucy). J Hum Evol 15:237-255.

Tobias, P.V., 1998. Ape-like *Australopithecus* after seventy years. Was it a hominid? J. Roy. Anthropol. Inst. 4, 283-308.

Trevathan W, Rosenberg K. 2001. The evolution of human birth. Sci Amer 285:72-77.

Trinkaus E, Wolpoff M. 1992. Brain size in post-habiline archaic *Homo*. Am J Phys Anthropol Supp 14:163.

Trotter M. 1929. The vertebral column in whites and in American negroes. Am J Phys Anthropol 9(4):95-107.

Ubelaker DH, Volk CG. 2002. A test of the Phenice method for the estimation of sex. J Foren Sci 47:19-24.

Walrath D, Glantz M. 1996. Sexual dimorphism in the pelvic midplane and its relationship to Neandertal reproductive patterns. Am J Phys Anthropol 100:89-100.

Ward CV. 1993. Torso morphology and locomotion in *Proconsul nyanzae.* Am J Phys Anthropol 92:291-328.

Washburn SL. 1948. Sex differences in the pubic bone. Am J Phys Anthropol 6:199-207.

Whitcome KK. 1999. Sexual dimorphism of the human lumbar spine. Am J Phys Anthropol 276-276 Suppl. 28.

Whitcome KK. 2000. A functional examination of sexual dimorphism in human lumbar vertebrae. Masters thesis. Southern Illinois University, Carbondale.

White AA. 2006. Clinical biomechanics of the spine. Williams and Wilkins:

Wood BA and Quinney PS. 1996. Assessing the pelvis of AL 288-1. J Hum Evol 31:563-568.

Chapter 2: Kinematics of Human Obstetric Spinal Loading

INTRODUCTION

The mature kinematic pattern of modern human locomotion is characterized in part by lumbar lordosis and sagittal pelvic tilt (Thurston and Harris, 1983; Crosbie et al., 1997). Lordosis and pelvic tilt are morphologically determined by skeletal shape and joint orientation on the one hand while kinematically defined by movement through a range of joint rotation on the other hand. The kinematic aspects of lordosis and pelvic tilt are largely constrained by morphology of the lumbar vertebrae and pelvis and the location of muscle attachments relative to the joints across which they act (i.e., Cunningham, 1886; von Lackam, 1924; Jenkins, 1974; Rose, 1975; Gilad and Nissan, 1985; Bogduk, 1997). The skeletal anatomy of the lumbar vertebral lordotic complex in early bipeds, to the extent that we know it from the hominin fossils A.L. 288-1, Sts 14 and Stw 431 is broadly similar in modern humans and these early australopithecines (Robinson, 1972; Sanders, 1998; Haeusler, 2002; Toussaint et al., 2003). Lumbar lordosis and sagittal pelvic tilt appear to be basal adaptations in the evolution of hominin bipedality, as evidenced by an extensive suite of postcranial traits shared exclusively within the Hominini. Non musculo-skeletal determinants of positional behavior present in modern humans include ligamentous structure (Leong et al., 1987; Sanders, 1998), size and shape parameters of upper body segments (Jensen et al, 1996a; Whittle and Levine, 1999) and relative positions of body segments with respect to one another (Levine and Whittle, 1996). For example, load carrying is a context-specific condition in which individuals self-select biomechanically stable positions (Granata and Sanford, 2000; Wilson and Granata, 2003). Within the range of angular excursions that the collective anatomical parameters allow, there is a conservative degree of self-selected positional arrangement possible.

While spinal loading forces generated during bipedal locomotion are generally similar for all adults (Pal and Routal, 1987; Pal, 1989), the lengthy duration and recurrent nature of obstetric fetal load cleaves two distinct loading groups, one male and one female, based entirely in reproductive physiology. In spite of this obvious biological dichotomy and decades of locomotor study, we know relatively little about spinal loading during pregnancy or its skeletal correlates. Our lack of knowledge is all the more surprising considering the likelihood that obstetric locomotor biomechanics are influential in evolutionary reproductive success.

As the fetus grows and its supporting tissues increase in mass, the maternal abdomen expands, undergoing incremental changes in shape and mass distribution. In humans as in other orthograde primates, expansion of the abdomen occurs largely along its fore-aft dimension, resulting in anterior translation of segmental center of mass (e.g., Taves et al., 1982; Mittlemark et al., 1991; Abitbol, 1996). Within bipeds, for whom the two-footed base of positional support is relatively small, bending moments at the hip are greatly increased under conditions of obstetric load because gravitational force draws the torso downward at a center of mass (COM) increasingly distant from the biacetabular axis. The fetus in its positional relationship to the maternal orthograde orientation reduces upper body stability when it induces a directional shift in the location of the maternal COM (Dumas et al., 1995; Jensen et al., 1996a; Jensen et al., 1996b).

The relative location of the total body COM holds implications for the kinematics of pregnant posture and gait (Stokes et al., 1989). In the absence of positional mechanistic adjustments, the temporal and biomechanical demands of human obstetric load would quickly fatigue the erector spinae muscle group, otherwise needed to resist the obstetric rotational hip moments (Ortengren and Andersson, 1977). Angular adjustments in maternal lumbar lordosis and sagittal pelvic tilt often characterize human pregnancy (Bullock et al., 1987; Franklin and Conner-Kerr, 1998; Foti et al., 2000). In isolation or in tandem, these lumbopelvic adjustments are capable of repositioning the maternal COM in a biomechanically efficient position relative to the major joints of the lower body and the bipedal support base. While these segmental shifts during pregnancy may be favorable for upper body control, through the redistribution of proportional loading within the vertebral column, they are likely to increase spinal loads along the bony structures that under nonparous conditions are less heavily loaded.

Posture and gait in human pregnancy

Pregnancy imposes considerable modifications in the structure and function of the female body to allow for development and parturition of the fetus. Many of these changes, including weight gain (Thompson, 1995), ligamentous laxity (Block et al., 1985) and shape alterations in body segments (Culver and Viano, 1990) contribute to the characteristic posture and gait associated with the pregnant human female. These changes, transient but cyclical, redefine biomechanics of the positional system.

Analyses of the temporal and angular kinematics of pregnant gait have produced equivocal results. While velocity, stride length and cadence appear unchanged with pregnancy (Taves et al., 1982; Foti et al., 2000), compensatory mechanisms may in effect normalize pregnant gait. For instance, a widened base of support is characteristic of near term pregnancy, as evidenced by increased inter ankle diameter (Bird et al., 1999; Foti et al., 2000; Lymbery and Gilleard, 2005). So, while conventional parameters of bipedal locomotor performance suggest that pregnant gait is remarkably unchanged from non pregnant gait, minor mechanistic differences may underlie the similarities.

Normalcy in pregnant gait is not without question. Contrary to earlier results (Taves et al., 1982; Foti et al., 2000), Wu and colleagues (2004) report a significant reduction in comfortable walking velocity during pregnancy, realized only when subjects were asked to self-select a preferential walking speed. Methodological differences then are likely to account for some discrepancy in documented gait parameters, and this presents some difficulty in assessing study of pregnant gait. Taves et al. (1982) potentially constrained subject performance by dictating three pre-determined treadmill speeds during which gait parameters were recorded. While Foti et al. (2000) found no change in gait velocity, stride length or cadence in their comparison of self-selected pregnant and postpartum gait, a significant difference occurred in support phase timing. Double-support phase contributed to a significantly larger percent of the gait cycle during pregnancy than after, and the hip abduction moment was significantly greater in the first peak of stance phase during pregnancy than in the period postpartum. The former result suggests a conservative locomotor strategy during parity by increased reliance on a more stable two-footed support. The latter result, in combination with a wide base of support (Dumas et al., 1995; Bird et al., 1999; Foti et al., 2000; Lymbery and Gilleard, 2005), suggests that additional recruitment of the hip abductors compensates for increased gravitational draw on the unsupported side of the body during single-support phase. These mechanisms of balance may be in response to a general increase in maternal body mass during pregnancy or a widening of pelvic dimensions (Foti et al., 2000) induced by joint laxity, perhaps both.

If pelvic widening is a true gravid phenomenon, one might predict an increase in stride length during pregnant gait, due to increased angular excursion in the transverse plane. However, stride length is consistently unchanged in pregnancy (Taves et al., 1982; Foti et al., 2000). One explanation for this unexpected result may be the relatively smaller amplitudes of pelvic rotation that characterize pregnant walking (Wu et al., 2004). Pelvic rotation is coupled with thoracic rotation in normal human gait (Cappozzo, 1981; Gracovetsky, 1985; Crosbie et al., 1997; Lamoth et al., 2002) and may be constrained during pregnancy by the presence of the fetal body. Alternatively, reduction of gravid pelvic rotation may be a response to increased moments of inertia imposed by maternal weight gain. Segmental mass of the lower torso, which includes the maternal abdomen and fetal tissues, increases at a greater rate (from 21.6 kg at two months gestation to 28.4 kg at nine months) than other body segments (for example, the upper trunk from 10.4kg to 11.7kg) (Jensen at al., 1996a).

While a relationship between change in gravid center of mass and change in lumbopelvic kinematics during pregnancy is often invoked as an introductory premise in biomechanical and clinical studies (e.g., Rhodes, 1958; Ostgaard et al., 1993; Lou et al., 2001; Noren et al., 2002), it has rarely been tested. Direct analysis of the relationship between the anatomical position of gravid center of mass and pregnant positional behavior has not been achieved and is the major focus of this study.

Maternal center of mass

The potential relationship between gravid center of mass and postural adjustment was initially and singularly investigated by Dumas et al., (1995) in a study on the effectiveness of exercise in mediating back pain during pregnancy. Data were collected during self-selected postures, photographically from spinal landmarks and kinetically from torque platform recordings of the body's line of gravity. Two results relevant to the current investigation were obtained: 1) curvature of the lumbar region increased during pregnancy; and 2) position of the line of gravity during pregnancy remained unchanged, leading to the inference that pregnant women posturally adjust to achieve stable equilibrium. To some extent, the inference remains assumptive since data captured no information on the position of center of mass in the absence of postural adjustments. The conclusion that segmental adjustments function to manage change in center of mass during pregnancy is explicitly unsupported; the study provided no evidence that gravid center of mass would otherwise translate toward postural instability.

Statement of purpose

The purpose of this study is to examine spinal loading patterns associated with human fetal load through kinetic identification of maternal center of mass and kinematic assessment of lumbar lordosis and pelvic tilt during pregnancy and a period postpartum.

Once identified, obstetric loading patterns can be applied in functional analyses of human lumbopelvic sexual dimorphism (see Chapter 3). The goal of the current study was achieved, in part by methodological design of a reference posture in which body angles were held constant. This ensured a means to identify the anatomical position of maternal center of mass in the absence of self-selected positional adjustments. These data were then compared with those collected in self-selected postures, to directly assess any relationship between adjustments in lumbar lordosis and pelvic tilt. Adjustments were of interest relative to the fore-aft location in maternal center of mass, as gauged by the position of the center of mass in the reference posture and in self-selected positional behaviors of natural stance.

Hypotheses

1. As fetal mass increases, the anteroposterior position of the maternal total body center of mass will shift anteriorly, when body segment angles are held constant.

2. Under natural conditions of increasing fetal load, the angle of lumbar lordosis will also increase, enhancing lordosis during natural stance and self-selected walking.
3. Under natural conditions of increasing fetal load, the pelvis will rotate clockwise in the sagittal plane, increasing the angle of sagittal pelvic tilt during natural stance and self-selected walking.
4. Postural and locomotor kinematic changes in lumbar lordosis and sagittal pelvic tilt will correlate with the anterior migration of the maternal total body center of mass.
5. As fetal mass increases, the anteroposterior position of the maternal total body center of mass will remain unchanged, when body segment angles are self-selected during natural stance.

Significance of study

The goal of this research is to better understand biomechanical change in pregnancy, particularly, to identify the role that increasing fetal load plays in the position of maternal center of mass and to accurately characterize the context-specific spinal loading patterns of bipedal pregnancy. Ultimately, with these phenomena clearly understood, we gain mechanistic tools necessary to better reconstruct the evolution of lumbopelvic sexual dimorphism in modern humans and to further identify adaptations that enhance the reproductive success of females.

Investigation of the biomechanical challenges presented by obstetric spinal load and the kinematic mechanisms of resolution will broaden the study of the evolution of hominin lumbopelvic morphology and further clarify the nature of shape sexual dimorphism in the lumbopelvic complex in humans, human ancestors and other primates.

MATERIALS AND METHODS

Sample

Twenty-five pregnant women, all healthy adults between the ages of 20 and 40 years, were selected to participate in a longitudinal study spanning seven sessions, initiated at the commencement of the third month of pregnancy and concluded in the third month of post parity.

Sample recruitment

Participants were solicited from Austin, Texas reproductive clinics and health promoting organizations (Appendix A: Recruitment flyer 1; Appendix B: Recruitment flyer 2; Appendix C: Recruitment web site). Potential volunteers were excluded if they evidenced life histories characterized by joint illness/injury or previous pregnancy-related difficulties leading to medical treatment, restricted physical activity, or persistent discomfort (Appendix D: Screening Questionnaire).

Actual sample size decreased from twenty-five to nineteen women due to various physiological and exogenous factors during the course of the study. One subject (10401) withdrew due to miscarriage in her 21st week of pregnancy. Three subjects (10403, 110305, 120307) missed one mid partum session as a result of obstetric complications managed by physician prescribed bed rest. One subject (10412) experienced multiple bouts of premature contractions for which she was repeatedly hospitalized over an extended period, precluding completion of the final two pre partum sessions. One subject (10402) did not return for the concluding postpartum session.

Six of the fully participatory nineteen subjects delivered two to three weeks earlier than their anticipated due dates and as a result missed Session 6, the final pre partum session. Since birth weights of these six “early” neonates were robust and within the expectation of healthy American live birth weights as reported by Alexander et al. (1996), these subjects were not excluded, and variates collected at Session 5 were treated as their “term” data for the analysis.

Maternal body weight was recorded each session and assessed by the Institute of Medicine standards (1990) which recommend an increase of 1.36 to 1.81 kilograms in the first three months and 1.36 to 1.81 kilograms per month in the later trimesters. Subjects whose prenatal weight gain exceeded 12.75 kilograms would have been excluded from the analyses, but none eclipsed the stated parameter.

Subject protection

The study protocol received University of Texas at Austin IRB approval for human research (IRB Protocol # 2002-05-0067). Participants gave their written consent confirming willingness to participate in study trials and their comprehension of project protocols (Appendix E: Consent Form and Appendix F. Consent Form Amendment). Subjects were compensated for their time and commitment to the study in the amount of $200.00.

Schedule of data collection

In order to investigate the impact of fetal load on maternal center of mass, lumbar lordosis and pelvic tilt, longitudinal data were collected during pregnancy and a period postpartum. To ensure equity in sampling schedules so that comparisons across subjects matched as closely as possible their corresponding stages of fetal load, data collection sessions targeted parity windows. Two factors determined the timing.

First, an incremental scale of increasing fetal load was chosen to standardize the contrasts according to predicted fetal growth. Intersession periods enveloped predicted 20% increases in fetal load following Alexander et al., (1996) and are depicted in Figure

2.1. A complete series included data collected from periods of 0%, 20%, 40%, 60%, 80% and 100% fetal mass and a final session postpartum.

Second, the onset of percentage progression in fetal mass was matched to dates of conception based on parturition “due” dates, provided by subjects in consultation with their obstetricians and other pregnancy care providers. Although as a predictor, the estimated day of delivery (EDD) given by clinicians is only a general approximation of parturition (Mongelli et al., 1996), the lack of preterm testing to identify the date of zygote generation made it the preferred source of estimation. Additionally, calendar prediction of parturition is not date specific and is better generalized by weeks, because gestation periods vary from individual to individual and from pregnancy to pregnancy (Mittendorf et al., 1993). Fewer than 5% of pregnancies reach delivery on the EDD (Baskett and Nagele, 2000).

An alternate approach to scheduling was considered in which session partitioning was directed according to expected maternal weight gain. This design was rejected due to the greater likelihood of fluctuations and broader range of variation in maternal mass (Scholl et al., 1995) when compared to such likelihoods in fetal mass (Alexander et al., 1996), the independent variable of interest in this study. Additionally, it was not possible to predict with a degree of acceptable certainty when an individual subject would reach a targeted weight, and therefore, the advance scheduling necessary in rigorous sampling protocol would be more vulnerable to error in the comparisons across subjects.

By partitioning longitudinal data collection into relatively broad increments of 20% predicted fetal mass change, inherent error in targeting exact dates due to imprecise predictions of both conception and delivery were minimized. Sampling parity at 20% increments tracked study variables through six successive stages of pregnancy and uniquely signifies one of the benefits of this study, for previous studies of pregnant posture and gait sampled less specific time frames and therefore were less likely to fully characterize patterns of kinematic and kinetic change.

The total load exerted on the gravid female extends beyond the aforementioned fetal mass (25%) to include such additional soft tissues as the placenta (5.5%), amniotic fluids (6.5%), uterus (8%), breasts (3%), increased blood volume (10%), increased water volume (14%) and maternal fat (28%), all of which introduce additional load during pregnancy (U.S. residents, American College of Obstetrics and Gynecology). Because these associated tissues increase proportionally with increases in the mass of the fetus, fetal mass provides the reference framework in tracking change in fetal load.

Anthropometric Measurements

Anthropometric variables were recorded for all subjects at each session, by a single observer (Table 2.1). A fiberglass measuring tape was used to quantify circumferences and stature to the nearest millimeter. Body mass was captured on the force plate. The vertical vector component of the ground reaction force, recorded in newtons, was adjusted for the baseline reading and then converted into kilograms for entry into the subjects' databases. The body mass variable was needed to calculate total body COM and was a relevant measure in recruitment criteria, as well as in monitoring change in maternal body mass during pregnancy. Although stature was not expected to vary, it was collected for use in calculating the Body Mass Index. In the event angular adjustments in lumbar lordosis and pelvic tilt influenced stature, height was recorded each session. Skinfold was measured to the nearest millimeter using a Lange Skinfold Caliper (accurate to +/- 1mm), as an indicator of percent body fat. The segment circumferences were recorded for shape information. Mid abdominal circumference was selected as a target measure in the prediction of change in maternal center of mass during pregnancy. Landmark based measurements (e.g., acromial and ASIS circumferences) were directed by palpation of bony structures through overlying skin and, in cases of some landmarks, additionally through thin, taut spandex clothing. Soft tissue defined measurements (e.g., areole and mid abdominal circumferences) were taken maximally. To more closely investigate shape change in the maternal abdomen throughout pregnancy a Girth-Mass Index was generated by dividing the maximum abdominal circumference by body mass:

$$\frac{\text{Abdominal circumference (cm)}}{\text{mass (kg)}} \text{ x } 100$$

In order to test the study hypotheses, subject body proportions were required to remain within hypothetical limits of an early human female model (Ruff et al., 2005) and follow the pattern of anthropometric change characteristic of contemporary women in the U.S. (U.S. National Institutes of Health, 1998).

Kinematic Procedure

All data were collected in the Developmental Motor Control Laboratory at the University of Texas at Austin. A Vicon motion analysis system (Vicon Peak) was used to capture three-dimensional positional data (60 Hz sampling rate) of each subject during quiet stance and while walking freely though a two cubic meter viewing volume. Five infrared cameras recorded positional data and trajectories of noninvasive lightweight 25mm reflective markers externally adhered by removable two-sided tape to thirty-three landmarks of the spine, innominates, and thirteen body segments (Table 2.2, Figure 2.2). The location of anatomical landmarks was identified by palpation. The time reference of heel strike and toe-off was identified by the onset and cessation of vertical force, respectively, as registered on a Bertec four axial transducing force plate (600 Hz sampling rate). Midstance reconstructed from 3D video was defined as occlusion of the support leg by the toe marker of the swing leg.

Prior to each data collection session the viewing volume was calibrated following static and dynamic protocols. Sensitivity of each of the five cameras was independently adjusted to maximize power of reflection. Camera sensitivity was then adjusted just below blooming effect of centroid distortion to prevent over sensitivity that would otherwise introduce noise into the data signals. Static calibration was achieved using a solid L-frame device; dynamic calibration was set using a 500mm wand. Residuals for all cameras were consistently within a range of 0.594 and 0.400mm, representing less than 0.1% of the $2m^3$ viewing volume. The mean wand visibility approached 84.0%.

Kinematic Measurements

Vicon 3D data files were transferred to a personal computer where lordotic and sagittal pelvic tilt angles were algorithmically calculated from positional data derived from lumbar and pelvic markers, using BodyBuilder software (Vicon Peak) (Appendix G: Angle Model). Angles were exported as ASCI to Excel files for further analysis.

Lumbar Lordosis (Figure 2.3)

Three points defined by the vertebral markers L1, L4 and S2 allowed quantification of the lordotic angle between Segments 1 and 2 defined by markers L1-L4 and L4-S2, respectively. Larger angle values indicated more acute lumbar lordosis.

Sagittal Pelvic Tilt (Figure 2.4):

A line extended through markers externally adhered to the right anterior and right posterior superior iliac spines (ASIS and PSIS) defined a parasagittal axis of the pelvis. Sagittal pelvic tilt was computed from the positional data, measuring the angle between the two lines defined by points PSIS and ASIS and PSIS and a global point sharing the PSIS x-coordinate. The degree of pelvic tilt in the sagittal plane impacts the radius of the lumbar curve. Larger angle values indicated more acute lumbar lordosis.

Kinetic Measurements

Maternal Center of Mass:

Kinematic and force plate analog data were captured to calculate the maternal total body center of mass in both the reference and self-selected postures. The static measure of COM taken in the consistent reference posture was needed to identify the translation of the resultant COM. Angular changes in lumbar lordosis and sagittal pelvic tilt were functionally assessed relative to the translation of this reference posture COM. To obtain as consistent a reference posture COM as possible, a portable plywood wall 3’ x 6’ was supported above the floor on a wheeled assembly spanning the Bertec Force Plate. Subjects stood with head, shoulders, and buttocks in contact with the vertical panel (Figure 2.5). Once a stable posture was attained, the portable wall was retracted. A second static measure of maternal COM was taken during natural stance to determine any self-selected kinematic repositioning of the COM. Reference posture center of mass was predicted to significantly change during pregnancy, as the segmental angles of lumbar lordosis and pelvic tilt were held constant from session to session through postural alignment with the reference panel. In contrast, the self-selected position of the maternal center of mass was expected to remain relatively constant throughout the study, its stability achieved through natural adjustments in lumbar lordosis and pelvic tilt.

The fore-aft vectors of the ground reaction force and center of pressure from which center of mass values were calculated were recorded using a Bertec K70501 Type 4550-08 force plate. The force plate was located in the center of an open laboratory space allowing subjects to achieve natural postures and steady state speeds of natural walking before striking the plate (Figure 2.6). This force plate measures applied forces using four tri-directional strain-gauged load transducers installed on a raised platform. When forces are applied to the plate, strain in the transducers changes resistances proportional to the forces. Voltages from the force platform were amplified externally using an adjustable gain amplifier and scaled to adjust for amplification (with channel and scaling factors of 1) -0.596484; 2) -0.588425; 3) -0.934066; 4) -288.9377; 5) -202.8327; 6) -138.8523). All collection trials were preceded by auto zeroing. The auto zero function of the external amplifier only approximates zero. True zero was attained by post-collection subtraction of baseline readings from the analog data averaged across five baseline trials. Maternal body mass was recorded from the force plate as the z force component adjusted for the plate's baseline measure taken during the corresponding session.

To obtain the maternal COM during both reference posture and natural stance, the horizontal position of the static center of gravity was calculated from vectors measured by the force plate following the *zero-point-to-zero-point integration* technique introduced by Zatsiorsky and King (1998) using the formula:

$$X_{\mathrm{GLP}}(t) = \left[\int\int_{\mathrm{t_n} | -\delta < Fx < \delta}^{\mathrm{t_n}+1 | -\delta < Fx < \delta} \ddot{X}(t) \right] + \dot{X}(t_n) \bullet t + X_{\mathrm{COP}}(t_n)$$

where, $X_{\mathrm{GLP}}(t)$ is the horizontal position of the static center of gravity, t_n = time (n), $|$ stands for 'under the condition that", F_x = horizontal ground reaction force, δ = incremental value, $\ddot{x}$ = acceleration, $\dot{x}$ = velocity, XCOP = center of pressure location along the x-axis.

The method is based on the postulation that the horizontal position of the total body line of gravity and the total body center of pressure on the force plate coincide when the horizontal ground reaction force, F_x, is zero. At this instant the torque about the intersection between the vertical axis through the ankles and the supporting substrate is either zero or negligible. The algorithm used to calculate the position of the center of mass was validated by Zatsiorsky and King (1998) with videography-based segment mass. There was no significant difference (at the 0.05 level) and coefficients of correlation were high (0.79 – 0.96) (Zatsiorsky and King, 1998) (Appendix H: MatLab algorithm for calculating fore-aft position of COM).

Position of the maternal center of mass in both the reference posture and in natural stance was determined relative to a point of reference. Global points provide no consistent reference due to the fact that subjects vary their stance position relative to global landmarks. While the positions of points in a global framework are permanent, the coordinates of the body with respect to those points vary whenever a subject re-enters the global space.

By precluding a kinematic response to postural challenges associated with fetal load, the reference posture served to target a rigid anatomical reading of the position of the COM. The C7 marker was expected to be the most relevant and accurate body marker for calculation of reference posture COM position, as it is the marker least likely to directionally shift in anatomical position relative to the location of the COM (among the non dependent variable markers). Because the torso is a relatively solid segment, the C7 marker, adhered to the external palpable spinous process of the seventh cervical vertebra, provided a consistent reference for determining the fore-aft position of the maternal center of mass in the experimental condition on the reference board. The Heel marker by virtue of its anatomical distance from the predicted COM was considered as an alternative to the C7 reference. However, the Heel marker defined a partial perimeter of the body's base of postural support. Therefore, the distance calculated between the COM and Heel marker would be readily mitigated by any self-selected subject adjustment. In spite of rigorous postural constraints imposed by the reference panel, the brief period of time required to both retract the device and capture marker positional data introduced the possibility of unintentional subject adjustment. As subjects became increasingly loaded and less flexible in pregnancy, stationary retention of the reference posture required more subject effort. The C7 marker was more likely to retain positional integrity with the true anatomical location of the COM in reference posture than was the Heel marker.

Under conditions of natural stance in which subjects were free to self-adjust, the position of the COM was expected to remain unchanged, therefore stable relative to the supporting joints and postural base. In order to test this prediction, the location of COM was made relative to a supporting landmark. Markers of the hip, knee, ankle, heel and metatarsal I head represented either supporting joints or the postural base. Accuracy in external placement of markers over anatomical landmarks is best achieved at sites where bony structures are easily palpable (McKenzie and Taylor, 1997). Because the heel and metatarsal head reflect the actual base of support for the body and are relevant to the location of the COM in terms of postural stability, each were considered as the natural stance reference marker. Hormonal effects are potential confounding factors in the position of the metatarsal head during pregnancy. Ligamentous laxity in the longitudinal arch of the foot lengthens the forefoot of some women (Bird at al., 1999), making the metatarsal head a less reliable reference for determining the position of natural stance COM. The heel position is independent of the longitudinal arch. Utility of the C7 marker in determining the relative position of the COM in natural stance is negated by the largely fixed position of the seventh cervical vertebra on the thorax. For instance, if a subject performs as predicted by dorsally repositioning her upper body, the C7 marker will translate along with the COM. In the context of determining the position of the COM in self-selected postures, the C7 and Metatarsal I Head markers are clearly less relevant than the Heel marker. The experimental set-up for all data sessions is depicted in Figure 2.6, and subject placement (in natural stance) relative to the laboratory space is illustrated in Figure 2.7.

Accuracy of the kinematic data

Accuracy of data is the degree to which a given measurement reflects the actual value it represents and its consideration is essential to a valid kinematic study (Sokal and Rohlf, 2004). In order to test the accuracy of the angular calculations made by the Vicon Peak Motion Capture System, a goniometer of calibrated linear and angular dimensions was recorded using the five motion capture cameras employed for data collection on study subjects. The goniometer was placed in the center of the viewing volume following protocol designed for subject quiet stance capture. The device was positioned to orient the ventrodorsal gape of the unit in the sagittal plane according to laboratory system coordinates. The free arm of the goniometer was then rotated within the transverse plane to create four excursions relating to different angular values. Three-dimensional data were collected and reconstructed in Vicon then processed in BodyBuilder. Angles derived from data capture, reconstruction and algorithm processing were then compared to the actual mechanical angles defined by the goniometer. Results of the protocol accuracy test are reported in Figure 2.8 and indicate good capture and reconstruction of the true measurement. Subsequently, all posture and gait trials were reconstructed from captured data. An example of gait reconstruction is shown in Figure 2.9.

Data Analyses

Group Design

First, a multi-trial Group Design accommodated testing for mean differences across all subjects. Repeated measures analysis of variance (RM ANOVA time x condition) was used to assess whether maternal gait kinematics and maternal center of mass differed with incremental increases in fetal growth for Predictions 1.1-1.3. Both linear and nonlinear models were included because mass increase during pregnancy is nonlinear (Jensen et al., 1996a). Repeated measures design is appropriate for longitudinal data of this type, by providing a more precise estimate of the experimental error. The technique identifies variability due to individual differences because the same subjects take part in each condition. Since the variance caused by differences between individuals is not helpful in deciding whether there is difference between occasions, the known individual differences can be isolated from the analysis by subtraction from the error variance. This step increases the power of the analysis. Repeated measures are also appropriate because it models correlation between the repeated measures, important since the longitudinal series violates assumptions of independence. To test for the presence of significant differences in dependent variables at early stage fetal load and at full term fetal load at the group level, the non parametric Wilcoxon rank sums test was applied. Statistical significance for the analyses was determined *a priori* at a level of $P \leq 0.05$ for the independent variable of fetal load and three dependent variables of maternal COM, maternal lumbar lordosis angle (LLA) and maternal pelvic tilt angle (PTA). Adjustments for repeated tests were made using the Bonferroni correction. Repeated measures ANOVA assessed the three measures (COM, LLA and PTA) over three activities (reference posture, self-selected posture and gait) sampled under the six conditions of proportionally increasing fetal load and a period postpartum. Pearson correlation tests were run to summarize the strength of the relationship between lumbar lordosis and pelvic tilt during pregnancy and between the position of the reference posture center of mass and the two kinematic variables. Pearson's r was considered significant at the $P \leq 0.05$ level.

Single subject design

In addition to the Group Design, a Single Subject Design was used to isolate patterns that occur as the result of postural and locomotor options subjects might choose in controlling movements. These are idiosyncratic in nature and are expected to some degree in lumbar lordosis and pelvic tilt under conditions of fetal load. For example, within the pliability range of the musculoskeletal system, one subject may opt to control maternal COM by increasing the angle of lumbar lordosis alone, while another may manage COM by additionally increasing the angle of sagittal pelvic tilt. Such performance differences may reduce the statistical power of a Group Design and generate a Type II error, false support for the null hypothesis. Therefore, multi-trial Single Subject Design was used to assess change within subjects using both graphical analyses of variability, trend and slope across multiple data sessions, as well as the parametric C statistic (Tryon, 1982; Nourbakhsh and Ottenbacher, 1994; Crosbie, 1995). This statistical technique initially evaluates baseline data; if no significant trend is detected in the baseline set, baseline and subsequent condition influenced datasets are combined to determine if a significant change has occurred. In this study a moving baseline was computed in order to compare each subsequent conditional session with the preceding session, which was treated as the immediate baseline. In this approach trends across all conditional data points including natural withdrawal of the fetal load postpartum are detectable (Jones, 2003). In order to obtain a consistent number of C-statistic test trials across all subjects, eight of the fifteen trials collected per session were included in the C-statistic analysis. Appropriate statistical power for the test is established with eight variates (Tryon, 1982) and this minimum was applied to accommodate any incomplete trials, resulting from occlusion of positional markers during limb segment excursion. If more than the statistical minimum number of trials were collected per session, the first eight of record were included in the C-statistic analysis.

RESULTS

Reliability of variables associated with retesting

As a follow-up to the reliability tests applied in the research design phase of this study for variables of COM, lumbar lordosis and pelvic tilt, a sample series of six trials from each of ten sessions was randomly drawn from study data to test reliability of the collected measurements. Consistency with retesting of postural and gait variables was good, supporting previous findings for trial-to-trial repeatability in postural and locomotor alignment (Hart and Rose, 1986; Bullock-Saxton, 1993; Whittle and Levine, 1997). The ICC values between eight trials were equal to or greater than 0.994 ($P<0.0001$) demonstrating strong agreement between the trials within a single session (Table 2.3).

Body mass intake measures

Intake measures of body mass, stature, body mass index, parity number, and week of gravidity were collected at subject orientation, in chronological occurrence with Session 1 (0% fetal load). Individual subject measurements and the mean and standard deviation of the study group are reported in Table 2.4.

The mean gravidity week at intake was 14.5 (sd 2.5). At this early gestational age fetal mass is predicted to be 56.5 g or 1.6% of estimated fetal mass at term gestation. Gravidity week ranged from 11 to 19 weeks, corresponding to a span of 0% to 7% of estimated term mass. Ten participants entered the study at 0% fetal load, seven under 5%, and two at 7%.

Since body mass alone is an inadequate indicator of body proportion, a Body Mass Index of maternal weight relative to stature served as an entry criterion, ranked according to the U.S. National Institutes of Health (1998) (Table 2.5). Body Mass Index (BMI) is calculated by dividing weight (kg) by stature squared (m^2).

The group mean BMI of 23.2, sd 2.8, (Table 2.4) fell well within the adult normal weight classification. Two “over weight” subjects (120301, 120303) with intake BMIs of 29.3 and 29.4 were further examined for body fat composition and relative muscle mass. Measurement by skin fold calipers quantified body fat at 22% and 24%, respectively, falling within the normal range of 15-25% for adult U.S. females (Department of Health and Human Services, 1983). Manual palpation of limb and hip musculature indicated a high percentage of muscle mass relative to body fat, further supporting inclusive status in the present study.

Body mass during pregnancy

According to the Institute of Medicine of the National Academies (1990), women whose pre pregnant BMI is below 19.8 are expected to gain between 12.5 and 18 kg during pregnancy; those whose BMI before pregnancy ranged from 19.8 to 26 should gain between 11.5 and 16 kg, and women whose pre pregnant BMI was greater than 26 are expected to gain 7 to 11.5 kg. Group mean maternal body mass during pregnancy is reported in Table 2.6. Overall, the mean gain from baseline/Session 1 to term/Session 6 was 11.2 kg.

Mean maternal term body mass (Session 6) of the group was 74.5 kg with a standard deviation of 10.3 kg. The result accords well with Lindsay et al. (1997) who report late mean gestational body mass for twenty-seven non-obese women at 73.3 kg ± 8.3, derived from data collected between 33-36 weeks. The slightly larger mean maternal mass of 74.5 kg reported in this study represents late gestational data collected between weeks 38 and 39 for participants whose pregnancies went to full term (defined as $\geq$ 39 weeks) and between week 37 and 38 for subjects whose parturitional events occurred before the expected due date. Within body mass gain parameters, the study group performed normally. Trajectories of change in body mass throughout pregnancy are plotted in Figure 2.10.

Individually, cumulative weight gain for two of the participants was lower than expected (Table 2.6). Subject 110303 gained only 6.7 kg in the full term pregnancy, nearly 60% less than the recommended change. Percent body fat gauged by the triceps skin fold measurement recorded during Sessions 5 and 6 dropped below the intake baseline. During this period the participant reported loss of appetite and energy reserve and shortly after delivery was clinically treated for postpartum depression. Despite these adverse events, neonatal growth was unaffected; live birth weight at 40 weeks gestational age was 4.6 kg, a robust measure of body mass for a neonatal length of 55.9 cm (Koo et al., 2004). Therefore, maternal departures from normative values of BMI and percent body fat present in this participant were not omissive of the subject 110303 data.

Weight gain in subject 30401 was also below expected values. Her weight plateaued through Sessions 2, 3 and 4, and in the final three weeks of pregnancy, she gained less than 0.7 kg, reaching a conservative peak of 3.4 kg above the intake measure. Concurrent with Session 3, she was physician directed to supplement her diet with high calorie liquids. The birth outcome was favorable, with normal delivery at gestational age 37 weeks. The neonatal birth weight was 2.7 kg with a body length of 48 cm. Because birth weight diverged from the average of 3.0 kg by less than 10% and is considered average for its gestational age (Koo et al., 2004), data from the participant's pregnancy was determined to be valid for inclusion in the analysis.

In using obstetric load in modern humans as an operational model for the investigation of fetal loading in general for Hominini, the inclusion of subjects 110303 and 30401 was appropriate, as both experienced reproductive successes within the events under study, evidenced by delivery of healthy neonates. From an evolutionary perspective, early hominin females were as likely as or more so than modern American women to have experienced variability within successful reproductive outcomes, most likely as a result of environmental stresses that are presently mediated, at least to some degree, by contemporary cultural and technological factors.

Gravid abdominal shape

The midabdominal circumference is presented in Table 2.7. Group means for the measure increase across sequential sessions. The mean circumference at term peaks at 107 cm, exceeding intake by 19.9 cm. This represents a 23% increase in abdominal girth through pregnancy. The mean value recorded postpartum closely approximates the intake measure; indicating a near complete return to baseline once the condition of fetal load was withdrawn.

To further identify maternal shape change in pregnancy, the abdominal circumference was plotted against maternal body mass at intake and at term (Figures 2.11 and 2.12. Dispersion of girth relative to body mass is similar at intake and at term, in that the same subjects represent the disparate extremes. Scatter reduced at term as each subject approached her maximum gravid expanse.

The Girth-Mass Index (GMI) across all sessions is reported in Table 2.8. The Girth-Mass Index is reported from Session 1 (0% fetal load) through Session 6 (100% fetal load) for those subjects whose pregnancies reached due date, and from Session 1 to Session 5 (100%fetal load) for others whose pregnancies resolved one to two weeks prior to expected due date. Girth-Mass Indices of the group can be sorted into two groups (Table 2.9), contrasting four subjects with modest change in GMI, varying from slight decrease (10411: -1.6; 10416: -0.6) to slight increase (110303: +1.5; 10404: +1.7) to the remaining fifteen subjects with more substantial increases in GMI. Taken separately the measures of abdominal girth and body mass from intake through term increase for all subjects, but the GMI does not. For subjects whose intake to term change in GMI was markedly high, change in abdominal size increased at a faster rate than did change in body mass.

Maternal center of mass

Reference Posture

The static measure of COM taken in the consistent Reference Posture was needed to identify the translation of the resultant center of mass. The Reference Posture constrained subjects from self-positioning their postural segment alignment, and therefore, allowed tracking of the anatomical center of mass in the absence of postural adjustments.

The group mean maternal COM recorded under conditions defined by the Reference Posture increased throughout the partum period, as predicted in Hypothesis H1. By term, the mean fore-aft position of the maternal center of mass increased to 3.14 cm. This represents a 25% anterior migration of the COM, roughly equivalent to the percent increase in abdominal girth. Only 3% of the overall translation in COM was recorded in the first trimester, while 22.6% of the translation occurred in the second trimester (Figure 2.13). The preponderance of change in fore-aft position of the Reference Posture COM, 74.3%, occurred in the third trimester.

Figure 2.14 plots the mean translational distance of the fore-aft position of the maternal COM recorded in each of the six sessions, corresponding with the expected increasing 20% increments of term phase fetal load. Maternal COM in the first gestational week is estimated through substitution of the postpartum value. The group mean reference posture COM translated 3.14 cm from Session 1, 0% fetal load to Session

6, 100% fetal load. The mean fore-aft position of COM at 0% fetal load was 10.92 cm ± 1.70, relative to the position of seventh cervical marker. The mean had shifted anteriorly to 14.00 cm ± 1.50 at 100% fetal load (Table 2.10). The Wilcoxon rank sums test of matched pairs was significant with a p value less than 0.0001 at an alpha level of 0.05 (Figure 2.15).

Results for the repeated measures ANOVA test of time effect on center of mass in the reference posture were significant (F ratio 28.81; F = 0.000; alpha 0.05 adjusted for multiple comparisons using Bonferroni correction) (Table 2.11). The level of significance was adjusted for multiple comparisons using the Bonferroni correction. Sessions 3, 4, 5 and 6 differ significantly from the baseline Session 1, demonstrating that fetal load at 40%, 60%, 80% and 100% of its expected term mass had a significant effect on maternal COM (in the reference posture). The postpartum Session 7 comparison differed significantly from Sessions 3, 4, 5, and 6 and did not differ from either Session 1 or Session 2, indicating that maternal center of mass returned to near baseline value once the condition of fetal load was withdrawn.

Individual participant values for Session 1 and Session 6 are plotted in Figure 2.16 and reported in Table 2.9. All participants experienced an anterior migration of reference posture COM from Session 1 to Session 6, although the increase in COM translation ranged from 1.0cm to 4.9cm.

Participants whose change in reference posture COM from intake to term was high also showed a high rate of increase in abdominal girth relative to body mass, as indicated by their GMI (Table 2.9). Those subjects whose GMI fell below zero during pregnancy experienced the smallest increase in COM change during pregnancy. Gravid change in GMI as a function of the translation in Reference Posture COM is plotted in Figure 2.17. The two subjects with negative change in gravid GMI experienced the most conservative anterior migration in COM (Figure 2.17, a). Two additional subjects experienced only modest increase in GMI and relatively small translational change in COM (Figure 2.17, b). Among the most GMI robust subjects, the group mean for translation of COM was 3.4 cm (Figure 2.17, c). Included within the majority Group c are four participants whose COM migrations did not surpass those of Group b. Three of these subjects (120301, 120303, 120305) began the study with large body masses (Table 2.6). Mass gain and abdominal expansion directly associated with the fetal body of these subjects represented a relatively smaller percentage of maternal starting values than did those of participants of lighter body weight. The fourth subject in this quartet had the smallest intake body mass (20401). Participant 20401 experienced a 2.5 cm migration of center of mass, less than that of many other members of Group c, and this reflected her diminutive stature and body size. A raw increase of 2.5 cm is proportionate for a woman of her small stature and slender proportions.

Lumbar lordosis and sagittal pelvic tilt

The angles of lumbar lordosis and sagittal pelvic tilt were computed to investigate positional adjustments of the upper body during gravid natural stance and gait. Hypotheses H2 and H3 were supported in that both kinematic angles increased during pregnancy.

Self- selected natural stance

There was a 56% group mean increase (18°) in lumbar lordosis from Session 1, 0% fetal load, at 32.10° ± 12 degrees to Session 6, 100% fetal load, at 50.05° ± 12 degrees (Figure 2.18). The inferential t-test of matched pairs produced a t stat of 6.6047, with the significant probability of $p < 0.0001$ (at alpha = 0.05). The 1st trimester results of this study are consistent with those of Franklin and Conner-Kerr (1998) who report a gravid lumbar lordosis, quantified by metricom digitizer in quiet stance, of 31.9° ± 9 in the 1st trimester and 37.8° ± 10 in the 3rd trimester. The larger term angle of lumbar lordosis reported in this study (50.05°) likely reflects the fact that results were derived from data collected within two advance weeks of parturition, corresponding to 100% fetal, while the Franklin and Conner-Kerr 3rd trimester angle (37.8°) was calculated from data sampled randomly across a broader time range beginning earlier in pregnancy and corresponding to a span of 40% to 100% fetal load. Franklin and Conner-Kerr (1998) do not report which anatomical landmarks of the lumbar spine were selected to define the angle of lordosis, so methodological agreement in angular measures employed in their study and this analysis is uncertain. However, overall changes in angle of lordosis determined by the two studies concur.

Individual comparisons of lumbar lordosis in natural stance at 0% and 100% fetal load are presented in Figure 2.19. Eighteen of the nineteen participants experienced an increase in lumbar lordosis. The angular excursion in one of those subjects was conservative at 1.7°. By the term session, lordosis in the remaining participant had decreased by -0.8°.

Results for the repeated measures ANOVA test of effect on lumbar lordosis were significant (F ratio 5.91; F = 0.007; alpha 0.05 adjusted for multiple comparisons using Bonferroni correction). Table 2.12 presents the pairwise comparisons of the time effect of increasing fetal load on the angular values of maternal lumbar lordosis. Fetal load exerted a significant effect on lumbar lordosis at Session 3 (40% fetal load), Session 4 (60% fetal load), Session 5 (80% fetal load) and Session 6 (100% fetal load) relative to the baseline value recorded at 0% fetal load. While lordosis at Session 7 (postpartum) differed significantly from the baseline angle taken at Session 1 and that recorded at Session 2 (20% fetal load), it did not differ significantly from later gestational angles taken at

Sessions 3, 4, and 5. The angle of lumbar lordosis decreased postpartum from its peak at term, falling just shy of Bonferroni significance with a value of 0.05.

There was a 61% mean increase (5.6°) in pelvic tilt from Session 1, 0% fetal load, at 9.25° to Session 6, 100% fetal load, at 14.87° (Figure 2.20). Sixteen of the nineteen subjects experienced increased sagittal tilt (Figure 2.21). The inferential t-test of matched pairs produced a t stat of 5.3732, with the significant probability of $p < 0.0001$. The 1st trimester results of this study (9.25°) are similar to those derived by Franklin and Conner-Kerr (1998) at 7.0° ± 7. Again, as in the case of lumbar lordosis the term angle reported here for sagittal pelvic tilt (14.87°) exceeds that of Franklin and Conner-Kerr at 11.2° ± 8, and may be due to the temporal differences from which the data derive.

Results for the repeated measures ANOVA test of effect on sagittal pelvic tilt were significant (F ratio 4.61; F = 0.043; alpha 0.05 adjusted for multiple comparisons using Bonferroni correction). Table 2.13 presents the pairwise comparisons of the time effect of increasing fetal load on the angular values of maternal pelvic tilt. Fetal load exerted a significant effect on pelvic tilt at Session 4 (60% fetal load), Session 5 (80% fetal load) and Session 6 (100% fetal load) relative to the baseline value recorded at 0% fetal load. The mean angle of pelvic tilt (8.7°) at Session 7 (postpartum) differed significantly from the term peak angle (14.8°), and was not significantly different from the mean angle at Session 1. The postpartum angle of pelvic tilt returned to the baseline value once the condition of fetal load was withdrawn.

Fetal load had a significant effect on both lumbar lordosis and sagittal pelvic tilt. In fact, the segment angles changed similarly under conditions of increasing fetal load (Figure 2.22). Each increased incrementally throughout pregnancy and each reached a peak increase at term, representing 100% fetal load. Upon natural withdrawal of the fetal load condition, both postpartum angles decreased.

Self-selected walking

Lumbar lordosis and sagittal pelvic tilt also increased during gait throughout pregnancy. Figure 2.23 plots the mean values at midstance for the two variables at each session. Both angles increased incrementally through pregnancy and reached their peak values at Session 6, the term session, corresponding to 100% fetal load. The angles are tightly correlated across Sessions 1, 2, 3, 4, 5 and 6 ($r = 0.97$, $p = 0.0012$). However, the postpartum values for the two angles differed. Pelvic tilt reduced markedly once fetal load was withdrawn, and while lumbar lordosis decreased, it did so conservatively. These postpartum patterns of lumbar lordosis and pelvic tilt during self-selected walking are consistent with those in natural stance.

Figures 2.24 and 2.25 show the single subject design visual pattern across sessions, using data collected from subject 120301, as illustration of the most prevalent subject pattern. The angle of lumbar lordosis during midstance of natural gait (Figure 2.23) remained relatively unchanged across Sessions 1 and 2 (0% - 20% fetal load). Significant increases in lumbar lordosis occurred across Sessions 3, 4, 5 and 6, corresponding to 40%, 60%, 80% and 100% of term fetal load. Data acquired in the multiple trials that comprise the first, second and third session units were consistently close in angular value, producing a flat plot pattern in each session. At 60% fetal load the intertrial data within sessions became more variable (generating scatter in the plotted points). There was a significant decrease in the angle of lumbar lordosis postpartum. The time series pattern of change in the angle of sagittal pelvic tilt during pregnancy closely followed that of lumbar lordosis (Figure 2.25). Again, a significant increase occurred at 40% fetal load with mean increases sequentially following through term (100% fetal load). The decrease in angle of pelvic tilt postpartum for subject 120301 was also consistent with the mean result for the study group in its significant drop compared to intake levels.

The C-statistic tests for session trends in lumbar lordosis and sagittal pelvic tilt during gait were run for each of the nineteen participants. Results for subject 10407 are presented in Tables 2.14 and 2.15, as a general representation of the group findings. Table 2.14 shows the C-statistic, z score and p value for eight trials within each of the seven fetal load defined sessions. Within-session trials for subject 10407, as for the mean group, were horizontally stable, indicating that there was no significant variation in angles of lumbar lordosis or pelvic tilt across trials within any of the seven sessions. There was consistency in results across trials at any one fetal loading phase of pregnancy. Table 2.15 reports the trends across sessions. While the group means for angles of lumbar lordosis and pelvic tilt increased through successive stages of fetal load, some of the idiosyncrasies present in the individual participant data files are apparent. Overall, through pregnancy there was increase in the segment angles for subject 10407, she experienced decreases in lumbar lordosis between Sessions 1-2 and Sessions 6-7. The Sessions 1-2 decrease was not predicted. The decrease that occurred between Sessions 6 and 7 supports the prediction that the angle of lumbar lordosis would decrease once obstetric load was withdrawn. During the period defined between 60%-80% fetal load, the participant values for lumbar lordosis neither significantly increased nor decreased. Significant increase in the angle of sagittal pelvic tilt did not occur in subject 10407 until pregnancy reached 40% of expected fetal load; this result precedes the significant landmark of 60% fetal load for the group. Subject 10407 experienced a significant decrease in the angle of pelvic tilt once fetal load was withdrawn, consistent with the group results. Additional periods of angular stability across sessions for subject 10407 occurred at 80-100% fetal load (unlike the group mean) and in the period defined postpartum (0% fetal load to post partum), the latter result also represents the group performance in that the angle of pelvic tilt postpartum returned to the intake (0% fetal load) value.

Effects of fetal load

Table 2.16 presents the combined results of the repeated measures ANOVA test with a subject factor of percent fetal load. Time was defined as seven sequential sessions, scheduled to correspond to 20% incremental increases in expected term fetal load and the single postpartum period. Fetal load exerted significant effects on reference posture COM, natural stance lordosis and natural stance pelvic tilt. The Greenhouse-Geisser and Huynh-Feldt corrections were used to reduce the likelihood of a Type 1 error because the assumption of sphericity did not hold across all time levels. The sphericity violation was expected since measures close in time (e.g., 20% and 40% fetal load sessions) were likely to be more highly correlated with one another than with measures more distant in time.

Predicted relationships between variables quantified during pregnancy and the postpartum period were supported by the analytical results. The fore-aft position of maternal COM in the reference posture and the angle of lumbar lordosis in natural stance were highly correlated ($r = 0.9732$, $p = 0.0011$). Similarly, a strong correlation between the position of maternal COM in reference posture and the angle of sagittal pelvic tilt in natural stance was identified ($r = 0.9755$, $p = 0.0009$). The two kinematic variables of lumbar lordosis and pelvic tilt as predicted were also highly correlated ($r = 0.9337$, $p = 0.0064$).

Maternal center of mass

Self-selected posture

When postural data were collected from subjects directed to stand comfortably in a self-selected posture, different results were attained from those identified in the reference posture. Whereas position of COM significantly translated from session to session when subjects assumed the reference posture, their COM in natural, self-selected stance remained entirely stationary. The mean fore-aft position of COM in natural stance at intake Session 1 (0% fetal load) was 10.44 cm, and the mean term position recorded at Session 6 (100% fetal load) was 10.24 cm (Figure 2.26). The -0.2 cm translational distance between to the two positions was nonsignificant ($p = 0.5695$, at alpha 0.05). In fact, no significant mean differences were found in any one of the six periods of increasing fetal load, or in the period postpartum.

Individual results show that sixteen of the nineteen participants experienced either a posterior retraction (-0.9 to -1.5 cm) of COM through pregnancy or near fixity in position (-0.4 to +0.1 cm) (Figure 2.27). In contrast, the natural stance center of mass for the three remaining subjects migrated anteriorly (+0.5 to +0.9). In each of these atypical cases, the COM translation was less than 1.0 cm, a substantially shorter translational distance than the group mean identified in the reference posture (3.2 cm).

When positions of maternal center of mass in natural stance and in reference posture are contrasted (Table 2.17), the conservative nature of fore-aft position of COM in the self-selected posture is clearly evident. Overall, the total translation of natural stance COM during human pregnancy is -0.28 cm, posteriorly directed. Although maternal shape changed dramatically along with fetal growth, and abdominal circumference increased significantly (Table 2.6), the mean position of maternal COM recorded in natural stance remained statistically stationary. Examined at the incremental phases of increasing fetal load that give, in part, this study its explanatory power over previous work (Dumas et al., 1995), the relevance of angular adjustment in gravid posture to the positioning of maternal center of mass is clarified. In early pregnancy, bridging the first and second trimesters (0% - 20% fetal load), maternal COM migrated anteriorly by 0.45 cm (Table 2.17). When positional adjustments were activated in self-selected posture, position of COM retracted posteriorly 0.79 cm. A substantial anterior translation in reference posture COM occurred as the fetus approached 40% of its expected term mass (1.36 cm), yet when subjects self-selected their posture, the position of COM modestly translated 0.31 cm. Throughout the third trimester, defined by periods of substantial fetal growth from 40% - 100%, the fore-aft position of COM in the reference posture continued to advance anteriorly by 1.39 cm. Yet, in self-selected posture, the third trimester change in maternal COM was a conservative 0.20 cm. Under conditions of obstetric load, the study group in natural stance maintained a relatively consistent position in maternal center of mass, restricting translation of the fore-aft location of COM to less than 0.3 cm.

General findings of the hypotheses testing are summarized in Figures 2.28 and 2.29. As obstetric load increased, mean reference posture COM translated anteriorly. When positional constraints were released, both mean lumbar lordosis and mean sagittal pelvic tilt increased. In the resulting natural stance, position of the COM remained stable throughout pregnancy. Upon withdrawal of obstetric load, reference posture center of mass and the lumbar and pelvic angles reversed trajectories. The angular kinematics of natural gait followed those of natural stance, both during pregnancy and in the period post partum.

DISCUSSION

Results from this study indicate that under conditions of increasing fetal load, human females positionally adjust their lower back and pelvic segments in association with anterior translation of maternal center of mass. In so doing, the effective fore-aft position of maternal center of mass is biomechanically recovered and its displacement throughout pregnancy restricted within a narrow window of efficiency relative to the supporting joints of the lower body. These positional mechanisms of lumbar lordosis and pelvic tilt occur in both quiet stance and natural gait, signaling a consistent biomechanical strategy in the bipedal behavior of gravid human females.

The power of this analysis to identify any relationship between fetal load and angles of lumbar lordosis and pelvic tilt was strengthened by frequent and consistent sampling of the independent and dependent variables throughout pregnancy, at the gestational landmarks of 0%, 20%, 40%, 60%, 80% and 100% fetal load.

During human pregnancy females are able to maintain postural and locomotor stability in spite of the challenging dynamic of gravitational force on the orthograde body. Positional adjustments in lumbar lordosis and sagittal pelvic tilt were triggered by accumulation of 40% fetal load. As pregnancy progressed through 40%, 60%, 80% and 100% fetal load, lumbar lordosis and sagittal pelvic tilt increased significantly and the changes in segment angles were tightly correlated. The angular values for these variables continued to increase in tandem with the growth of the fetus, attaining peak change at the recorded term event of 37 weeks gestation. In the absence of self-selected postural adjustments, externally imposed by the reference posture apparatus, the maternal center of mass underwent 3.2 cm of anterior translation in the period defined between the end of the first trimester and the close of the third. While the absolute distance of migration in center of mass (COM) may seem small in linear terms, the effective change in fore-aft location of COM relative to the biacetabular axis can exert a marked effect. The obstetric load-induced position of maternal COM shifted anterior to all of the major supporting joints and their respective axes, including not only the hips (inferred from positional constraint against the reference panel), but also the knees and ankles. Thus, shifts in COM position relative to the lower body imposed by fetal load introduced substantial change in the biomechanical mechanisms of balance and stability during bipedal posture and locomotion. Increased intertrial variability in the angle of lumbar lordosis recorded within sequential sessions of the third trimester suggests that some instability and perturbation characterize human gait during advanced pregnancy.

While the data reported here were drawn only from humans and not from other orthograde primates that similarly maintain habitual upright postures and also utilize vertical locomotion, comparative inferences are appropriate because the nature of human erect positional behavior is biomechanically distinct from others by the absence of upper body support in achieving balance and stability. In effect, the upper body of the human biped is an unwieldy cylinder stabilized only at its base by articulation with the sacrum and tethering via muscles and ligament to the pelvis. The sway and pitch of the bipedal upper body is controlled by skeletal alignment of uniquely wedged lumbar vertebrae. Bipedalism is unlike the vertical clinging and leaping postures and locomotion of many other orthograde primates in which forelimbs provide anchor on the vertical substrates across which the animals travel. In aerial phase locomotion, vertical clingers and leapers are less challenged by upper body control because the hindlimbs, although held vertically below the torso, do not oscillate during travel as do the hindlimbs of bipeds. In addition, the start phase and end phase of the leaping stride are often assisted by forelimb action (Preuschoft et al., 1979; Demes et al., 1996). Although forelimb suspensory primates often assume erect postures, the torso loading regimes in forelimb suspension are predominantly tensile in nature not compressive, so positional challenges differ (Ruff and Runestead, 1992; Llorens et al., 2001), and in suspension the fore-aft position of maternal center of mass relative to the support limbs presents less of a stability issue. Therefore, it is reasonable to conclude that bipedalism is more markedly challenged under conditions of obstetric load than are other orthograde positional behaviors. Inclusive studies however are needed to comparatively test hypotheses that postural and locomotor kinematics differ under conditions of obstetric load in bipedal, suspensory and vertical clinging and leaping primates.

This study clearly demonstrates that significant angular increases in female lumbar lordosis and sagittal pelvic tilt co-occur during human pregnancy. Both positional mechanisms are activated near the same fetal growth landmark, suggesting they share the same center of mass trigger point and function similarly to resolve instability induced by increasing fetal load. Quantification of these angular excursions and the spatial translation of maternal COM provide detailed parameters for an obstetric spinal loading model in modern humans, a model that exclusively characterizes female spinal loading. While obesity is prevalent in both sexes of many modern human populations and influences the position of COM, the weight gain associated with increased body fat due to excessive caloric intake is distributed differently than the weight acquired during pregnancy (Bjorntorp, 1996). More importantly, obesity is a relatively recent human phenomenon and therefore not relevant to the deep history of modern human evolution.

The routine duration of human fetal load is a uniquely female experience. The obstetric loading forces induced by pregnancy and the associated adjustment in upper body position achieved to resist the migration of maternal COM introduce a pattern of dorsal shifting in compressive and shearing stress onto the vertebral laminae and zygapophyses that otherwise experience relatively little of the spinal load (Adams and

Hutton, 1980, 1983). Results of this study support all five hypotheses (1.1 – 1.5, p 25-26). When maternal body angles were held constant in the reference posture throughout pregnancy, there was a significant anteroposterior translation in total body COM. In self-selected postures and natural gait, pregnant females increased the angles of lumbar lordosis and sagittal pelvic tilt as the fetal load became greater. These angular changes correlated significantly with the translation of maternal COM taken in reference posture. The position of maternal COM captured in self-selected postures throughout pregnancy did not vary, did not significantly translate. The COM remained stationary indicating that the angular adjustments in lordosis and pelvic tilt, at least partially, constrained displacement of the COM, in spite of the increasing anterior load of fetal mass.

The functional role of increasing lordosis and pelvic tilt in managing the position of obstetric COM is further supported by the near full return to pre-pregnant angular values once fetal load was withdrawn. In fact, the postpartum position of the reference posture center of mass and the postpartum angle of pelvic tilt so closely approximated their respective intake values that no significant differences between postpartum and 0% fetal load were identified. While the angle of lumbar lordosis significantly decreased from the full term value at 100% fetal load to the postpartum value at fetal load withdrawal, the postpartum angle of lordosis did not fully revert to its initial 0% fetal load value.

One might predict that measures of maternal body mass and shape would differ postpartum from those attained at intake, in part, due to lactation load; nearly all of the study participants were breast feeding at the time of the final data collection session. In fact, the mean upper torso anthropometrics of acromion, areole and xiphoid circumferences were slightly higher postpartum than at intake. If the postpartum anthropometrics impacted lumbar lordosis under the same biomechanical parameters as the gravid anthropometrics, one would expect to find persistent reference posture COM displacement. However, the fore-aft mean position of maternal COM postpartum had fully reverted to the intake value, suggesting that lactation load did not influence postpartum lordosis. An alternative explanation for the relatively acute postpartum lumbar lordosis might be an effect of lingering compromise in abdominal muscle leverage due to shape change in the gravid abdomen (Gilleard et al., 1996), at least temporarily. Support for this explanation is modestly evidenced in the dispersion of angular values for lumbar lordosis in the postpartum scatter. Angular values were higher in those participants who returned soon after parturition, within eight to twelve weeks of delivery, while the angle of lumbar lordosis was lower, and more closely approximated the intake values for those participants whose postpartum session occurred more than twelve weeks after delivery. This suggests there is a recovery period after pregnancy in which the abdominal muscles regain their antagonistic role relative to the erector spinae group.

SUMMARY

Increase in the angles of lumbar lordosis and sagittal pelvic tilt during human pregnancy provides a biomechanical solution to the problem of anterior translation in the position of maternal COM, imposed by increasing obstetric load. Effective balance of the bipedal upper body over the supporting lower body is achieved, at least in part, by mere shifting of the upper body into greater extension at the lower back and lumbosacral regions. In this manner, pregnant females avoid both the fatigue and energy cost of muscle recruitment that would otherwise be needed to stabilize the torso against the force of gravity acting anterior to the hips on the translated center of mass. Sustained recruitment of muscle effort throughout the second and third trimesters of human pregnancy would further inflate the risks of back and hip injury to women. In this sense, effective management of the stability issues of bipedal pregnancy contributes to the reproductive success of human females.

In summary, as human fetal load approached half of its expected term mass, gravid women began to alter their posture and gait by significantly increasing lumbar lordosis (mean increase of 18°) and anterior pelvic tilt (mean increase of 5.6°), repositioning their anteriorly translating center of mass over supporting joints of the lower limbs. As pregnancy reached term, lordosis and pelvic tilt peaked, shifting spinal loads onto the delicate and complex bony features of the vertebral arch. The postural constraint imposed by the experimental reference posture revealed a 3.2 cm mean anterior translation in center of mass during pregnancy. Yet, when gravid women self-positioned in natural stance, they maintained a relatively consistent center of mass, restricting translation of its fore-aft location to less than 0.3 cm. The gravid adjustments in maternal lumbar lordosis and pelvic tilt appear to mediate the biomechanical instability of the fetal load-induced position of the COM by shifting it posteriorly into vertical realignment with the supporting joints and the body base.

The functional implications of obstetric spinal loading in the evolution of the vertebrae and pelves of modern humans are investigated in Chapter 3, where the adult lumbopelvic morphology of human males and females is quantified and contrasted.

Table 2.1 Anthropometric variables defined

Anthropometric variables	Measurements defined	Conditions
Height (cm)	floor to crown	body aligned in stance with dorsal surfaces of buttocks, thorax and head in contact with vertical wall
Body mass (kg)	vertical ground reaction force	captured by force place in newtons, adjusted for force plate baseline and converted to kg
Acromial circumference (cm)	planar circumference relative to horizontal floor and landmarked by lateral margins of left and right acromia	natural stance
Areole circumference (cm)	planar circumference relative to horizontal floor and landmarked by left and right areole apices	natural stance
Xiphoid circumference (cm)	planar circumference relative to horizontal floor and landmarked by xiphoid process	natural stance
Midabdominal circumference (cm)	planar circumference relative to horizontal floor and landmarked by maximum anterior reach of the abdomen	natural stance
Lower lumbar circumference (cm)	planar circumference relative to horizontal floor and landmarked by the midcraniocaudal height of the L4 spinouis process	natural stance
Anterior superior iliac spine circumference (cm)	planar circumference relative to horizontal floor and landmarked by the anteriormost process of the left and right anterior superior iliac spines	natural stance
Gluteal circumference (cm)	planar circumference relative to horizontal floor and landmarked by maximum posterior reach of the buttocks	natural stance
% body fat (mm)	skini fold thickness of the triceps region of the upper arm	natural stance

Table 2.2. Reflective marker identity and placement for kinematic data collection

Marker	# of markers	Position	Description
glabella	1	sagittal midline	most anterior point of the forehead in sagittal midline at the level of the supraorbital ridges
mastoid	2	left and right	bony protuberance of the inferior temporal bone, behind and below the ear
acromion	2	left and right	bony process on the lateral reach of the scapula, cranial and lateral surface of the shoulder
upper arm	2	left and right	midway between the elbow and shoulder, laterally along the brachialis-deltoid junction
elbow	2	left and right	bony expansion of the lateral epicondyle of the humerus
radius	2	left and right	styloid process of the radius
ulna	2	left and right	styloid process of the ulna
ASIS	2	left and right	anterior superior iliac spine
PSIS	2	left and right	posterior superior iliac spine
sacrum	1	sagittal midline	spinous process of the second sacral vertebra
thigh	2	left and right	midway between the knee and hip, laterally along vastus lateralis
knee	2	left and right	bony expansion of the lateral condyle of the femur
tibia	2	left and right	midway between the ankle and knee, laterally along peroneus longus
ankle	2	left and right	lateral malleous of the fibula
heel	2	left and right	bony calcaneal tuberosity
toe	2	left and right	head of the second metatarsal
cervical	1	sagittal midline	spinous process of the seventh cervical vertebra
xiphoid	1	sagittal midline	caudal base of the xiphoid process
lumbar (1)	1	sagittal midline	spinous process of the first lumbar vertebra
lumbar (2)	1	sagittal midline	spinous process of the fourth lumbar vertebra

Table 2.3. Intraclass correlation coefficients for angles of lumbar lordosis and sagittal pelvic tilt in Natural Stance and Gait for test-retest reliability in eight replicate determinations of full series data for six randomly selected subjects

		ICC (2,1)	95% C I		
Event	Measurment	Single measures	Lower bound	Upper bound	Significance
Natural stance					
	Lumbar lordosis (degrees)	0.974	0.947	0.991	$p < 0.0001$
	Sagittal pelvic tilt (degrees)	0.977	0.950	0.993	$p < 0.0001$
Gait (midstance)					
	Lumbar lordosis (degrees)	0.960	0.897	0.992	$p < 0.0001$
	Sagittal pelvic tilt (degrees)	0.989	0.977	0.996	$p < 0.0001$

Table 2.4. Intake variables of active study participants

Subject #	Body mass (kg)	Height (m)	BMI (kg/m^2)	Pregnancy #	Gravidity week	Sessions completed
10411	52.7	1.68	18.7	1	14	1, 2, 3, 4, 5, 6, 7
20401	50.1	1.59	19.8	1	12	1, 2, 3, 4, 5, 6, 7
10404	58.1	1.65	21.3	1	15	1, 2, 3, 4, 5, 6, 7
30402	56.2	1.62	21.4	2	12	1, 2, 3, 4, 5, 6, 7
110301	57.6	1.63	21.7	1	17	1, 2, 3, 4, 5, 6, 7
10413	56.7	1.61	21.9	2	19	1, 2, 3, 4, 5, 6, 7
120302	59.9	1.63	22.5	2	14	1, 2, 3, 4, 5, 6, 7
110302	65.3	1.70	22.6	1	12	1, 2, 3, 4, 5, 6, 7
110303	69.9	1.73	23.4	1	11	1, 2, 3, 4, 5, 6, 7
10407	68.2	1.68	24.2	2	13	1, 2, 3, 4, 5, 6, 7
120305	73.8	1.67	26.5	1	17	1, 2, 3, 4, 5, 6, 7
120301	77.8	1.63	29.3	1	15	1, 2, 3, 4, 5, 6, 7
120303	83.0	1.68	29.4	1	13	1, 2, 3, 4, 5, 6, 7
10416	53.7	1.60	21.0	1	17	1, 2, 3, 4, 5, 7
10405	58.8	1.63	22.1	1	13	1, 2, 3, 4, 5, 7
20403	68.3	1.73	22.8	1	19	1, 2, 3, 4, 5, 7
10414	59.0	1.60	23.0	2	16	1, 2, 3, 4, 5, 7
120306	66.1	1.68	23.4	1	11	1, 2, 3, 4, 5, 7
30401	67.3	1.63	25.3	2	15	1, 2, 3, 4, 5, 7
Mean	**63.3**	**1.65**	**23.2**	**1.3**	**14.5**	
Std Dev	**8.9**	**0.04**	**2.8**	**0.48**	**2.5**	

Table 2.5 Body weight classifications by Body Mass Index for adults[a]

Weight Status	BMI (kg/m^2)
Under weight	> 18.5
Normal weight	18.5 - 25.9
Over weight	26 - 29.9
Obese	≥ 30

[a] National Institutes of Health (1998)

Table 2.6. Body mass (kg) during pregnancy

Subject	Session 1 *0% fetal load*	Session 2 *20% fetal load*	Session 3 *40% fetal load*	Session 4 *60% fetal load*	Session 5 *80% fetal load*	Session 6 *100% fetal load*
110301	57.6	58.3	63.2	64.4	67.2	68.1
110302	65.3	72.3	74.7	74.5	78.0	78.9
110303	**69.9**	**71.3**	**72.9**	**73.5**	**75.0**	**76.6**
120301	77.8	79.2	82.6	83.9	87.2	87.9
120302	59.9	62.5	64.7	66.8	68.0	69.7
120303	83.0	86.8	90.9	92.8	94.8	95.4
120305	73.8	78.1	80.9	81.5	82.7	83.9
10404	58.1	63.2	65.4	68.0	70.3	70.3
10407	68.2	71.7	74.2	75.9	77.6	78.2
10411	52.7	57.6	60.0	61.2	62.7	62.3
10413	56.7	59.8	59.8	65.0	66.3	67.5
20401	50.1	56.0	56.2	57.0	58.6	59.3
30402	56.2	62.2	65.3	66.0	68.0	70.4
10414	59.0	63.6	64.0	68.0	69.0	-
120306	66.1	69.8	72.3	74.9	78.6	-
10405	58.8	62.3	63.8	66.9	67.7	-
10416	53.7	58.7	60.2	62.7	64.0	-
20403	68.3	70.4	72.7	76.3	77.5	-
30401	**67.3**	**69.1**	**69.4**	**69.4**	**71.1**	**-**
mean	63.3	67	69.1	71	72.9	74.5
st dev	8.9	8.4	9.0	8.7	9.0	10.3
change		3.7	2.1	1.9	1.9	1.6

Table 2.7. Midabdominal circumference (cm)

Subject	Session 1	Session 2	Session 3	Session 4	Session 5	Session 6	Session 7
	0% fetal load	*20% fetal load*	*40% fetal load*	*60% fetal load*	*80% fetal load*	*100% fetal load*	*post partum*
110301	82.5	87.5	95.7	99.0	103.3	104.0	80.7
110302	80.5	96.0	99.5	104.5	105.0	110.8	99.5
110303	93.0	93.8	94.0	98.0	102.0	103.0	88.0
120301	93.0	97.0	101.5	106.5	107.8	110.5	91.0
120302	81.0	90.8	97.0	100.5	102.5	104.0	84.0
120303	106.0	117.3	122.0	122.3	130.3	129.5	108.5
120305	95.0	101.5	104.8	109.8	108.0	112.0	109.0
10404	92.0	95.5	99.5	104.5	107.0	112.5	-
10407	86.0	98.0	96.5	108.5	106.0	105.5	82.8
10411	81.5	90.0	87.0	91.0	94.0	95.3	83.0
10413	83.0	92.0	94.2	103.3	104.8	106.0	75.0
20401	73.8	83.3	85.5	85.0	89.5	92.8	74.5
30402	74.5	93.8	99.5	106.0	106.5	105.8	87.0
10414	80.3	91.6	95.3	104.5	105.0	-	89.0
120306	77.0	91.0	96.0	102.5	106.0	-	79.5
10405	79.8	89.3	95.8	97.8	100.8	-	79.0
10416	80.0	87.5	86.5	94.0	95.0	-	78.3
20403	85.0	95.5	98.3	103.0	110.0	-	95.0
30401	99.0	101.0	103.5	104.5	108.0	-	96.0
mean	87.1	94.3	97.8	102.1	104.6	107.0	87.6
std dev	8.7	7.5	8.4	7.8	8.2	9.0	10.4
mean change		7.2	3.5	4.3	2.5	2.4	-19.4

Table 2.8. Maternal GMI[1] during pregnancy and post partum

Subject	**Session 1** *0% fetal load*	**Session 2** *20% fetal load*	**Session 3** *40% fetal load*	**Session 4** *60% fetal load*	**Session 5** *80% fetal load*	**Session 6** *100% fetal load*	**Session 7** *post partum*
110301	143.2	150.1	151.4	153.7	153.7	152.7	140.6
110302	123.3	132.8	133.2	140.3	134.6	140.4	143.8
110303	133.0	131.5	128.9	133.3	136.0	134.5	149.2
120301	119.5	122.5	122.9	126.9	123.6	125.7	124.0
120302	135.2	145.3	149.9	150.4	150.7	149.2	145.1
120303	127.7	135.1	134.2	131.7	137.4	135.7	137.0
120305	128.7	130.0	129.5	134.7	130.6	133.5	147.3
10404	158.3	151.1	152.1	153.7	152.2	160.0	158.3
10407	126.1	136.7	130.1	143.0	136.6	134.9	124.1
10411	154.6	156.3	145.0	148.7	149.9	153.0	162.4
10413	146.4	153.8	157.5	158.8	158.1	157.0	121.2
20401	147.2	148.7	152.1	149.1	152.7	156.4	146.4
30402	132.6	150.7	152.4	160.6	156.6	150.2	145.7
10414	146.6	144.0	148.8	153.7	152.2		155.9
120306	116.5	130.4	132.8	136.8	134.9		125.4
10405	135.6	143.3	150.1	146.1	148.8		143.1
10416	149.0	149.1	143.7	149.9	148.4		146.8
20403	124.5	135.7	135.1	135.0	141.9		139.1
30401	147.1	146.2	149.1	150.6	151.9		142.0
mean	136.6	141.5	141.8	145.1	144.8	144.9	142.0
sd	12.4	9.4	10.3	9.2	9.6	11.1	11.6

[1] abdominal circumference (cm) / body mass (kg) *100

Table 2.9.Total gestational change in GMI[1]

Subject	Intake *0% fetal load*	Term *100% fetal load*	Change
10411	154.6	153.0	**-1.7**
10416	149.0	148.4	**-0.5**
110303	133.0	134.5	**1.4**
10404	158.3	160.0	**1.7**
120305	128.7	133.5	4.8
30401	147.1	151.9	4.8
10414	146.6	152.2	5.6
120301	119.5	125.7	6.2
120303	127.7	135.7	8.0
10407	126.1	134.9	8.8
20401	147.2	156.4	9.2
110301	143.2	152.7	9.5
10413	146.4	157.0	**10.7**
10405	135.6	148.8	**13.2**
120302	135.2	149.2	**14.0**
110302	123.3	140.4	**17.1**
20403	124.5	141.9	**17.4**
30402	132.6	150.2	**17.6**
120306	116.5	134.9	**18.4**

[1] abdominal circumference (cm) / body mass (kg) *100

Table 2.10 Fore-aft position of the COM in Reference Posture relative to C7 marker

Subject	**session 1**	**session 2**	**session 3**	**session 4**	**session 5**	**session 6**	**session 7**
	0% fetal load	*20% fetal load*	*40% fetal load*	*60% fetal load*	*80% fetal load*	*100% fetal load*	*post partum*
30402	10.0	10.9	11.7	10.1	12.2	12.4	5.5
110302	10.2	11.7	14.0	14.8	15.3	15.5	13.4
120306	11.6	13.9	14.2	15.6	15.6	15.6	10.7
120303	14.2	15.1	15.5	16.9	17.1	16.1	12.2
10404	10.7	11.1	13.8	13.5	12.8	13.4	11.1
10413	10.8	10.9	13.5	15.5	13.0	15.0	11.4
110301	9.0	11.5	11.7	12.1	12.7	13.0	10.4
10416	9.5	10.4	10.6	10.9	10.7	10.7	9.1
10414	10.3	12.5	12.9	12.5	13.3	13.3	10.8
120301	12.6	12.7	14.7	14.4	14.3	14.7	13.2
120305	13.1	12.7	13.2	13.1	15.6	15.8	13.1
120302	9.5	11.2	12.7	12.2	13.5	14.0	8.2
10407	12.4	13.8	15.6	15.1	15.6	15.6	12.0
20401	10.8	12.3	12.7	13.3	12.3	12.7	9.7
10411	9.9	8.6	10.9	12.7	12.8	13.1	10.3
10405	8.7	8.4	11.1	12.6	12.6	12.6	11.0
20403	8.9	13.7	13.8	13.2	13.1	13.7	9.7
110303	10.1	10.3	10.3	10.7	12.3	12.6	10.7
30401	13.6	13.8	14.8	14.9	16.0	16.0	13.5
Mean	**10.92**	**11.90**	**13.00**	**13.40**	**13.80**	**14.00**	**10.80**
Std Dev	**1.70**	**1.80**	**1.60**	**1.80**	**1.70**	**1.50**	**2.00**

Table 2.11 Pairwise comparisons of repeated measures ANOVA for center of mass in reference posture

					95% confidence Interval for Difference ^{a}	
(x) time	(y) time	mean difference (x-y)	Std Error	Significance ^{a}	Lower Bound	Upper Bound
(1) 0% fetal load	2	-1.076	0.352	0.159	-2.346	0.193
	3	-2.212	0.355	**0.000**	-3.491	-0.932
	4	-2.832	0.402	**0.000**	-4.283	-1.382
	5	-3.124	0.239	**0.000**	-3.985	-2.262
	6	-3.329	0.254	**0.000**	-4.245	-2.413
	7	0.218	0.500	1.000	-1.583	2.018
(2) 20% fetal load	1	1.076	0.352	0.159	-0.193	2.346
	3	-1.135	0.286	**0.023**	-2.164	-0.106
	4	-1.756	0.368	**0.004**	-3.081	-0.403
	5	-2.047	0.366	**0.001**	-3.365	-0.729
	6	-2.253	0.380	**0.000**	-3.623	-0.883
	7	1.294	0.585	0.878	-0.814	3.402
(3) 40% fetal load	**1**	2.212	0.355	**0.000**	0.932	3.491
	2	1.135	0.286	**0.023**	0.106	2.164
	4	-0.621	0.207	0.180	-1.368	0.126
	5	-0.912	0.229	**0.022**	-1.736	-0.087
	6	-1.118	0.250	**0.008**	-2.018	-0.217
	7	2.429	0.472	**0.002**	0.730	4.129
(4) 60% fetal load	**1**	2.832	0.402	**0.000**	1.382	4.283
	2	1.756	0.368	**0.004**	0.430	3.081
	3	0.621	0.207	0.180	-0.126	1.368
	5	-0.291	0.270	1.000	-1.265	0.683
	6	-0.497	0.291	1.000	-1.545	0.551
	7	3.05	0.491	**0.000**	1.281	4.819
(5) 80% fetal load	**1**	3.124	0.239	**0.000**	2.262	3.985
	2	2.047	0.366	**0.001**	0.729	3.365
	3	0.912	0.299	**0.022**	0.087	1.736
	4	0.291	0.279	1.000	-0.683	1.265
	6	-0.206	0.087	0.642	-0.519	0.107
	7	3.341	0.464	**0.000**	1.671	5.012
(6) 100% fetal load term session	**1**	3.329	0.254	**0.000**	2.413	4.245
	2	2.253	0.380	**0.000**	0.883	3.623
	3	1.118	0.250	**0.008**	0.217	2.018
	4	0.497	0.291	1.000	-0.551	1.545
	5	0.206	0.087	0.642	-0.107	0.519
	7	3.547	0.505	**0.000**	1.728	5.366
(7) post partum	1	-0.218	0.500	1.000	-2.018	1.583
	2	-1.294	0.585	0.878	-3.402	0.814
	3	-2.429	0.472	**0.002**	-4.129	-0.730
	4	-3.05	0.491	**0.000**	-4.819	-1.281
	5	-3.342	0.464	**0.000**	-5.012	-1.671
	6	-3.547	0.505	**0.000**	-5.366	-1.728

bold-faced values are significant of the 0.05 level

significance reports p values and is adjuested for multiple comparisons: Bonferroni

Table 2.12 . Pairwise comparisons of repeated measures ANOVA for lumbar lordosis in natural stance

(x) time	(y) time	mean difference (x-y)	Std Error	Significance[a]	95% confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
(1) 0% fetal load	2	-1.606	2.054	0.466	-5.984	2.772
	3	-11.444	2.546	**0.000**	-16.871	-6.017
	4	-12.325	2.687	**0.000**	-18.052	-6.598
	5	-13.625	3.523	**0.002**	-21.133	-6.117
	6	-15.913	2.727	**0.000**	-21.724	-10.101
	7	-10.756	2.538	**0.001**	-16.165	-5.347
(2) 20% fetal load	1	1.606	2.054	0.446	-2.772	5.984
	3	-9.838	2.798	**0.003**	-15.801	-3.874
	4	-10.719	2.996	**0.003**	-17.105	-4.333
	5	-12.019	3.255	**0.002**	-18.957	-5.08
	6	-14.306	2.820	**0.000**	-20.317	-8.296
	7	-9.15	2.087	**0.001**	-13.598	-4.702
(3) 40% fetal load	**1**	11.444	2.546	**0.000**	6.017	16.871
	2	9.838	2.798	**0.003**	3.874	15.801
	4	-0.881	3.308	0.795	-7.932	6.169
	5	-2.181	3.629	**0.557**	-9.916	5.554
	6	-4.469	3.421	**0.211**	-11.761	2.824
	7	0.688	2.445	0.782	-4.524	5.899
(4) 60% fetal load	**1**	12.325	2.687	**0.000**	6.598	18.052
	2	10.719	2.996	**0.003**	4.333	17.105
	3	0.881	3.308	0.794	-6.169	7.932
	5	-1.3	2.955	0.666	-7.599	4.999
	6	-3.588	2.428	0.160	-8.763	1.588
	7	1.569	2.241	**0.495**	-3.208	6.346
(5) 80% fetal load	**1**	13.625	3.523	**0.002**	6.177	21.113
	2	12.019	3.255	**0.002**	5.08	18.957
	3	2.181	3.629	0.557	-5.554	9.916
	4	1.3	2.955	0.666	-4.999	7.599
	6	-2.288	2.865	0.437	-8.394	3.819
	7	2.869	3.124	0.373	-3.79	9.527
(6) 100% fetal load term session	**1**	15.913	2.727	**0.000**	10.101	21.724
	2	14.306	2.820	**0.000**	8.296	20.317
	3	4.469	3.421	0.211	-2.824	11.761
	4	3.588	2.428	0.160	-1.588	8.763
	5	2.288	2.865	0.437	-3.819	8.394
	7	5.156	2.423	0.050	-0.009	10.321
(7) post partum	**1**	10.756	2.538	**0.001**	5.347	16.165
	2	9.15	2.087	**0.001**	4.702	13.598
	3	-0.688	2.445	0.782	-5.899	4.524
	4	-1.569	2.241	0.495	-6.346	3.208
	5	-2.869	3.124	0.373	-9.527	3.79
	6	-5.156	2.423	0.050	-10.321	0.009

bold-faced values are significant of the 0.05 level

significance reports p values and is adjuested for multiple comparisons: Bonferroni

Table 2.13 . Pairwise comparisons of repeated measures ANOVA for pelvic tilt in natural stance

(x) time	(y) time	mean difference (x-y)	Std Error	Significance ^{a}	95% confidence Interval for Difference ^{a}	
					Lower Bound	Upper Bound
(1) 0% fetal load	2	-2.158	1.554	1.000	-8.255	3.938
	3	-3.475	0.913	0.061	-7.058	0.108
	4	-4.642	1.111	**0.032**	-8.999	-0.285
	5	-6.617	1.163	**0.003**	-11.179	-2.054
	6	-6.692	1.316	**0.007**	-11.853	-1.530
	7	-0.567	1.661	1.000	-7.083	5.950
(2) 20% fetal load	1	2.158	1.554	1.000	-3.938	8.255
	3	-1.317	1.162	1.000	-5.877	3.244
	4	-2.483	1.359	1.000	-7.814	2.848
	5	-4.458	1.562	0.329	-10.586	1.670
	6	-4.533	1.852	0.680	-11.800	2.733
	7	1.592	1.808	1.000	-5.500	8.683
(3) 40% fetal load	1	3.475	0.913	0.061	-0.108	7.058
	2	1.317	1.162	1.000	-3.244	5.877
	4	-1.167	0.878	1.000	-4.612	2.279
	5	-3.142	0.800	0.500	-6.279	-0.005
	6	-3.217	1.290	0.627	-8.277	1.844
	7	2.908	1.697	1.000	-3.749	9.566
(4) 60% fetal load	**1**	4.642	1.111	**0.032**	0.285	8.999
	2	2.483	1.359	1.000	-2.848	7.814
	3	1.167	0.878	1.000	-2.279	4.612
	5	-1.975	0.867	0.919	-5.377	1.427
	6	-2.050	1.135	1.000	-6.502	2.402
	7	4.075	1.660	0.672	-2.437	10.587
(5) 80% fetal load	**1**	6.617	1.163	**0.003**	2.054	11.179
	2	4.458	1.562	0.329	-1.670	10.586
	3	3.142	0.800	0.050	0.005	6.279
	4	1.975	0.867	0.919	-1.427	5.377
	6	-0.075	0.623	1.000	-2.518	2.368
	7	6.050	1.401	**0.026**	0.555	11.545
(6) 100% fetal load term session	**1**	6.692	1.316	**0.007**	1.530	11.853
	2	4.533	1.852	0.680	-2.733	11.800
	3	3.217	1.290	0.627	-1.844	8.277
	4	2.050	1.135	1.000	-2.402	6.502
	5	0.075	0.623	1.000	-2.368	2.518
	7	6.125	1.362	**0.019**	0.783	11.467
(7) post partum	1	0.567	1.661	1.000	-5.950	7.083
	2	-1.592	1.808	1.000	-8.683	5.500
	3	-2.908	1.697	1.000	-9.566	3.749
	4	-4.075	1.660	0.672	-10.587	2.437
	5	-6.050	1.401	**0.026**	-11.545	-0.555
	6	-6.125	1.362	**0.019**	-11.467	-0.783

bold-faced values are significant of the 0.05 level

significance reports p values and is adjuested for multiple comparisons: Bonferroni

Table 2.14. Within session trends: midstance of natural gait[1] for Subject 10407

	Lordosis				Pelvic Tilt			
Session	C-Statistic	z score	p	trend	C-Statistic	z score	p	trend
1, *0% fetal load*	0.354	1.098	0.136	horizontal stability	0.222	0.689	0.245	horizontal stability
2, *20% fetal load*	-0.002	-0.006	0.502	horizontal stability	-0.582	-1.805	0.964	horizontal stability
3, *40% fetal load*	0.473	1.465	0.071	horizontal stability	-0.307	-0.869	0.807	horizontal stability
4, *60% fetal load*	0.071	0.221	0.412	horizontal stability	0.473	1.467	0.071	horizontal stability
5, *80% fetal load*	-0.392	-1.215	0.887	horizontal stability	0.392	1.217	0.111	horizontal stability
6, *100% fetal load*	-0.260	-0.805	0.789	horizontal stability	0.012	0.036	0.485	horizontal stability
7, *post partum*	0.081	0.251	0.400	horizontal stability	-0.465	-1.441	0.925	horizontal stability

[1] n = 8 trials per session

Table 2.15. Across session trends : midstance of natural gait[1] for Subject 10407

	Lordosis				Pelvic Tilt			
Sessions	C-Statistic	z score	p	trend	C-Statistic	z score	p	trend
1 and 2, *0% to 20% fetal load*	0.870	3.509	**0.001**	**non random decrease**	-0.050	-0.202	0.580	horizontal stability
2 and 3, *20% to 40% fetal load*	0.580	2.338	**0.009**	**non random increase**	0.734	2.776	**0.002**	**non random increase**
3 and 4, *40% to 60% fetal load*	0.736	2.970	**0.001**	**non random increase**	0.812	3.073	**0.001**	**non random increase**
4 and 5, *60% to 80% fetal load*	0.387	1.560	0.059	horizontal stability	0.525	2.116	**0.017**	**non random increase**
5 and 6, *80% to 100% fetal load*	0.645	2.601	**0.004**	**non random increase**	0.090	0.035	0.362	horizontal stability
6 and 7, *100% fetal load to post partum*	0.613	2.471	**0.006**	**non random decrease**	0.769	3.007	**0.001**	**non random decrease**
1 and 7, *0% fetal load to post partum*	0.806	3.251	**0.001**	**non random increase**	-0.420	-1.693	0.954	horizontal stability

[1] n = 8 trials per session

Table 2.16 . Within subjects design time effects, with time defined by seven stages of fetal load: 0%, 20%, 40%, 60%, 80%, 100%, and a period post partum

		p value		
Maternal variables	F-ratio [1]	F	Greenhouse-Geisser	Huynh-Feldt
COM reference posture	28.81	**< 0.0001**	**< 0.0001**	**< 0.0001**
Lordosis natural stance	5.91	**0.007**	**< 0.0001**	**< 0.0001**
Pelvic tilt natural stance	4.61	**0.043**	**< 0.0001**	**< 0.0001**

[1] Repeated Measures ANOVA
Values in bold-face are statistically significant at alpha 0.05 (Bonferroni corrected)

Table 2.17 Center of mass translation (cm) in reference posture and in natural stance, presented as group means [1]

	Reference Posture [2] COM change	Natural Stance [3] COM change
0% - 20% fetal load	0.45	-0.79
20% - 40% fetal load	1.36	0.31
40% - 60% fetal load	0.51	-0.19
60% - 80% fetal load	0.29	-0.01
80% - 100% fetal load	0.59	0.40
0% through 100% fetal load	3.20	-0.28

[1] Positive values indicate anterior translation. Negative values indicate posterior translation. COM change is the linear difference in fore-aft position during the period defined by the % transition of fetal load

[2] The reference posture was secured by body alignment to a retractable wall by which segmental angles of lumbar lordosis and pelvic tilt were were held constant across all session

[3] The natural stance allowed subjects to self-select a comfortable posture

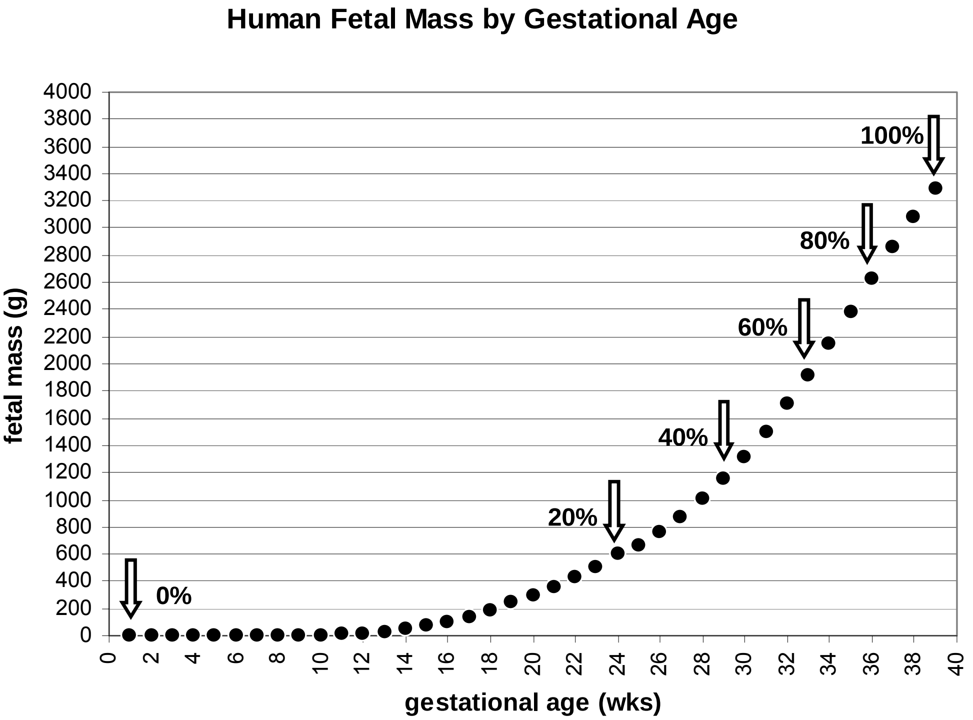
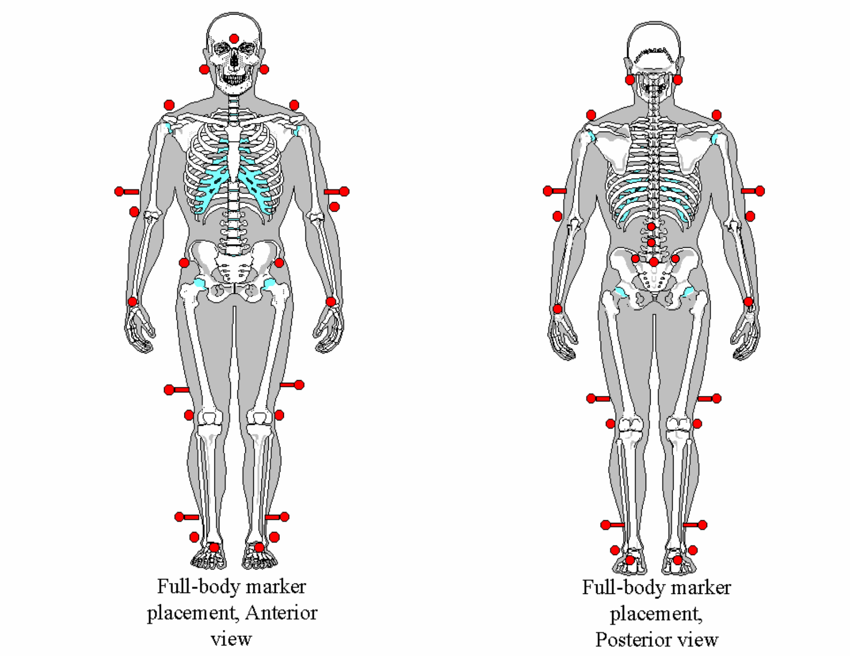


Figure 2.1. Fetal mass is negligible in the first twelve weeks of pregnancy (less than 14g, 4% of full term mass). At the end of the following twelve weeks, the fetus attains 20% of its term weight, typically at week twenty-four. Fetal growth accelerates after the twenty-fourth week, increasing 20% in each of the four successive and increasingly shorter periods, comprised of four, three, two and two week spans, respectively (modified from Alexander et al., 1996).



Full-body marker placement, Anterior view

Full-body marker placement, Posterior view

Figure 2.2. Marker positions for kinematic data collection, modified from Eames et al., 1999.

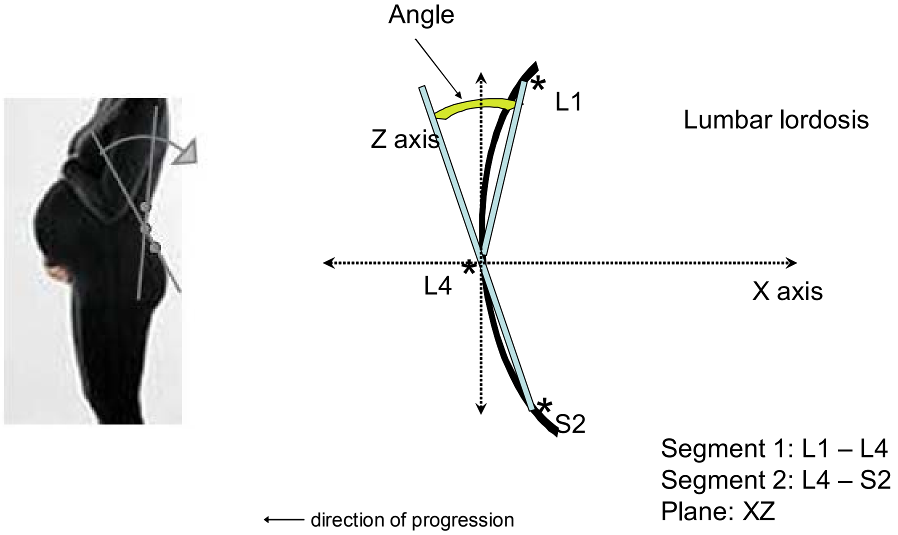


Fig 2.3. Kinematic angular method of calculating lumbar lordosis from marker positions. L1 = first lumbar vertebra, L4 = fourth lumbar vertebra. S2 = second sacral vertebra. Markers were adhered externally over palpated spinous processes. XZ plane refers to sagittal plane of the body and is spatially defined in Figure 2.6.

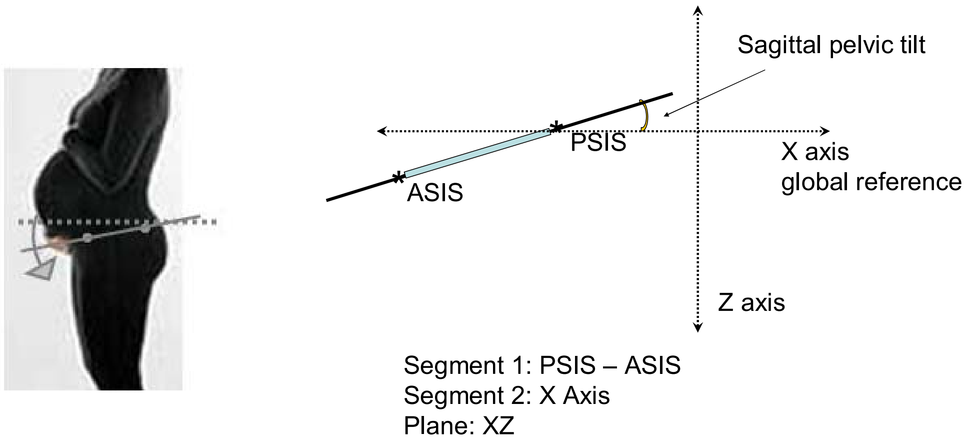


Figure 2.4. Kinematic angular method of calculating sagittal pelvic tilt from marker positions. ASIS = anterior superior iliac spine, PSIS = posterior superior iliac spine. Markers were adhered externally over bony processes. XZ plane refers to sagittal plane of the body and is spatially defined in Figure 2.6.

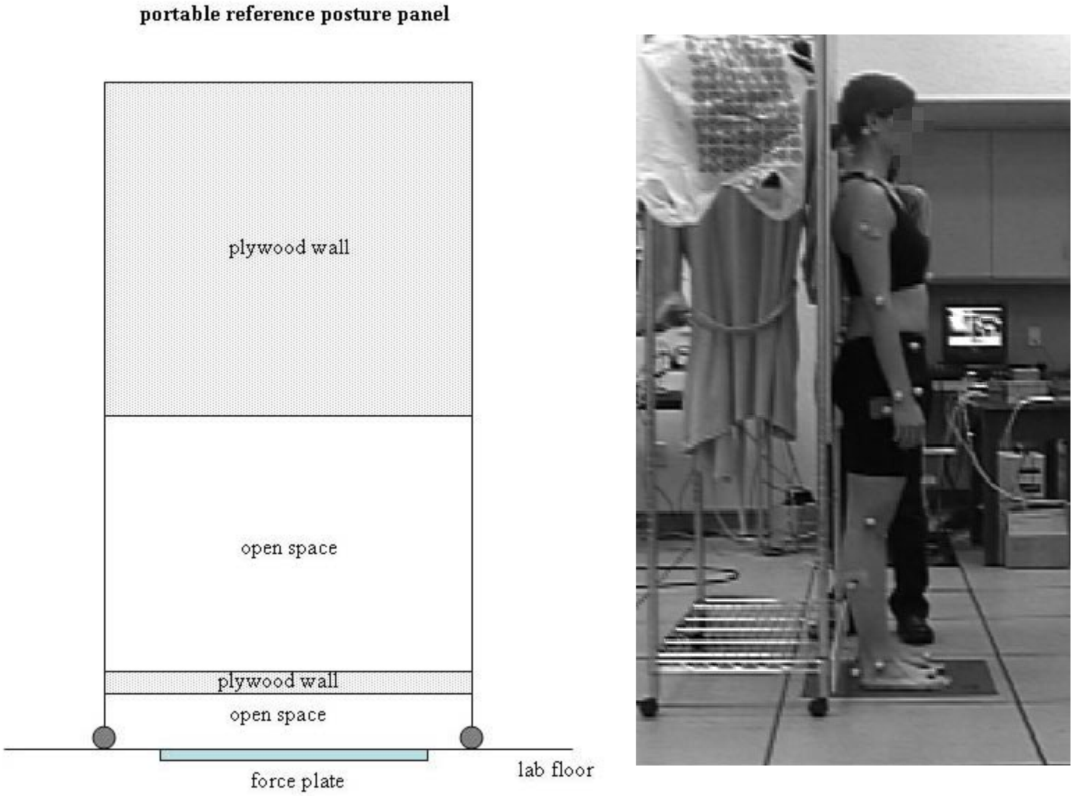


Figure 2.5. Portable reference posture apparatus. Left, frontal view of apparatus with labeled components. Right, lateral view of apparatus indicating subject position.

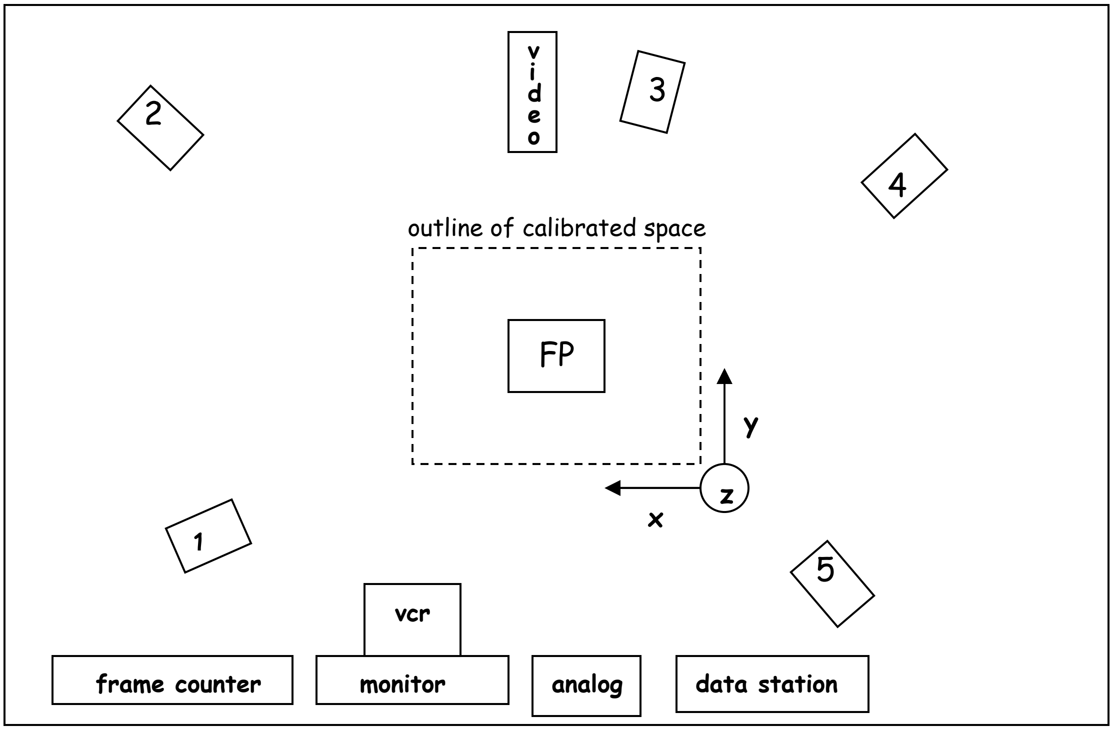


Figure 2.6. Experimental lab set-up. Objects numbered 1-5 are cameras of the Vicon 250 data acquisition system and were used for kinematic data collection. The object labeled FP is the Bertec 4550-08 force platform used for kinetic data collection. The calibrated space and lab coordinate system is also indicated. The distance from camera 3 to the force platform is 3 m. Subjects stood facing the positive x direction and walked in a forward trajectory along the positive x.

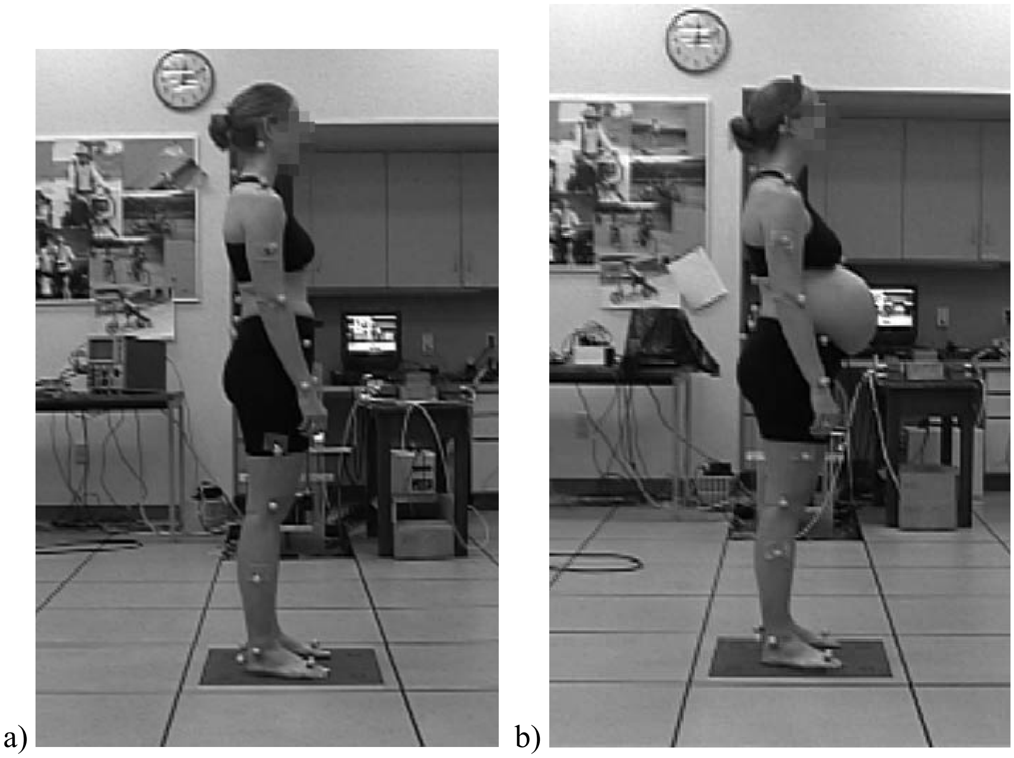


Figure 2.7. Subject and marker placement during data acquisition in natural stance. Subject 110302. Left, Session 1, 0% fetal load. Right, Session 6, 100% fetal load.

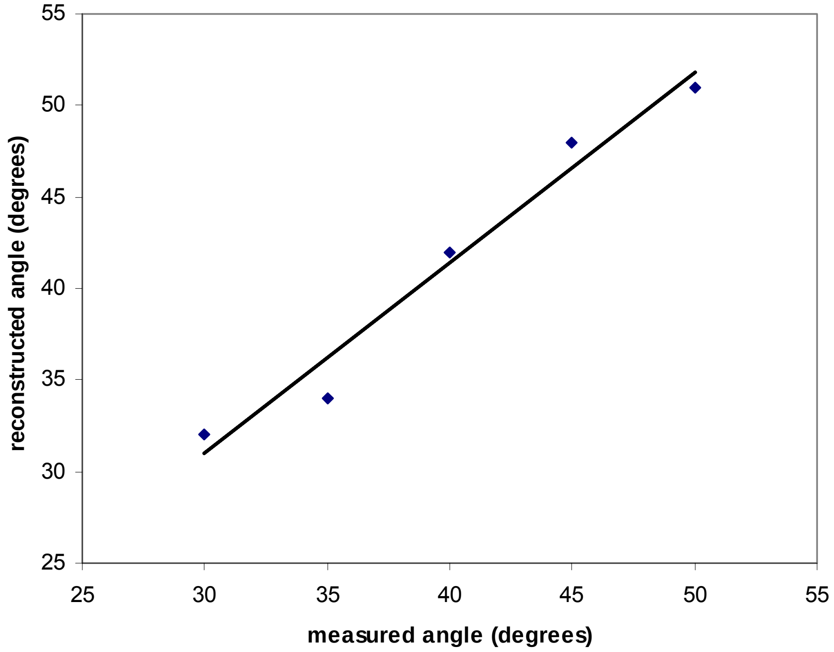


Figure 2.8. Measured vs. reconstructed angle using a calibrated goniometer for direct measurement and 3D positional capture of goniometer markers from which angular values were reconstructed. The line represents least-squared regression (r = 0.969, slope (95% CI) = 1.04).

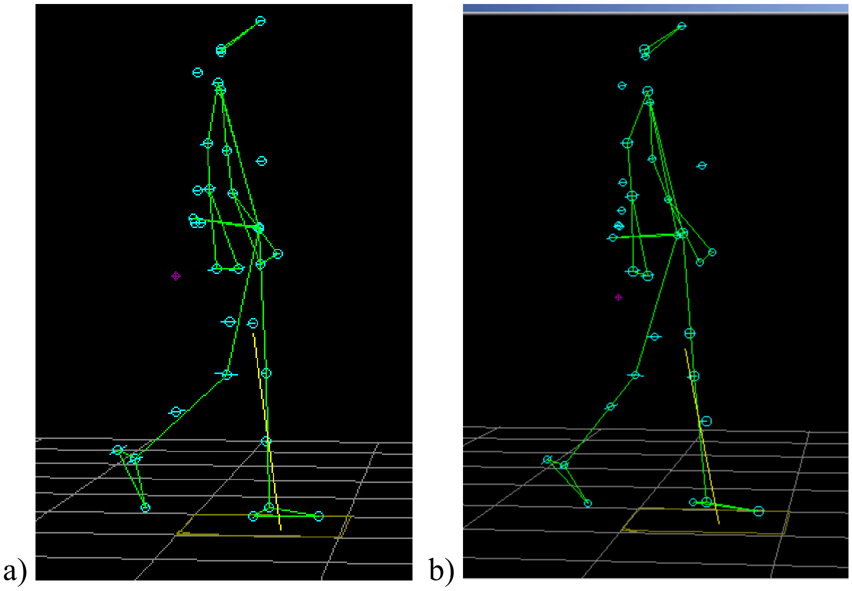


Figure 2.9. Vicon 3D gait trial reconstruction in right lateral view, a) Session 1, 0% fetal load; b) Session 6, 100% fetal load.

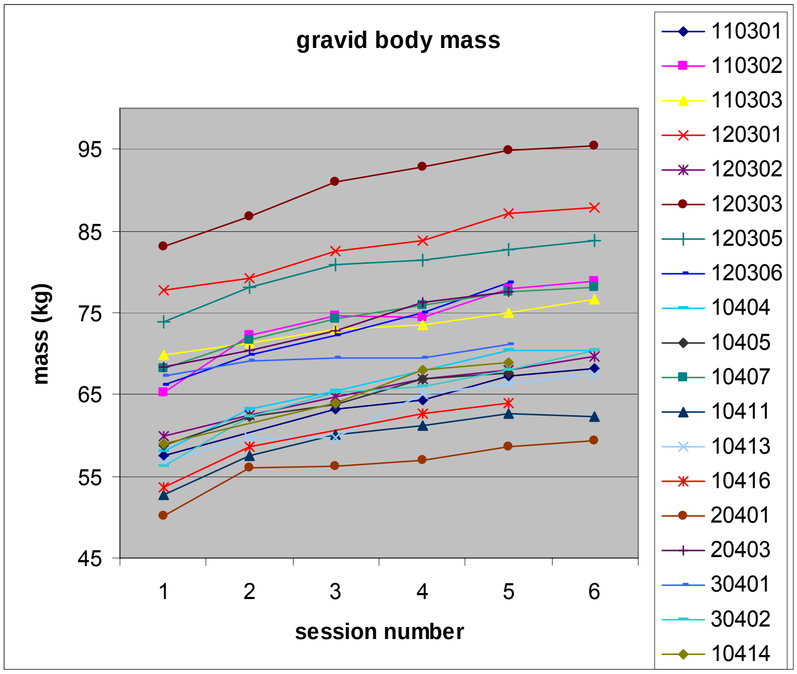


Figure 2.10. Participant body mass (kg) plotted by session (intake Session 1 through term Session 6). Trajectories truncated at Session 5 derive from subjects who reached term neonate delivery during the time lapse between completion of Session 5 and the scheduled Session 6.

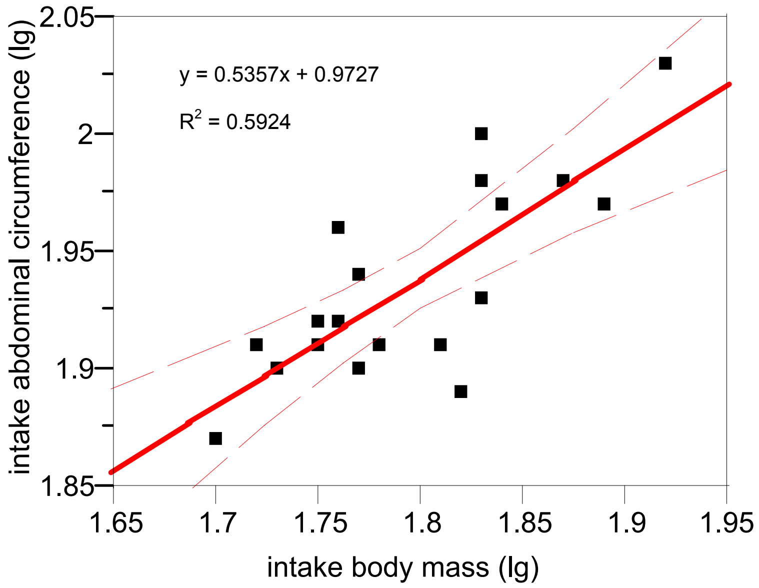


Figure 2.11. Abdominal circumference (lg) plotted against body mass (lg) at intake (Session 1). The solid line represents the best fit. The dotted lines represent 95% confidence limits.

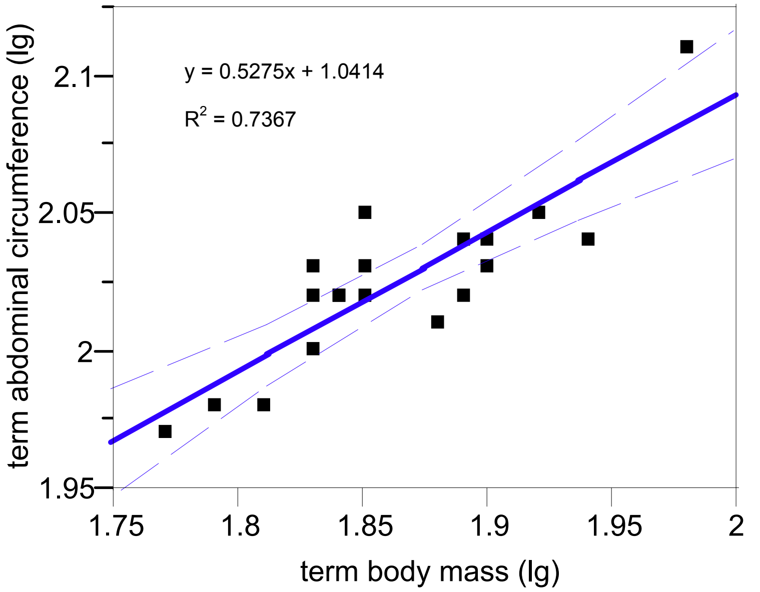


Figure 2.12. Abdominal circumference (lg) plotted against body mass (lg) at term (Session 6). The solid line represents the best fit. The dotted lines represent 95% confidence limits.

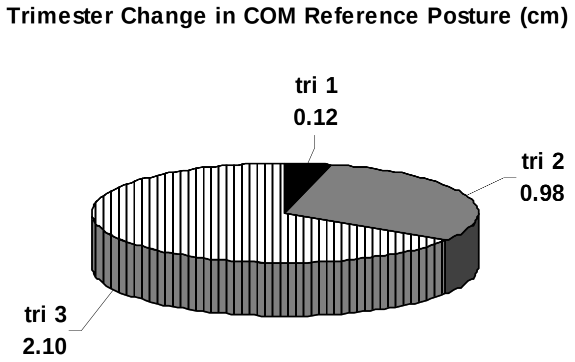


Figure 2.13. Total mean translation of maternal center of mass in the fore-aft direction during pregnancy (3.2 cm), reported by trimester.

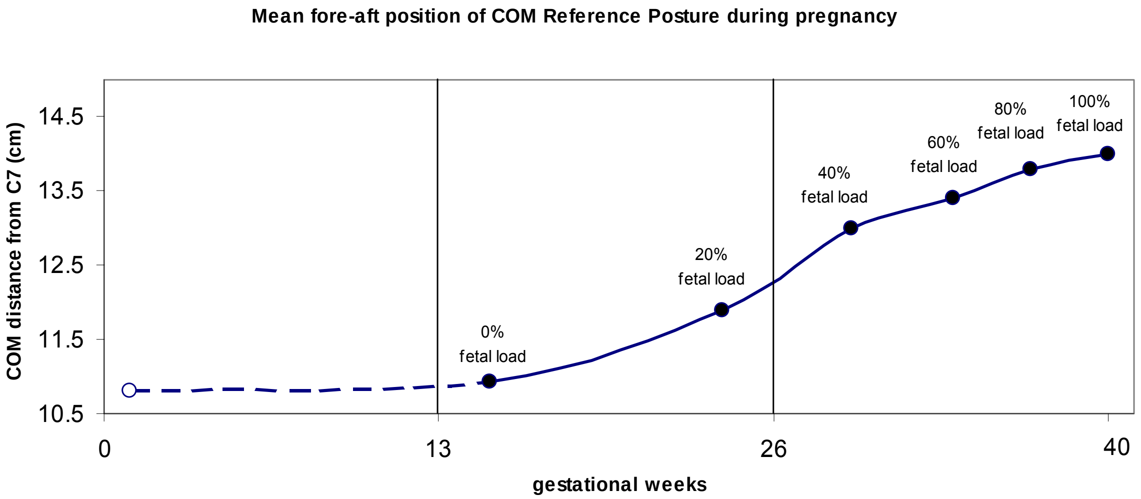


Figure 2.14. Mean fore-aft position of the maternal center of mass relative to position of the C7 marker. Solid circles denote six consecutive sessions corresponding to 0%, 20%, 40%, 60%, 80% and 100% of expected term fetal load. The open circle is estimated. The partitioned triplet represents the three gravid trimesters.

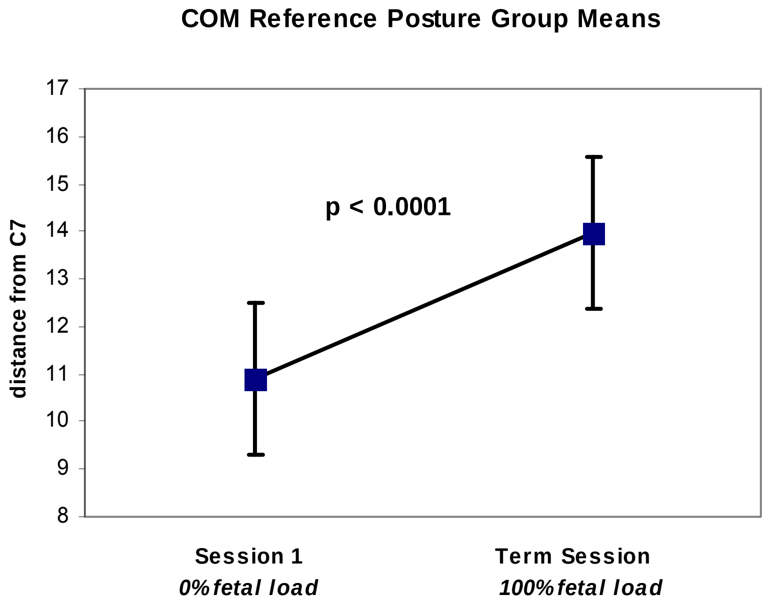


Figure 2.15. Change in the mean fore-aft position of the maternal center of mass relative to position of the C7 marker in the Reference Posture during pregnancy. Squares represent mean points; vertical lines represent standard deviation. The alpha level was set at 0.05.

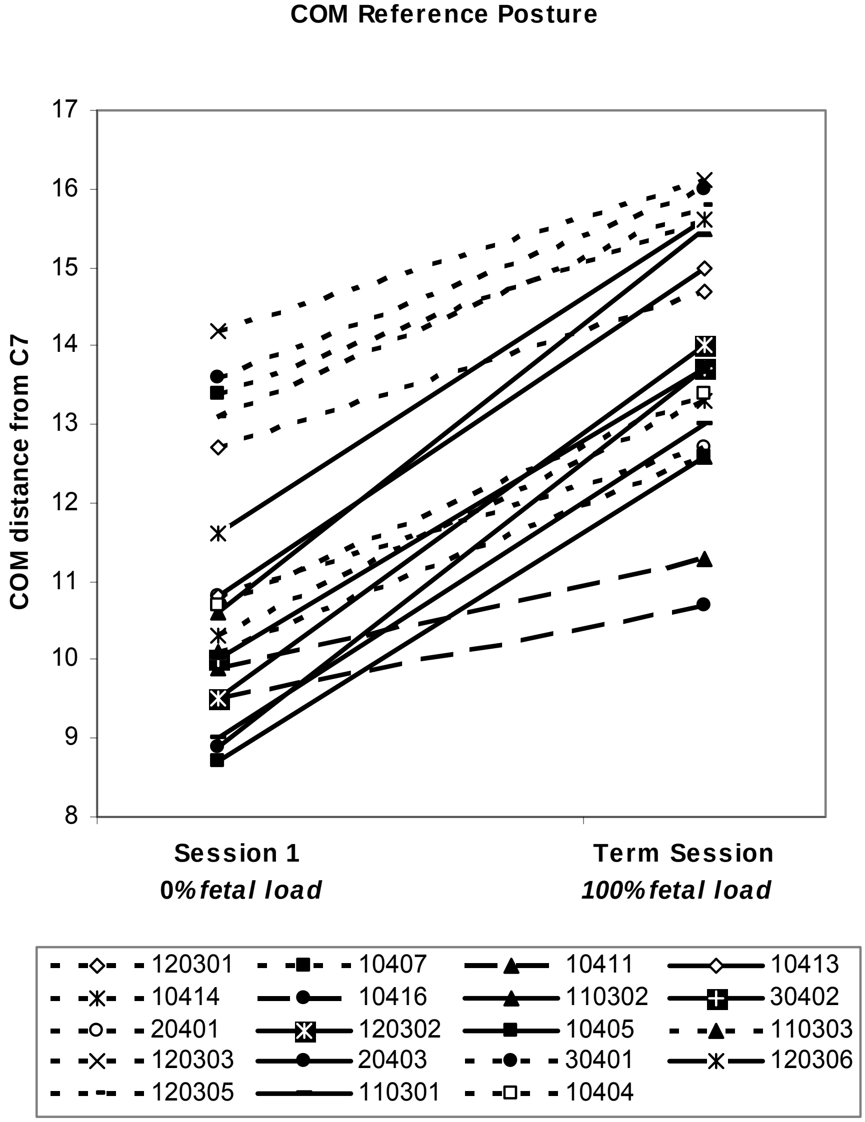


Figure 2.16. Change in individual subject's fore-aft positions of the maternal center of mass relative to position of the C7 marker in the Reference Posture during pregnancy. Dashed lines indicate COM translation less than 1.5 cm, dotted lines greater than 1.4 and less than or equal to 3.0 cm; and solid lines indicate translation greater than 3.1 cm.

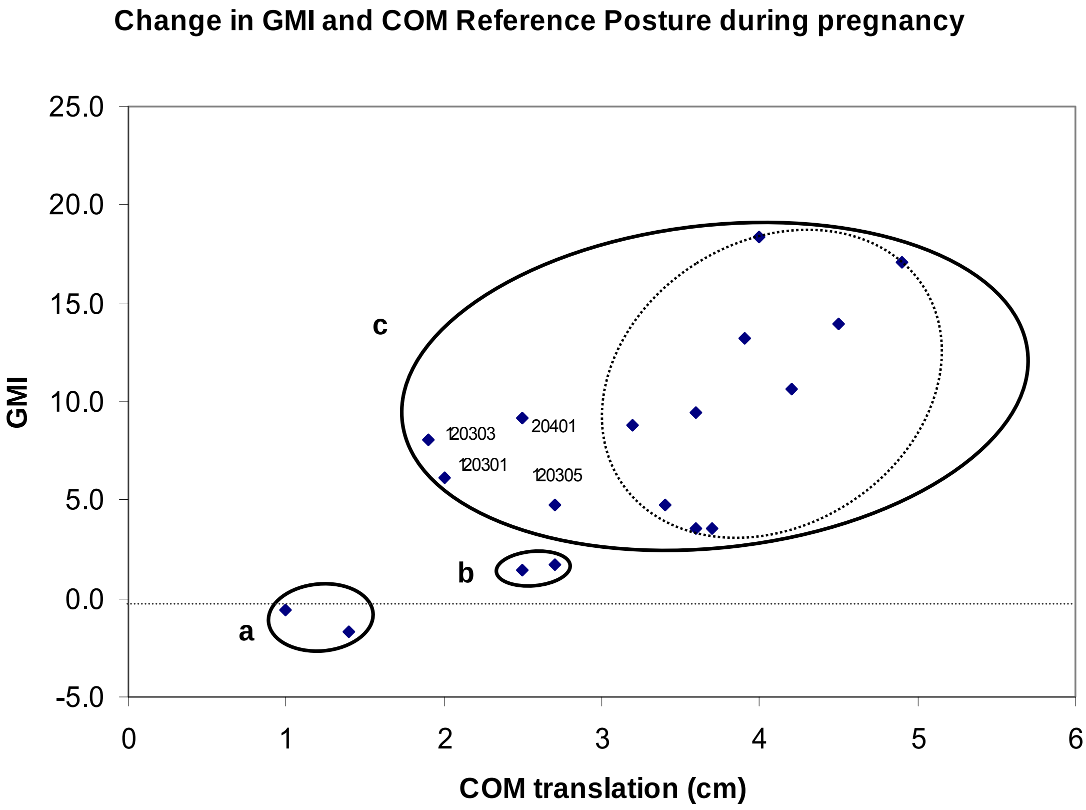


Figure 2.17. Gravid change in Girth-Mass Index plotted against fore-aft translation of maternal center of mass in the reference posture.

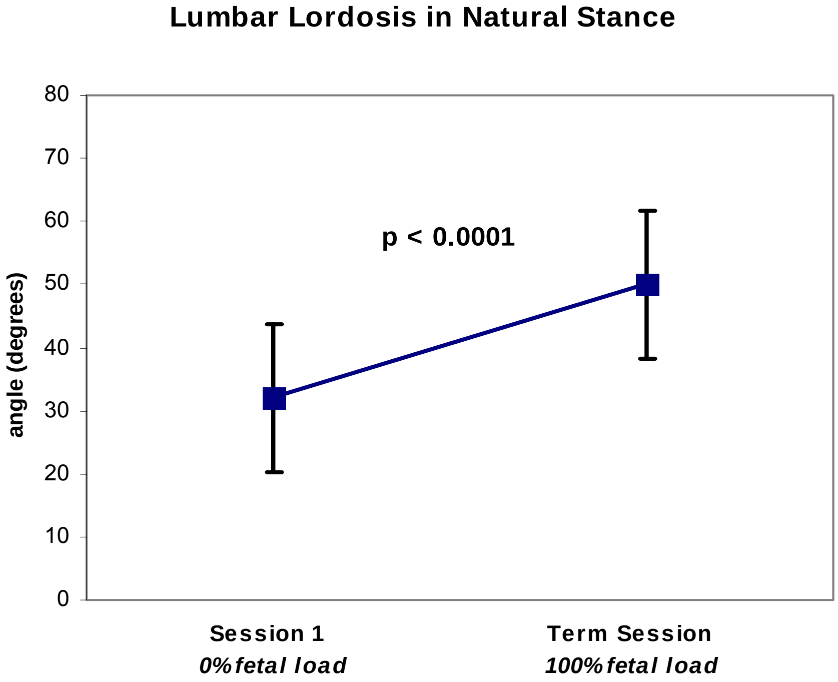


Figure 2.18. Angle of lumbar lordosis compared at 0% fetal load and 100% fetal load. Squares represent group means; vertical lines represent standard deviation. Mean differences are significant at alpha 0.05, $p < 0.0001$.

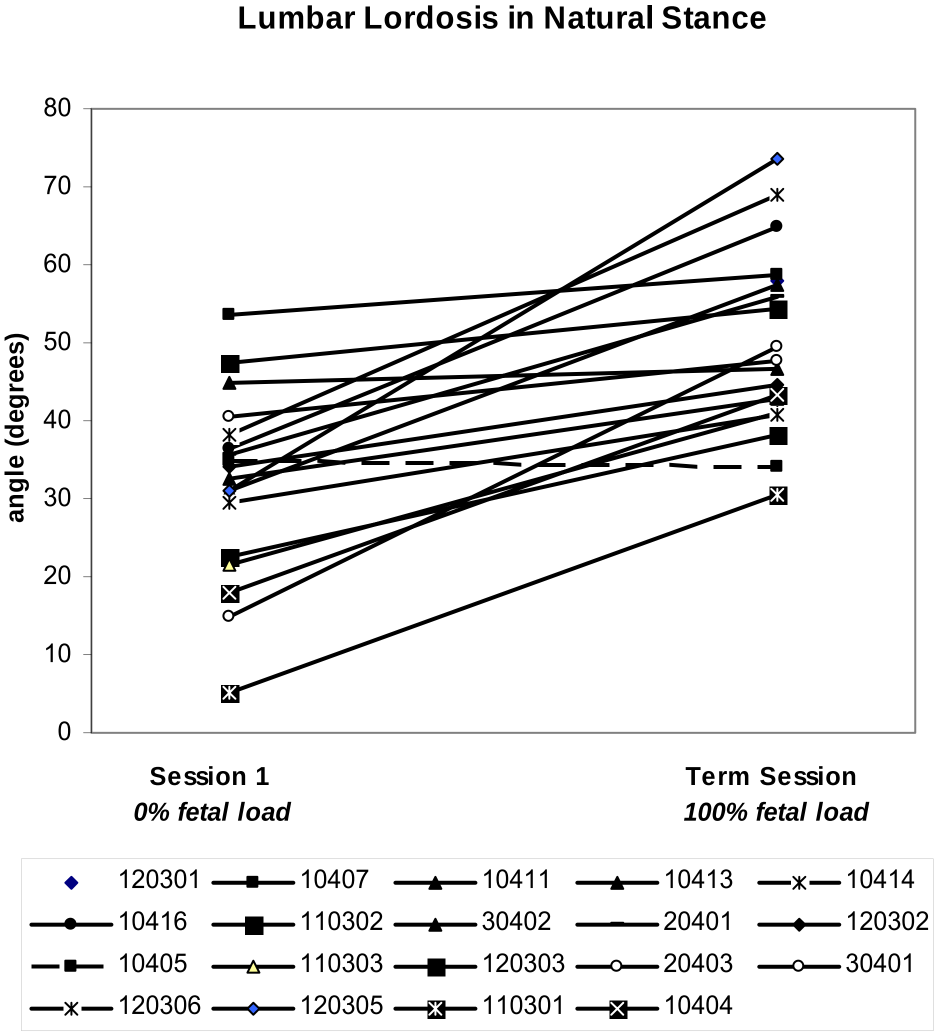


Figure 2.19. Angle of lumbar lordosis compared at 0% fetal load and 100% fetal load for each study participant. Solid lines represent increases in lumbar lordosis. Dashed line represents decrease in lumbar lordosis.

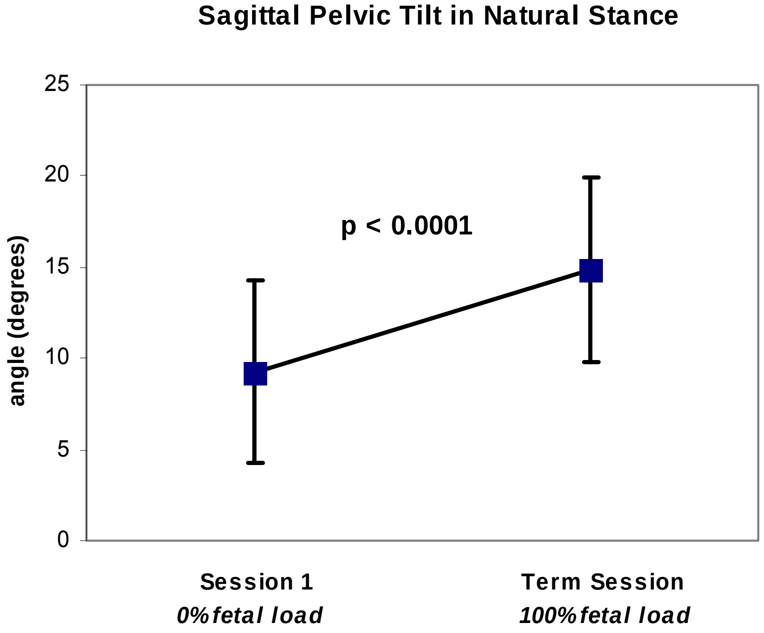


Figure 2.20. Angle of sagittal pelvic tilt compared at 0% fetal load and 100% fetal load. Squares represent group means; vertical lines represent standard deviation. Mean differences are significant at alpha 0.05, $p < 0.0001$.

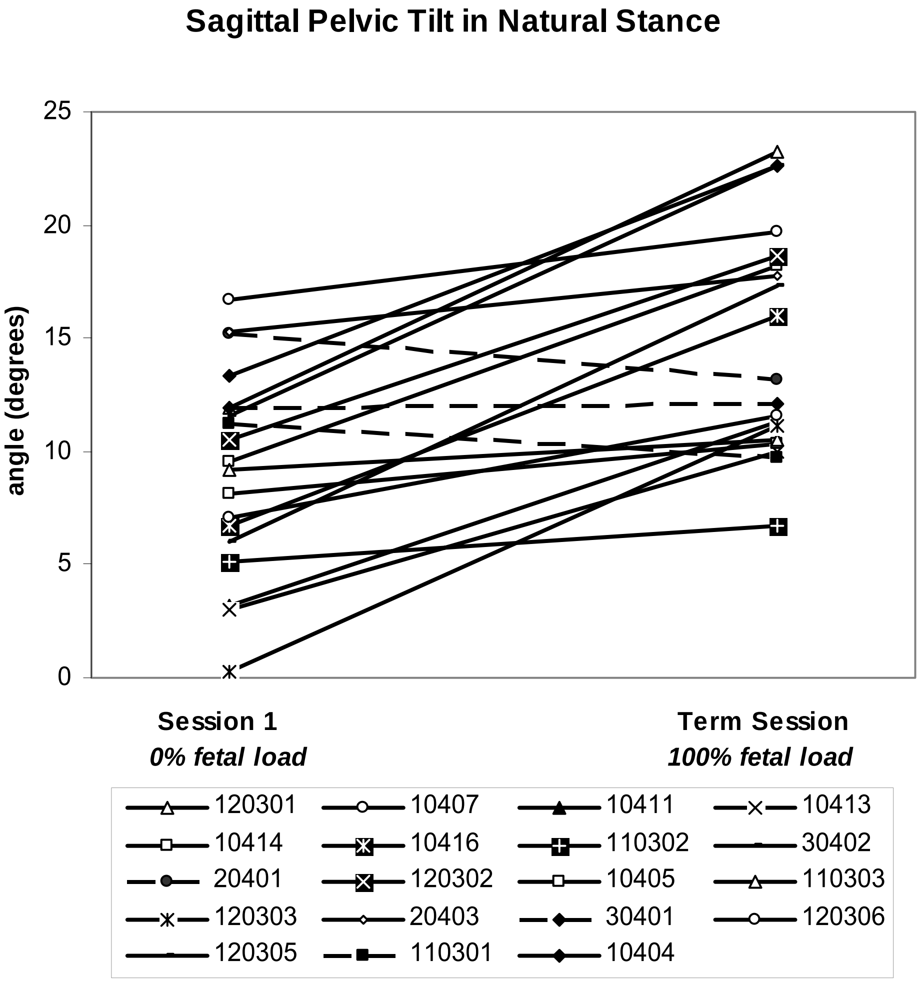


Figure 2.21. Angle of sagittal pelvic tilt compared at 0% fetal load and 100% fetal load for each study participant. Solid lines represent increases in pelvic tilt. Dashed line represents decrease in pelvic tilt.

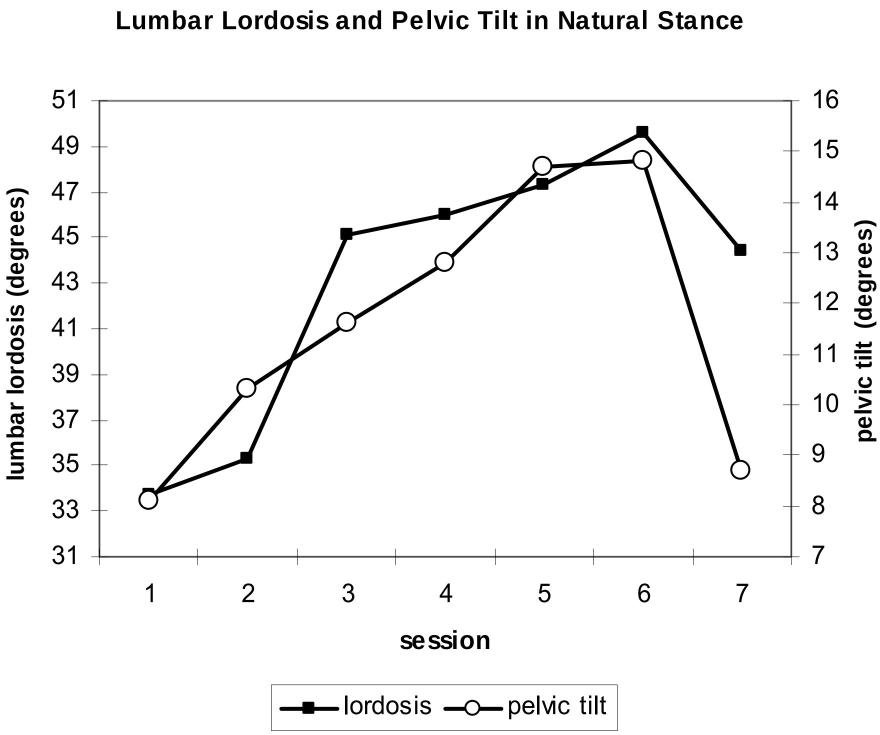


Figure2.22. Angles of lumbar lordosis and sagittal pelvic tilt in Natural Stance throughout pregnancy (Sessions 1-6) and a period postpartum (Session 7). Points represent mean values for study group (n=19).

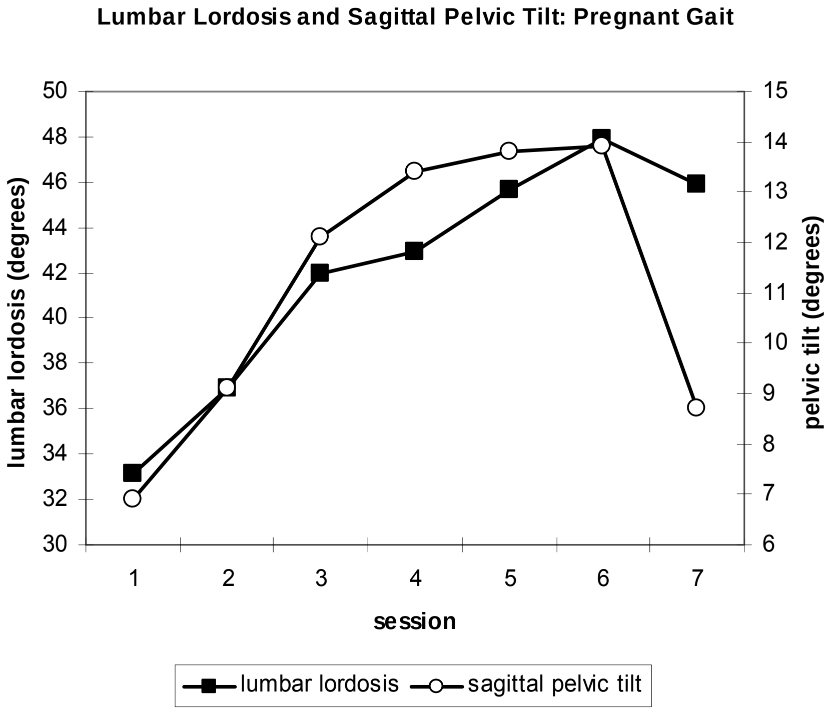


Figure 2.23. Angles of lumbar lordosis and sagittal pelvic tilt in midstance of natural gait throughout pregnancy (Sessions 1-6) and a period postpartum (Session 7). Points represent mean values for study group (n=19).

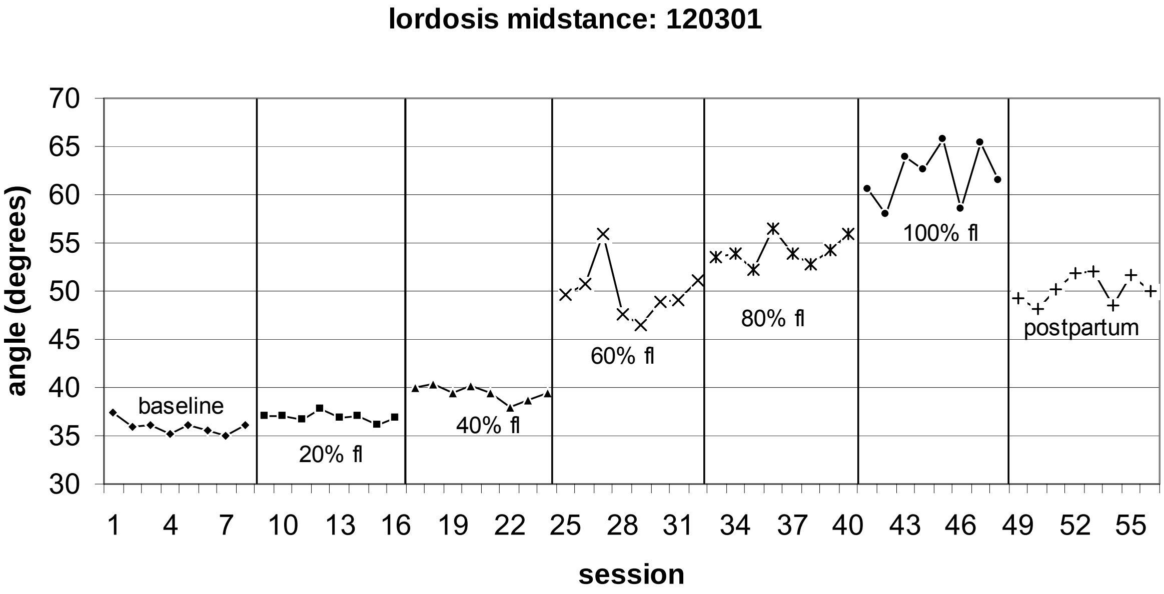


Figure 2.24. Time series chart of the angle of lumbar lordosis for subject 120301in midstance phase of natural gait plotted by session trials. Each partitioned series of points represents a different data collection stage. Stages are shown in sequence as: Sessions 1, 2, 3, 4, 5, 6, and 7. Each session is labeled according to the relevant obstetric phase. The baseline series was recorded at intake Session 1. Percentage labels refer to expected percentage of term fetal mass. The postpartum series was recorded at the final session and was defined by withdraw of the fetal load condition.

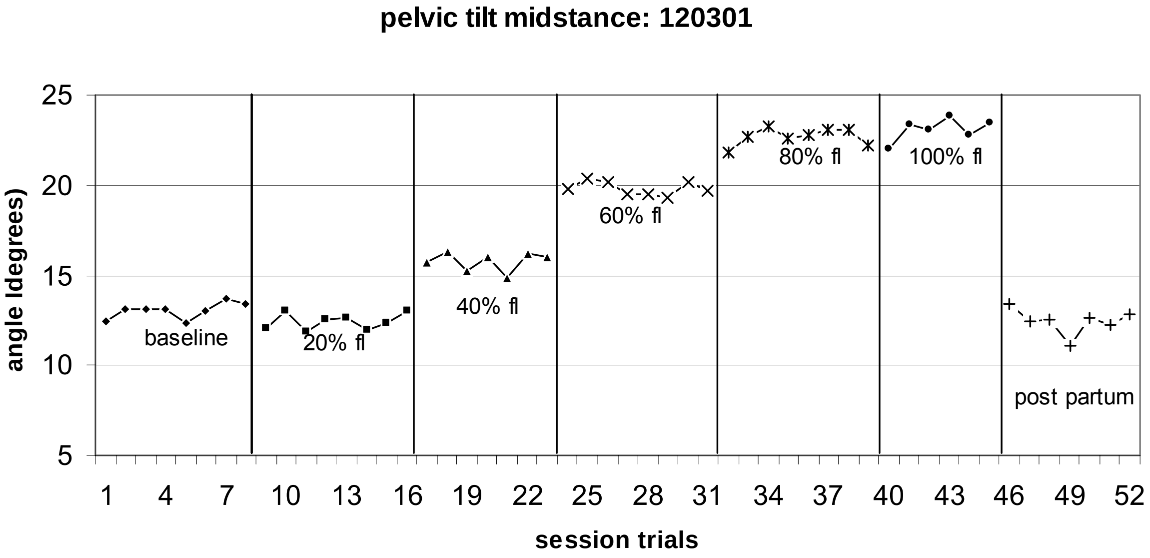


Figure 2.25. Time series chart of the angle of sagittal pelvic tilt for subject 120301 during midstance phase of natural gait plotted by session trials. Each partitioned series of points represents a different data collection stage. Stages are shown in sequence as: Sessions 1, 2, 3, 4, 5, 6, and 7. Each session is labeled according to the relevant obstetric phase. The baseline series was recorded at intake Session 1. Percentage labels refer to expected percentage of term fetal mass. The postpartum series was recorded at the final session and was defined by withdraw of the fetal load condition.

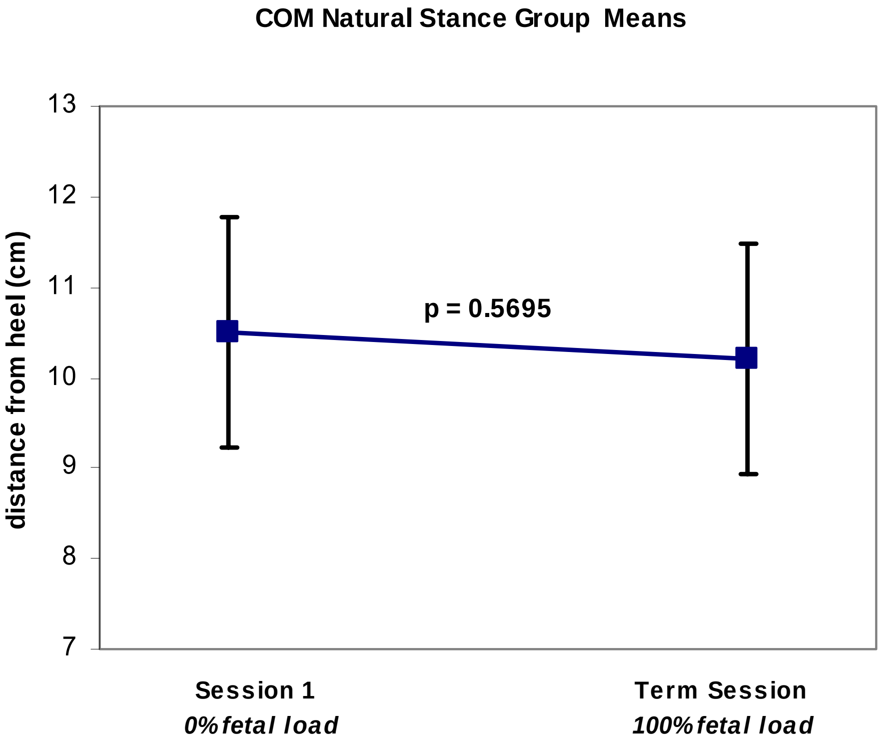


Figure 2.26. Mean fore-aft position of maternal center of mass at intake Session 1, 0% fetal load, and at term Session 6, 100% fetal load, plotted with group standard deviation. Means do not significantly differ (at alpha 0.05, p = 0.5695).

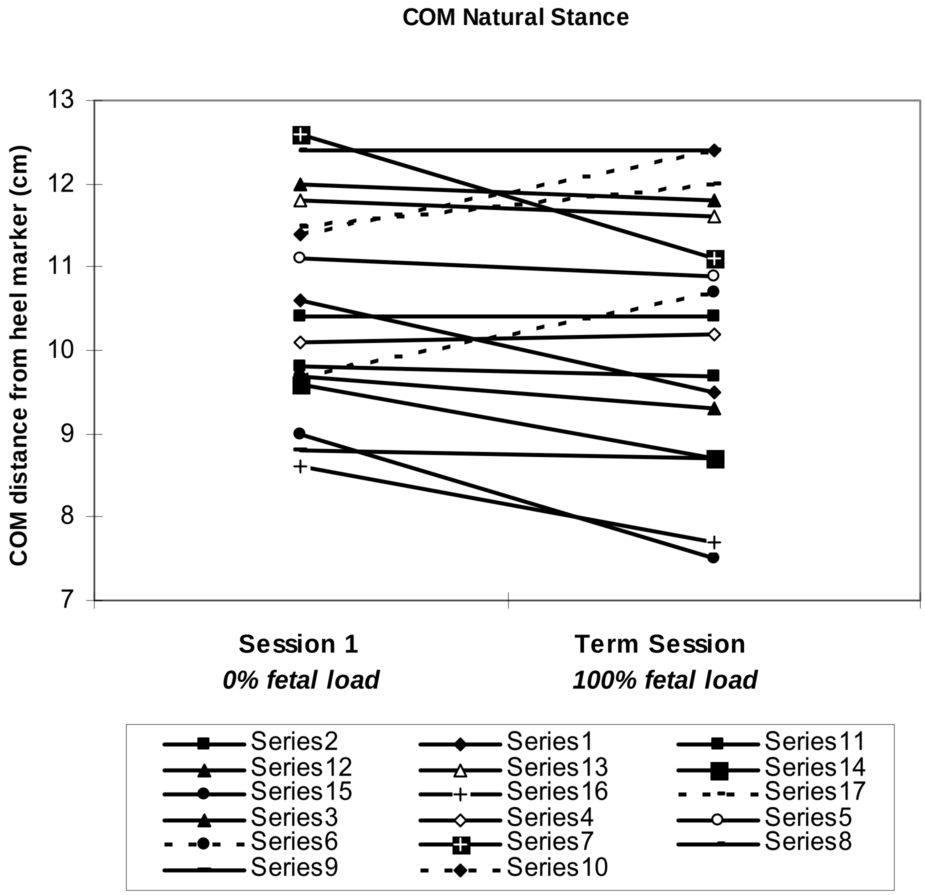


Figure 2.27. Mean fore-aft position of maternal center of mass at intake Session 1 (0% fetal load) and at term Session 6 (100% fetal load) plotted for each subject. Solid lines represent near fixity of position or posterior retraction. Dashed lines represent anterior translation.

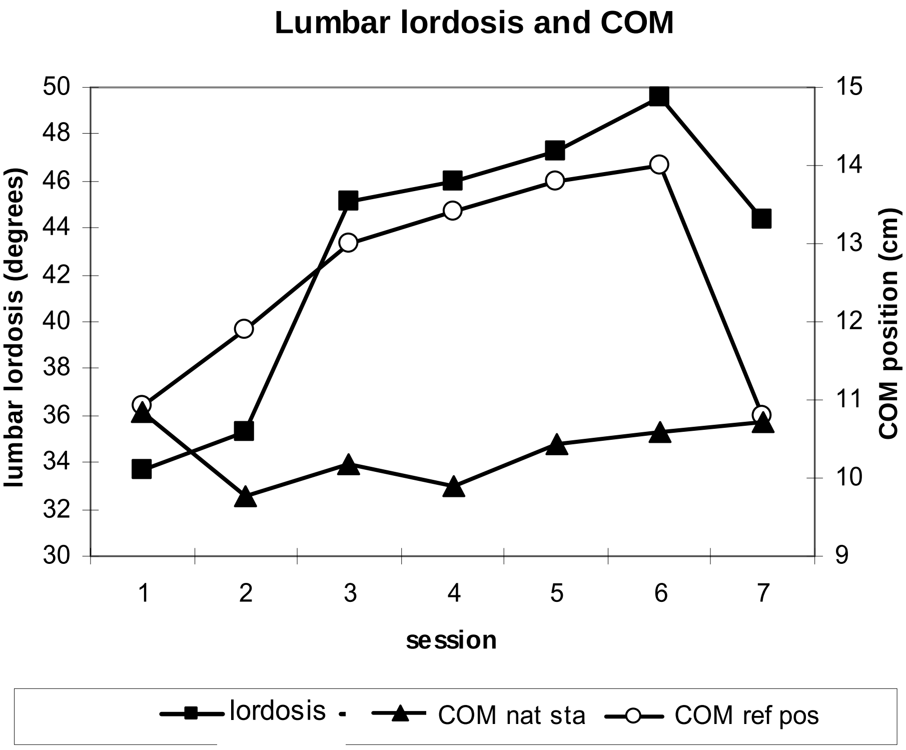


Figure 2.28. Mean angle of lumbar lordosis in natural stance across all sessions with mean position of center of mass in reference posture and natural stance (self-selected posture).

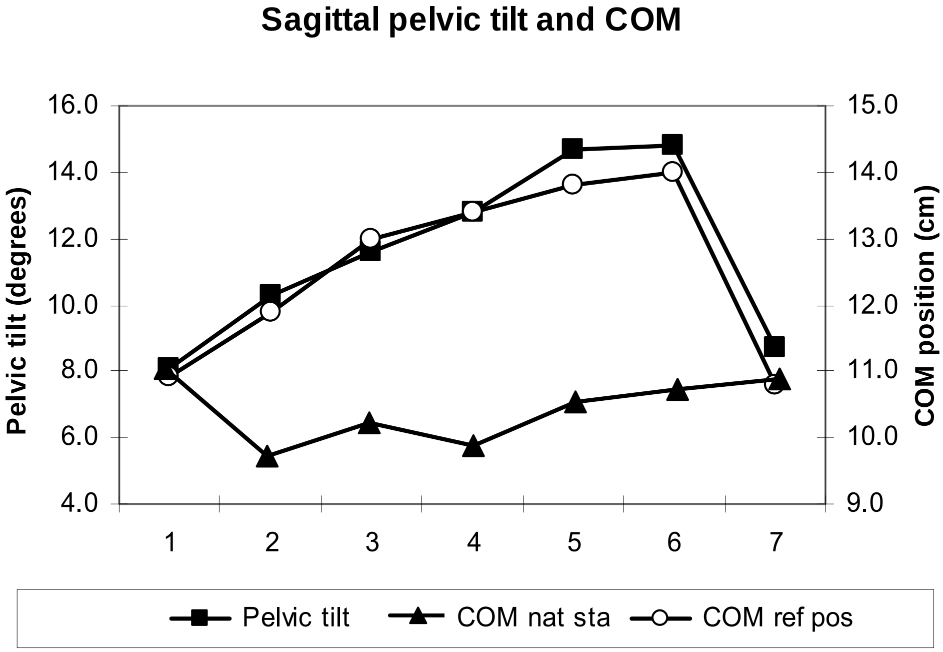


Figure 2.29. Mean angle of sagittal pelvic tilt in natural stance across all sessions with mean position of center of mass in reference posture and natural stance (self-selected posture).

REFERENCES

Abitbol M. 1996. Birth and human evolution: anatomical and obstetrical mechanics in primates. Westport, Conn: Bergin and Garvey.

Adams MA, Hutton WC. 1980. The effect of posture on the role of the apophyseal joints in resisting intervertebral compressive forces. J Bone Joint Surg 62B:358-362.

Adams MA, Hutton WC. 1983. The mechanical function of the lumbar apophyseal joints. Spine 8:327-330.

Alexander GR, Himes JH, Kaufman RB, Mor J, Kogan M. 1996. A United States national reference for fetal growth. Obstet Gyn 87:163-168.

Baskett TF, Nagele F. 2000. Naegele's rule: a reappraisal. British J Obstet Gyn 107:1433-1435.

Bird AR, Menz HB, Hyde CC. 1999. The effect of pregnancy on footprint parameters: a prospective investigation. Journal of the American Podiatric Medical Association 89:405-409.

Bjorntorp P. 1996. The regulation of adipose tissue distribution in humans. Int J Obesity 20:291-302.

Bogduk N. 1997. Clinical anatomy of the lumbar spine and sacrum. 3rd edition. New York:Churchill Livingstone.

Block RA, Hess LA, Timpano EV, Serlo C. 1985. Physiologic changes in the foot during pregnancy. J Amer Pod Med Assoc 75:297-299

Bullock J, Jull G, Bullock M.1987. The relationship of low back pain to postural changes during pregnancy. Aust J Phys 33:10-17.

Bullock-Saxton J. 1993. Postural alignment in standing: a repeatability study. Aust. J Physiother 39:25-29.

Cappozzo A. 1981. The forces and couples in the human trunk during level walking. J Biomech 265-277.

Crosbie J. 1995. Interrupted time series analysis with short series: why it is problematic; how it can be improved. In: The analysis of change, Gottman JM (ed). Mahwah, NJ: L Erlbaum Associates.

Crosbie J, Vachalathiti R, Smith R. 1997. Patterns of spinal motion during walking Gait Post 5: 6-12.

Culver CC, Viano DC. 1990. Anthropometry of seated women during pregnancy. Defining a fetal region for crash protection research. Hum Factors 32:625-636.

Cunningham DJ. 1886. Cunningham's manual of practical anatomy. Oxford, NY: Oxford University Press.

Davis PR. 1961. Human lower lumbar vertebrae: some mechanical and osteological considerations. J Anat 95:337-344.

Department of Health and Human Services. 1983. Obese and overweight adults in the United States. Publication No (PHS) 83-1680.

Demes B, Jungers WL, Fleagle JG, Wunderlich RE, Richmond BG, Lemelin P. 1996. Body size and leaping kinematics in Malagasy vertical clingers and leapers. J Hum Evol 31:367-388.

Dumas GA, Reid JG, Griffin MP, McGrath MJ. 1995. Exercise, posture, and back pain during pregnancy. Clin Biom 10(2):98-105.

Eames MHA, Cosgrove A, Baker R. 1999. Comparing methods of estimating total body center of mass in three-dimensions in normal and pathological gait. Hum Move Sci 18: 637-646.

Foti T, Davids J, Bagley A. 2000. A biomechanical analysis of gait during pregnancy. J Bone Joint Surg 82A:625-632.

Franklin M, Conner-Kerr T. 1998. An analysis of posture and back pain in the first and third trimesters of pregnancy. J Ortho Sports Phys Ther 28:133-138.

Gilad I, Nissan M. 1985. Sagittal evaluation of elemental geometric dimensions of human vertebrae. J Anat 143:115-120.

Gilleard D, Brown W, Brown JM. 1996. Structure and function of the abdominal muscles in primigravid subjects during pregnancy and the immediate postbirth period. Phys Ther 76: 750-762.

Gracovetsky S. 1985. A hypothesis for the role of the spine in human locomotion: a challenge to current thinking. J Biomed Eng 7:205-216.

Granata KP, Sanford AH. 2000. Lumbar-pelvic coordination is influenced by lifting task parameters. Spine 25:1413-1418.

Hart DL, Rose SJ. 1986. Reliability of a noninvasive method for measuring the lumbar curve. J Orthop Sports Phys Ther 8:180-184.

Haeusler M, Martelli S, Boeni T. 2002. Vertebrae numbers of the early hominid lumbar spine. J Hum Evol 43:621-643.

Institute of Medicine of the National Academies. 1990. Nutrition during pregnancy. Part1. Weight gain. Washington DC: National Academy Press.

Jenkins FA. 1974. Primate locomotion. New York: Academic Press.

Jensen RK, Doucet S, Treitz T. 1996a. Changes in segment mass and mass distribution during pregnancy. J Bio 29:251-256.

Jensen RK, Treitz T, Doucet S. 1996b. Prediction of human segment inertias during pregnancy. J Appl Biom 12:15-30.

Jones WP. 2003. Single-case times series with Bayesian analysis: a practitioner's guide. Measurement and Evaluation in Counseling and Development 36:28-35.

Koo WWK, Walters JC, Hockman EM. 2004. Body composition in neonates: relationship between measured and derived anthropometry with dual-energy x-ray absorptiometry measurements. Pediat Res 56:694-700

Lamoth CJC, Beek PJ, Meijer OG. 2002. Pelvis-thorax coordination in the transverse plane during gait. Gait Posts 16:101-114.

Leong JCY, Luk KDK, Chow DHK, Woo CW. 1987. The biomechanical functions of the iliolumbar ligament in maintaining stability of the lumbosacral junction. Spine 12, 669–674.

Levine D, Whittle MW. 1996. The effects of pelvic movement on lumbar lordosis in the standing position. J Orthoped Sports Phys Ther 24: 130-135.

Lindsay CA, Huston L, Amini SB, Catalano PM. 1997. Longitudinal changes in the relationship between body mass index and percent body fat in pregnancy. Obs Gyn 89:377-382.

Llorens L, Casinos A, Berge C, Majoral M, Jouffroy FK. 2001. A biomechanical study of the long bones in platyrrhines. Fol Primatol 72:201-216.

Lou SZ, Chou YL, Chou PH, Lin CJ, Chen UC, Su FC. 2001. Sit-to-stand at different periods in pregnancy. Clin Biom 16:194-198.

Louis R. 1985. Spinal stability as defined by the three-column spine concept. Anat Clin 7:33-42.

Lymbery JK, Gilleard W. 2005. The stance phase of walking during late pregnancy: Temperospatial and ground reaction force variables. J Amer Pod Med Asso 95:247-253.

McKenzie AM, Taylor NF. 1997. Can physiotherapists locate lumbar spinal levels by palpation? Physiother 83:235-239.

Mittendorf R, Williams MA, Berkey CS, Lieberman E, Monson RR. 1993. Predictors of human gestational length. Am J Obstet Gynecol 168:480-484.

Mittlemark R, Wiswell R, Drinkwater B. 1991. Exercise in pregnancy. Baltimore: Williams and Wilkins.

Mongelli MB, Wilcox M, Gardosi J. 1996. Estimating the date of confinement: ultrasonographic biometry versus certain menstrual dates. Amer J Obstet Gynecol 174:278-281.

National Institutes of Health. 1998. Clinical guidelines on the identification, evaluation and treatment of overweight and obesity in adults. Bethesda, MD: NIH National Heart, Lung and Blood Institute.

Nourbakhsh MR, Ottenbacher KJ. 1994. The statistical analysis of single-subject data: a comparative examination. Phys Ther 74:768-776.

Ortengren R, Andersson G. 1977. Electromyographic studies of trunk muscles with special reference to the anatomy of the lumbar spine. Spine 2:44-52.

Pal GP. 1989. Weight transmission through the sacrum in man. J Anat 162:9-17.

Pal GP, Routal RV. 1986. A study of weight transmission through the cervical and upper thoracic regions of the vertebral column in man. J Anat 148:245-261.

Pal GP, Routal RV. 1987. Transmission of weight through the lower thoracic and lumbar regions of the vertebral column in man. J Anat 152: 93-105.

Preuschoft H, Fritz M, Niemitz C. 1979. Biomechanics of the trunk in primates and problems of leaping in *Tarsius*. In Morbeck ME, Preuschoft H, Gomberg M, Eds., Environment, behavior and morphology: dynamic interactions in primates, pp. 327-345. New York: Fischer Verlag.

Rhodes P. 1958. Orthopaedic conditions associated with childbearing. Practitioner 181:304-312.

Robinson J. 1972. Early hominid posture and locomotion. Chicago: The University of Chicago Press.

Rose MD. 1975. Functional proportions of primate lumbar vertebral bodies. J Hum Evol 4:21-38.

Ruff CB, Runestead JA. 1992. Primate limb bone adaptations. Ann Rev Anthropol 21:407-433.

Ruff CB, Niskanen M, Junno J-A, Jamison P. 2005. Body mass prediction from stature and bi-iliac breadth in two high latitude populations, with application to earlier higher altitude humans. J Hum Evol 48:381-392

Sanders WJ. 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. J Hum Evol 34:249-302.

Scholl TO, Hediger ML, Schall JI, Ances IG, Smith WK. 1995. Gestational weight gain, pregnancy outcome, and postpartum weight retention. Obstet Gyn 86:423–427.

Sokal RR, Rohlf FJ. 2004. Biometry: the principles and practice of statistics in biological research. New York: WH Freeman.

Stokes V, Andersson C, Forssberg H. 1989. Rotational and translational movement features of the pelvis and thorax during adult human locomotion. J Biom 22:43-50.

Taves C, Charteris J, Wall JC. 1982. The kinematics of treadmill walking during pregnancy. Physiother Canada 34:321-323.

Thompson E. 1995. Introduction to maternity and pediatric nursing, 2nd ed., Philadelphia: WB Saunders Company.

Thurston AJ, Harris JD. 1983. Normal kinematics of the lumbar spine and pelvis. Spine 8: 199-205.

Toussaint M, Macho GA, Tobias PV. 2003. The third partial skeleton of a late Pliocene hominin (Stw 431) from Sterkfontein, South Africa. S Afr J Sci 99:215-223.

Tryon W. 1982. A simplified time-series analysis for evaluating treatment interventions. J Appl Beh Anal 15:432-429.

von Lackum HL. 1924. The lumbosacral region. An anatomic study and some clinical observations. J Am Med Assoc. 82:1109-1114.

Whittle MW, Levine D. 1997. Measurement of lumbar lordosis as a component of clinical gait analysis. Gait Post 5:101-107.

Whittle MW, Levine D. 1999. Three-dimensional relationships between the movements of the pelvis and lumbar spine during normal gait. Hum Move Sci 18:681-692.

Wilson SE, Granata KP. 2003. Reposition sense of lumbar curvature with flexed and asymmetric lifting postures. Spine 28: 513-518.

Wu WH, Meijer OG, Lamoth CJC, Uegaki K, van Dieen JH, Wuisman PIJM, de Vries JIP, Beek PJ. 2004. Gait coordination in pregnancy: Transverse pelvic and thoracic rotations and their relative phase. Clin Bio 19:480-488.

Zatsiorsky V, King D. 1998. An algorithm for determining gravity line location from posturographic recordings. J Biom. 31:161-164.

Chapter 3: Human Lumbopelvic Sexual Dimorphism

INTRODUCTION

Arguably, one of the most distinct features of the human lumbopelvic complex is its lumbar curve. Positioned between the sacrum and the thorax, the lumbar curve opens dorsally and recedes ventrally, its arc referred to as a lordosis. Structurally, lumbar lordosis is comprised of wedge-shaped vertebral bodies and intervertebral discs.

Functionally, lumbar lordosis translates the human vertebral column anteriorly so that it overlies the hip joints in bipedal stance (Latimer and Ward, 1993). This marked and novel orientation facilitates balance and stability in the largely unsupported upper body. When the upper body center of mass aligns vertically above the biacetabular axis of the supporting hip joints, it concomitantly aligns well over the body support base. The overall alignment of center of mass achieved through inherent lordosis minimizes torque that would otherwise require counter balance by sustained muscle effort. In this way, lordosis provides an energy efficient solution to a biped challenge.

Lordosis is so fundamental to bipedal posture and locomotion that it appears early in hominin evolution (Robinson, 1972; Latimer and Ward, 1993; Sanders, 1995, 1998). Although the extent of behavioral commitment to bipedality in early hominins is debated (Leakey and Hay, 1979; Lovejoy, 1979, 1980; Day and Wickens, 1980; Stern and Susman, 1983; Susman et al., 1984; Latimer and Lovejoy, 1990; Stern, 2000), morphological adaptations to bipedal locomotion are clearly evident in the fossil record as early as 7 million years ago, in the anterior position of the foramen magnum and the thin compact architecture of the superior femoral neck of *Sahelanthropus tchadensis* (Zollikofer et al., 2005) and *Orrorin tugenensis* (Galik et al., 2004), respectively. Direct evidence of lumbar lordosis in early hominins is present in the australopithecine specimens AL 288-1 (*Australopithecus afarensis*) and Sts14 (*Australopithecus africanus*) whose lumbar vertebral bodies though degraded are morphologically consistent with the modern bipedal mechanism of lumbar lordosis (Sanders, 1995, 1998).

The bony contribution to lordosis derives, in part, from vertebral body and disc shape, and is determined by relative differential length in the ventral and dorsal aspects of the centrum. The cranial portion of the lordotic arc is formed by vertebrae whose bodies are ventrally wedged (Figure 3.2). Ventrally wedged vertebral bodies predominate in the thoracic spinal region cranially adjacent to the lumbar spine. Thoracic vertebrae in the approximate lumbar region sequentially decrease in the degree of ventral wedging, flattening out to some extent the kyphotic arc of the thoracic spine. Within the lumbar region vertebral body wedging transitions from the kyphotic ventrally-wedged state to a lordotic dorsally-wedged state. Collectively along the lumbar spine, the sequential decrease in kyphotic wedging and increase in lordotic wedging give the human lumbar spine its distinctive structural lordosis.

The lumbar vertebrae of nonhuman primates are typically kyphotic, their ventral length reduced relative to their dorsal length (i.e., Cunningham, 1933; Schultz, 1961; Rose, 1975; Latimer and Ward, 1993; Sanders, 1995). Kyphotic wedging accumulates along the column and produces an anterior concavity which is continuous with the thoracic curve, generating large loads on the vertebral bodies.

The distinct human lumbar curve, achieved predominantly by dorsal lordotic wedging of the vertebral body, further complicates the loading regime of the human vertebral column. The human commitment to bipedality amplifies compression, torsion, and shearing forces directed through the lumbar vertebrae (Adams and Hutton, 1980, 1983; Davis, 1961; Latimer and Ward, 1993; Louis, 1985, Pal and Routal, 1987, 1988; Sanders, 1995; Shapiro, 1991, 1993a, 1993b, 1995).

Lordosis, particularly the long arc of human lumbar lordosis, directs a portion of the spinal load from the vertebral bodies to the zygapophyses, articular processes less well adapted to manage complex loads. In accordance, human prezygapophyseal facets are relatively large compared to those of other primates (i.e., Cunningham, 1933; Schultz, 1961; Rose, 1975; Latimer and Ward, 1993; Shapiro, 1993b; Sanders, 1995).

Human spinal loading model

Human spinal loading then is particularly complex due to the presence of lumbar lordosis. Pal and Routal's (1986, 1987) load transfer model defines two pillars through which spinal loads travel, a ventral pillar comprised of vertebral centra and intervertebral discs and a dorsal pillar formed by the neural arch components of pedicles, laminae and zygapophyses (Figure 3.1). Proportional loading shifts between the two pillars as a result of both static morphology, particularly centrum wedging in the lumbar region (Figure 3.2), and movements initiated along the vertebral column. The load bearing capacity of the ventral pillar is relatively high as a result of centrum endplate size and transverse orientation (Pal and Routal, 1987, 1991). Nonetheless, human lumbar lordosis increases the magnitude of load through the dorsal pillar's zygapophyses (Davis, 1961; Louis, 1985), and nearly 25% of static lower lumbar load is transferred through the laminae (Adams and Hutton, 1980).

Obstetric Spinal Loading

While spinal loading forces generated during bipedal locomotion are generally similar for all adults (Pal and Routal, 1987; Pal, 1989), the lengthy duration and recurrent nature of obstetric fetal load cleaves two distinct loading groups, one male and one female, based entirely in reproductive physiology. In spite of this obvious biological dichotomy and decades of locomotor and vertebral study, we know relatively little about the skeletal correlates of intraspecific spinal loading.

Because pregnancy exerts marked, recurrent biomechanical stress on the postural and locomotor skeleton, obstetric load is likely to have influenced the evolution of human lumbopelvic morphology, particularly given the unique spinal loading patterns associated with bipedal lumbar lordosis. Because the lumbar and sacral vertebrae provide the main load bearing capacity of the axial skeleton, adaptations in the female skeleton to the stresses of obstetric load are likely to be evident among them.

Three obstetric factors are of relevance to spinal loading. First, the growing fetus and its attendant soft tissues, localized in the upper body, incrementally increase compressive load on the maternal axial skeleton. Second, because maternal shape and mass distribution change as abdominal muscles stretch and separate to accommodate fetal growth (Abitbol, 1996; Gilleard et al., 1996), the obstetric load is applied tangentially to the axial spine, compounding bending stress on the vertebral column. Finally, related to the location of the obstetric load, the more ventrally positioned maternal center of mass inherent in pregnancy generates strong moments about the hip (Dumas et al., 1995; Jensen et al., 1996). So while the added tangential load in and of itself exacerbates stress on the vertebral column, any positional adjustments in lumbar lordosis and anterior sagittal pelvic tilt selected by the gravid female to alleviate the need for muscle counter balance of a translating center of mass would direct a greater proportion of spinal load through the dorsal pillar zygapophyses.

The hypotheses tested in this study propose that loading bearing structures of the human lumbopelvic complex are sexually dimorphic in that human females express lumbar and sacral morphologies consistent with a greater proportion of spinal load directed through the dorsal pillar. The hypothesis is part of a broader collection of hypotheses that attempt to explain aspects of human lumbopelvic sexual dimorphism as female adaptations to resist the structural risks associated with bipedal obstetric load. Although pregnancy is intermittent, the duration and recurrence of fetal load exert marked stress on the postural and locomotor skeleton, holding implications not only for modern humans, but also for earlier hominins, whose vertebral column evidenced a common biomechanical theme of lumbar lordosis.

Two explicit predictions were investigated:

1) The lumbar and sacral vertebrae of human adult females will present larger *dorsal* pillar structures relative to overall vertebral size than those of human adult males.

2) Lumbar and sacral vertebrae of human adult males will present relatively larger *ventral* pillar structures relative to overall vertebral size than those of human adult females.

MATERIALS AND METHODS

Sample

The sample population chosen to test the study hypothesis was drawn from two well studied 20th Century osteological archives of known age and sex: the Hamann-Todd collection curated at the Cleveland Museum of Natural History; and the Terry Collection housed at the National Museum of Natural History in Washington DC. Each collection is supported by morgue records that provide general biological profiles for specimens, including sex, age, stature and gross pathologies. Ancestry-related differences within the sample population (morgue identified and morgue parlanced as black or white) were tested for ethnicity effect using ANOVA cross (sex and ethnicity). No significant ethnicity response by sex was obtained. Specimens were selected to represent each of the three polymorphisms in human lumbar vertebral number: a modal group comprised of individuals with five lumbar vertebrae; an extra-modal group of individuals with six lumbar vertebrae, referred to herein as the L6 variant; and an alternate nonmodal group comprised of individuals with four lumbar vertebrae, referred to as the L4 variant. The L6 variant is particularly relevant to the question of early hominin bipedal adaptation as australopithecines appear to have had lumbar column length equal to the extra-modal variant in modern humans (Robinson, 1972; Sanders, 1998; Tobias, 1998, but see Haeusler et al., 2002).

Sample size

The modal group consisted of 59 males and 54 females. Nonmodal variants occur with less frequency than the modal type, between 5% and 8% (Bornstein and Peterson, 1966; de Beer Kaufman, 1974; Ward and Latimer, 1993), making it difficult to obtain robust sample sizes for both variants. Their infrequent representation in skeletal collections limited sample sizes for the variants to: 20 males and 12 females in the L6 Variant group; and 7 males and 8 females in the L4 Variant group.

Sex determination

Museum records were initially consulted to identify specimen sex. In addition to reported sex, morgue photos were examined whenever available. To further ensure correct sexing, specimens were assessed according to the modified Phenice method (Phenice, 1969; Ubelaker and Volk, 2002). Individuals whose sex was ambiguous according to either collection records or observer assessment were excluded.

Age determination

Specimens were selected within an adult age range of 20 to 40 years. This criterion targeted individuals whose skeletal development had reached maturity but whose aging effects had not yet eclipsed osteophytic deposition, typical in synovial and symphyseal joint margins with aging, e.g. spondylosis deformans (Latimer and Ward, 1993). Chronological age was obtained through morgue records and further evaluated by visual confirmation of postcranial epiphyseal fusion. If skeletal age was found to fall outside the inclusion range the specimen was omitted from the study. Pathological specimens, whether determined by collection records or gross observation by the study author were not analyzed. Specimens included in the analysis are listed in Table 3.1 along with sex, vertebral number and the institutions from which they derive.

Lumbar vertebral identification

Lumbar vertebrae were defined according to their zygapophyseal orientation (Washburn and Buettner-Janusch, 1952; Shapiro, 1993a). This facet-based designation differs from the widely used non rib-bearing alternative (Schultz, 1930) in its functional emphasis on the range of motion between vertebral elements; type and range of movement in the lumbar column are largely influenced by facet direction. The medial and lateral orientation of lumbar superior and inferior facets, respectively, guide sagittal flexion and extension while resisting both rotation (Rockwell et al., 1938) and ventral displacement (Latimer and Ward, 1993; Bogduk and Twomey, 1997).

Lumbopelvic Osteological Measurements

Predictions of lumbopelvic sexual dimorphism were tested on fourteen vertebral variables at each lumbar vertebral level, four sacral variables and two innominate measures, chosen to define the relative size and shape of the lumbar vertebrae and pelvis. The structures quantified receive and transfer postural and locomotor forces generated within the lumbopelvic complex, and are therefore subject to biomechanical stresses introduced by fetal load. Variables are illustrated and anatomically defined in Figure 3.3. Surface area and cross-sectional area were constructed from linear variables. One areal measurement was digitally derived from scaled photographs. Each variable captured a dimension of structural function in load resistance, range of motion and/or muscle leverage, and was therefore potentially relevant to biomechanical stresses that would be introduced by obstetric load. Each variable is defined anatomically and functionally below.

Linear measurements were collected with a Mitutoyo 500-171 needle point digital caliper and were recorded to the nearest 0.01mm. Angular measurements were collected with an SPI 0-180 degree protractor. Auricular surface area was photographed with a Nikon CoolPix 10x camera. ImageJ digitizing software, version 1.34n (Rasband WS.,U.S. National Institutes of Health, USA, 1997-2006) was used to measure surface area of the sacral auricular facet.

Lumbar Vertebrae (Figure 3.3a):

*Vertebral Body***:** The vertebral body (centrum) is the primary load bearing structure of the vertebral column (Bogduk, 2005), and its joint surfaces are generally proportional to the magnitude of forces they transmit (Pal and Routal, 1986, 1987; Pal, 1989). Following the hypotheses presented in this study, it was predicted that males would present relatively larger centrum areas than females in accordance their reliance on ventral pillar load resistance. Lumbar body area was calculated from the cranial centrum endplate dimensions, based on the area of an ellipse as follows: (CMD/2) x (CAD/2) x 3.1416. Sacral body area was similarly derived as: (SMD/2) x (SAD/2) x 3.1416. Vertebral wedging, the bony contribution to lumbar lordosis occurs when ventral and dorsal body lengths differ. To more effectively dissipate compressive load and shearing forces associated with obstetric load, females were expected to present a longer lordotic curve (either a greater number of more dorsally wedged vertebral bodies or an equal number of dorsally wedged lumbar vertebrae but with a greater degree of dorsal wedging) than were males. Linear measurements were analyzed separately then used to calculate an angular variable of vertebral body wedging following Digiovanni et al., (1989):

$$\text{Wedging angle} = 2 \text{ arctangent } (((\text{CDH}-\text{CVH})/2)/\text{CAD})$$

Positive angles were kyphotic while negative angles were lordotic. A vertebra was determined to be neutral, neither kyphotic nor lordotic, when its value fell within the range 0.5 to -0.5 degrees. Graphic representation and mathematical calculation of the bony lordotic curve was obtained in MATLAB script written for this analysis in consultation with Dr. Tim Eakin (University of Texas at Austin, ITS, Senior Systems Analyst). See Appendix H for MATLAB script.

Pedicle: The vertebral pedicle provides structural continuity between the two pillars of the spine and is subject to increased bending stress when loads are transferred between them (Davis, 1961; Adams and Hutton, 1980, 1983). Since human females were predicted to carry a greater proportion of spinal load along the dorsal pillar structures than males, the pedicle cross-sectional area was expected to be relatively larger in human females than in males. Pedicle cross-sectional area was calculated as PW x PL, length times width.

Transverse Process: Transverse processes provide attachment sites for many of the erector spinal muscles that act to extend of the back. Females were expected to present larger and more dorsally oriented processes relative to body size than were males for effective leverage under conditions of obstetric inertia. These expectations were measured by transverse process length (TPL) and obliquity of the transverse process (ATP).

Zygapophyses: Zygapophyses are secondary load bearing structures. These synovial joints guide intervertebral movements and support a proportionately greater load under conditions of acute lumbar lordosis (Adams and Hutton, 1980; Pal and Routal, 1987). It was therefore predicted that females would present relatively large prezygapophyseal facets to manage increased load. The following formula defined prezygapophyseal area:

$$[(SCC/2 + SOM/2)/2] \times [(SML/2) + (SOC/2)/2] \times 3.1416$$

The angle of prezygapophyseal obliquity (POB) was taken to investigate potential range of motion in spinal rotation and flexion/extension as well as resistance to ventral shear stress. Obliquity is exemplified in humans in that the crainiocaudally sequential lumbar vertebrae bear prezygapophyses that are increasingly more coronal in their facet orientation (Odgers, 1933; Shapiro, 1991; Latimer and Ward, 1993). To increase resistance to shear force inherent between dorsally wedged vertebral bodies, female zygapophyses were expected to be more obliquely oriented than those of males.

Sacrum (Figure 3.3b):

Sacral Body: The vertebral body and the paired prezygapophyses of the first sacral vertebra function similarly to those of the lumbar vertebrae. The medio-lateral expanse of the sacral body provides, in part, attachment sites for muscles controlling the upper body. Where extensive erector spinae muscles benefit torso stability, a relatively broad sacrum is predicted. Females were predicted to have relatively broader sacra than males to better resist hip moments exacerbated by fetal load. The auricular area across which upper body-hindlimb load transfers, was also expected to be larger in females than in males, as a reflection of female obstetric load. The sacrum performs a dual role as the axial load bearing base of the spine and the dorsal bony continuum of the pelvic girdle, the latter role relevant to spatial dimensions at parturition. The parsing of functional roles in a multi-functional element is often problematic. Should sacral breadth differ by sex, identification of significant sex differences in auricular area would lend support for an obstetric leverage function. Sacral auricular area was calculated digitally from scaled photographs using JImage areal software (version 1.34n, NIH, USA).

Innominate (Figure 3.3c):

Ilium: The ilium provides attachment of the lesser gluteal muscles that function as abductors in humans stabilizing the upper body in bipedal locomotion, particularly, during single support phase. Additionally, the posterior reach of the iliac crest augments the lever advantage of the erector spinae group in stabilizing the upper body over the pelvis. Females are expected to present relatively long and broad innominates in accordance with fetal load.

Statistical Analyses

The null hypothesis in all comparisons was no difference in lumbopelvic shape parameters in males and females. JMP 5.0.1.2 (SAS Institute, 2003) and SPSS 12.0 (SPSS, Inc, 2003) software packages were used for statistical analyses. MATLAB 7, release 14 (The MathWorks) was used for mathematical and graphical analyses.

Size standardization

Without adjusting for body size variation within the sample population, any significant differences identified by contrasting males and females might reflect little more than stochastic distribution of body size differences within the samples. To test for the presence of shape sexual dimorphism, data were size-adjusted. The effectiveness of various methods for the study of size and shape have been well studied (for a recent review, see Klingenberg, 1996). For the purpose of this study, the representative measure of gross size used to remove the general isometric phenomenon (Jungers, 1984a, 1984b; Corruccini, 1987, 1995; Falsetti et al., 1993; Jungers et al., 1995) was the scale free geometric mean (Mosimann, 1970; Darroch and Mosimann, 1985) derived from the forty-eight linear variables of the lumbar vertebrae, twelve from each of the first, second, penultimate and last lumbar levels (see linear measures in Figure 3.3a). Mosimann's method (1970) removes the effects of size for each variable on an individual basis using a directly measured index of individual size. Variates obtained for each individual were standardized by dividing the raw values by the geometric mean of the relevant specimen (the 48th root of the product of the variables). The overall size of the lumbar vertebrae as defined here by many and varied measures of the dorsal and ventral pillar structures represents the relative upper body load in both males and females, and therefore captures the specific target of obstetric mass.

Principal Component Analysis

Principal component analyses (PCA) investigate the dependence structure in a suite of observations. The first linear combination of the analysis maximizes the variance of resulting scores. Successive linear combinations maximize variance of resulting scores subject to the condition that they are uncorrelated with the previous linear combination.

In order to assess whether the human modal and variant groups share similar patterns of association among the study's linear variables (Figures 3.3a, 3.3b, 3.3 c, linear variables only), a Q-mode Principal Component Analysis was performed on a correlation matrix. This matrix is preferred over a co-variance matrix due to differing units of measurement among the variables (Blackith and Reyment, 1971). In Q-Mode analysis, rows are variables, and columns are cases; the inverse factor analysis from the common R-Mode.

Because total number of lumbar vertebral levels differed among the three morphotypes, it was not possible to perform a complete level-by-level comparison. As an alternative, principal component analyses included the L1, L2, Penultimate and Last lumbar levels of each group. The anatomical levels that comprise the comparative categories for each of the three morphotypes are presented in Table 3.2. The resultant omission of vertebral level L3 from the modal group and levels L3 and L4 from the L6 variant introduces the possibility of functional discontinuity for inferences drawn from the analyses. Although the inferential value of the comparisons is somewhat restricted by this selective vertebral level comparison, it nonetheless provides an initial examination of intergroup relationships within the data. The tests of sexual dimorphism that follow the principal component analyses were performed on complete lumbar series for each group (i.e., lumbar levels L1, L2, L3, L4 and L5 for the modal group).

Since many of the lumbopelvic variables were not independent, a multivariate R-Mode analysis served to identify the percentage contribution to lumbopelvic shape variation separating the modal and variant groups and isolate similarities within human lumbar vertebral columns, regardless of vertebral number. Variables that are functionally or developmentally related were expected to share high coefficients within a factor.

Subsequent sex partitioned analyses were conducted on complete lumbar series within each morphotype to obtain initial pattern information on the relationship of variables both within the morphotype and according to sex.

Inferential test of sexual dimorphism in lumbopelvic variables

In accordance with the biomechanical principles outlined in the two-pillar model of spinal force transmission (Pal and Routal, 1987, 1988), the variables tested in this portion of the analysis represent the major load-bearing and load-resistant structures operating under conditions of bipedal obstetric load. The variables tested include: centrum wedging, surface area, medio-lateral breadth; transverse process angle and length; pedicle cross-sectional area; prezygapophyseal surface area and angle; interfacet breadth; sacral body breadth; and auricular area. Variables were tested for normality using the single sample Shapiro-Wilk W test. A between-sex test for homoscedasticity was performed as a two-tailed Fmax test with a 0.05 alpha. Because distribution assumptions of normality and homoscedasticity were not met for many of the variates, tests of significance in comparing male and female specimens were obtained using the Wilcoxon Rank Sums test using a multiple comparisons adjustment to limit Type I errors (Sokal and Rholf, 1995) following Jaccard and Wan (1996), who advocate a modified Bonferroni procedure. The Wilcoxon Rank Sums test is a nonparametric test of the null hypothesis that both male and female samples for each variable derive from the same distribution. Means, standard deviations, z-values and probabilities were reported for all comparisons. The null hypothesis in all comparisons was no sex difference in the lumbopelvic structures within each species level sample population.

Association between centrum wedging and spinal load resistance

To investigate the relationship between vertebral body wedging and shift of loading forces as indicated by articular surface area, Spearman's rank order correlation coefficient was calculated between the angle of vertebral wedging and the size adjusted centrum surface area, pedicle cross-sectional area and prezygapophyseal area, at each vertebral level. A comparison of centrum articular area and prezygapophyseal area was also performed.

RESULTS

Pooled morphotypes: Q-mode principal component analysis

Figure 3.4 presents the Q-Mode PCA for the correlation matrix of pooled morphotypes: modal; L6 variant; and L4 variant. Principal Component 1 is heavily loaded with 99.2% of the variance partitioned. All cases (cases are individuals in Q-mode analyses) are equal in eigenvector score, indicating that the association of variables is homogenous across all column types. Separation on PC1 is driven by *relative* size, as all variates were geomean size-adjusted prior to the analysis. For example, linear dimensions of the vertebrae are inherently smaller in scale than are the linear dimensions of the ilia. Variables projected to the right of the axis are large (iliac and sacrum breadth and iliac height) relative to the variables plotted to the left (lumbar vertebral pedicles and zygapophyses). The remaining variance differentiated on subsequent axes is less than 1% of the total. Principal Component 2 captures 0.2% of the overall variance. While this axis contrasts increasing interfacet breadth with pedicle dimensions of the second lumbar vertebra, the small percentage of variance it represents is not likely to be of biological relevance in this study. Each of the remaining axes captures less than 0.10% of the pooled sample variance. In general, Q-mode PCA indicates that variables are largely distinguished from one another according to size. The size sorting of variables is consistent across all three morphotypes and their inclusive cases/individuals. Therefore, while each morphotype is distinct in terms of the number of lumbar vertebrae that comprise its total length, the structural relationship of the variables chosen to describe the shape of the lumbopelvic elements in this study do not differ across morphotypes.

Pooled morphotypes: R-mode principal component analysis

Principal Components 1 and 2 of the R-mode PCA are shown in Figure 3.5. Scatter of cases within each morphotype overlap indicating homogeneity of the sample groups. PC1 accounts for 49.2% of the variance and contrasts pelvic breadth and height, with positive loadings, against prezygapophyseal diameters, with negative loadings. Individuals plotted to the right have relatively large pelves with small vertebral dimensions. PC2 isolates 12.9% of the variance in contrasting centrum mediolateral diameters and sacral body breadth. Individuals near the positive loading pole have large lumbar vertebral centra and relatively narrow sacra (Figure 3.6). The wide dispersion of specimens and lack of morphotype separation shown on PC1 and PC2 also characterizes PC3. This third axis isolates 7.5% of the total variance and contrasts variables of the pelvis (3.6). Positive loadings emphasize sacral body breadth in contrast to negative loadings that feature sacral centrum breadth and iliac height and breadth. However, the axis is calibrated across a narrow range of values, so the dispersion within the combined groups is limited.

Overall, this R-Mode PCA shows that the modal and L4 and L6 variants are not distinguishable from one another in pooled morphospace. Rather, the groups under study are homogeneous in expression of all variables, when pooled.

Modal human group: Principal component analysis and tests of sexual dimorphism

Principal Component Analysis

Figure 3.7 shows the first and second principal component scores for the human modal sample. The first three PC scores account for 66.5% of the total shape variance, PC1 47%, PC2 13%, and PC3 6.5%. The right pole of PC1 is occupied by individuals with relatively large pelves (sacral breadth, iliac breadth and height) and small pedicles and zygapophyses. Because variates used in the analyses were geomean adjusted for raw size differences among individuals prior to analysis, the contrast of pelvic and vertebral variables that is captured on PC1 is not driven by "absolute size". Instead the variance loading pattern is due to the presence of individuals who have large pelves (high loading) as well as individuals who have small pelves (low loading), relative to respective "absolute size". Specimen 2923 in the bottom right corner of Figure 3.7 is characterized by a raw sacral breadth of 118.8mm, a value not among the broadest of the group. However, her size-adjusted sacral breadth value of 7.22 is among the most extreme of the large sacral values, indicating that the pelvis of individual 2923 is large relative to body size. In contrast, specimen 2120 falls to the far left of the plot. Raw sacral breadth for this individual is 113.7mm and is not among the narrowest. Yet the size-adjusted value for 2120 is 5.39, and this value is very low within the group, indicating the individual has a small pelvis relative to body size.

The information on PC2 best separates individuals by sex. Figure 3.8 presents PC3 on PC2. In the PC2 domain of 13% variance, the larger scores derive from males while the smaller scores derive from females. While there is considerable overlap of sexes along PC2, the disparate ends of the axis are dominated by only one sex. The high loadings on PC2 derive from increasing centrum breadth along the entire lumbar column and contrast with increasing pelvic breadth in the low loading region to the left. Individuals, mostly male, who plot to the far right of PC2, specimen 3052 for example, have relatively broad lumbar centra yet relatively narrow sacral bodies. The morphospace domain at the left pole of the PC2 axis is predominantly occupied by females, specimen 1289 for example. Individuals, mostly female, who plot in this region present relatively broad sacral bodies and relatively small lumbar vertebral centra. This typical female pattern is expressed by a few males, 2941 for example. The mid morphospace of the PC2 axis captures numerous males and females sharing the same relative proportions in centrum breadth and sacral breadth.

Tests of sexual dimorphism

Results for the tests of sexual dimorphism in the modal group are presented in Table 3.3. Relative to body size, modal human males have significantly larger vertebral centra and pedicle cross-sectional area than do modal females at lumbar levels L1-L4 and L1-L3, respectively. The wedging angle of lumbar vertebrae differs in males and females through four of the five lumbar levels leading to the last lumbar vertebra where wedging in the sexes does not differ significantly. The differences in wedging patterns of males and females are further examined later in this chapter. Female prezygapophyseal angle significantly exceeds that of males along the entire lumbar column, L1-L5. Also, relative to body size, females have both a broader sacrum and ilium than found in males.

Nonmodal variants: Principal component analysis and tests of sexual dimorphism

L6 variant: Principal component analysis

Figure 3.9 shows the first and second principal component scores for the L6 variant group. Results are similar in many respects to those obtained for the modal human sample. While PC1 of the L6 variant analysis captures only 26.4% of the variance, the major contrast on the axis is between sacral breadth which increases to the right, and dorsal column structures, all of which increase to the left. Individuals who plot to the right have relatively broad pelves compared to their zygapophyses and pedicles.

Individuals on the left express the opposite proportional relationship, narrow pelves with relatively large zygapophyses and pedicles. There is no separation by sex on PC1.

Figure 3.10 shows the PC2 and PC3 results with 17.2% and 13.9% of the total variance, respectively. While males on the second principal component axis are widely scattered, females plot almost entirely to the left of the midpoint. Only one female falls in the right side morphospace, otherwise dominated by males. The PC2 axis contrasts medio-lateral and antero-posterior diameters of the vertebral centra, which increase to the right, with the interfacet breadth, which increases to the left. With respect to the relationship between the variables contrasted on PC2, females are less variable. They don't attain the expansive centrum breadth of males and their interfacet breadths remain wide relative to the vertebral centra. Fourteen percent of the variance is isolated on PC3. On this axis, interfacet breadth increases in the positive direction in contrast to prezygapophyseal diameters increasing toward the negative pole. Although females cluster to the left of the PC 2 axis, males are widely dispersed along the expanse, indicating that little separation among the sexes in the principal component analysis.

L6 variant: Tests of sexual dimorphism

Results of the tests of sexual dimorphism for the L6 variant are presented in Table 3.4. With respect to lumbar vertebral wedging, differences between males and females are significant at vertebral levels L1 and L2. Sex differences in centrum surface area are significant at level L1, where the male mean is larger than the female mean. No signal of sexual dimorphism occurs in the transverse process angle. Relative length of the transverse process differs significantly at L2 and L3 where male mean length exceeds that of females. The cross-sectional area of the pedicles significantly differs in much of the cranial end of the lumbar column where male means exceed those of females at lumbar levels L2, L3, L4 and L6. Male pedicular cross sectional area exceeds that of females at L5, but the means do not statistically differ. Area of the prezygapophyses does not reach statistical significance at any level along the column.

In many respects the results obtained for the L6 variant are similar to those of the modal group. In both morphotypes females express significantly more oblique angles of the zygapophyses at all five lumbar levels, orienting the prezygapophyseal articular surfaces in a more coronal plane along the entire lumbar column. Sacral breadth and iliac breadth in females are larger than those of males. Males of both morphotypes are characterized by broad lumbar centra at each level along the lumbar column.

To some extent the L6 variant is less sexually dimorphic than the modal group. Significant sex differences in both lumbar vertebral body wedging and centrum surface area in the L6 variant are limited to the most cranial reach of the lumbar column, L1-L2 and L1, respectively. By comparison sexual dimorphism in these vertebral traits extends more caudally in the modal group to encompass all but the last lumbar level. Although the degree of sexual dimorphism in the mid and lower lumbar regions of the L6 variant do not reach statistical significance, male values exceed female values as they do in the modal group. It should be noted that sample size in the L6 variant is relatively small and may be a factor in the absence of statistically significant results for this morphotype.

L4 variant: Principal component analysis

Results of the principal component analysis of the L4 variant are presented in Figures 3.11 and 3.12. The first three principal components account for 70.5% of the total shape variance, PC1 for 45.5%, PC2 for 15.8% and PC3 for 9.1%. On PC1 the positive scores plotted to the right emphasize broad pelvic breadth while the negative scores to the left reflect increasing prezygapophyseal diameters. The contrast sorts individuals whose pelves are relatively large for their body size. The variables featured on this axis are consistent with those of the modal and L6 variant PCA. The second PC contrasts the breadth of the sacral body with positive scores and the breadth of the sacral centrum with negative scores. Individuals who have relatively broad sacra yet narrow sacral centra plot within the positive pole. Males fall to the negative side of the axis. More females fall to the positive pole, and the positive domain is entirely occupied by females.

Sexes separate more clearly on PC3. The majority of points in the negative pole of PC3 are female while the preponderance of points in the positive domain are male. The third PC contrasts broad interfacet distances with iliac breadth. Most males in this group have broadly spaced facets yet relatively narrow pelves compared to females, although there is no distinct sex separation.

L4 variant: Tests of sexual dimorphism

Table 3.5 reports results of the statistical tests for sexual dimorphism in the L4 variant. Sample sizes for each sex in this morphotype are small and results from these tests are more likely to reflect crude differences rather than fine differences that are possible with more robust sampling as in the modal group (Sokal and Rohlf, 1995). Results of this portion of the analysis must be considered preliminary at best and require subsequent testing when larger sample sizes are obtained. Because the L4 variant is the least prevalent morphotype, its low frequency in skeletal collections currently limits its utility for study of human lumbopelvic sexual dimorphism. Nonetheless, a few significant results were obtained, all of which are consistent with the more robust results of the modal and L6 variant analyses. As in the other groups, sexual dimorphism is present in the cranialmost region of the lumbar column where male lumbar vertebral centra are relatively large compared to those of females.

Wedging angle: All morphotypes

Wedging of the vertebral bodies is the result of the dimensional relationship of body length in both the ventral and dorsal margins and the antero-posterior diameters. While each of these linear dimensions differs significantly by sex at one or more vertebral levels and are larger in males than in females, the structural effect of these significant differences is not simply that the male lumbar vertebral centra exceed the relative size of the female centra. The relationship of the variables influences the specific shape of each vertebral body, and a closer examination of their cumulative effect on vertebral shape reveals important distinctions in the lumbar wedging sequence of males and females.

Lumbar vertebral wedging angles are reported in Table 3.6. Regardless of modal, L4 variant or L6 variant membership, the entire sequence of dorsal wedging in males spans the penultimate and last lumbar vertebrae, at the two caudalmost lumbar levels. The female wedging pattern is also consistent across the morphotypes but differs entirely from the male pattern in respect to the total number of lumbar levels that are dorsally wedged. The dorsal wedging sequence in the female lumbar column expands over three lumbar levels, to include the pre penultimate, penultimate and last lumbar levels. The modal morphotype is distinguished by the occurrence of statistically significant sex differences in four sequential lumbar levels (L1-L4), contrasted with the two (L1-L2) and one (L1) lumbar levels that characterize the L6 variant and the L4 variant, respectively. The kyphotic pattern of body wedging characterizes both sexes at the cranial end of the lumbar column and in turn the caudal end of the lumbar region is comprised of vertebral bodies shaped in the lordotic pattern. However, the sexes are distinguished from one another at the transitional level where kyphotic wedging gives way to lordotic wedging. The wedging angles enclosed by boxes in Table 3.6 demonstrate that female lumbar lordosis is initiated more cranially in the lumbar region than is the lordosis of males, regardless of numeric morphotype. The consistency of this sex-related pattern across all three morphotypes suggests an inherent pervasiveness of morphological distinction in the bony lordosis of modern humans. Females present a longer series of dorsally wedged lumbar vertebrae and in the common modal morphotype sexes differ markedly in the degree of wedging that characterizes all the pre terminal lumbar vertebrae. The effects of lumbar vertebral body wedging on the curvature of the human vertebral column are mathematically and graphically represented as the radius of curvature in Figures 3.13 through 3.18.

Radius of lumbar lordotic curve: All morphotypes

Lumbar vertebral curves are reported and plotted in Figures 3.13 – 3.18. For the purpose of explicitly isolating the bony contribution to the lordotic curve, the vertebral level of neutral body wedging served as the starting position of the lordotic arc and the caudalmost vertebral level of dorsal body wedging served as the end position. Cumulative wedging across these vertebral levels produced a measurable radius of lordotic curvature. A different approach was employed in examination of lordotic curvature within the L4 variant column due to the fact that neither sex presented a distinct neutrally wedged vertebral level. In this case, all four lumbar vertebral levels were included in the calculation for each sex within the L4 group.

The radius of curvature in the modal group is presented in Figures 3.13 and 3.14. Patterns of sexual dimorphism in the modal lordotic curve can be compared across figures. The obvious difference between male and female lordosis is the number of vertebral bodies that contribute to the curve: three levels in the modal male and four levels in the modal female. The mean radius of curvature in modal males is 114.22mm while that of modal females is 111.01mm, a difference of 3.21mm. A smaller radius of curvature indicates a tighter curve.

As in the modal group, the L6 variant males have a shorter lordotic sequence than do females (Figures 3.15 and 3.16). However, there is almost no difference in the radius of curvature between the sexes. The male mean is 111.94mm and the female mean is 112.26mm. The difference is 0.30mm. This result is consistent with the fact that wedging angles differ significantly only at the L1 and L2 levels in the L6 group (see Table 3.6).

Results are presented for the L4 variant in Figures 3.17 and 3.18. Again, because the L4 variant does not express a distinct neutral/transitional level of wedging in the lumbar region, all four vertebral levels of the lumbar column are plotted in the radius of curvature graphical analysis for each sex. Recall that the pattern of wedging in the L4 variant is consistent with that of both the modal and L6 variant in that females have a series of three dorsally wedged lumbar vertebrae while males have shorter series of two dorsally wedged lumbar vertebrae. When the radius of curvature is computed for the L4 variant sexes, a slight difference in radius is detected. The male mean is 112.69mm while the female mean is 111.63mm, a difference of 1.06mm. As in the modal group, females express a tighter radius of curvature along the lumbar column.

In general and relative to males, females present a smaller and tighter radius of lumbar curvature, derived across a longer sequence of dorsally wedged lumbar vertebrae.

Association between centrum wedging and spinal load resistance: All morphotypes

Spearman's rank order correlation coefficient was used to test for a relationship between centrum surface area and pedicle cross-sectional area and between vertebral body wedging and loading signals in the areal measures. Table 3.7 presents the Spearman's correlation coefficient (rs) between surface areas relative to body size and body wedging in the modal group, according to sex. The results show that the correlations are significant between centrum surface area and pedicle cross-sectional area. The correlations are strong for both males and females at lumbar vertebral levels L2-L5. The female contrast is also significant at the first lumbar level. While pedicles are typically included among the dorsal pillar structures and viewed functionally as struts subject to bending forces due to differential loading of the ventral and the dorsal pillars (Bogduk, 1999), they are intermediary connectors between the two pillars, in so far as loads transfer to and from the centra and zygapophyses. The functional resultant site of force application to the pedicle is uncertain. Therefore, it may not be surprising if increased centrum loading impacts pedicle loading, regardless of whether or not load is actively transferred between the centrum and zygapophyses. The similar correlation patterns between centrum surface area and pedicle cross-sectional area in males and females indicate a lack of sex-based differentiation in the functional relationship. The remaining contrasts of vertebral body wedging and areas of the centrum, pedicle and prezygapophyses by sex are non significant, with the exception of the modal female L1 pedicle area.

Auricular Area

A reduced major axis regression of auricular area on the geometric mean of the modal group is presented in Figure 3.19. The slope of the regression line (2.106) approximates the expected isometric slope of 2.0 for area (squared) on geomean (linear). The correlation is low (0.31). While seventy-five percent of the female dispersion falls above the regression line, male dispersion is broadly cast both above and below the line. Table 3.8 shows the geomean-adjusted values for the three morphotypes grouped by sex. Results of the significance test for sex differences are presented in Figure 3.20. For their size, modal females have a significantly larger auricular area than do modal males, $p < 0.0017$.

DISCUSSION

Results of this study demonstrate that the lumbopelvic complex of human males and females differs significantly in fundamental features related to upper body control and spinal loading. Most importantly, the sex-specific vertebral body wedging sequences and their resultant radii of curvature suggest that the crucial bipedal mechanism of lumbar lordosis is differentially constructed in males and females.

Table 3.9 summarizes the significant findings of the analysis for the modal human group and offers a regional perspective on the patterns of sex difference along the lumbar column. While all vertebral levels are sexually dimorphic, the least dimorphic is the last, lumbar level L5. This result is somewhat surprising given its proximity to the pelvis. The pelvis is arguably the most sexually dimorphic structure in the human skeleton. For instance, sexual dimorphism in the pelvic canal is well documented and its functional role in parturition incontrovertible (e.g., Berge et al., 1984; Tague and Lovejoy, 1986; Abitbol, 1987, 1996; Rosenberg, 1988, 1992; Hager, 1989, 1996; Ruff, 1995; Walrath and Glantz, 1996; Trevathan and Rosenberg, 2001). One might argue that the last lumbar vertebra in its articulation with the sacral platform would be expected to reflect some element of shape sexual dimorphism due to pelvic proximity. To the contrary, the near lack of shape sexual dimorphism in the last lumbar vertebra suggests that sex differences in the more cranial levels of the lumbar spine are less influenced by pelvic parturitional demands than postural and locomotor pressures.

The most prevalent expression of lumbar sexual dimorphism occurs in the mid lumbar region, levels L2 and L3. This area is the transitional zone of vertebral body wedging where kyphotic vertebral bodies reach their caudal limit. Lumbar level two is the neutral or transitional level in females while lumbar level three is the level of wedge transition in males. Wedging properties when viewed cranio-caudally in the lumbar region are either less kyphotic or more lordotic in females than in males. Female vertebral bodies therefore are less heavily loaded, proportionally, than those of males at any one level in the lumbar region. The relatively large centrum surface areas in males from L1 through L4 and S1 also indicate that males bear more of their axial load along the ventral pillar centra. The greater obliquity of the prezygapophyses in the female lumbar spine is functionally consistent with a more dorsally directed spinal loading pattern, as resistance to an increase in shear stress with dorsal wedging. While these results generally support the hypotheses that dorsal pillar loading is greater in females than in males, the nature of transverse process sexual dimorphism is unexpected. In fact, females were expected to present longer and more dorsally oriented transverse processes relative to body size than were males as effective leverage under conditions of obstetric inertia, but male processes were relatively longer.

Pedicles were found to be more robust relative to body size in males than in females. This result was also unexpected. While speculative, it is worth mentioning that a functional relationship between transverse process length and pedicle robusticity may be a component of ventral and dorsal pillar loading regimes. Why males have relatively longer transverse processes than females at the L2 and L3 lumbar levels is not immediately clear. Nonetheless, the presence of relatively long transverse processes would increase bending stress on the pedicles during unilateral flexion as well as during sagittal extension. Therefore, the mutual relationship in relative size of the transverse processes and pedicles is apparent. It is worth noting that while vertebral body shape is similar in males and females at the cranialmost and caudalmost reaches of the lumbar region (kyphotic at L1 and lordotic at both L4 and L5), vertebral shape differs by sex at lumbar levels L2 and L3. The male L2 vertebra is kyphotic while the female element is non-wedged, and the male L3 vertebra is non-wedged while the female vertebral body is lordotic. Spinal loading along the L2-L3 levels of the lumbar spine are likely to be different in males and females as this is the critical region of shape change in the vertebral bodies.

The smaller radius of curvature expressed in females produces a tighter curve relative to males. Although female lumbar lordosis is more acute than that of males, it is distributed across a greater number of vertebrae. By distributing the proportionally larger dorsal pillar load across a longer expanse of vertebrae, the female lumbar spine may confer additional structural safety to a column that must resist obstetric load.

While the degree of sexual dimorphism in both the L6 variant and L4 variant is less than that expressed in the modal group, some common features further clarify the nature of sex differences in the human lumbar column. In all three groups, males present relatively large centrum surface areas in the more cranial margin of the lumbar spine.

A greater number of similarities characterize the modal and L6 variant groups. The most important of which is the prezygapophyseal obliquity of the female lumbar spine. Female prezygapophyses are more oblique than males at every level of the lumbar spine. In the modal group, obliquity is correlated with vertebral body wedging. However, the pervasiveness of female obliquity in the L6 variant is not paralleled by the same pattern of female wedging characteristic of the modal group. While lumbar prezygapophyseal orientation is functionally relevant to shear resistance, and the greater obliquity of the female vertebrae confers increased resistance compared to that of males, orientation of the prezygapophyses is also a relevant factor in the range of motion permissible between lumbar vertebrae. Greater obliquity limits sagittal flexion and extension and allows greater axial rotation. However the potential relevance of these factors in the context of obstetric load is not readily apparent.

SUMMARY

In conclusion, the lumbar and sacral vertebrae of human females differ significantly from those of human males in aspects of their relative size and shape. Female vertebrae are dorsally wedged, contributing to the bony lordosis at lumbar levels L3, L4 and L5. At these lordotic levels, female vertebrae bear markedly oblique prezygapophyses. Conversely, lordotic wedging in human males is less extensive along the lumbar column, occurring at the lumbar levels L4 and L5. Human female vertebral morphology is consistent with the spinal loading patterns of the kinematic analyses (see Chapter 2), indicating that female vertebrae are adapted to resist structural risks of bipedal lordosis, which shift a larger proportion of compressive load from the vertebral bodies to the dorsally located zygapophyses.

Table 3.1. List of specimens included in the study, number of vertebrae in lumbar region, sex, and collection

Specimen	Lumbar Vertebrae	Sex	Collection
HTH1062	L5 Modal	Male	CMNH
HTH1080	L5 Modal	Male	CMNH
HTH1100	L5 Modal	Male	CMNH
HTH1139	L5 Modal	Male	CMNH
HTH1146	L5 Modal	Male	CMNH
HTH1201	L5 Modal	Male	CMNH
HTH1241	L5 Modal	Male	CMNH
HTH1261	L5 Modal	Male	CMNH
HTH1281	L5 Modal	Male	CMNH
HTH1327	L5 Modal	Male	CMNH
HTH1373	L5 Modal	Male	CMNH
HTH1393	L5 Modal	Male	CMNH
HTH1410	L5 Modal	Male	CMNH
HTH1474	L5 Modal	Male	CMNH
HTH2193	L5 Modal	Male	CMNH
HTH2401	L5 Modal	Male	CMNH
HTH2451	L5 Modal	Male	CMNH
HTH2474	L5 Modal	Male	CMNH
HTH2584	L5 Modal	Male	CMNH
HTH2602	L5 Modal	Male	CMNH
HTH2763	L5 Modal	Male	CMNH
HTH2831	L5 Modal	Male	CMNH
HTH2846	L5 Modal	Male	CMNH
HTH2852	L5 Modal	Male	CMNH
HTH2941	L5 Modal	Male	CMNH
HTH3052	L5 Modal	Male	CMNH
HTHHTH3077	L5 Modal	Male	CMNH
HTH3097	L5 Modal	Male	CMNH
HTH3265	L5 Modal	Male	CMNH
NMNH 1352	L5 Modal	Male	NMNH
NMNH 1388	L5 Modal	Male	NMNH
NMNH 1415R	L5 Modal	Male	NMNH
NMNH 1470	L5 Modal	Male	NMNH
NMNH 14R	L5 Modal	Male	NMNH
NMNH 1564	L5 Modal	Male	NMNH
NMNH 1569	L5 Modal	Male	NMNH
NMNH 1598	L5 Modal	Male	NMNH
NMNH 1607	L5 Modal	Male	NMNH
NMNH 187R	L5 Modal	Male	NMNH
NMNH 196	L5 Modal	Male	NMNH
NMNH 235	L5 Modal	Male	NMNH
NMNH 269	L5 Modal	Male	NMNH
NMNH 301R	L5 Modal	Male	NMNH
NMNH 302R	L5 Modal	Male	NMNH
NMNH 30R	L5 Modal	Male	NMNH
NMNH 331	L5 Modal	Male	NMNH
NMNH 424	L5 Modal	Male	NMNH
NMNH 465	L5 Modal	Male	NMNH
NMNH 477	L5 Modal	Male	NMNH
NMNH 509	L5 Modal	Male	NMNH
NMNH 594	L5 Modal	Male	NMNH
NMNH 595	L5 Modal	Male	NMNH
NMNH 606	L5 Modal	Male	NMNH
NMNH 62RR	L5 Modal	Male	NMNH
NMNH 675	L5 Modal	Male	NMNH
NMNH 719	L5 Modal	Male	NMNH
NMNH 755	L5 Modal	Male	NMNH
NMNH 802	L5 Modal	Male	NMNH
NMNH 876	L5 Modal	Male	NMNH
HTH1119	L5 Modal	Female	CMNH
HTH1157	L5 Modal	Female	CMNH
HTH1213	L5 Modal	Female	CMNH
HTH1214	L5 Modal	Female	CMNH
HTH1215	L5 Modal	Female	CMNH
HTH1277	L5 Modal	Female	CMNH
HTH1345	L5 Modal	Female	CMNH
HTH1350	L5 Modal	Female	CMNH
HTH1427	L5 Modal	Female	CMNH
HTH1489	L5 Modal	Female	CMNH
HTH1515	L5 Modal	Female	CMNH
HTH1539	L5 Modal	Female	CMNH
HTH1554	L5 Modal	Female	CMNH
HTH1558	L5 Modal	Female	CMNH
HTH1600	L5 Modal	Female	CMNH
HTH1747	L5 Modal	Female	CMNH
HTH1785	L5 Modal	Female	CMNH
HTH1900	L5 Modal	Female	CMNH
HTH1924	L5 Modal	Female	CMNH
HTH1973	L5 Modal	Female	CMNH
HTH1978	L5 Modal	Female	CMNH
HTH2041	L5 Modal	Female	CMNH
HTH2086	L5 Modal	Female	CMNH
HTH2116	L5 Modal	Female	CMNH
HTH2120	L5 Modal	Female	CMNH
HTH2125	L5 Modal	Female	CMNH
HTH2363	L5 Modal	Female	CMNH
HTH2848	L5 Modal	Female	CMNH
HTH2857	L5 Modal	Female	CMNH
HTH2923	L5 Modal	Female	CMNH
NMNH 1010	L5 Modal	Female	NMNH
NMNH 1287	L5 Modal	Female	NMNH
NMNH 1289R	L5 Modal	Female	NMNH
NMNH 12R	L5 Modal	Female	NMNH
NMNH 1311	L5 Modal	Female	NMNH
NMNH 1333	L5 Modal	Female	NMNH
NMNH 1354	L5 Modal	Female	NMNH
NMNH 135R	L5 Modal	Female	NMNH
NMNH 1396	L5 Modal	Female	NMNH
NMNH 1402	L5 Modal	Female	NMNH
NMNH 1417R	L5 Modal	Female	NMNH
NMNH 146R	L5 Modal	Female	NMNH
NMNH 1482R	L5 Modal	Female	NMNH
NMNH 1563	L5 Modal	Female	NMNH
NMNH 1599	L5 Modal	Female	NMNH
NMNH 1617	L5 Modal	Female	NMNH
NMNH 162R	L5 Modal	Female	NMNH
NMNH 330	L5 Modal	Female	NMNH
NMNH 41R	L5 Modal	Female	NMNH
NMNH 568	L5 Modal	Female	NMNH
NMNH 627R	L5 Modal	Female	NMNH
NMNH 657R	L5 Modal	Female	NMNH
NMNH 729R	L5 Modal	Female	NMNH
NMNH 847	L5 Modal	Female	NMNH

Table 3.1 continued . List of specimens in the study, number of vertebrae in lumbar region, sex, and collection

Specimen	Lumbar Vertebrae	Sex	Collection
HTH 0445	L6 Variant	Male	CMNH
HTH 1075	L6 Variant	Male	CMNH
HTH 1389	L6 Variant	Male	CMNH
HTH 1392	L6 Variant	Male	CMNH
HTH 1501	L6 Variant	Male	CMNH
HTH 2192	L6 Variant	Male	CMNH
HTH 2409	L6 Variant	Male	CMNH
HTH 2863	L6 Variant	Male	CMNH
HTH 3230	L6 Variant	Male	CMNH
NMNH591	L6 Variant	Male	NMNH
NMNH608	L6 Variant	Male	NMNH
NMNH619	L6 Variant	Male	NMNH
NMNH645	L6 Variant	Male	NMNH
NMNH654	L6 Variant	Male	NMNH
NMNH707	L6 Variant	Male	NMNH
NMNH971	L6 Variant	Male	NMNH
NMNH999	L6 Variant	Male	NMNH
NMNH1131	L6 Variant	Male	NMNH
NMNH111R	L6 Variant	Male	NMNH
NMNH311R	L6 Variant	Male	NMNH
HTH 1622	L6 Variant	Female	CMNH
NMNH455	L6 Variant	Female	NMNH
NMNH610	L6 Variant	Female	NMNH
NMNH880	L6 Variant	Female	NMNH
NMNH921	L6 Variant	Female	NMNH
NMNH970	L6 Variant	Female	NMNH
NMNH1119	L6 Variant	Female	NMNH
NMNH1120	L6 Variant	Female	NMNH
NMNH1222	L6 Variant	Female	NMNH
NMNH1523	L6 Variant	Female	NMNH
NMNH1594	L6 Variant	Female	NMNH
NMNH405R	L6 Variant	Female	NMNH
HTH 562	L4 Variant	Male	CMNH
HTH 65	L4 Variant	Male	CMNH
HTH 799	L4 Variant	Male	CMNH
NMNH551	L4 Variant	Male	NMNH
NMNH555	L4 Variant	Male	NMNH
NMNH1529	L4 Variant	Male	NMNH
HTH 1117	L4 Variant	Male	CMNH
HTH 2298	L4 Variant	Female	CMNH
HTH 886	L4 Variant	Female	CMNH
NMNH996	L4 Variant	Female	NMNH
NMNH1122	L4 Variant	Female	NMNH
NMNH1413	L4 Variant	Female	NMNH
NMNH1553	L4 Variant	Female	NMNH
NMNH151R	L4 Variant	Female	NMNH
NMNH554R	L4 Variant	Female	NMNH

Table 3.2. Lumbar vertebral levels used in the Q-Mode Principal Component Analysis

Comparative	Anatomical Level		
Level	Modal	L4 Variant	L6 Variant
L1	L1	L1	L1
L2	L2	L2	L2
Penultimate	L4	L3	L5
Last	L5	L4	L6

Table 3.3. Sexual dimorphism in Human Modal type lumbopelvic variables: magnitude and results of Wilcoxon Rank Sums test [1]

		Magnitude of sexual dimorphism (probability)					
	(n)	Lumbar Level					Sacrum
Variable	(M,F)	1	2	3	4	5	
Centrum wedging	(59,54)	**- 5.245********	**- 4.521********	**- 2.664******	**- 3.498*******	1.753 (ns)	
Centrum surface area	(59,53)	**- 4.953********	**- 4.272********	**- 3.392*******	**- 2.279*****	- 0.962 (ns)	**- 2.823******
Centrum medio-lateral breadth	(59,51)	**- 5.044********	**- 4.506********	**- 4.105********	**- 3.484*******	- 1.788 (ns)	**- 3.165******
Transverse process angle[2]	(55,45)	- 0.383 (ns)	- 0.489 (ns)	- 1.004 (ns)	0.093 (ns)	0.882 (ns)	
Transverse process length	(55,45)	- 1.219 (ns)	**- 3.303******	**- 2.800******	- 0.795 (ns)	1.219 (ns)	
Pedicle cross-sectional area	(59,50)	**- 3.773*******	**- 3.773*******	**- 2.386******	- 1.379 (ns)	0.318 (ns)	
Prezygapophyseal surface area	(59,53)	1.415 (ns)	1.673 (ns)	1.451 (ns)	0.670 (ns)	0.927 (ns)	- 0.599 (ns)
Prezygapophyseal angle [2]	(59,52)	**2.080*****	**2.779******	**4.088********	**2.134*****	**2.121*****	**2.053*****
Interfacet breadth	(59,51)	1.858 (ns)	1.253 (ns)	1.636 (ns)	0.384 (ns)	0.132 (ns)	-
Sacral body breadth	(59,51)	-	-	-	-	-	**4.771********

1 Two-tailed test of significance used. M, male; F, female; ns, P > 0.05. Some of these data were presented in Whitcome (1999).

[2] Raw variate

Positive scores indicate that female mean exceeds male mean

Negative scores indicate that male mean exceeds female mean

* $P = 0.05$.

** $P = 0.01$.

*** $P = 0.001$.

**** $P = 0.0001$.

Table 3.4. Sexual dimorphism in Human L6 Variant type lumbopelvic variables: magnitude and results of Wilcoxon Rank Sums test[1]

		Magnitude of sexual dimorphism (probability)						
	(n)	Lumbar Level						Sacrum
Variable	(M,F)	1	2	3	4	5	6	
Centrum wedging	(20,12)	**- 2.083***	**- 2.044***	- 1.440 (ns)	- 1.460 (ns)	- 0.214 (ns)	- 0.078 (ns)	
Centrum surface area	(20,12)	**- 2.199***	- 1.888 (ns)	- 1.538 (ns)	- 1.285 (ns)	- 0.623 (ns)	- 0.136 (ns)	0.227 (ns)
Centrum medio-lateral breadth	(20,12)	**- 5.044*******	**- 4.506*******	**- 4.105*******	**- 3.484******	**- 1.788***	**- 1.788***	0.640 (ns)
Transverse process angle[2]	(20,12)		- 0.331 (ns)	0.249 (ns)	0.090 (ns)	0.641 (ns)	0.766 (ns)	
Transverse process length	(20,12)		**- 2.261***	- 1.926 (ns)	- 0.472(ns)	0.391 (ns)	- 0.237 (ns)	
Pedicle cross-sectional area	(20,12)	0.156 (ns)	**- 2.396*****	**- 2.496*****	**- 2.415*****	- 1.156 (ns)	**- 2.126***	
Prezygapophyseal surface area	(20,12)	- 0.876 (ns)	0.487 (ns)	1.109 (ns)	0.642 (ns)	- 0.176 (ns)	- 0.176 (ns)	**3.056*****
Prezygapophyseal angle[2]	(20,12)	**2.080***	**2.779*****	**4.088*******	**2.134***	**2.121***	**2.121***	
Interfacet breadth	(20,12)	**2.086***	0.434 (ns)	0.000 (ns)	-1.343 (ns)	-1.384 (ns)	-0.950 (ns)	
Sacral body breadth	(20,12)	-	-	-	-	-	-	**3.311******

1 Two-tailed test of significance used. M, male; F, female; ns, P > 0.05. Some of these data were presented in Whitcome (1999).
Positive scores indicate that female mean exceeds male mean
Negative scores indicate that male mean exceeds female mean
* P = 0.05.
** P = 0.01.
*** P = 0.001.
**** P = 0.0001.

Table 3.5. Sexual dimorphism in Human L4 Variant type lumbopelvic variables: magnitude and results of Wilcoxon Rank Sums test [1]

		Magnitude of sexual dimorphism (probability)				
	(n)	Lumbar Level				Sacrum
Variable	(M,F)	1	2	3	4	
Centrum wedging	(7,8)	__- 2.488**__	- 1.794 (ns)	- 0.984 (ns)	- 1.678 (ns)	
Centrum surface area	(7,8)	__- 2.604**__	__- 2.141*__	- 1.562 (ns)	- 0.637 (ns)	__2.269*__
Centrum medio-lateral breadth	(7,8)	__- 2.951**__	__- 2.488**__	__- 2.141*__	- 1.215 (ns)	- 1.976 (ns)
Transverse process angle[2]	(7,8)	0.943 (ns)	0.641 (ns)	0.517 (ns)	0.575 (ns)	
Transverse process length	(7,8)					
Pedicle cross-sectional area	(7,8)	- 1.794 (ns)	__- 2.257*__	- 1.794 (ns)	- 0.405 (ns)	
Prezygapophyseal surface area	(7,8)	- 0.794 (ns)	0.405 (ns)	0.752 (ns)	- 1.794 (ns)	1.872 (ns)
Prezygapophyseal angle [2]	(7,8)	- 0.523 (ns)	- 0.870 (ns)	- 0.195 (ns)	0.649 (ns)	- 0.000 (ns)
Interfacet breadth	(7,8)	0.868 (ns)	- 0.174 (ns)	- 0.058 (ns)	- 0.058 (ns)	
Sacral body breadth	(7,8)	-	-	-	-	- 1.537 (ns)

1 Two-tailed test of significance used. M, male; F, female; ns, P > 0.05.
Positive scores indicate that female mean exceeds male mean
Negative scores indicate that male mean exceeds female mean
* *P* = 0.05.
** *P* = 0.01.
*** *P* = 0.001.
**** *P* = 0.0001.

Table 3.6. Lumbar vertebral wedging angle in degrees for human Modal, L4 variant and L6 variant by sex, means reported with (standard deviation).

	Female			Male		
Vertebral Level[1]	L6 Variant *n = 12*	Modal *n = 59*	L4 Variant *n = 8*	L6 Variant *n = 20*	Modal *n = 59*	L4 Variant *n = 7*
a	**3.55 *** **(2.07)**			**5.57** **(2.73)**		
b	**1.89 *** **(2.62)**	**2.21 ***** **(1.83)**		**3.54** **(1.66)**	**4.26** **(1.86)**	
c	-0.33 (2.18)	**0.09 ***** **(2.46)**	**1.2 *** **(1.54)**	1.1 (2.90)	**2.42** **(2.30)**	**3.32** **(1.50)**
d	-2.25 (2.81)	**-1.17 *** **(2.46)**	-0.77 (2.22)	-0.46 (2.48)	**0.15** **(2.47)**	1.87 (2.48)
e	-2.81 (2.48)	**-3.17 **** **(2.19)**	-2.5 (2.21)	-2.56 (2.04)	**-1.60** **(2.42)**	-1.25 (2.78)
f	-7.56 (2.75)	-5.54 (2.96)	-7.15 (1.24)	-7.39 (2.35)	-6.65 (2.88)	-3.41 (1.32)

Vertebral Level[1]: levels are listed in order from cranialmost to caudalmost position.

Boldface indicates significant result. Wilcoxon Rank Sums Test, Bonferroni adjusted.

* indicates $P < 0.01$, ** indicates $P < 0.001$, *** indicates $P < 0.0001$.

Positive angles are kyphotic. Negative angles are lordotic. Vertebrae are transitional, neither kyphotic not lordotic, when -0.5° > angle < 0.5°.

Lordotic vetebral series enclosed by boxes.

Table 3.7a. Spearman's correlation coefficients (r_s) between lumbar centrum articular area and pedicle cross-sectional area [1] in human modal, reported by sex

Vertebral Level	Male	Female
	r_s (probability)	r_s (probability)
L1	0.1652 (*P* = 0.2111)	**0.3112 (*P* = 0.0278)**
L2	**0.3033 (*P* = 0.0195)**	**0.3145 (*P* = 0.0261)**
L3	**0.3411 (*P* = 0.0076)**	**0.4974 (*P* = 0.0002)**
L4	**0.3489 (*P* = 0.0068)**	**0.3019 (*P* = 0.0313)**
L5	**0.2413 (*P* = 0.0656)**	**0.3512 (*P* = 0.0115)**

[1] Two-tailed test of significance used, pairwise correlation

Table 3.7b. Spearman's correlation coefficients (r_s) between lumbar vertebral wedging and centrum surface area [1] in human modal, reported by sex

Vertebral Level	Male	Female
	r_s (probability)	r_s (probability)
L1	0.0859 (*P* = 0.5179)	0.2299 (*P* = 0.0977)
L2	-0.0686 (*P* = 0.6056)	0.0969 (*P* = 0.4899)
L3	0.1863 (*P* = 0.1578)	0.1505 (*P* = 0.2822)
L4	0.0936 (*P* = 0.4809)	0.0094 (*P* = 0.9470)
L5	-0.1463 (*P* = 0.2687)	0.0638 (*P* = 0.6500)

[1] Two-tailed test of significance used, pairwise correlation

Table 3.7c. Spearman's correlation coefficients (r_s) between lumbar vertebral weding and pedicle cross-sectional area [1] in human modal, reported by sex

Vertebral Level	Male	Female
	r_s (probability)	r_s (probability)
L1	0.0171 (*P* = 0.5894)	**0.3578 (*P* = 0.0107)**
L2	-0.0940 (*P* = 0.4878)	0.1398 (*P* = 0.3330)
L3	0.1214 (*P* = 0.3597)	0.1897 (*P* = 0.2044)
L4	- 0.0807 (*P* = 0.5437)	0.1547 (*P* = 0.2785)
L5	0.0433(*P* = 0.7390)	0.1874 (*P* = 0.1878)

[1] Two-tailed test of significance used, pairwise correlation

Table 3.7d. Spearman's correlation coefficients (r_s) between lumbar vertebral wedging and prezygapophyseal area [1] in human modal, reported by sex

Vertebral Level	Male	Female
	r_s (probability)	r_s (probability)
L1	0.1234 (*P* = 0.3518)	**0.3301 (*P* = 0.0169)**
L2	0.1560 (*P* = 0.2382)	-0.1600 (*P* = 0.2479)
L3	0.0273 (*P* = 0.8372)	-0.0608 (*P* = 0.6653)
L4	0.0183 (*P* = 0.8907)	0.1545 (*P* = 0.2647)
L5	-0.0726 (*P* = 0.5845)	-0.0244 (*P* = 0.8611)

[1] Two-tailed test of significance used, pairwise correlation

Table 3.8. Sacral auricular area, mean and (standard deviation) by sex, raw area and size-adjusted geomean area [1] in the three human lumbar vertebral number morphotypes

		Modal		L6 Variant		L4 Variant	
Auricular variable		mean area	(std dev)	mean area	(std dev)	mean area	(std dev)
Raw area [2]	male	1282.53	(222.2)	1269.90	(134.9)	1269.53	(264.4)
	female	1256.58	(196.7)	1201.87	(197.2)	1194.75	(258.0)
Size-adjusted area [3]	male	**1.872**	**(0.162)**	1.680	(0.141)	1.830	(0.299)
	female	**1.999**	**(0.182)**	1.741	(0.109)	1.882	(0.208)
	p value	**< 0.0017**		= 0.2005		= 0.5309	

[1] Two-tailed test of significance used, pairwise correlation

[2] Raw area reported in mm^2

[3] Size-adjusted area unitless, $\boxed{\sqrt[2]{aurarea}}$/geomean

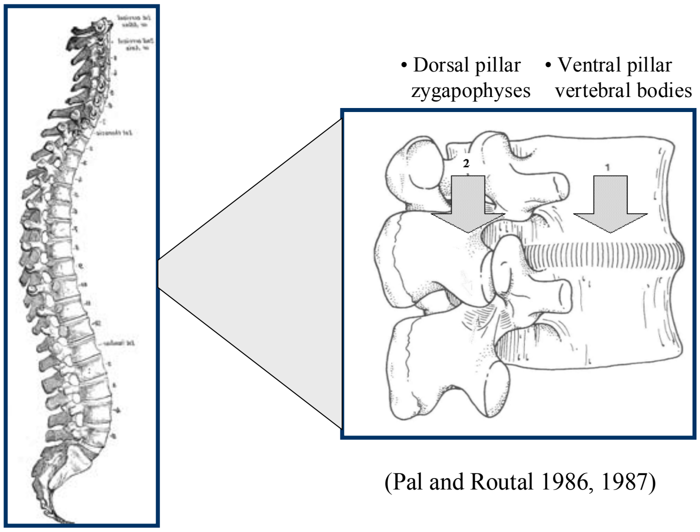
Modal n: male = 53, female = 49. L6 variant n: male = 20, female = 12. L4 variant n: male = 5, female = 5

Table 3.9. Significant variables by their respective vertebral levels and relevant sex in the modal sample [1]

Female					Male		
Sacrum Aricular Area	**Sacrum Breadth**	**Prezygapophyseal Obliquity**	**Vertebral Wedging**	**Vertebral level**	**Centrum Surface Area**	**Pedicle Cross-Sectional Area**	**Transverse Process Length**
		↕	↕	**L1**	↕	↕	
		↕	↕	**L2**	↕	↕	↕
		↕	↕	**L3**	↕	↕	↕
		↕	↕	**L4**	↕		
		↕		**L5**			
↕	↕			**Sacrum**	↕		

[1] Arrows indicate significant results and denote which sex presents the larger value. Arrow span includes vertebral levels for which significant results were obtained.

Two-Pillar Spine Model



(Pal and Routal 1986, 1987)

Figure 3.1. Pair of adjacent lumbar vertebrae, dorsolateral view from right, in anatomical position. Arrows indicate directionality of the two biomechanical pillars. Arrow 1: ventral pillar comprised of vertebral bodies. Arrow 2: dorsal pillar comprised of laminar structures and zygapophyses.

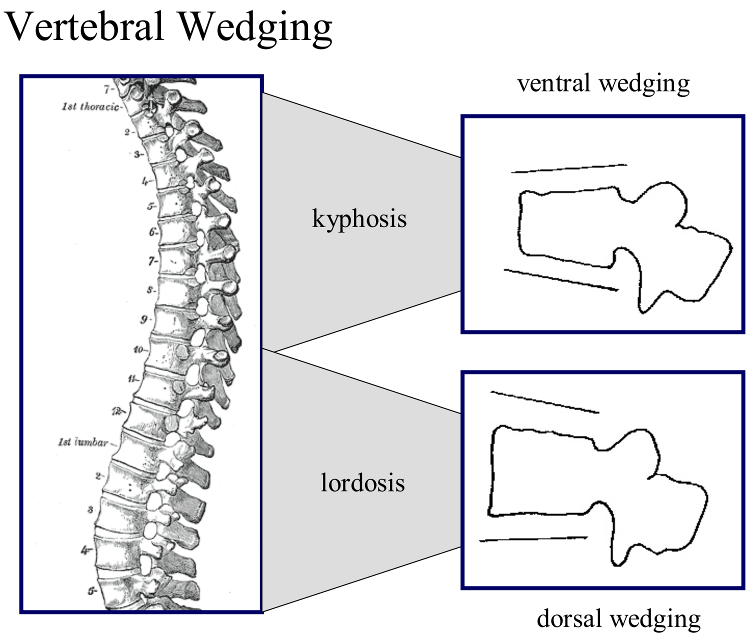


Figure 3.2. Vertebral body wedging results from differing heights of the ventral and dorsal margins of the centrum. Ventral wedging results from reduced ventral length relative to dorsal length and characterizes the thoracic spinal region, generating kyphosis. Dorsal wedging results from increased ventral length relative to dorsal length and characterizes the lordotic region of the spine, generating lumbar lordosis. Proportional loading shifts between the two pillars as a result of both bony morphology and movements initiated along the vertebral column.

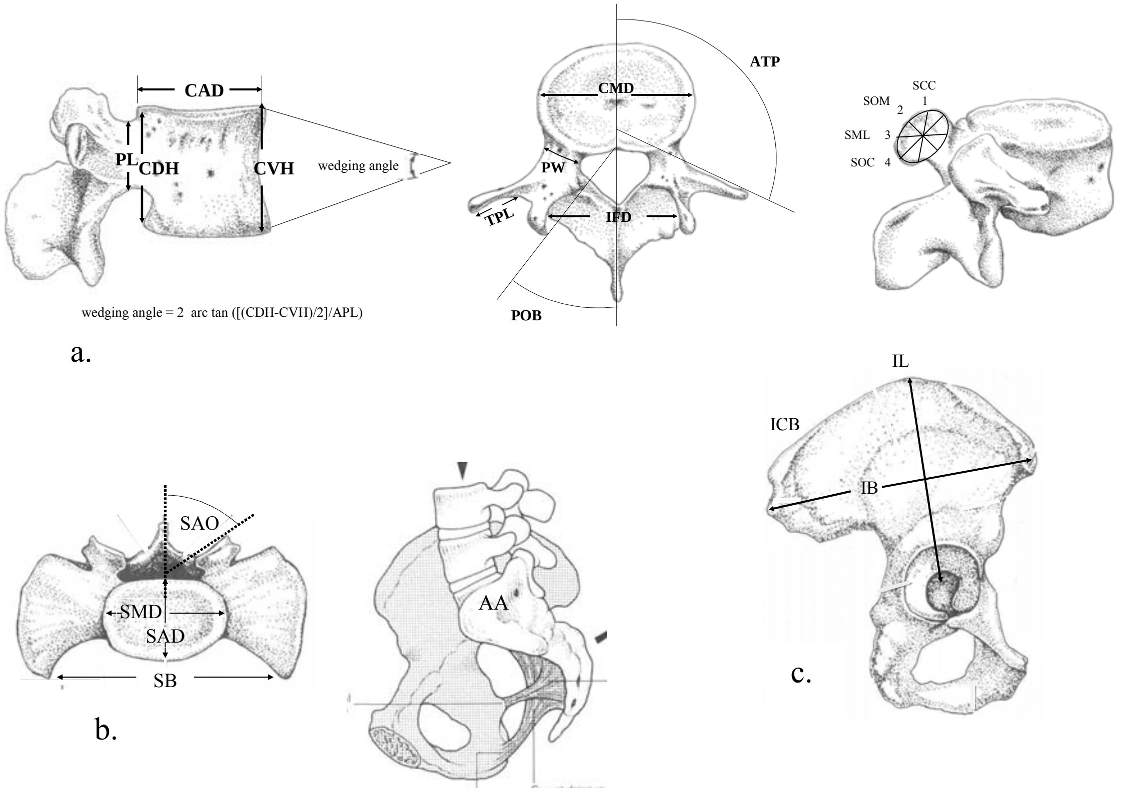


Figure 3.3. Morphometric measurements. a.) Lumbar vertebra. Vertebral body: CAD - Anteroposterior length of centrum cranial surface at midline; CMD - Maximum mediolateral width of centrum cranial surface; CVH - Craniocaudal height of centrum at ventral midline; CDH - Craniocaudal height of centrum at dorsal midline. Pedicle: PL - Minimum craniocaudal length of pedicle; PW - Minimum mediolateral length of pedicle. Transverse process: TPL - Dorsal distance from base of transverse process to process tip; ATP - Angle of transverse process taken from centrum midline to process tip. Zygapophyses: IFD - Linear distance between the most lateral reach of paired prezygapophyses; POB - Angle of prezygapophysis from centrum midline to lateral reach of facet; SCC - Craniocaudal diameter of prezygapophyseal facet; SML - Mediolateral diameter of prezygapophyseal facet; SOC - Oblique craniocaudal diameter of prezygapophyseal facet; SOM - Oblique mediolateral diameter of prezygapophyseal facet. b.) Sacrum: SAD - Anteroposterior length of centrum cranial surface at midline; SMD - Maximum mediolateral width of centrum cranial surface; SB - Maximum mediolateral width on ventral surface; SAO - Angle of sacral prezygapophysis from centrum midline to lateral reach of facet; AA - Area of the auricular surface computed digitally. c.) Innominate: IL –Maximum craniocaudal length of the ilium; IB - Maximum mediolateral breadth of the ilium; ICB - Maximum curvilinear length of the mediolateral margin of the iliac crest.

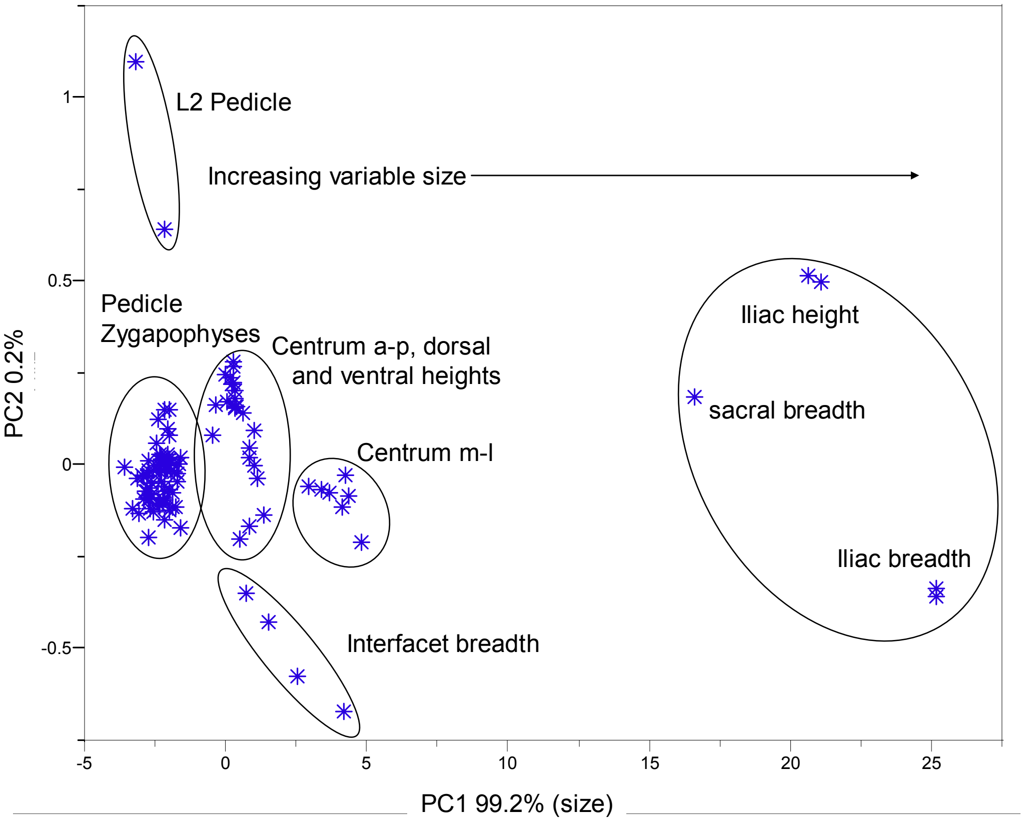


Figure 3.4. Plot of first two principal components from the Q-Mode Principal Component Analysis of the variables.

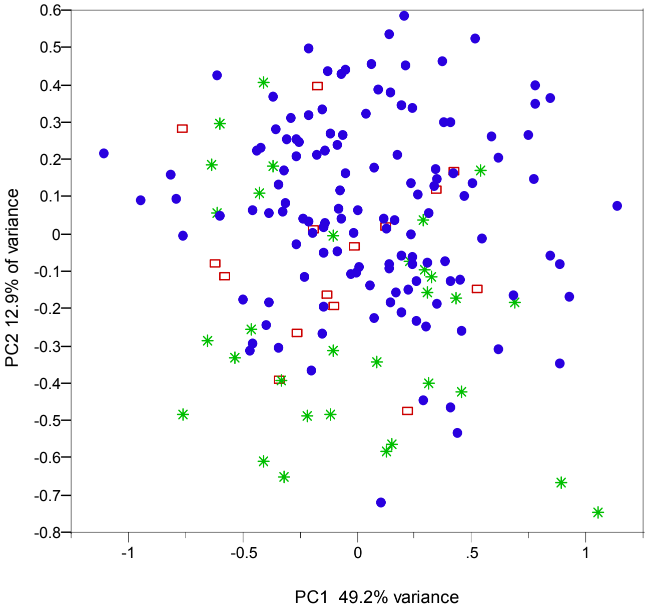


Figure 3.5. Plot of PC1 and PC2 of R-mode principal component analysis of three human groups: modal, L4 variant and L6 variant. ∗ L6 variant, □ L4 variant, ● modal.

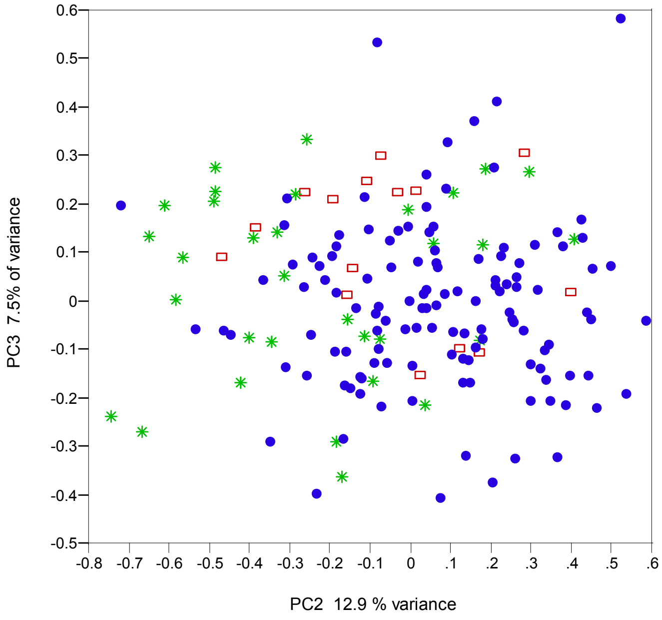


Figure 3.6. Plot of PC2 and PC3 of R-mode principal component analysis of three human groups: modal. L4 variant and L6 variant. ∗ L6 variant, □ L4 variant, ● modal.

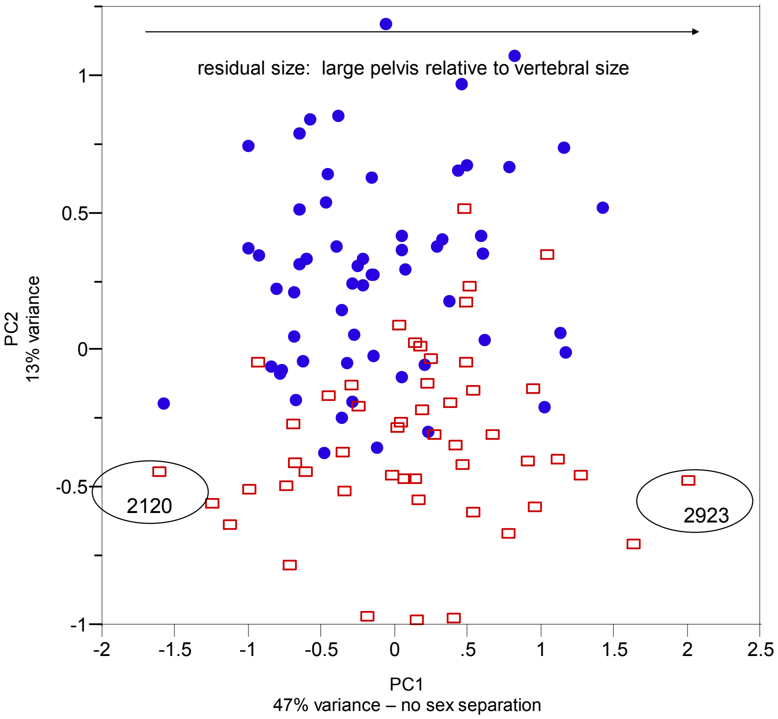


Figure 3.7. Plot of PC1 and PC2 for human modal group. □ female, ● male.

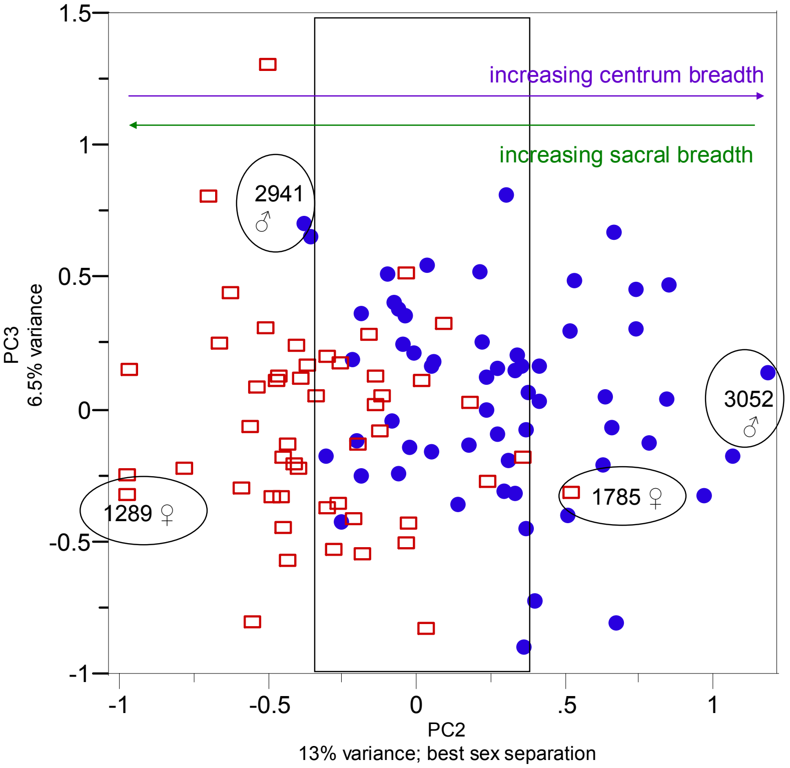


Figure 3.8. Plot of PC 2 and PC3 human modal group. □ female, ● male.

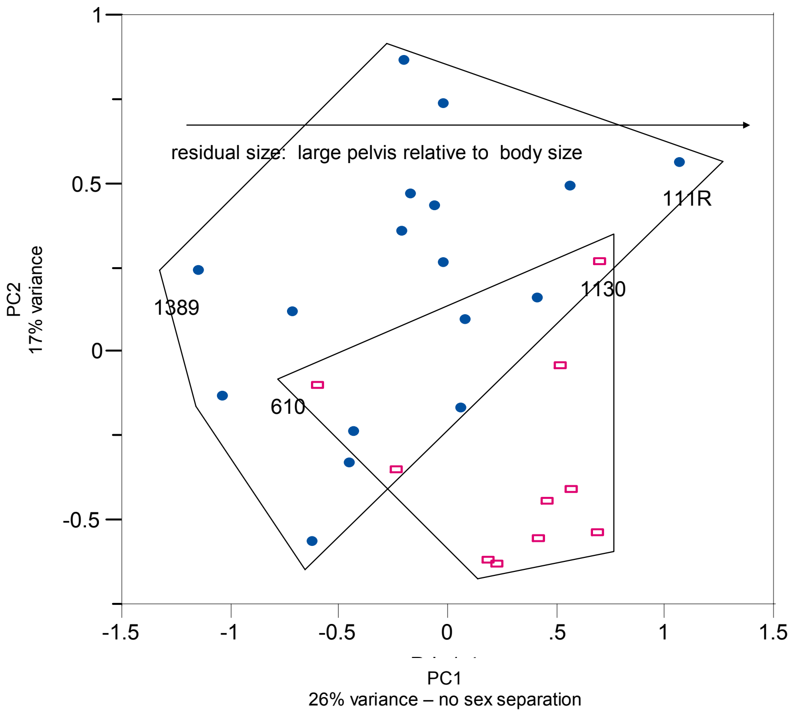


Figure 3.9. PC1 and PC2 human L6 variant group. □ female, ● male.

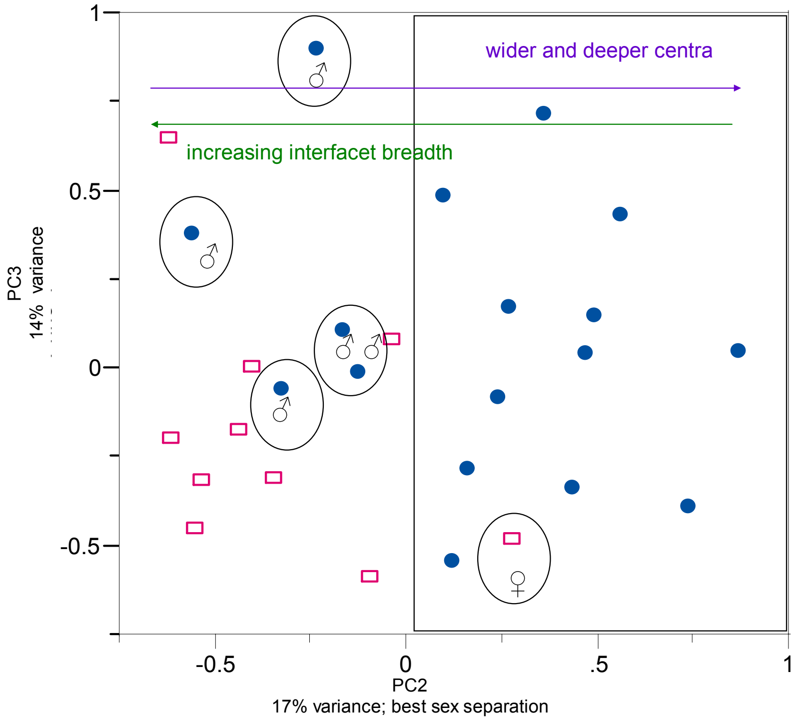


Figure 3.10. PC 2 and PC3 human L6 variant group. □ female, ● male.

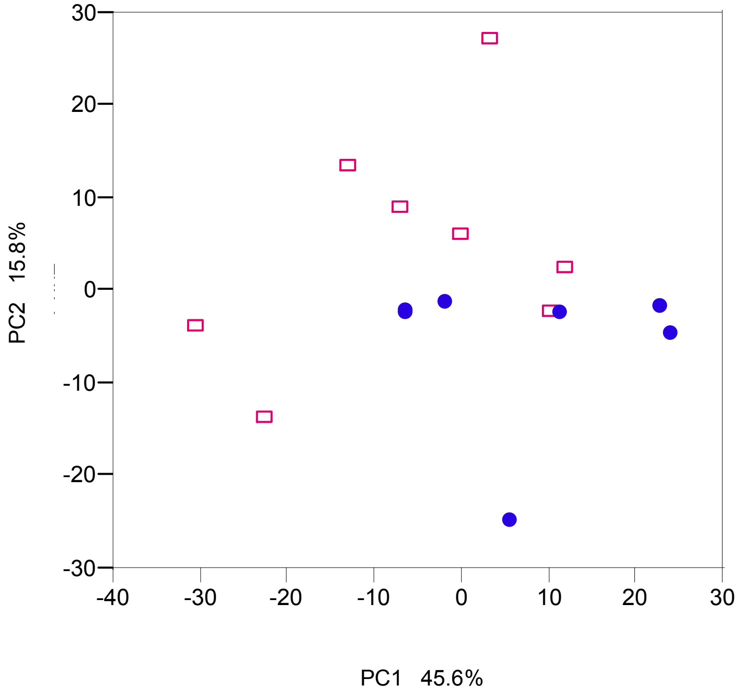


Figure 3.11. PC 1 and PC2 human L4 variant group. □ female, ● male.

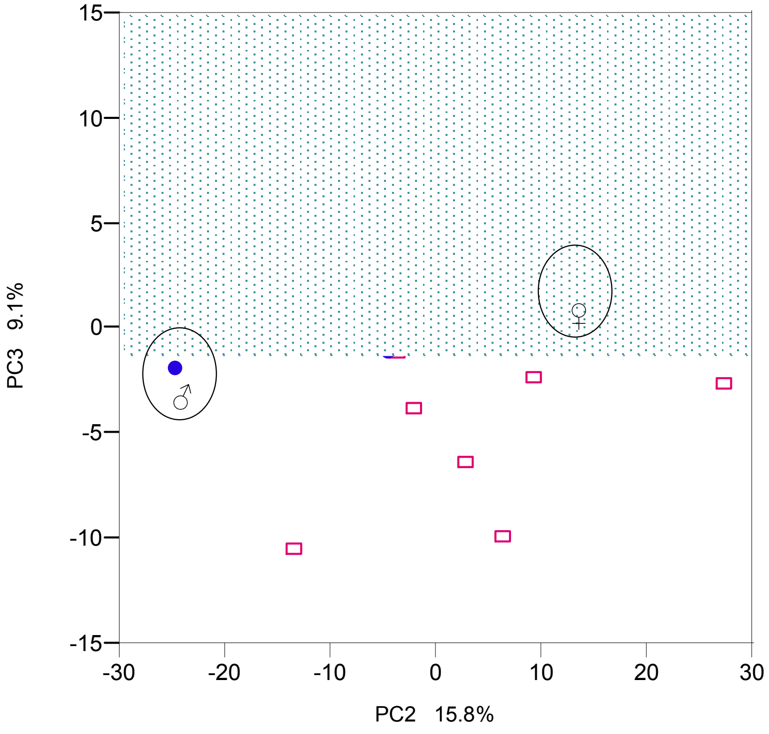


Figure 3.12. PC2 and PC3 human L4 variant group. □ female, ● male.

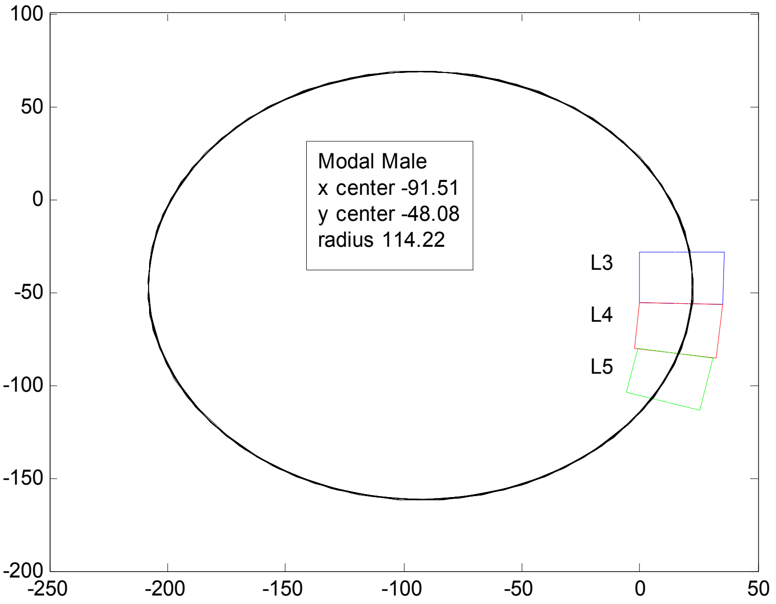


Figure 3.13. Radius of lumbar curvature in human modal males (n = 59), derived from mean values of vertebral dorsal height, ventral height and antero-posterior diameter.

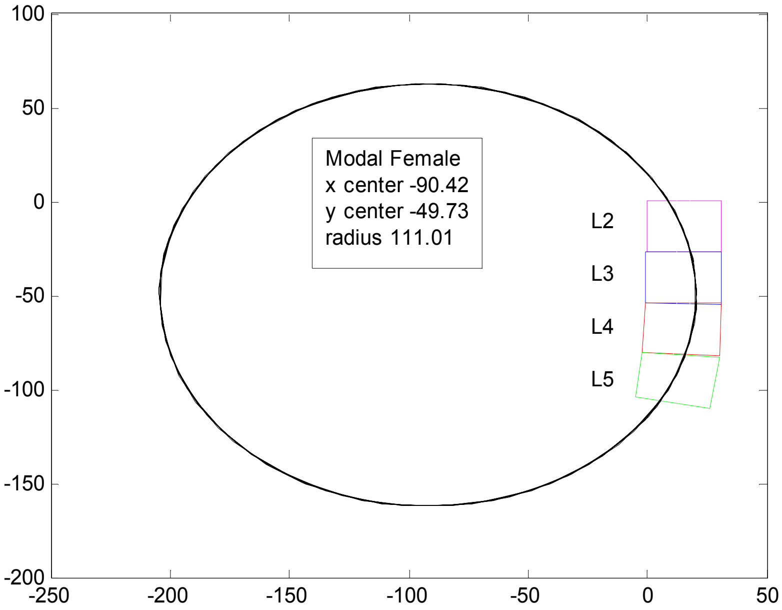


Figure 3.14. Radius of lumbar curvature in human modal females (n = 59), derived from mean values of vertebral dorsal height, ventral height and antero-posterior diameter.

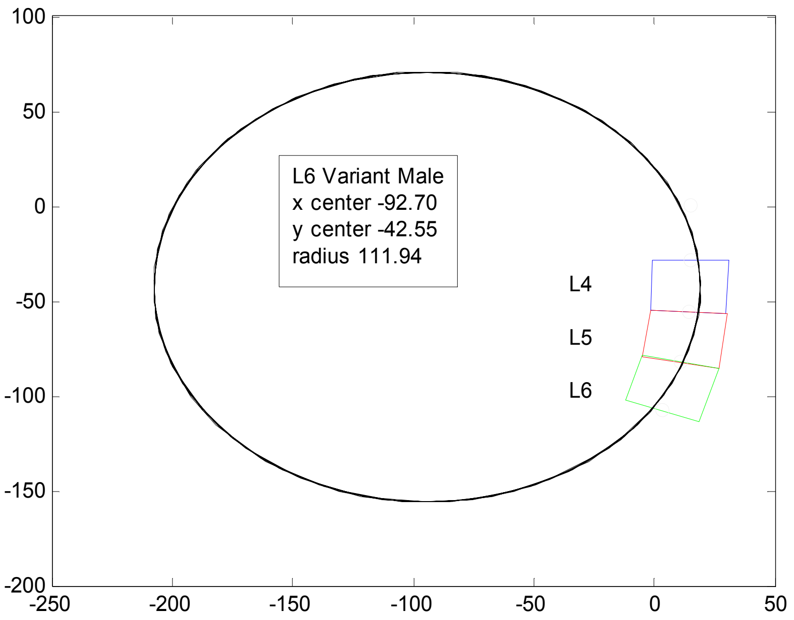


Figure 3.15. Radius of lumbar curvature in L6 variant males (n = 20), derived from mean values of vertebral dorsal height, ventral height and antero-posterior diameter.

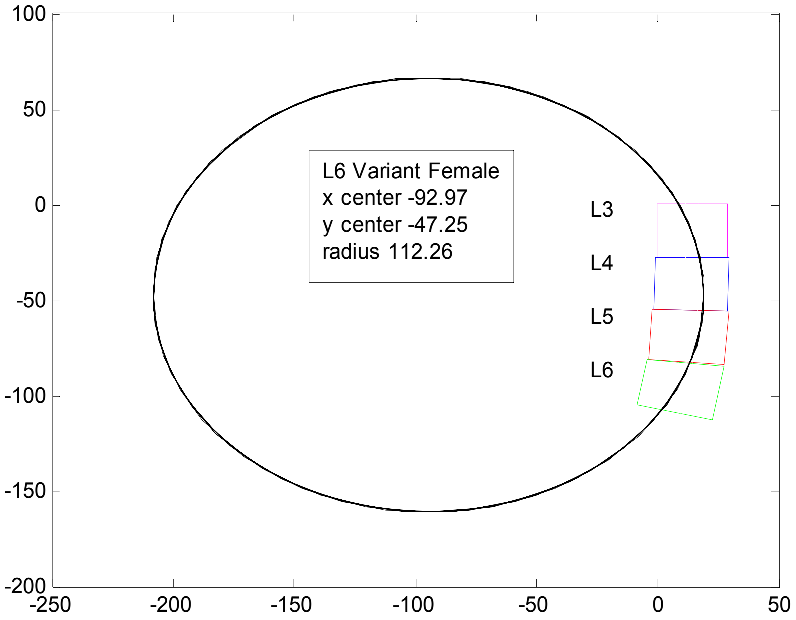


Figure 3.16. Radius of lumbar curvature in L6 variant females (n = 12), derived from mean values of vertebral dorsal height, ventral height and antero-posterior diameter.

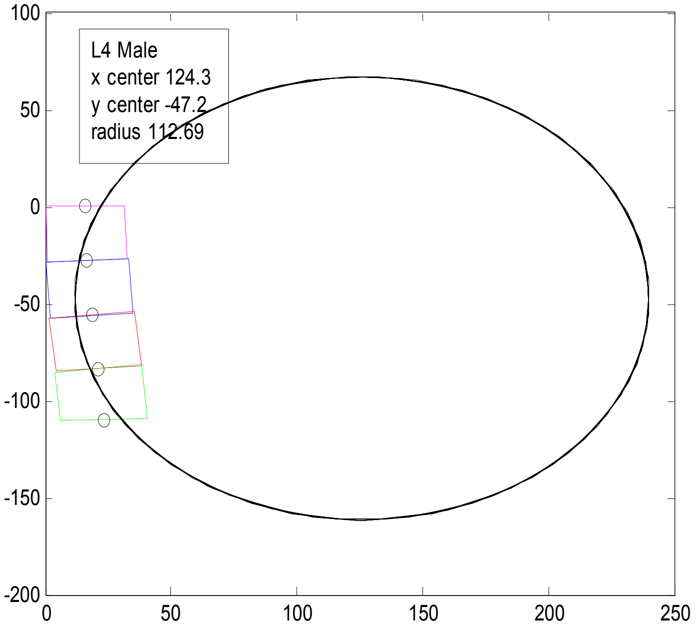


Figure 3.17. Radius of lumbar curvature in L4 variant males (n = 7), derived from mean values of vertebral dorsal height, ventral height and antero-posterior diameter.

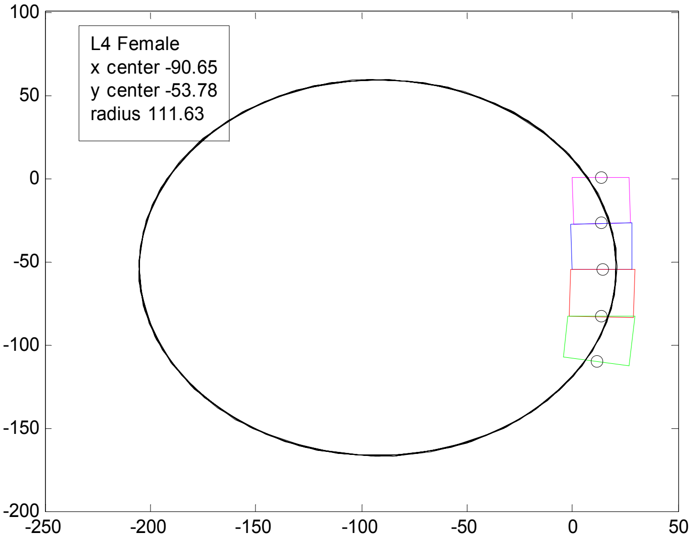


Figure 3.18. Radius of lumbar curvature in L4 variant females (n = 8), derived from mean values of vertebral dorsal height, ventral height and antero-posterior diameter.

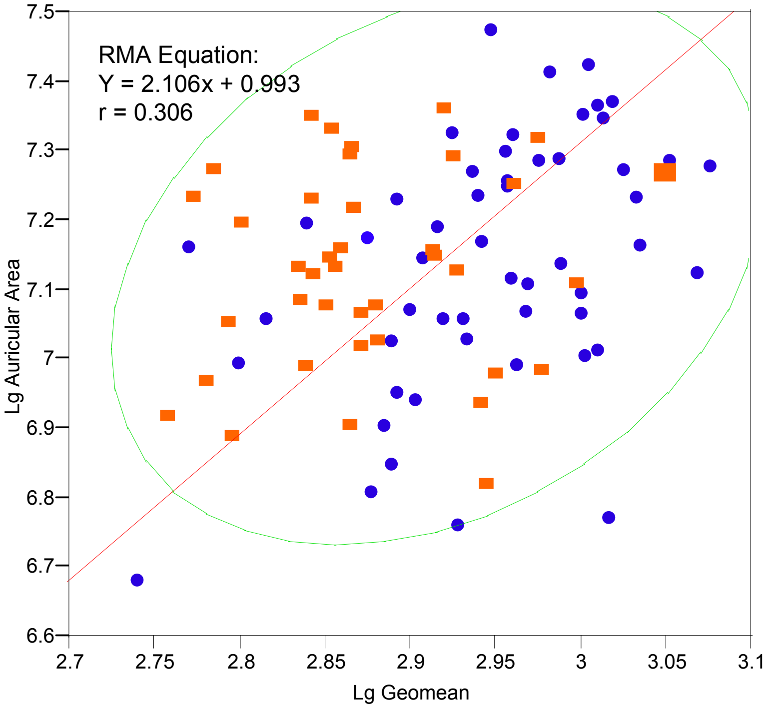


Figure 3.19. Reduced major axis regression of modal human auricular area on geomean with 95% confidence ellipse. Slope of isometry is 2.0. Slope of the regression line is 2.106, approximating isometry. The confidence intervals for the slope do include true isometry. ■ female, ● male.

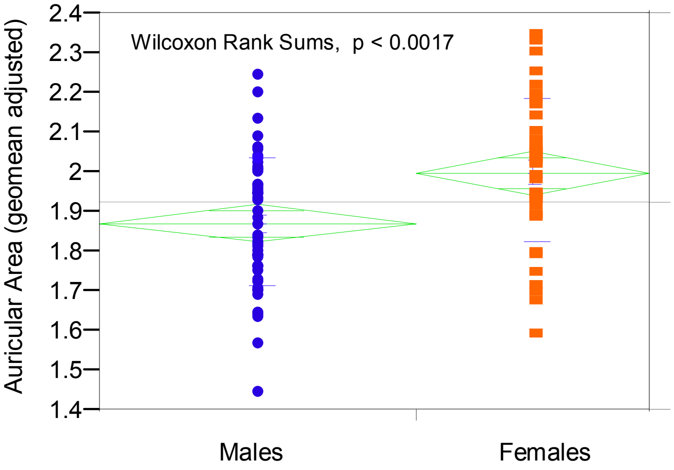


Figure 3.20. Distribution and mean comparisons of modal human auricular area, geomean adjusted for overall body size difference between males and females. Diamonds represent mean (center line) and 95% confidence intervals (apices). Box midline is total response sample mean. Short lines in data point columns represent one standard deviation.

REFERENCES

Abitbol M. 1987. Obstetrics and posture in pelvic anatomy. J Hum Evol 16:243-256.

Adams MA, Hutton WC. 1980. The effect of posture on the role of the apophyseal joints in resisting intervertebral compressive forces. J Bone Joint Sur 62B:358-360.

Adams MA, Hutton WC. 1983. The mechanical function of lumbar apophyseal joints. Spine 8:327-330.

Berge C. 1984. Multivariate analysis of the pelvis for hominids and other extant primates: Implications for the locomotion and systematics of the different species of australopithecines. J Hum Evol 13:555-562.

Berge C. 1990. Size and locomotion-related aspects of hominid and anthropoid pelves: an osteometrical multivariate analysis. In: FK Jouffroy, MH Stack, C Niemitz, editors. Gravity, Posture and Locomotion in Primates. Firenze: Il Sedicesimo. p 97-108.

Berge C, Orban-Segebarth R, Schmid P. 1984. Obstetric interpretation of the australopithecine pelvic cavity. J Hum Evol 13:573-587.

Blacke SP, Connors AM. 2004. Sacral insufficiency fracture. Brit J Radiol 77:891-896.

Blackith R, Reyment RA. 1971. Multivariate morphometrics. Academic Press, New York.

Bogduk N, Twomey LT. 1997. Clinical anatomy of the lumbar spine and sacrum. Churchill Livingston: New York.

Bornstein P, Peterson R. 1966. Numerical variation of the presacral vertebral column in three population groups in North America. Am J Phys Anthropol 25:139-146.

Corruccini RS. 1987. Shape in morphometrics: comparative analyses. Am J Phys Anthropol 73: 289-303.

Cunningham D. 1886. The lumbar curve of man and apes, with an account of the topographical anatomy of the chimpanzee, orangutan, and gibbon. Cunningham Memorial, Royal Irish Academy, No. 2.

Darroch J, Mosimman J. 1985. Canonical and principal components of shape. Biometrika 72:241-252.

Davis PR. 1961. Human lower lumbar vertebrae: some mechanical and osteological considerations. J Anat 95:337-344.

Day MH, Wickens EH. 1980. Laetoli Pleiocene hominid footprints and bipedalism. Nature 286:385-387.

DeBeer Kaufmann P. 1974. Variation in the number of presacral vertebrae in Bantu-speaking South African Negroes. Am J Phys Anthropol 40:369-374.

Digiovanni B, Scoles P, Latimer B. 1989. Anterior extension of the thoracic vertebral bodies in Scheuermann's kyphosis: an anatomic study. Spine 14(7): 712-716.

Elftman HO. 1932. The evolution of the pelvic floor of primates. Am J Anat 51*:*307-346.

Fajardo RJ, Müller R. 2001. Three-dimensional analysis of nonhuman primate trabecular architecture using micro-computed tomography. Am J Phys Anthrop 115: 327–336.

Falsetti AB, Jungers WL, Cole TM. 1993. Morphometrics of the callitrichid forelimb: A case study in size and shape. Int J Primatol 14(4):551-572.

Galik K, Senut B, Pickford M. 2004. External and internal morphology of the BAR 1002'00 *Orrorin tugenensis* femur. Science 305:1450-1453.

Gingerich PD. 1972. The development of sexual dimorphism in the bony pelvis of the squirrel monkey. Anat Rec 172*:*589-595.

Hager LD. 1996. Sex differences in the sciatic notch of great apes and modern humans. Am J Phys Anthropol 99*:*287-300.

Haeusler, M., Martelli, S., Boeni, T., 2002. Vertebrae numbers of the early hominid lumbar spine. J Hum Evol 43, 621-643.

Huiskes R, Ruimerman R, Van Lenthe GH, Janssen JD. 2000. Effects of mechanical forces on maintenance and adaptation of form in trabecular bone. Nature 405: 704–706.

Jaccard J, Wan CK. 1996. LISREL approaches to interaction effects in multiple regression. Thousand Oaks, CA: Sage Publications.

Jenkins FA. Jr. 1974. Tree shrew locomotion and the origins of primate arborealism. In Jenkins FA Jr. (ed), Primate locomotion. New York: Academic Press. pp 85-115.

Johnson SE, Shapiro LJ. 1998. Positional behavior and vertebral morphology in atelines and cebines. Am J Phys Anthropol 105:333-354.

Jorgensen MJ, Marras WS, Granata KP, Wiand JW. 2001. MRI-derived moment-arms of the female and male spinal loading muscles. Clin Biom 16:182-193.

Jorgensen MJ, Marras WS, Gupta P, Waters TR. 2003. Effect of torso flexion of the lumbar torso extensor muscle sagittal plane moment arms. Spine J 3:363-369

Jungers WL. 1984. Aspects of size and scaling in primate biology with special reference to the locomotor skeleton. Yrbk Phys Anthropol 27:73-97.

Jungers WL, Falsetti AB, Wall CE. 1995. Shape, relative size, and size-adjustments in morphometrics. Yrbk Phys Anthropol 38:137-161.

Keith A. 1923. Man's posture and its evolution and disorders. II. The evolution of the orthograde spine. Brit Med J 1:499-502.

Klingenberg CP. 1996. Multivariate allometry. In Marcus LF, Corti M, Loy A, Naylor G, Slice D (eds) Advances in morphometrics. Plenum Press: New York. Pp 23-49.

Knussman R, Finke E. 1980. Studies on the sex-specificity of the human spinal profile. J Hum Evol 9:615-620.

Krogman WM. 1951. The scars of human evolution. Sci Am December 1951:54-57.

Latimer B, Lovejoy CO. 1990. Hallucal tarsometatarsal joint in *Australopithecus afarensis*. Am J Phys Anthropol 82:125-133.

Latimer B, Ward CV. 1993. The thoracic and lumbar vertebrae. In: Walker A, Leakey REF, editors. The Nariokotome *Homo Erectus* Skeleton. Cambridge: Harvard University Press p 266-293.

Leakey MD, Hay RL. 1979. Pliocene footprints in the Laetoli Beds at Laetoli, northern Tanzania. Nature 27:317-323.

Leutenegger W. 1972. New born size and pelvic dimensions of *Australopithecus*. Nature 240:568-569.

Leutenegger W. 1974. Functional aspects of pelvic morphology in simian primates. J Hum Evol 3*:*207-222.

Leutenegger W. 1982a. Sexual dimorphism in nonhuman primates. In: Hall RL, editor. Sexual Dimorphism in *Homo Sapiens*: A Question of Size. New York: Praeger p 11-33.

Leutenegger W. 1982b. Encephalization and obstetrics in primates with particular reference to human evolution. In: Armstrong E, Falk D, editors. Primate Brain Evolution: Methods and Concepts. New York: Plenum Press p 85-95.

Louis R. 1985. Spinal stability as defined by the three-column spine concept. Anat Clin 7:33-42.

Lovejoy CO. 1979. A reconstruction of the pelvis of AL 288 (Hadar Formation, Ethiopia). Am J Phys Anthropol 50:460.

Lovejoy CO. 1980. Hominid origins: the role of bipedalism. Am J Phys Anthropol 52:250.

Merbs CF. 1983. Patterns of activity-induced pathology in a Canadian Inuit population. Otttawa: National Museum of Man Mercury Series, Archaeological Survey of Canada paper no 199.

Merbs CF. 1996. Spondylolysis and spondylolythesis: A cost of being an erect biped or a clever adaptation? Yrbk Phys Anthropol 39:201-228.

Merbs, CF. 2002. Asymmetrical spondylolysis. Am J Phys Anthropol 119:156-174.

Merbs CF. 2004. Sagittal clefting of the body and other vertebral development errors in Canadian Inuit skeletons. Am J Phys Anthropol 123:236-249.

Morinaga Y, Kimura M, Ienaga T, Higuchi K. 1997. Clinical study of pelvic insufficiency fractures. Orthop Sur Tram 40:219-228.

Mosimann J. 1970. Size allometry: Size and shape variables with characterizations of the log normal and gamma distributions. J Am Stat Assoc 56:930-945.

Odgers P. 1933. The lumbar and lumbosacral diarthrodial joints. J Anat 67:301-317.

Pal GP. 1989. Weight transmission through the sacrum in man. J Anat 162:9-17.

Pal GP, Routal RV. 1986. A study of weight transmission through the cervical and upper thoracic regions of the vertebral column in man. J Anat 148:245-261.

Pal GP, Routal RV. 1987. Transmission of weight through the lower thoracic and lumbar regions of the vertebral column in man. J Anat 152:93-105.

Pal GP, Routal RV. 1991. Relationship between the articular surface-area of a bone and the magnitude of stress passing through it. Anat Rec 230:570-574.

Phenice TW. 1969. A newly developed visual method of sexing in the *Os pubis.* Am J Phys Anthropol 30:297-301.

Preuschoft H, Fritz M, Niemitz C. 1979. Biomechanics of the trunk in primates and problems of leaping in *Tarsius*. In: M Morbeck, H Preuschoft, N Gomberg, editors. Environment, behavior and morphology: dynamic interactions in primates. New York: Gustov Fischer. p 327-345.

Preuschoft H. 1998. The shape of the pelvis and trunk in primates. Folia Primatol 69*:*187.

Rasband WS., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://rsb.info.nih.gov/ij/, 1997-2006.

Robinson J. 1972. Early Hominid Posture and Locomotion. Chicago: The University of Chicago Press.

Rockwell H, Gaynor Evans F, Pheasant H. 1938. The comparative morphology of the vertebrate spinal column: its form as related to function. J Morphol 63:87-117.

Rose MD. 1975. Functional proportions of primate lumbar vertebral bodies. J Hum Evol 4:21-38.

Rosenberg KR. 1992. The evolution of modern human childbirth. Yrbk Phys Anthropol 35*:*89-124.

Rosenberg KR, Trevathan W. 1996. Bipedalism and human birth: the obstetrical dilemma revisited. Evol Anthropol 4*:*161-168.

Rosenberg KR, Trevathan W. 2002. Birth, obstetrics and human evolution. BJOG – Internat J Obstet Gynecol 109: 1199-1206.

Sanders WJ. 1990. Weight transmission through the lumbar vertebrae and sacrum in australopithecines. Am J Phys Anthropol Annual Mtg Issue 81:2 Abstract.

Sanders WJ. 1995. Function, allometry, and evolution of the australopithecine lower precaudal spine. PhD dissertation, New York University.

Sanders WJ. 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. J Hum Evol 34:249-302.

Sanders WJ, Bodenbender BE. 1994. Morphometric analysis of lumbar vertebra UMP 67-28: Implications for spinal function and phylogeny of the Miocene Moroto Hominoid. J Hum Evol 26:203-237.

Schultz AH. 1930. The skeleton of the trunk and limbs of higher primates. Hum Biol 2:303-409.

Schultz AH. 1949. Sex differences in the pelves of primates. Am J Phys Anthropol 7:401-423.

Schultz AH. 1961. Vertebral column and thorax. Primatol 4:1-66.

Shapiro LJ. 1991. Functional morphology of the primate spine with special reference to orthograde posture and bipedal locomotion. PhD Dissertation. State University of New York at Stony Brook.

Shapiro LJ. 1993a. Evaluation of "unique" aspects of human vertebral bodies and pedicles with a consideration of *Australopithecus africanus.* J Hum Evol 25:433-470.

Shapiro LJ. 1993b. Functional morphology of the vertebral column on primates. In: Gebo DL, editor. Postcranial Adaptation in Nonhuman Primates. DeKalb: Northern Illinois University Press p 121-149.

Shapiro LJ. 1995. Functional morphology of Indrid lumbar vertebrae. Am J Phys Anthropol 98:323-342.

Shapiro LJ, Simons CVM. 2002. Functional aspects of strepsirrhine lumbar vertebral bodies and spinous processes. J Hum Evol 42:753-783.

Slijper EJ. 1946. Comparative biolog-anatomical investigations on the vertebral column and spinal musculature of mammals. Verh K Ned Akad Wet 42: 1-128.

Snijders CJ, Vleeming A, Stoeckart R. 1993. Transfer of lumbosacral load to iliac bones and leg. Part 1. Biomechanics of self-bracing of the sacroiliac joints and its significance for treatment and exercise. Clin Biom 8:285-294.

Sokal RR, Rohlf FJ. 1995. Biometry: The Principles and Practice of Statistics in Biological Research. 3rd Edition. New York: W.H. Freeman and Company.

Stern JT Jr. 2000. Climbing to the top: A personal memoir of *Australopithecus afarensis*. Evol Anthropol 9:113-133.

Stern, JT Jr, Susman RL. 1983. The locomotor anatomy of *Australopithecus afarensis*. Am J Phys Anthropol. 60:279–317.

Steudal K. 1981a. Sexual dimorphism and allometry in primate *os coxae*. Am J Phys Anthropol 55:209-215.

Steudel K. 1981b. Functional aspects of primate pelvic structure: a multivariate approach. Am J Phys Anthropol 55:399-410.

Stoller M. 1995. The obstetric pelvis and mechanism of labor in nonhuman primates. PhD dissertation, University of Chicago, Chicago, Illinois.

Straus WL. 1927. The human ilium: Sex and stock. Am J Phys Anthropol 11:1-28.

Sturesson B, Uden A, Vleeming A. 2000. A radiostereometric analysis of movements of the sacroiliac joint during the standing hip flexion test. Spine 25:364-368.

Susman RL, Stern JT Jr, Jungers WL.1984. Arboreality and bipedality in the Hadar hominids. Fol Primatol 43: 113–156.

Tague RG. 1986. Obstetric adaptations of the human bony pelvis. PhD dissertation, Kent State University.

Tague RG. 1992. Sexual dimorphism in the human bony pelvis with a consideration of the Neanderthal pelvis from Kebara Cave, Israel. Am J Phys Anthropol 88:1-21.

Tague RG, Lovejoy CO. 1986. The obstetric pelvis of A.L. 288-1 (Lucy). J Hum Evol 15:237-255.

Tague RG, Lovejoy CO. 1986. The obstetric pelvis of AL 288-1 (Lucy). J Hum Evol 15*:*237-255.

Tague RG, Lovejoy CO. 1998. AL 288-1 - Lucy or Lucifer: gender confusion in the Pliocene. J Hum Evol 35*:*75-94.

Taylor J, Twomey L. 1984. Sexual dimorphism in human vertebral body shape. J Anat 138:281-286.

Trevathan WR. 1987. Human Birth: An Evolutionary Perspective. New York: Aldine de Gruyter.

Trevathan W. 1988. Fetal emergence patterns in evolutionary perspective. Am Anthropol 90*:*19-26.

Trevathan W. 1996. The evolution of bipedalism and assisted birth. Med Anthropol Q 10*:*287-290.

Tveit P, Daggfeldt K, Hetland S, Thorstensson A. 1994. Erector spinae level arm length variations with changes in spinal curvature. Spine 19:199-204.

Ubelaker DH, Volk CG. 2002. A test of the Phenice method for the estimation of sex. J Foren Sci 47:19-24.

Vleeming A, Volkers ACW, Snijders CJ, Stockart R. 1990. Relation between form and function in the sacroiliac joint: II. Biomechanical aspects. Spine 15:133-135.

Wang M, Dumas GA. 1998. Mechanical behavior of the female sacroiliac joint and influence of the anterior and posterior sacroiliac ligaments under sagittal loads. Clin Biom 13:293-299.

Ward CV. 1993. Torso morphology and locomotion in *Proconsul nyanzae.* Am J Phys Anthropol 92:291-328.

Ward C. 1994. Locomotor and obstetric constraints in hominoid pelvic evolution. Am J Phys Anthropol Supplement 18*:*204.

Ward CV, Latimer B. 2005. Human evolution and the development of spondylolysis. Spine 30:1808-1814.

Washburn SL. 1948. Sex differences in the pubic bone. Am J Phys Anthropol 6:199-207.

Washburn SL. 1950. The analysis of primate evolution with particular reference to the origin of man. Cold Spring Harb Symp Quant Biol 15:67-78.

Washburn SL, Buettner-Janusch J. 1952. The definition of thoracic and lumbar vertebrae. Am J Phys Anthropol 10:251.

Whitcome KK. 2000. A functional examination of sexual dimorphism in human lumbar vertebrae. Masters thesis. Southern Illinois University, Carbondale.

Woollard H. 1925. The anatomy of *Tarsius spectrum.* Proc Zool Soc Lond 70:1071 -1184.

Zollikofer CPE, Ponce de Leon MS, Lieberman DE, Guy F, Pilbeam D, Likius A, Mackaye HT, Vignaud P, Brunet M. 2005. Virtual cranial reconstruction of *Sahelanthropus tchadensis*. Nature 434 (7034):755-759.

Zuckerman S, Ashton EH, Flinn RM, Oxnard CE, Spence TF. 1973. Some locomotor features of the pelvic girdle in primates. Symp Zool Soc Lond 33:71-165.

Chapter 4: Comparative Lumbopelvic Sexual Dimorphism

INTRODUCTION

A readily apparent yet unexplored factor in spinal loading derives from a dichotomy in reproductive physiology, one that cleaves two distinct loading groups within all primate species. Females grow a fetus, incrementally over time, incrementally gram by gram. In many primate species, female reproductive success requires a relatively long period of gestation (Ardito, 1976; Kiltie, 1982; Little, 1989). This physiological phenomenon holds implications for the biomechanics of posture and locomotion that are unique to females. During the protracted period of primate gestation, the fetus and its supporting soft tissues increase maternal body mass and alter maternal mass distribution, concentrating load in the abdominal cavity (Abitbol, 1996; Gilleard et al., 1996). In both pronograde and orthograde primates, those that are quadrupedal and those that frequently maintain an upright position, respectively, the ventrodorsal dimension of the maternal abdomen offers the greatest potential for expansion in accommodation of increasing fetal mass. However, the functional relevance of the abdominal wall differs obstetrically in pronogrady and orthogrady. With respect to the former, the abdominal wall and rectus muscles provide the major support for fetal load (Abitbol, 1993, 1996), and the vertical force generated by fetal load transfers to and is largely constrained by abdominal wall integrity. And although the maternal center of mass shifts ventrally as a result of ventrodorsal abdominal expansion, it is not assumed in pronograde contexts to translate in a fore-aft direction beyond the usual line of gravity.

In contrast, obstetric load in orthograde postures and locomotion is resisted not only by the maternal abdominal wall but also by the musculoskeletal structure of the pelvic floor (Elftman, 1932; Abitbol, 1993, 1996; Gillard et al., 1996). The vertical force generated by orthograde obstetric load increases compression through the axial skeleton, particularly the vertebrae and pelvis. Furthermore, while the maternal center of mass translates ventrally, its progression is anterior to the supporting structures, and therefore increases bending stress on the lumbopelvic complex. In light of the reproductive-based loading exerted on the female skeleton, functionally related differences in primate male and female lumbopelvic morphology are expected. Because the magnitude of loading forces through the vertebrae and pelvis are likely to be greater in orthograde contexts than in pronograde contexts, primates species that engage in a preponderance of upright positional behaviors are expected to express a greater degree of lumbopelvic sexual dimorphism in features related to load resistance than those of pronograde habits.

All primate species express some degree of sexual dimorphism in one or more dimension of the pelvis (Straus, 1927; Washburn, 1948; Schultz, 1949; Black, 1970; Gingerich, 1972; Leutenegger, 1973, 1987; Zuckerman et al., 1973; Steudel, 1981a, 1981b; Berge, 1984; Trinkaus, 1984; Tague and Lovejoy, 186; Rosenberg, 1986, 1988, 1992; Trevathan, 1987, 1988; Tague, 1989, 1990, 1991, 1993, 1995; Berge, 1990; Pissinatti and Dasilva, 1992; LaVelle, 1995; Ruff, 1995; Stoller, 1995; Hager, 1996, 1996; Walrath and Glantz, 1996) (but see Leutenegger, 1973 for *Perodicticus potto)*. The most extensive pelvic research has been conducted on the pelvic canal, or true pelvis, as considerable attention has been afforded to parturitional events as the fundamental selection pressure on female pelvic morphology (i.e., Leutenegger, 1974; Lindberg, 1982; Tague, 1986; Abitbol, 1987a; Trevathan, 1988, 1996; Rosenberg, 1992; Stoller, 1995, Rosenberg and Trevathan, 1996). Failure of the fetus to navigate the birth canal terminates pregnancy in primates (Stoller, 1995), and without effective intervention, induces death of the fetus and mother. Therefore, the relationship between fetal body and maternal pelvic dimensions is critical to female reproductive success.

However, it is important to note that the obstetric events of female reproductive success are not limited to parturition. Regardless of how definitive parturitional success is to fitness, the reproductive events preceding parturition must execute properly to advance pregnancy to successful term. While traditionally we have not acknowledged the biomechanical challenges of reproductive load on the posture and locomotion of females, our broad and detailed understanding of vertebral and pelvic functional morphology provides a foundation on which to investigate a potential relationship between lumbopelvic sexual dimorphism and obstetric load.

Primates as an order present a diverse range of positional behaviors. Among them, arboreal and terrestrial quadrupedalism are performed with the long axis of the body held horizontally, in a positional alignment referred to as pronograde. Other primate positional behaviors such as vertical clinging and leaping and below branch suspension typically place the body's long axis in a vertical orientation, along the line of gravity. Positional behaviors performed in a vertical context are known as orthograde. Even among those primate species that travel exclusively in a pronograde quadrupedal manner, feeding and resting behaviors are often performed in an orthograde or semi-orthograde posture (i.e., Wrangham, 1980; Gebo and Chapman, 1995; Hunt, 1996; Walker and Ayres, 1996; Youlatos, 1999; Stanford, 2006). Therefore, all primates engage in some degree of orthogrady (Slijper, 1946; Rose, 1975). Those committed to it, such as tarsiers (Niemitz, 1984; Dagosto et al., 2001), indrids (Dagosto, 1995), gibbons (Vereecke et al., 2005) and humans, display a wide range of body sizes, locomotor modes and body proportions.

The concepts of orthogrady and pronogrady underscore the varied biomechanical challenges different axial orientations impose. Erect postures characterizing orthogrady generate vectors with strong vertical components (Preuschoft et al., 1979). In large part, these force vectors are received and transferred from the upper body to the lower body along the vertebrae of the flexible spine and the fused sacrum (Kapjandji, 1982; Pal and Routal, 1986, 1987; Pal, 1989; Shapiro, 1991). Many researchers have noted that variation in vertebral size and shape reflects differences in function of the lumbosacral spine and positional behaviors (Rockwell et al., 1938; Schultz, 1953; Ankel, 1972; Rose, 1975; Halpert et al., 1987; Shapiro, 1991, 1993a, 1993b, 1995, 2002; Sanders, 1995, 1998; Johnson and Shapiro, 1998; Shapiro and Simons, 2002; Chen et al., 2005). Primate species that engage in orthograde positional behaviors present a suite of vertebral characteristics that differ from those of habitually pronograde primates. Their vertebral bodies are relatively short, as is lumbar regional length overall (Rose, 1975; Shapiro, 1991, 1995; Sanders, 1995; Johnson and Shapiro 1998; Shapiro and Simons, 2002), and the processes to which spinal muscles attach, both transverse and spinous, are oriented more dorsally (Shapiro, 1991, 1995; Johnson and Shapiro 1998; Shapiro and Simons, 2002). For example, distinctions in relative proportions of lumbar vertebral bodies between cercopithecoids and apes, between lorids and cheirogaleids, and between generalized lemurs and indrids, correspond with the importance of orthograde postures (Schultz, 1953; Ankel, 1967, 1972; Rose, 1975; Shapiro, 1993a, 1995; Sanders and Bodenbender, 1994; Sanders, 1995; Johnson and Shapiro, 1998; Shapiro and Simons, 2002). For instance, although the gibbon, a slightly built diminutive ape is as small as some cercopithecines, the vertebrae of the gibbon are relatively wider and shorter than those of the baboon, a large-bodied cercopithecine monkey (Rose, 1975; Sanders, 1995). By comparison the baboon, a terrestrial quadruped, has relatively larger vertebral dimensions than the domestic greyhound, a similarly sized nonprimate terrestrial quadruped (Chen, 2005). The behavioral inference from such comparison is that the baboon like all primates engages in a greater proportion of orthograde or semi-orthograde climbing and feeding behaviors than do many other mammals (Slijper, 1946; Rose, 1975).

The size and orientation of muscle attachment sites on the vertebrae of orthograde primates provide efficient leverage to counter large bending moments inherent in an erect upper body (Slijper, 1946; Benton, 1967, 1974). Reduction in vertebral length resists bending forces that are further exacerbated by angular excursions of the upper body over the sacral support base (Slijper, 1946; Badoux, 1974; Rose, 1975).

This morphometric analysis aims to identify sexual dimorphism in load bearing structures of the lumbopelvic complex and to test the hypothesis that sexual dimorphism, at least in part, represents female adaptations to the biomechanical risks associated with orthograde fetal load. Specifically, the prediction in this analysis is: The degree of lumbopelvic sexual dimorphism will be relatively greater in orthograde primate taxa than in pronograde primate taxa.

MATERIALS AND METHODS

Sample

The primate sample is comprised of 141 individuals from 9 species (Table 4.1). A similar analysis was performed exclusively on humans (see Chapter 3). To identify to the presence of lumbopelvic sexual dimorphism in nonhuman primates that differ in preferred trunk orientation, lumbar and sacral vertebrae were contrasted by sex within three orthograde, four semi-orthograde, and two pronograde species (Table 4.2). The taxonomic sampling is diverse, representing varied locomotor behaviors, diverse phylogenetic groups and a range of adult body sizes. The importance of targeting geographically and taxonomically coherent samples in studies of sexual dimorphism has been emphasized by several authors (e.g., Leutenegger and Larson, 1985; Plavcan and van Schaik, 1997, Lague, 2003), who note extensive interpopulational variation in the degree of body mass dimorphism within some species. When possible, samples in this study were restricted to geographically local conspecifics. The *Ateles, Propithecus* and *Indri* sample groups were not locally constrained due to the small number of available sex-certain specimens. For all taxa, only wild collected specimens were included.

Behavioral bases for positional groupings

Hylobates lar is a specialized brachiator of the dense tropical forest of SE Asia where it employs a variety of locomotor modes including leaping, bipedal walking, running, and scrambling (Carpenter, 1964; Ellefson, 1967; Fleagle, 1976; Gittins, 1983; Hollihn, 1984; Cannon and Leighton, 1994; Satie and Alfred, 2002, Vereecke et al., 2005). The majority of these behaviors are performed with the torso inclined vertically, 10-12% of which derive from arboreal bipedal walking (Vereecke et al., 2005). Therefore, *Hylobates lar* was considered orthograde in this study.

Indrids are Malagasy vertical clingers and leapers of relatively large body size (Gebo, 1987; Dagosto, 1995; Warren & Crompton, 1997). They utilize ricochetal tree-to-tree leaping in which one leap is rapidly followed by another (Petter, 1962; Oxnard et al., 1990), and they travel terrestrially via large hindlimb-powered bounds (Petter, 1962; Walker, 1979; Gebo, 1987; Terranova, 1995, 1996; Demes et al., 1999). Like all vertical clinging and leaping primates, *Indri indri* and *Propithecus verreauxi* maintain vertical trunk positions in the majority of their postural and locomotor behaviors, and were therefore included among the orthograde taxa in the analyses.

The great apes present a suite of positional adaptations that facilitate efficient terrestrial and arboreal behaviors. Orangutans are the most arboreal of the great apes (Knott, 1999), and as much as 80% of their travel modes are performed in forelimb suspension, typically with the torso held vertically below the supporting forelimbs (Cant, 1987). Whether traveling arboreally or terrestrially, both chimpanzees and gorillas remain anti-pronograde while climbing, suspending or knuckle-walking (see Stern, 1975 for term "anti-pronograde"; Remis, 1995; Isler, 2005). *Gorilla gorilla gaueri* and *Pan troglodytes schweinfurthii* are included in this study, along with *Pongo pygmaeus,* as semi-orthograde primates.

Ateles, a large-bodied suspensory platyrrhine, is known to move rapidly through the forest by arm-swinging, climbing and leaping (Fleagle and Mittermeier, 1976; Mittermeier, 1978; Cant, 1986; Fontaine, 1990; Johnson and Shapiro, 1998). Members of this genus spend nearly one third of their feeding time in forelimb suspension (Bergeson, 1996; Johnson and Shapiro, 1998; Cant et al., 2001). When traveling, *Ateles geoffroyi* frequently utilizes arboreal quadrupedalism. Mittermeier (1979) reported just 25% quadrupedalism in *A. geoffroyi* (Barro, Panama) locomotor bouts. Fontaine (1970) observed 50% locomotor quadrupedalism studying a population geographically approximate to the group recorded by Mittermeier (1979), also in Barro, Panama. Cant (1986) reported that 52% of *Ateles geoffroyi* (Tikal, Guatemala) were quadrupedal. Based on the substantial frequency of quadrupedal locomotion in the positional repertoire of *Ateles geoffroyi,* the species was treated as a semi-orthograde primate in the analyses, along with the great apes.

Alouatta seniculus travels predominantly in an arboreal quadrupedal mode (Altmann, 1959; Richard, 1970; Cant, 1986). Nearly 80% of this platyrrhine's arboreal travel is performed in slow quadrupedal progression (Fleagle and Mittermeier, 1980). *Macaca fascicularis* is a highly arboreal quadrupedal cercopithecoid (Rodman, 1979; Cant, 1988). These two species represent the pronograde positional mode in the analyses.

Sample Size

Sample size by sex varied across taxa from as many as sixteen individuals to as few as two (Table 4.1). Robust samples were planned for all taxa according to available collection records. Once pulled, many of the designated specimens proved to be incomplete, immature, and/or of questionable sex assignment. Generally, within primate osteological collections, *Propithecus verreauxi* and *Indri indri* are relatively under-represented. Among them, many specimens include only craniodental material. Where postcranial elements are present, long bones predominate and vertebrae and pelves are scarce. Often where vertebrae are available, regional elements of the vertebral column are missing, and lumbar regions are incomplete.

Sex Determination

Only specimens of curation-recorded sex were included in the study. Specimen tags and field records were reviewed for corroboration of sex assignment when available. No attempt was made to identify sex from either comparative body size or canine size alone. Where museum records failed to indicate sex or where multiple records differed, specimens were precluded from the analyses.

Skeletal age

Samples were comprised of adult specimens. Collection records initially determined skeletal maturity. Specimens noted as infant, juvenile or subadult were excluded. In some cases, researcher-observed skeletal maturation contradicted reported developmental status. Purported adults presenting any unfused epiphyses were omitted.

Scoliotic individuals were rejected, as were those with visible skeletal trauma (other than lead shot clearly associated with the field acquisition event), osteophytic deposition or visible bone remodeling.

Lumbar vertebral identification

As with the human specimens reported in Chapter 3, the lumbar vertebrae of nonhuman primates were defined according to their zygapophyseal orientation (Washburn and Buettner-Janusch, 1952; Shapiro, 1993a). This facet-based designation differs from the widely used non rib-bearing alternative (Schultz, 1930) in its functional emphasis on the range of motion between vertebral elements; type and range of movement in the lumbar column are largely influenced by facet direction. The dorso-medial and ventro-lateral orientations of lumbar superior and inferior facets, respectively, guide sagittal flexion and extension while resisting both rotation (Rockwell et al., 1938) and ventral displacement (Latimer and Ward, 1993; Bogduk, 2005).

Spinal loading model

Functional implications of lumbopelvic sexual dimorphism were explored in the context of a two-pillar spine human model conceptualized by Pal and Routal (1986, 1987). According to the model, direction and magnitude of spinal loads are channeled through two pillars, a ventral pillar comprised of vertebral centra and intervertebral disks and a dorsal pillar formed by laminae and zygapophyses (Figure 4.4). Pedicles function in the model system as conduits of force distribution between the two pillars. Proportional loading shifts between the two pillars as a result of both static morphology, particularly centrum wedging (Figure 4.5), and movements initiated along the vertebral column. The model is predicated on a functional relationship between structural size and loading capacity. The ventrally located vertebral centra form the major load bearing pillar while the neural arch structures of the dorsal pillar resist forces applied by epaxial muscles and additionally bear load directed dorsally through static configuration and segmental movement.

While the model presents a biomechanical explanation of force distribution in the human sinusoidal column, its utility extends to weight bearing properties in all primates (Shapiro, 1993a; Sanders, 1995, 1998; Sanders and Bodenbender, 1994), and has been applied to the study of orthograde mammals (Chen et al., 2005).

Lumbopelvic Osteological Measurements

Predictions of lumbopelvic sexual dimorphism in nonhuman primates were tested on fourteen vertebral variables at each lumbar vertebral level and four sacral variables, chosen to define the relative size and shape of the lumbar vertebrae and pelvis. The structures quantified receive and transfer postural and locomotor forces generated within the lumbopelvic complex, and are therefore subject to biomechanical stresses introduced by fetal load. Variables are illustrated and anatomically defined in Figure 4.1. Data collection followed the protocol established for human specimens as reported in Chapter 3.

Lumbar Vertebrae (Figure 4.1a):

Vertebral Body: The vertebral body (centrum) is the primary load bearing structure of the vertebral column (Bogduk, 2005). Vertebral joint surfaces are generally proportional to the forces they transmit (Pal and Routal, 1986, 1987; Pal, 1989). If sexes differ in the proportion of load transmitted along the lumbar vertebra and sacrum, endplate dimensions relative to body size are expected to be larger in the more heavily loaded sex. Among the orthograde taxa females are predicted to have relatively larger vertebral surface areas than those of males, in accordance with vertical obstetric load. Lumbar surface area was calculated from the cranial centrum endplate dimensions as follows: (CMD/2) x (CAD/2) x 3.1416. Sacral surface area was similarly derived as: (SMD/2) x (SAD/2) x 3.1416, based on the formula for area of an ellipse.

Vertebral wedging contributes to the bony curvature of the lumbar spine. Cunningham (1886) and Schultz (1961) suggested that humans might not be alone in the presence of a marked lumbar curve. In a comparative anthropoid sample Rose (1975) found significant lordotic wedging in gorillas and humans, although the gorilla lordosis occurred only at the last lumbar level. Sanders (1995) found a similar gorilla trend, although the result was not statistically significant. As wedging relates directly to the orientation of the trunk and positional behaviors (Cunningham, 1886; Rose, 1975; Clauser, 1980; Sanders, 1995), orthograde females were predicted to present relatively greater ventral wedging than were males. Linear measurements were analyzed separately then used to calculate an angular variable of vertebral body wedging following Digiovanni et al., (1989):

$$\text{Wedging angle} = 2 \text{ arctangent } (((\text{CDH}-\text{CVH})/2)/\text{CAD})$$

Positive angles were kyphotic while negative angles were lordotic. A vertebra was determined to be neutral, neither kyphotic nor lordotic, when its value fell within the range 0.5 to -0.5 degrees.

Pedicle: The vertebral pedicle provides structural continuity between the centrum and the neural arch and is subject to varying magnitudes of bending stress under different spinal loading regimes (Davis, 1961; Pal and Routal, 1986, 1987; Sanders, 1995, 1998; Shapiro, 1991, 1993a, 1995). Pedicular sexual dimorphism is characteristic of humans (Chapter 3). Male pedicles present significantly greater relative cross-sectional area at the first, second and third lumbar levels than do females. Differences are not significant at lumbar levels four and five. The change along the human vertebral column most likely accords with the more kyphotic vertebral body wedging in males at the three cranialmost lumbar vertebrae. Bogduk (2005) emphasizes the role of pedicles in resistance to bending forces exerted by spinal muscles attached to dorsal elements. More muscle effort may be required to generate extension of the lumbar spine in the region of the kyphotic vertebrae than in the lordotic vertebrae. Since the human male lumbar region is more kyphotic than that of human females at lumbar levels L1-L3, their relatively large pedicles may reflect this resistance to muscle action. While lumbar lordosis is a bipedal positional mechanism and not expected to characterize the comparative taxa in this analysis, any significant difference in vertebral wedging was expected to impact pedicle morphology. Since females experience obstetric spinal loading and males do not, greater pedicle robusticity in the form of cross-sectional area was predicted in females, as resistance to stronger loading forces that would shift between the spinal pillars during flexion and extension. Pedicle cross-sectional area was calculated as PL x PW.

Transverse Process: Transverse processes provide attachment sites for many of the spinal muscles that contribute to extension of the back. Females of the orthograde taxa are expected to present larger and more dorsally oriented processes to facilitate upper body stability under conditions of obstetric load.

Zygapophyses: Zygapophyses are secondary load bearing structures. These synovial joints guide intervertebral movements and support a proportionately greater load under conditions of acute lumbar lordosis (Adams and Hutton, 1980; Pal and Routal, 1987).

Orientation of the zygapophyseal facets plays a role in resistance to vertebral shear stress and are expected to be relatively larger for load bearing and more oblique in females, as added resistance to shear stress that would be produced by fetal load. Loading comparisons between sexes were performed on zygapophyseal area according to the formula: $[(SCC/2 + SOM/2)/2] \times [(SML/2) + (SOC/2)/2] \times 3.1416$

The angle of prezygapophyseal obliquity (POB) was taken to investigate potential range of motion in spinal rotation and flexion/extension as well as resistance to ventral shear stress. The latter is exemplified in humans whose sequential lumbar vertebrae bear prezygapophyses increasingly more coronal in their facet orientation (Odgers, 1933; Shapiro, 1991; Latimer and Ward, 1993).

Sacrum (Figure 4.1b):

Sacral Body: The vertebral body and prezygapophyses of the first sacral vertebra function similarly to those of the lumbar vertebrae. The medio-lateral expanse of the sacral body provides, in part, attachment sites for muscles controlling the trunk. Where extensive erector spinae muscles benefit torso stability, a relatively broad sacrum is predicted. Therefore, orthograde females are predicted to have relatively broader sacra than males. The sacrum in its dual role as the axial load bearing base of the spine and the dorsal bony continuum of the pelvic girdle is expected to have greater relative breadth in females than in males. The latter functional role is relevant to primate taxa in which the fetal body dimensions closely approximate the maternal pelvic canal. For instance, the female macaque pelvis is proportional to relative neonate size while the maternal pelvis is roomy relative to fetal size in each of the great apes (Schultz, 1949). Greater relative breadth is predicted in the female macaque rather than the male due to shape selection pressure for successful delivery of the neonate, while in the great apes, a relatively broad female sacrum would not be predicted as an accommodation to fetal size, since great apes give birth to relatively small neonates (Schultz, 1949). Rather, female great ape sacra are predicted to be relatively wider than male sacra due to the increased magnitude of spinal forces in semi-orthograde obstetric load. Further, the obstetric load functional prediction extends to the auricular area across which torso-hindlimb loads transfer. Sacral auricular area was calculated digitally from scaled photographs using JImage areal software (version 1.34n, NIH, USA).

Size standardization

***Geometric mean*:** Many of the sampled species are sexually dimorphic in body size. Without size standardization of the variates, tests of lumbopelvic sexual dimorphism might identify nothing more than gross size differences or fail to identify shape difference because they are masked by body size. For instance, if the prezygapophyses of females are larger relative to body size than are those of conspecific males and the species in question is sexually dimorphic in body size such that males are markedly larger than females, the analyses of raw variates may confound the two factors and generate a result that dilutes or exacerbates the phenomena. Size standardization of the data was achieved through division of the raw linear variates by the scale-free geometric mean of linear variables for each specimen drawn from four lumbar levels: the first (L1), the second (L2), the penultimate (PL) and the last (LL) (Mosimann, 1970; Darroch and Mosimann, 1985). In this analysis, the geometric mean was constructed as the 48th root of the product of the linear measures of the lumbar vertebrae (see linear variables in Figure 4.1a)

***Validity of geometric mean*:** To assess the validity of the geometric mean as a specimen-specific proxy for gross size, reduced major axis regression of the species' geomean on reported species' body mass (Smith and Jungers, 1997) is shown in Figure 4.2. The 0.3 slope of the regression line is isometric, as predicted for a regression of linear dimension on cubic volume. Among the sampled taxa, there is good agreement between the geometric mean of lumbar vertebral variables and published body mass. Therefore, results of this study are easily referenced to other studies drawn from mean body mass reported in Smith and Jungers (1997). A single mean point representing male *Gorilla gorilla gaueri* in the regression plots outside the lower bound of the 95% confidence limit. The geometric mean falls below the predicted value based on mean body mass reported in Jungers and Sussman (1984), whose n=4 generated a mean of 175.2 kg, a body mass 2.5 times larger than the stated female mass (71.0 kg). Lower means for male *G. g. gaueri* have been reported (Meder, 1993), demonstrating differences among sample populations from which body mass values have been derived. The incongruency between the geometric mean and referenced body mass of *G. g. gaueri* may result from error in one or both of the contrasted means. The differences in means reported in the literature suggest the Smith and Jungers (1997) may overstate the true parent population mean. On the other hand, the formula of calculation for the geometric mean (nth root of linear variates' product) in this study may have skewed the proxy as a result of geometric mean formulation in the gorilla. The geomeans of all other taxa in the analysis were drawn from the 48th root of variates among vertebrae L1, L2, PL and LL, while the gorilla mean was drawn as the 36th root from L1, PL and LL. A lumbar column of just three vertebrae characterized each gorilla specimen in the analysis.

Data Analyses

Linear Regression**:** Linear regressions were run on the full comparative sample for areal measures, as a means to assess any consistent sexual dimorphism in spinal loading patterns within the positional groups. The lumbar levels included in the full comparative regressions were: L1, L2, PL and LL. Model II, Reduced Major Axis (RMA) regression was used for the comparison since the x axis traits were not assumed to have less inherent error variance than the y axis traits. RMA fits lines that adjust for variability in X as well as Y (Figure 4.3). Where linear variates were plotted on the geometric mean (essentially a linear measure), the expected isometric slope was 1.0. In the case of areal measures plotted against the geometric mean, the expected slope of isometry was 2.0. Confidence limits were calculated as described in Tan and Inglewicz (1999).

Tests of sexual dimorphism**:** Tests of sexual dimorphism were run independently on each primate species to identify statistically significant sex differences. Variables were tested for normality using the single sample Shapiro-Wilk W test. A between-sex test for homoscedasticity was performed as a two-tailed Fmax test with a 0.05 alpha. To test hypotheses of lumbopelvic sexual dimorphism, the inferential two-tailed Student's unpaired *t*-test was performed on each species. The Student's *t*-test is sensitive to nonnormal distribution. Therefore, where the assumptions of normality and homoscedasticity were violated, the Welch's approximate *t*-test was performed. As multiple tests inflate the likelihood of Type I error, the sequential Bonferroni procedure, although conservative in precluding Type I error, was applied. Means, standard deviations, t-values and probabilities are reported for all comparisons. The null hypothesis in all comparisons was no sex difference in the lumbopelvic structures within each species level sample population.

Variables tested in the analysis of sexual dimorphism included: the centrum wedging angle, mediolateral breadth and surface area of the centrum; transverse process angle and length; pedicle cross-sectional area; prezygapophyseal angle and surface area; interfacet breadth; and sacral body breadth. These intraspecific tests of sexual dimorphism included all lumbar levels, as enumerated in each species modal number.

RESULTS

Linear Regression

Sacral breadth

Results of the RMA linear regression of sacral breadth (ln) against the geomean (ln) are presented in Figure 4.6 and Table 4.3. All taxa fall within the 95% confidence limits of the regression line, and the slope approximates isometry (1.06). The male mean of *Pan troglodytes* (Pt) lies along the margin of the lower confidence band. It plots close to the mean sacral breadth value of females and is lower than predicted based on its larger geomean measure. While *Macaca fascicularis* (Mf) lies in the lower pole of the regression space and its sexes plot higher relative to the regression line, the dispersion of space between the male and female means and their positions relative to one another is similar to that of the male and female *Pan troglodytes*. The taxa in the pronograde and semi-orthograde positional categories otherwise plot close to the regression line in accordance with their geometric mean differences. Among the orthograde taxa, *Hylobates lar, Indri indri* and *Propithecus verreauxi*, females plot above the conspecific males in space at positions greater than predicted by the regression line. In other words, the hypothetical lines formed between the male and female means of each orthograde taxon exceed the slope of the regression. Although *Ateles geoffroyi* (Ag) and *Alouatta seniculus* (As) are close phylogenetic taxa (Givnish and Sytsma, 1997; Horowitz et al., 1998; Canavez, 1999; Ruiz-Garcia and Alvarez, 2003; Steiper and Ruvolo, 2003; Collins, 2004) and both share specialized tail prehensility, they differ in the regression space. Both male and female means of *Alouatta seniculus* fall close to the regression line while those of *Ateles geoffroyi* plot above the line. Although both taxa occupy regression space within the 95% confidence limits, *Ateles* plots well above *Alouatta.* Sexes plot differently in the two platyrrhines; within pronograde *Alouatta* male sacral breadth plots above female breadth, while the opposite holds for semi-orthograde *Ateles.* Although *Ateles geoffroyi* is considered a semi-orthograde species in the overall analysis, its sexes follow the orthograde pattern in the sacral breadth-geomean comparison. Mean points for *Homo sapiens* (drawn from Chapter 3) were introduced to the plot after the regression analysis to allow comparison of human orthograde sexes with those of the nonhuman taxa. The human female mean plots above the nonhuman regression line, within the 95% confidence limit. The human male mean plots close to the nonhuman regression line, demonstrating a narrow sacrum relative to geomean measure, in comparison to female sacral breadth, a contrast that mirrors the dispersion of sexes in *Pan troglodytes.*

Centrum surface area

All nonhuman taxa fall within the 95% confidence bands of the centrum surface area regression on the geometric mean (Figure 4.7 and Table 4.3). The regression slopes at each vertebral and sacral level exceed the slope of isometry (2.0). There is a positive allometric effect to centrum surface area in these diverse primate species. Most sexes lie close to the regression line (r = 0.99 at all levels except L2 where r = 0.98). The exception occurs in *Hylobates lar* whose male mean straddles the upper confidence band and female mean lies close to the perimeter. For their respective geomean measures, each plots slightly higher than predicted by the regression line. Plotting positions between conspecific sexes are consistent across all vertebrae and the sacrum. No differences are observed between sexes in comparing the different positional orientations of orthogrady, semi-orthogrady and pronogrady.

Prezygapophyseal surface area

Results of linear regressions of prezygapophyseal surface area (PSA) on the geometric mean are presented in Figure 4.8 and Table 4.4. In all comparisons, L1 through S1, the regression slopes approximate the slope of isometry (2.0) and fall within 95% confidence limits. Male and female means of all comparative taxa plot within the confidence bands. Human males and females were plotted onto the nonhuman regression space after analysis and fall above the upper confidence limit at levels L2, LL and S1, indicating that humans have relatively large PSAs for their size compared to all other primates in the sample.

Pedicle cross-sectional area

Linear regressions of pedicle cross-sectional area (PedXS) against the geometric mean are presented in Figure 4.9 and Table 4.5. All levels, L1, L2, PL and LL present positive allometric slopes, exceeding the isometric slope of 2.0. Dispersion of the taxa around the regressions lines is similar at each lumbar level. All comparative taxa fall within or on the 95% confidence ellipse. Human data points were superimposed onto the regression space after analysis and fall below the lower confidence limit at lumbar levels L1 and L2. Cross-sectional area of the human pedicle is less than predicted by the comparative taxa regression. For their geometric size, humans have small pedicles at the cranial levels when compared to the other primate sampled in the analysis. Plotting points of sexes within species generally follow the regression slope. Relative to their geometric mean, pedicle cross-sectional area for females exceeds that of conspecific males, at all lumbar levels.

Auricular area

Log transformed auricular area is plotted against log geomean in Figure 4.10. The comparison is not strongly correlated (r = 0.84), and the regression slope (1.84) is negatively allometric (p = 0.05). Within the orthograde taxa (*Ii, Pv, Hl*), female means tend to exceed male means. This is also the case for the two prehensile-tailed taxa, *Ag* (semi-orthograde) and *As* (pronograde). Raw and size-adjusted means and standard deviations for auricular area are shown in Table 4.6, 4.7 and 4.8. P values are included, demonstrating that there were no significant differences between sexes of any species in any of the positional groups, including the orthograde primates.

Tests of Sexual Dimorphism

Orthograde primates

Tests of sexual dimorphism were performed on geomean adjusted variates of the sacrum and for all lumbar levels included in the modal number of lumbar vertebrae for each taxon. Results for the orthograde species *Hylobates lar* are reported in Table 4.9. Significant sex differences were identified in the lumbar centra, including relative centrum surface area, centrum medio-lateral breadth and pedicle cross-sectional area. Relative area of the centrum differed significantly by sex at the last lumbar level L5. Breadth of the centrum differed significantly at three lumbar levels, L1, L2, and L4. Sex differences in pedicle cross-sectional area reached significance by sex at lumbar level L2. Interfacet breadth differed at the last lumbar level. In all occurrences of lumbar sexual dimorphism in *Hylobates lar,* the male mean exceeded the female mean. No significant sex differences were identified in the sacral variables of *Hylobates lar.* Tests of sexual dimorphism performed on the other orthograde species, *Indri indri* and *Propithecus verreauxi* produced no significant results (Tables 4.10 and 4.11).

Semi-orthograde primates

Results of sexual dimorphism tests for *Gorilla gorilla gaueri* are presented in Table 4.12. Significant differences for this semi-orthograde primate were identified in the two of the three lumbar levels and in the sacrum. Centrum surface area significantly differed between males and females at lumbar levels L1 and L2. Medio-lateral centrum breadth also differed significantly at lumbar levels L1 and L2 and additionally at the sacral level. Male means exceeded female means in all significant results. Results for *Pongo pygmaeus* are presented in Table 4.13. Differences in male and female means did not reach Bonferroni significance for any variable, with the exception of sacral body breadth in which females are relatively larger than males. Table 4.14 reports tests of sexual dimorphism for *Pan troglodytes*. The male mean significantly exceeded the female mean for interfacet breadth at lumbar level L1 and centrum surface area at L3. Nearly results for semi-orthograde *Ateles geoffroyi* were nonsignificant (Table 4.15). At the last lumbar level, female transverse processes are more oblique and relatively longer than male processes.

Pronograde primates

Results for *Macaca fascicularis* are shown in Table 4.16. Male means significantly exceeded female means in centrum surface area at the first and last lumbar vertebral levels, L1 and L9. Test results for *Alouatta seniculus* are presented in Table 4.17. Two significant results were obtained. Centrum wedging at L4 and prezygapophyseal angle at L3.

Overall, a small number of variables reached significance in the comparative sampling, although no clear pattern of sex-related differences in size-adjusted variables was identified within the orthograde, semi-orthograde, or pronograde groups. The greatest number of significant results were identified in dimensions of the vertebral centra, and in all comparisons, male values exceeded female values. *Hylobates lar* was distinguished among the positional samples by its large number of significant results, at four it its five lumbar levels.

Vertebral Wedging

This formulated variable takes into account the cranio-caudal dimension of the ventral and dorsal walls of the vertebral body as well as the antero-posterior diameter of the body. Where ventral and dorsal heights differ, the shape of the vertebral body departs from geometric blocking. Wedging may be absent or neutral (zero angle value), kyphotic (positive angle value) in which case spinal loading is increased ventrally, lordotic (negative angle value) in which case a greater proportion of spinal load is shifted dorsally. The lumbar vertebrae of humans are kyphotic cranially and lordotic caudally (Whitcome, 1999, 2000 and see Chapter 3). Human male and female wedging differs significantly at all lumbar pre terminal levels. Females attain a transition from kyphotic to lordotic wedging at L2 while males reach transition at L3. Means, standard deviations and significance testing results for lumbar vertebral wedging in the comparative taxa are presented in Tables 4.18 – 4.20.

Orthograde primates

Wedging angles for the orthograde taxa are presented in Table 4.18. The lumbar vertebrae of both hylobatid sexes were kyphotic at all five lumbar levels, decreasing sequentially down the column. At all lumbar levels, female vertebrae were less kyphotic than male vertebrae, although the difference reached statistical significance only at the second and last lumbar levels. Sexes of *Indri indri* and *Propithecus verreauxi* were also kyphotic along the lumbar column. Female *Indri* were more kyphotic at all lumbar levels than were male *Indri*, but not significantly so. No significant differences were identified for *Propithecus verreauxi.*

Semi-orthograde primates

Wedging angles for the semi-orthograde species are presented in Table 4.19. The pattern of decreasing kyphosis in *Pan troglodytes* was similar in males and females. No significant differences were detected. The wedging angles in both sexes of *Pongo pygmaeus* decreased along the lumbar column. The male mean transitioned to lordotic wedging at the last lumbar level while the female mean remained slightly kyphotic. Differences in male and female wedging angles did not reach statistical significance at any lumbar levels. Wedging angles also decreased along the lumbar column in *Gorilla gorilla gaueri*. Both males and females transitioned from kyphosis to lordosis. No significant differences were identified. In contrast to the last lumbar level pattern in the great ape taxa, wedging at the last lumbar level in *Ateles* was strongly kyphotic. None of the male-female differences reach statistical significance.

Pronograde primates

Wedging angles of the pronograde taxa are shown in Table 4.20. All lumbar vertebrae of *Alouatta* and *Macaca* were kyphotic. Generally, vertebrae became less kyphotic toward the caudal margin of the lumbar column. No significant sex differences were present in the macaque lumbar column. Significant differences were identified in the mid lumbar levels of male and female *Alouatta* (L3 and L4), where female means were less kyphotic than male means. At all lumbar levels, females were either less kyphotic or equally kyphotic to males. Where standard deviations in the angle of wedging for both sexes were relatively small, statistically significant differences were noted.

Mean Comparisons

Sample sizes of some taxa were small, reducing power of the statistical testing.

Simple bar charts of male and female means provide visual examination and comparison of overall patterns of lumbar vertebral wedging by species sex. Means for each sex are graphically represented by taxon in Figures 4.11 through 4.19. Even in the absence of statistical significance, consistent intraspecies pattern in male and female proportions may reflect true anatomical variance of important biological meaning. For instance, Figure 4.11 presents lumbar vertebral wedging means for *Hylobates lar.* Male kyphosis exceeded female kyphosis at each of the five lumbar levels. Female kyphosis dropped markedly at the last lumbar level, and this change in progression differed significantly from the corresponding male kyphosis. In contrast, as Figure 4.12 demonstrates, *Indri indri*, another orthograde primate, is characterized by a contrasting pattern. Female kyphosis exceeded male kyphosis at seven consecutive vertebral levels, beginning with lumbar level L3. Cranially, female means matched male means at levels L1 and L2. While no statistical differences were noted, and the sample size is small (female n = 7, male n = 2), the consistent proportional difference between male and female lumbar wedging indicates that for this sample comparison, females were more kyphotic than males, and further demonstrates the importance of expanding the sample size for adequate statistical testing. Results for the third orthograde taxon, *Propithecus verreauxi*, show apparent randomness in the wedging sequences of both males and females (Figure 4.13). There were no consistent patterns either within or between the sexes. While these results may be indicative of parent population morphology, the sample size for this species (female n = 2, male n = 4) may simply fail to capture the true variation of the species and its sexes. The graphical comparison of the *Pan troglodytes* sample shows that the trends for male and female wedging were similar (Figure 4.14). While mean female kyphosis in *Pongo pygmaeus* decreased incrementally from the first lumbar vertebra to the last, males show an increase in kyphosis from L1 to L2 and a transition from kyphosis to lordosis at the last lumbar level (Figure 4.15). Again, small sample sizes severely limit inference beyond the sample of study. However, male and female means for *Gorilla gorilla gaueri* presented similar transitional steps leading from kyphosis at the first lumbar level to lordosis at the last. Sexes differed at the intermediate level where mean female wedging became modestly less kyphotic while mean male wedging became lordotic (Figure 4.16). A more robust sample is required to either confirm or dismiss the kyphosis- lordosis split in sexes at the L2 level. All lumbar vertebrae for *Ateles geoffroyi* are kyphotic (Figure 4.17). The mean male angle is relatively constant from the first to the penultimate vertebra. Female means are more varied with a decrease marked decrease in kyphosis at the penultimate level. Both sexes show increased kyphosis at the last lumbar level. The two pronograde taxa present different proportional patterns in their respective male and female comparisons. While male and female means follow the same trend within species, female *Macaca fascicularis* means are generally more kyphotic than male means (Figure 4.18), while the opposite holds for *Alouatta seniculus* (Figure 4.19); male means typically exceed those of females. The two pronograde species are similar in that kyphosis increases slightly at the cranial margin of the lumbar column followed by a long series of kyphotic reduction toward the caudal margin.

DISCUSSION

In light of the fact that humans express significant lumbopelvic sexual dimorphism (Whitcome, 2000, 2001, and see Chapter 3 of this dissertation) and given the loading biomechanics and functional morphology of orthograde primates (Shapiro, 1991, 1995), this study predicted the degree of lumbopelvic sexual dimorphism would be relatively greater in orthograde primate taxa than in pronograde primate taxa.

Most species sampled in this comparative study, whether orthograde, semi-orthograde, or pronograde, do not substantially differ by sex in the relative size and shape of lumbar and sacral vertebrae. Among those that do, *Hylobates lar* and *Gorilla gorilla gaueri* exhibit more sexual dimorphism than the rest, although not in the predicted direction, as males are relatively larger than females. These two taxa differ markedly from one another in overall body size, body size dimorphism, and positional behaviors. *Hylobates lar* exemplifies primate arboreal orthogrady while *Gorilla gorilla gaueri* is predominantly terrestrial and semi-orthograde in its positional behaviors. The two share a relatively close phylogenetic history having diverged from a common hominoid ancestor from which other great apes and humans descended. If the levels of lumbopelvic sexual dimorphism evidenced by *Hylobates* and *Gorilla* in this study shared evolved *de novo* in the last common ancestor of the hominoids, *Pongo pygmaeus* and *Pan troglodytes* would also express a similar degree of dimorphism, assuming parsimony principle. That expectation, unrealized here, is the consequence of phylogenetic reconstruction based on multiple lines of evidence that the orangutan lineage diverged sometime after that of the hylobatids and before that of the gorillas (i.e., Ruvolo, 1997; Rae and Koppe, 2000). While similarities in shape sexual dimorphism in the lumbar vertebral centra of *Hylobates lar* and *Gorilla gorilla gaueri* may be functionally related in terms of adaptive resistance to spinal loading, the selection factors that underlie the their respective sex differences are not necessarily one and the same. A discussion of each follows.

While not predicted in this analysis, the presence of significant sex differences in the lumbar and sacral vertebrae of *Gorilla gorilla gaueri* is less surprising than that of *Hylobates lar*. There is no functional basis on which to hypothesize that obstetric load would significantly impact the evolutionary loading structure of the female eastern lowland gorilla to the extent it morphologically differs from the male, but the extreme body size dimorphism of the large great ape species may exert a positive allometric effect on males. Previous analysis of gorilla vertebral morphology in *Gorilla gorilla gorilla* (western lowland gorilla) (Whitcome, 2000) showed no expression of lumbar shape sexual dimorphism. Reports of mean body mass by Smith and Jungers (1997) suggest the eastern and western lowland subspecies share similar body size dimorphism by sex, the western taxon with 170.4 kg and 71.5 kg for males and females respectively and 175.2 kg and 71.0 kg for the eastern taxon. Male and female mean body mass for the mountain gorilla (*Gorilla gorilla berengei)* was given at 162.5 and 97.5 kg. According to these data, the male eastern lowland gorilla attains the largest mass among all living primates. In contrast to males and females of the western subspecies, the thorax of both male and female eastern gorillas is relatively broad (Harcourt, 1985), suggesting that the difference in subspecies body mass may be concentrated in the upper body rather than equally distributed throughout. The pronounced body size dimorphism of lowland gorillas and particularly the likely preponderance of relatively large upper body mass in the eastern subspecies may be a factor in the significant sexual dimorphism in the lumbar centra of *Gorilla gorilla gaueri,* as identified in this analysis. The eastern and western lowland gorilla subspecies also differ in modal number of lumbar vertebrae; four vertebrae are characteristic of the western group while three vertebrae are common in the eastern gorilla (per obs). Reduced numbers of lumbar vertebrae are functionally related to orthograde load bearing and limited mobility of the spine (Fowler, 1885; Slijper, 1946; Benton, 1967; Rose, 1975). It is relatively easy to see that from a biomechanical standpoint, disparate adult body sizes, such as those present in the eastern lowland great ape *Gorilla gorilla gaueri* may drive shape change in conspecific sexes. Within primates in general, centrum surface area correlates closely with body size (Shapiro, 1991; Sanders, 1995; Johnson and Shapiro, 1998). While the results of this study support the correlation, the geometric prediction of isometry in centrum surface area was not realized in this analysis (i.e., contra to Sanders, 1995; Johnson and Shapiro, 1998). In contrast, the results reported here indicate a significant allometric relationship within the sample populations. This study-specific departure from isometry may derive to some extent from the geometric mean size "proxy" applied in the analyses. Vertebral linear measures taken from L1, L2, PL and LL were used to calculate the geomean, and while the study-specific geomean itself proved isometric in relation to reported body mass (Smith and Jungers, 1997), its inherent vertebral constitution provides a slightly different comparison in the case of centrum surface area. It is possible that primate centrum surface area does not vary proportionally to overall body size yet varies proportionally in reference to overall vertebral size. If centrum surface area is more size "responsive" to increasing spinal load than are the other structural features of vertebrae, the more direct comparison afforded by application of the vertebral geomean may detect that signal whereas comparison by gross body mass may not. Regression slopes of CSA on geomean for L1, L2, PL, LL and S1 in this study range from 2.42 to 2.94, well above the slope of isometry. That the largest of all living primates expresses further intraspecific allometry (sexual dimorphism) with respect to large male vertebral body size is not necessarily surprising.

Both male and female hylobatids have, for their respective geomean sizes, larger centrum surface areas at all vertebral levels than predicted by comparative regression. Sexes significantly differ in mediolateral breadth of the centrum at three of the five lumbar levels (Bonferroni sequential procedure), where mean male values exceed those of females. This phenomenon is not allometric as *Hylobates lar* is monomorphic in overall body size. Nor is it phylogenetic, for although the positive sexual dimorphism of the gibbon also characterizes humans (see Tables 3.3, 3.4, and 3.5, Chapter 3), it is not characteristics of all the hominoid taxa investigated here. Furthermore, gibbon lumbopelvic sexual dimorphism, while predicted in this study, appears functionally unrelated to obstetric load, as none of the sex differences indicate increased resistance to load-bearing stress among females, only among males.

What then accounts for the gibbon's preponderance of lumbopelvic sexual dimorphism among the primates in this comparative analysis? The first explanatory consideration lies in the sample constituents. Sample sizes for *Hylobates lar* males and females are relatively robust. So, while in comparison to the other primate taxa within the analysis, *Hylobates* is distinguished by its degree of sexual dimorphism, parent populations of the comparative taxa may be more sexually dimorphic than the study suggests. This point is particularly relevant to the other orthograde species, *Indri indri* and *Propithecus verreauxi* whose sample sizes were among the smallest. However, *Pan troglodytes*, a semi-orthograde species is represented by male and female samples of similar size to *Hylobates*. Tests of sexual dimorphism identified but one Bonferroni significant result for *Pan.*

In the absence of functional differences in male and female vertebral morphology, body size monomorphism should be equally reflected in similar vertebral size and shape within the sexes. The fact that medio-lateral breadth differs significantly in gibbon males and females along three of the five lumbar levels, indicates some degree of spinal loading differential between the sexes. Although the other features that significantly differ in gibbons, centrum surface area, pedicle cross-sectional area and interfacet breadth, are not as pervasive throughout the lumbar column, they do suggest a possible explanation for the large relative breadth of male centra related to spinal loading.

Behavioral data from field studies demonstrate that gibbon locomotor behaviors differ by sex, and given the ballistic ricochetal nature of gibbon suspensory travel, the spinal loading forces associated with brachiation may explain, to some degree, the robusticity in male centra identified in this analysis. Reichard and Sommer (1997) reported that among eleven groups of Thailand *Hylobates lar* 61% of observed encounters between groups involved chases during which all adult and subadult males actively participated. These chase-encounters were almost exclusively male-centered, as male-male interactions constituted 90% of all inter-group chases. Bartlett (2003) recently reported that 56% of intergroup encounters between *Hylobates lar* groups were agonistic involving rapid chases, principally between adult males.

The relatively large mediolateral breadth of *Hylobates lar* sexes may be functionally related to locomotor specialization. During gibbon brachiation, unilateral contraction of the iliocostalis muscle directs the orthograde torso toward the supporting forelimb via lateral flexion (Shapiro, 1991). As a determinant of gibbon gait, lateral spinal flexion routinely loads the vertebral body at its lateral margins. Mediolateral elongation of the vertebral body in *Hylobates lar* may be an adaptation to resist bending stress generated by gibbon forelimb suspensory locomotion. If the energetic intergroup agonistic behaviors, whether territory or mate defense in nature, so characteristic of *Hylobates lar* are exclusively male behaviors, selection pressures related to spinal loading biomechanics may be a factor in gibbon lumbopelvic sexual dimorphism and explain why male centra are even more robust than those of females. Centrum loading during explosive ricochetal brachiation would exacerbate bending stress on the lateral margins of the lumbar vertebral body. In this manner a functional element of gibbon social behavior may be a selection factor in anatomical adaptation. Testing of a formal hypothesis relating sex-specific spinal loading patterns to male defense behaviors in *Hylobates lar* would be possible through field application of sonomicrometry, which measures strain, length, area, thickness, volume, and geometry in muscle function. Recently modified for portability in the study of dynamic behavior in horses (Hoyt et al., 2005), further refinement of sonometric technology into smaller units holds promise for primate locomotor field study and may soon provide a method to directly quantify relationships between musculoskeletal function and positional behavior.

CONCLUSIONS AND SUMMARY

This study investigated the hypothesis that the degree of sexual dimorphism in load bearing features of the lumbar and sacral vertebrae would be relatively greater in orthograde primates than in pronograde primates. The prediction derives from a larger set of hypotheses that attempt to explain aspects of human lumbopelvic sexual dimorphism as adaptations to obstetric load. An important question in the larger investigation is whether human obstetric load dimorphism is a functional consequence of general orthogrady in primates or is a more positional specific phenomenon. In this analysis then, it was predicted that obstetric load in orthograde contexts impacts the functional morphology of lumbar and sacral vertebrae. In humans, male and female spinal loading patterns differ, with females carrying a greater proportion of the upper body load along the spine's dorsal pillar.

In this comparative primate sample no significant differences in dorsal pillar loading was evidenced in relative size and shape of vertebrae by sex. Obstetric load borne by nonhuman primates, orthograde, semi-orthograde and pronograde alike, does not appear to generate load distribution or load resistance in any identifiable pattern in the lumbopelvic complex of nonhuman primates. This comparative morphometric study of nonhuman primates places the analysis of human lumbopelvic sexual dimorphism into a broader phylogenetic and evolutionary context. In contrast to nonhuman primates, shape sexual dimorphism predominates the human lumbopelvic complex (Chapter 3). Females present a longer series of dorsally wedged lumbar vertebrae accompanied by greater prezygapophyseal obliquity. These features along with postural and locomotor adjustments in lumbar lordosis and pelvic tilt during pregnancy (Chapter 2) demonstrate a close functional relationship between the human female pattern of lumbar lordosis and obstetric loading. Although humans are not unique in their habitual use of orthograde postures and locomotion, they are distinct among all primates in their degree of lumbopelvic sexual dimorphism in features related to upper body load.

Sex differences are present in few taxa, the semi-orthograde eastern lowland gorilla (*Gorilla gorilla gaueri*) and the orthograde white-handed gibbon (*Hylobates lar*) whose males present relatively large centra surface areas, the major load bearing structures of the vertebral column. Because there are no anatomical or functional signals that the female lumbopelvic complex is adapted to manage obstetric load in the comparative species, traits unique to males are interpreted to be 1) in *Gorilla gorilla gaueri* a positive allometric effect of overall body size dimorphism on the relative size and shape of vertebral centra, and 2) in *Hylobates lar* a possible correlate to disproportionately high levels of male-male chase behavior, during which relatively strong bending force is applied through segmental alignment and iliocostalis contractive load stress on the vertebral body, particularly in lateral flexion during ricochetal brachiation. No pattern of orthograde spinal loading by sex is identified in the analysis.

Table 4.1. Sampled taxa

Sample taxa	Species abbreviation	CMNH	MCZ	NMNH	AMNH	MHNP	NNML	AIM	RMCA	MNB	Total
Hylobates lar lar	*Hl*		16/15								16/15
Indri indri	*Ii*						1/1			6/1	7/2
Propithecus verreauxi	*Pv*		0/1			1/1				3/0	4/2
Pan troglodytes schweinfurthii	*Pt*	8/6			3/0				3/4		14/10
Pongo pygmaeus	*Pp*	0/1	2/2	3/3	1/1			1/2		1/0	8/9
Gorilla gorilla graueri	*Gg*								7/6		7/6
Ateles geoffroyi	*Ag*	1/2						2/2	0/1		3/5
Alouatta seniculus	*As*						3/5	1/0			4/5
Macaca fascicularis	*Mf*		10/10					1/3			11/13
		9/9	28/28	3/3	4/1	1/1	4/6	5/7	10/11	10/1	74/67

CMNH = Cleveland Museum of Natural History; MCZ = The Museum of Comparative Zoology, Harvard; NMNH = National Museum of Natural History, Washington DC; AMNH = American Museum of Natural History, NY; MHNP = Muséum d'Histoire Naturelle, Paris; NNML = National Natuurhisorisch Meseum Leiden, Leiden; AIM = Anthropologisches Institut und Museum, Zurich; RMCA = Royal Museum for Central Africa, Tervuren, Belgium' MNB = Museum National, Berlin

Sample sizes are reported as males/females

Table 4.2. Positional category and body mass of comparative taxa

Positional category	Species	Body mass (kg) Male	Female
orthograde	*Hylobates lar*	5.90	5.34
orthograde	*Indri indri*	5.83	6.84
orthograde	*Propithecus verreauxi*	3.70	4.28
semi-orthograde	*Pan trog. schwein.*	42.70	33.70
semi-orthograde	*Pongo pygmaeus*	78.50	35.80
semi-orthograde	*Gorilla gorilla graueri*	175.20	71.00
semi-orthograde	*Ateles geoffroyi*	9.11	8.44
pronograde	*Aloutta seniculus*	6.69	5.21
pronograde	*Macaca fascicularis*	5.36	3.59

Body mass from Smith and Jungers (1997).

Table 4.3. Results of linear regressions on natural logarithm transformed data [1]

y variable x variable	Geomean Body Mass	Sacral Breadth Geomean	CSA[2] L1 Geomean	CSA L2 Geomean	CSA PL Geomean	CSA LL Geomean	CSA Sacrum Geomean
Correlation (*r*)	0.981	0.970	0.985	0.982	0.990	0.990	0.990
Observations	18	18	18	16	18	18	18
P value	< 0.0000	< 0.0000	< 0.0000	< 0.0000	< 0.0000	< 0.0000	< 0.0000
Intercept	1.524	1.502	-1.432	-0.952	-0.390	-0.310	-0.011
Slope (*k*)	0.302	1.064	2.940	2.775	2.603	2.581	2.420
k lower 95%	0.272	0.932	2.679	2.485	2.417	2.395	2.247
k upper 95%	0.336	1.215	3.226	3.099	2.803	2.782	2.606
Mean (y)	2.522	3.936	5.289	5.195	5.560	5.591	5.521
Standard deviation (*y*)	1.225	0.394	1.089	0.905	0.964	0.956	0.896
Mean (x)	2.286	2.286	2.286	2.215	2.286	2.286	2.286
Standard deviation (*x*)	0.370	0.370	0.370	0.326	0.370	0.370	0.370

[1] Regressions include all comparative taxa except those drawn from Lumbar Level 2, which lacks *Gorilla gorilla gaueri.* Its three lumbar levels were designated as L1, PL and LL.

[2] CSA indicates centrum surface area

Table 4.4. Results of linear regressions on natural logarithm transformed data [1]

y variable x variable	PSA[2] L1 Geomean	PSA L2 Geomean	PSA PL Geomean	PSA LL Geomean	PSA Sacrum Geomean
Correlation (*r*)	0.982	0.980	0.977	0.974	0.963
Observations	18	16	18	18	18
P value	< 0.0000	< 0.0000	< 0.0000	< 0.0000	< 0.0000
Intercept	-1.067	-1.015	-0.481	-0.321	-0.559
Slope (*k*)	2.055	2.097	1.888	1.803	1.855
k lower 95%	1.854	1.868	1.681	1.594	1.599
k upper 95%	2.277	2.354	2.121	2.039	2.153
Mean (y)	3.631	3.629	3.835	3.801	3.682
Standard deviation (*y*)	0.761	0.684	0.699	0.668	0.687
Mean (x)	2.286	2.215	2.286	2.286	2.286
Standard deviation (*x*)	0.370	0.326	0.370	0.370	0.370

[1] Regressions include all comparative taxa except those drawn from Lumbar Level 2, which lacks *Gorilla gorilla gaueri.* Its three lumbar levels were designated as L1, PL and LL.

[2] PSA indicates prezygapophyseal surface area

Table 4.5. Results of linear regressions on natural logarithm transformed data [1]

y variable x variable	PedXS[2] L1 Geomean	PedXs L2 Geomean	PedXS PL Geomean	PedXS LL Geomean
Correlation (*r*)	0.987	0.979	0.987	0.988
Observations	18	16	18	18
P value	< 0.0000	< 0.0000	< 0.0000	< 0.0000
Intercept	-1.881	-2.089	-1.802	-2.010
Slope (*k*)	2.491	2.598	2.526	2.649
k lower 95%	2.287	2.303	2.314	2.435
k upper 95%	2.712	2.930	2.758	2.882
Mean (y)	3.813	3.665	3.973	4.045
Standard deviation (*y*)	0.922	0.847	0.936	0.981
Mean (x)	2.286	2.215	2.286	2.286
Standard deviation (*x*)	0.370	0.326	0.370	0.370

[1] Regressions include all comparative taxa except those drawn from Lumbar Level 2, which lacks *Gorilla gorilla gaueri* . Its three lumbar levels were designated as L1, PL and LL.

[2] PedXS indicates pedicle cross-sectional area

Table 4.6. Sacral auricular area, mean and (standard deviation) by sex, raw area and size-adjusted geomean area [1] in the orthograde primates

		Hylobates lar lar	*Indri indri*	*Propithecus verreauxi*
Auricular variable		mean area (std dev)	mean area (std dev)	mean area (std dev)
Raw area [2]	male	145.76 (17.15)	159.36 (9.23)	128.19 (28.24)
	female	143.02 (16.79)	167.93 (na)	197.15 (0.381)
Size-adjusted area [3]	male	0.88 (0.072)	0.99 (0.065)	0.96 (0.065)
	female	0.87 (0.075)	0.93	1.03 (0.142)
	p value	= 0.9212	= 0.8026	= 0.7728

[1] Two-tailed test of significance used, pairwise correlation
[2] Raw area reported in mm^2
[3] Size-adjusted area unitless, auricular area$^{1/2}$/geomean

Table 4.7. Sacral auricular area, mean and (standard deviation) by sex, raw area and size-adjusted geomean area [1] in the semi-orthograde primates

		Pan troglodytes	*Pongo pygmaeus*	*Gorilla gorilla*	*Ateles geoffroyi*
Auricular variable		mean area (std dev)	mean area (std dev)	mean area (std dev)	mean area (std dev)
Raw area [2]	male	843.14 (15.93)	901.32 (112.61)	807.54	501.84 (69.76)
	female	548.38 (22.89)	532.77 (117.95)	704.15 (53.3)	657.57 (69.81)
Size-adjusted area [3]	male	1.72 (0.22)	1.68 (0.17)	1.52	2.98 (0.47)
	female	1.46 (0.22)	1.55 (0.11)	1.52 (0.11)	2.94 (2.88)
	p value	= 0.2159	= 0.5637	= 0.6547	= 0.6985

[1] Two-tailed test of significance used, pairwise correlation
[2] Raw area reported in mm^2
[3] Size-adjusted area unitless, auricular area$^{1/2}$/geomean

Table 4.8. Sacral auricular area, mean and (standard deviation) by sex, raw area and size-adjusted geomean area [1] in the pronograde primates

		Alouatta seniculus	*Macaca fascicularis*
Auricular variable		mean area (std dev)	mean area (std dev)
Raw area [2]	male	312.64 (27.63)	318.26 (-)
	female	355.20 (82.94)	290.48 (22.20)
Size-adjusted area [3]	male	2.15 (0.52)	1.87 (-)
	female	2.29 (0.34)	1.88 (0.15)
	p value	= 0.3865	= 0.5403

[1] Two-tailed test of significance used, pairwise correlation
[2] Raw area reported in mm^2
[3] Size-adjusted area unitless, auricular area$^{1/2}$/geomean

Table 4.9. *Hylobates lar lar* lumbopelvic sexual dimorphism: magnitude and results of Wilcoxon Rank Sums test [1] on size adjusted variates

		Magnitude of sexual dimorphism (probability)					
	(n)	Lumbar Level Lumbar vertebrea					Sacrum
Variable	(M,F)	1	2	3	4	5	
Centrum wedging	(16,15)	- 0.217 (ns)	- **2.223**	- 1.403 (ns)	- 1.374 (ns)	- **2.634**	-
Centrum surface area	(16,15)	- 1.640 (ns)	- **2.075**	- 1.798 (ns)	- **1.996**	- **1.950***	1.237 (ns)
Centrum medio-lateral breadth	(16,15)	- **2.908***	- **2.495***	- **2.593**	- **2.763***	- 1.805 (ns)	- 1.613 (ns)
Transverse process angle	(16,15)	- 0.223 (ns)	- 0.219 (ns)	- 0.852 (ns)	- 1.763 (ns)	- 1.158 (ns)	-
Transverse process length	(16,15)	- 1.362 (ns)	- 1.362 (ns)	0.217 (ns)	- 0.296 (ns)	- 0.731 (ns)	-
Pedicle cross-sectional area	(16,15)	- 1.542 (ns)	- **3.380***	- **2.668**	- 1.552 (ns)	0.507 (ns)	-
Prezygapophyseal surface area	(16,15)	1.541 (ns)	0.455 (ns)	0.376 (ns)	- 0.178 (ns)	- 0.913 (ns)	- 1.013 (ns)
Prezygapophyseal angle	(16,15)	0.198 (ns)	1.170 (ns)	- 0.644 (ns)	1.121 (ns)	- 0.229 (ns)	- 0.243 (ns)
Interfacet breadth	(16,15)	- 1.231 (ns)	- 1.030 (ns)	- 1.068 (ns)	- 0.989 (ns)	- **2.752***	1.231 (ns)
Sacral body breadth	(16,15)	-	-	-	-	-	1.843 (ns)

1 Two-tailed test of significance. M, male; F, female;

Negative scores indicate male mean > female mean.

Bold faced type indicates original significance of $P < 0.05$. Asterisks indicate significance reached sequential Bonferroni adjustment.

ns = non significance

Table 4.10. *Indri indri* lumbopelvic sexual dimorphism: magnitude and results of Wilcoxon Rank Sums test [1] on size adjusted variates

		Magnitude of sexual dimorphism (probability)					Magnitude of sexual dimorphism (probability)				
	(n)	Lumbar Level Lumbar vertebrea					Lumbar Level Lumbar vertebrea				Sacrum
Variable	(M,F)	1	2	3	4	5	6	7	8	9	
Centrum wedging	(7,2)	1.464 (ns)	1.464 (ns)	- 1.025 (ns)	- 1.903 (ns)	- 0.439 (ns)	- 1.318 (ns)	- 0.439 (ns)	- 0.439 (ns)	- 1.317 (ns)	-
Centrum surface area	(7,2)	- 0.439 (ns)	1.318 (ns)	1.025 (ns)	- 0.732 (ns)	0.146 (ns)	0.146 (ns)	0.732 (ns)	1.025 (ns)	0.439 (ns)	0.242 (ns)
Centrum medio-lateral breadth	(7,2)	- 1.610 (ns)	0.739 (ns)	0.146 (ns)	- 1.610 (ns)	- 1.025 (ns)	- 1.317 (ns)	- 0.732 (ns)	0.146 (ns)	- 0.146 (ns)	0.732 (ns)
Transverse process angle	(7,2)	0.272 (ns)	- 0.441 (ns)	0.769 (ns)	0.376 (ns)	0.135 (ns)	0.180 (ns)	- 0.441 (ns)	- 0.441 (ns)	0.146 (ns)	-
Transverse process length	(7,2)	-	0.663 (ns)	- 0.732 (ns)	- 1.023 (ns)	- 1.317 (ns)	- 0.732 (ns)	0.146 (ns)	0.439 (ns)	1.025 (ns)	-
Pedicle cross-sectional area	(7,2)	- 1.025 (ns)	- 1.620 (ns)	- 0.732 (ns)	0.146 (ns)	0.439 (ns)	0.146 (ns)	0.146 (ns)	0.439 (ns)	1.317 (ns)	-
Prezygapophyseal surface area	(7,2)	- 1.317 (ns)	- 0.732 (ns)	1.146 (ns)	1.317 (ns)	0.732 (ns)	0.732 (ns)	0.439 (ns)	0.146 (ns)	- 0.146 (ns)	1.903 (ns)
Prezygapophyseal angle	(7,2)	- 1.317 (ns)	- 0.732 (ns)	- 0.146 (ns)	1.317 (ns)	0.732 (ns)	0.732 (ns)	0.439 (ns)	0.146 (ns)	- 0.146 (ns)	-
Interfacet breadth	(7,2)	- 1.317 (ns)	- 0.732 (ns)	- 0.146 (ns)	- 0.146 (ns)	- 0.146 (ns)	- 0.146 (ns)	0.146 (ns)	0.146 (ns)	1.317 (ns)	-
Sacral body breadth	(7,2)	-	-	-	-	-	-	-	-	-	0.732 (ns)

1 Two-tailed test of significance. M, male; F, female; ns, $P > 0.05$.

Negative scores indicate male mean > female mean

Bold faced type indicates original significance of $P < 0.05$. Asterisks indicate significance reached sequential Bonferroni adjustment.

ns = non significance

Table 4.11. *Propithecus verreauxi* lumbopelvic sexual dimorphism: magnitude and results of Wilcoxon Rank Sums test [1] on size adjusted variates

		Magnitude of sexual dimorphism (probability)					Magnitude of sexual dimorphism (probability)				
	(n)	Lumbar Level Lumbar vertebrea					Lumbar Level Lumbar vertebrea				Sacrum
Variable	(M,F)	1	2	3	4	5	6	7	8	9	
Centrum wedging	(5,2)	0.694 (ns)	- 0.581 (ns)	1.253 (ns)	0.092 (ns)	- 0.959 (ns)	- 1.812 (ns)	- 1.386 (ns)	1.039 (ns)	- 1.187 (ns)	-
Centrum surface area	(5,2)	0.231 (ns)	0.194 (ns)	- 1.462 (ns)	- 1.004 (ns)	- 0.959 (ns)	0.107 (ns)	0.107 (ns)	0.095 (ns)	- 0.274 (ns)	, 0.959 (ns)
medio-lateral breadth	(5,2)	- 0.000 (ns)	- 1.173 (ns)	- 1.187 (ns)	- 0.325 (ns)	- 0.162 (ns)	- 0.325 (ns)	- 0.000 (ns)	- 0.325 (ns)	0.162 (ns)	, 1.137 (ns)
Transverse process angle	(5,2)	-	-	- 1.315 (ns)	- 0.000 (ns)	- 0.000 (ns)	0.959 (ns)	0.320 (ns)	- 0.475 (ns)	0.387 (ns)	-
Transverse process length	(5,2)	-	-	0.276 (ns)	0.456 (ns)	0.081 (ns)	0.081 (ns)	- 0.407 (ns)	- 0.162 (ns)	- 0.491 (ns)	-
Pedicle cross-sectional area	(5,2)	0.232 (ns)	0.581 (ns)	- 0.367 (ns)	1.004 (ns)	- 0.107 (ns)	- 0.107 (ns)	- 0.533 (ns)	1.039 (ns)	1.173 (ns)	-
Prezygapophyseal surface area	(5,2)	- 0.232 (ns)	1.743 (ns)	- 0.122 (ns)	- 0.857 (ns)	- 0.107 (ns)	- 0.107 (ns)	- 0.107 (ns)	- 0.320 (ns)	- 0.107 (ns)	0.367 (ns)
Prezygapophyseal angle	(5,2)	- 0.354 (ns)	- 0.171 (ns)	- 0.496 (ns)	- 0.375 (ns)	0.146 (ns)	- 0.886 (ns)	0.550 (ns)	- 0.644 (ns)	- 0.300 (ns)	-
Interfacet breadth	(5,2)	0.091 (ns)	0.000 (ns)	- 1.624 (ns)	- 0.456 (ns)	- 0.650 (ns)	- 0.162 (ns)	- 0.974 (ns)	- 1.137 (ns)	0.162 (ns)	-
Sacral body breadth	(5,2)	-	-	-	-	-	-	-	-	-	1.790 (ns)

1 Two-tailed test of significance. M, male; F, female; ns, $P > 0.05$.

Negative scores indicate male mean > female mean

Bold faced type indicates original significance of $P < 0.05$. Asterisks indicate significance reached sequential Bonferroni adjustment.

ns = non significance

Table 4.12. *Gorilla gorilla gaueri* lumbopelvic sexual dimorphism: magnitude and results of Wilcoxon Rank Sums test [1] on size adjusted variates

		Magnitude of sexual dimorphism (probability)			
	(n)	Lumbar vertebrea			Sacrum
Variable	(M,F)	1	2	3	
Centrum wedging	(7,6)	- 0.357 (ns)	- 0.929 (ns)	- 0.080 (ns)	-
Centrum surface area	(7,6)	- **2.786****	- **2.643****	- **2.322**	- **2.100***
Centrum medio-lateral breadth	(7,6)	- **2.786****	- **2.643****	- **2.214**	- 0.400 (ns)
Transverse process angle	(7,6)	0.530 (ns)	- **2.206**	- 0.185 (ns)	-
Transverse process length	(7,6)	- 1.274 (ns)	- **2.648**	1.004 (ns)	-
Pedicle cross-sectional area	(7,6)	- 1.500 (ns)	- 1.357 (ns)	- 1.500 (ns)	-
Prezygapophyseal surface area	(7,6)	0.071 (ns)	0.929 (ns)	1.786 (ns)	- 0.320 (ns)
Prezygapophyseal angle	(7,6)	1.362 (ns)	1.462 (ns)	0.741 (ns)	- 0.861 (ns)
Interfacet breadth	(7,6)	- 1.200 (ns)	- 0.500 (ns)	0.786 (ns)	-
Sacral body breadth	(7,6)	-	-	-	0.487 (ns)

1 Two-tailed test of significance. M, male; F, female; ns, P > 0.05.

Bold faced type indicates original significance of $P < 0.05$. Asterisks indicate significance reached sequential Bonferroni adjustment.

ns = non significance

Table 4.13. *Pongo pygmaeus* lumbopelvic sexual dimorphism: magnitude and results of Wilcoxon Rank Sums test [1] on size adjusted variates

		Magnitude of sexual dimorphism (probability)				
	(n)	Lumbar vertebrea				Sacrum
Variable	(M,F)	1	2	3	4	
Centrum wedging	(8,9)	- 1.101 (ns)	- 0.433 (ns)	- 1.017 (ns)	- 0.722 (ns)	-
Centrum surface area	(8,9)	- 1.684 (ns)	- 1.491 (ns)	- 1.203 (ns)	- 1.203 (ns)	0.625 (ns)
Centrum medio-lateral breadth	(8,9)	1.876 (ns)	- 0.722 (ns)	- 0.722 (ns)	- 1.876 (ns)	0.433 (ns)
Transverse process angle	(8,9)	- 0.097 (ns)	0.482 (ns)	0.097 (ns)	0.048 (ns)	-
Transverse process length	(8,9)	1.491 (ns)	0.529 (ns)	0.626 (ns)	1.010 (ns)	-
Pedicle cross-sectional area	(8,9)	- 1.010 (ns)	0.048 (ns)	**2.069**	0.914 (ns)	-
Prezygapophyseal surface area	(8,9)	0.144 (ns)	- 1.876 (ns)	- 0.144 (ns)	- 1.684 (ns)	- 1.300 (ns)
Prezygapophyseal angle	(8,9)	- 0.877 (ns)	0.194 (ns)	1.256 (ns)	0.289 (ns)	- 0.097 (ns)
Interfacet breadth	(8,9)	- 0.529 (ns)	1.300 (ns)	0.433 (ns)	- 0.144 (ns)	-
Sacral body breadth	(8,9)	-	-	-	-	- **1.972***

[1] Two-tailed test of significance. M, male; F, female; ns, P > 0.05.
Bold faced type indicates original significance of *P* < 0.05. Asterisks indicate significance reached sequential Bonferroni adjustment.
ns = non significance

Table 4.14. *Pan troglodytes schweinfurthii* lumbopelvic sexual dimorphism: magnitude and results of Wilcoxon Rank Sums test ^{1} on size adjusted variates

		Magnitude of sexual dimorphism (probability)				
	(n)	Lumbar vertebrea				Sacrum
Variable	(M,F)	1	2	3	4	
Centrum wedging	(14,10)	- 0.381 (ns)	- 0.746 (ns)	0.797 (ns)	- 1.054 (ns)	-
Centrum surface area	(14,10)	- 1.142 (ns)	- 1.672 (ns)	- **2.032***	- 0.489 (ns)	- 0.077 (ns)
Centrum medio-lateral breadth	(14,10)	- 1.260 (ns)	- 1.105 (ns)	0.180 (ns)	- 0.540 (ns)	- 0.231 (ns)
Transverse process angle	(14,10)	0.249 (ns)	- 0.550 (ns)	0.900 (ns)	1.281 (ns)	-
Transverse process length	(14,10)	- 1.191 (ns)	- 1.068 (ns)	1.605 (ns)	- 0.299 (ns)	-
Pedicle cross-sectional area	(14,10)	- 0.263 (ns)	0.900 (ns)	- 0.746 (ns)	- 0.694 (ns)	-
Prezygapophyseal surface area	(14,10)	- 0.439 (ns)	- 1.363 (ns)	- 0.232 (ns)	- 0.694 (ns)	- 0.849 (ns)
Prezygapophyseal angle	(14,10)	- 0.792 (ns)	- 0.026 (ns)	- 1.775 (ns)	0.180 (ns)	- 0.097 (ns)
Interfacet breadth	(14,10)	- **2.898***	- 0.849 (ns)	0.695 (ns)	- 0.437 (ns)	-
Sacral body breadth	(14,10)	-	-	-	-	0.129 (ns)

1 Two-tailed test of significance. M, male; F, female; ns, P > 0.05.
Bold faced type indicates original significance of $P < 0.05$. Asterisks indicate significance reached sequential Bonferroni adjustment.
ns = non significance

Table 4.15. *Ateles geoffroyi* lumbopelvic sexual dimorphism: magnitude and results of Wilcoxon Rank Sums test[1] on size adjusted variates

		Magnitude of sexual dimorphism (probability)					
	(n)	Lumbar vertebrea					Sacrum
Variable	(M,F)	1	2	3	4	5	
Centrum wedging	(3,5)	- 0.596 (ns)	- 0.894 (ns)	- 1.410 (ns)	- 0.596 (ns)	- 0.596 (ns)	-
Centrum surface area	(3,5)	0.000 (ns)	0.298 (ns)	0.298 (ns)	- 0.298 (ns)	0.298 (ns)	- 0.000 (ns)
Centrum medio-lateral breadth	(3,5)	1.193 (ns)	0.597 (ns)	0.298 (ns)	0.597 (ns)	0.298 (ns)	1.193 (ns)
Transverse process angle	(3,5)	rib bearing	1.746 (ns)	0.151 (ns)	- 0.596 (ns)	- **1.950***	-
Transverse process length	(3,5)	rib bearing	1.107 (ns)	- 0.750 (ns)	- 1.050 (ns)	- **1.950***	-
Pedicle cross-sectional area	(3,5)	- 0.000 (ns)	0.298 (ns)	0.298 (ns)	- 1.491 (ns)	- 1.789 (ns)	-
Prezygapophyseal surface area	(3,5)	1.193 (ns)	0.000 (ns)	- 0.597 (ns)	- 0.298 (ns)	- 0.000 (ns)	0.000 (ns)
Prezygapophyseal angle	(3,5)	1.193 (ns)	1.789 (ns)	1.500 (ns)	0.611 (ns)	0.894 (ns)	-
Interfacet breadth	(3,5)	1.193 (ns)	0.596 (ns)	0.298 (ns)	0.596 (ns)	0.298 (ns)	-
Sacral body breadth	(3,5)	-	-	-	-	-	0.298 (ns)

1 Two-tailed test of significance. M, male; F, female; ns, P > 0.05.

Bold faced type indicates original significance of $P < 0.05$. Asterisks indicate significance reached sequential Bonferroni adjustment.

ns = non significance

Table 4.16. *Macaca fascicularis* lumbopelvic sexual dimorphism: magnitude and results of Wilcoxon Rank Sums test [1] on size adjusted variates

		Magnitude of sexual dimorphism (probability)									
	(n)			Lumbar Level	Lumbar vertebrea			Lumbar Level	Lumbar vertebrea		Sacrum
Variable	(M,F)	1	2	3	4	5	6	7	8	9	
Centrum wedging	(11,13)	- 1.275 (ns)	- 1.448 (ns)	- 0.579 (ns)	- 0.753 (ns)	0.000 (ns)	- 1.738 (ns)	- 1.564 (ns)	- 0.116 (ns)	- 0.522 (ns)	-
Centrum surface area	(11,13)	**2.995****	1.159 (ns)	**2.202**	**2.375**	1.506 (ns)	1.506 (ns)	1.043 (ns)	1.448 (ns)	**2.028***	1.159 (ns)
Centrum medio-lateral breadth	(11,13)	1.479 (ns)	- 0.058 (ns)	0.640 (ns)	0.871 (ns)	- 0.872 (ns)	- 0.464 (ns)	- 0.726 (ns)	- 0.842 (ns)	- 0.435 (ns)	- 0.029 (ns)
Transverse process angle	(11,13)	rib bearing	rib bearing	- 1.106 (ns)	- 0.031 (ns)	**2.238**	0.125 (ns)	- 0.929 (ns)	- 0.808 (ns)	- 1.089 (ns)	-
Transverse process length	(11,13)	rib bearing	rib bearing	- 0.151 (ns)	0.609 (ns)	0.435 (ns)	- 0.261 (ns)	- 0.898 (ns)	- 1.594 (ns)	- **2.115**	-
Pedicle cross-sectional area	(11,13)	- 1.043 (ns)	0.058 (ns)	1.072 (ns)	- 1.623 (ns)	- 1.159 (ns)	- 1.680 (ns)	- 0.058 (ns)	0.232 (ns)	- 0.232 (ns)	-
Prezygapophyseal surface area	(11,13)	- 0.523 (ns)	- 0.339 (ns)	- 0.523 (ns)	- 0.729 (ns)	- 0.954 (ns)	- 0.954 (ns)	1.877 (ns)	1.166 (ns)	- 0.892 (ns)	-
Prezygapophyseal angle	(11,13)	- 0.058 (ns)	- 0.986 (ns)	- 0.290 (ns)	- 0.987 (ns)	- 1.654 (ns)	- 0.031 (ns)	- 1.103 (ns)	- 0.639 (ns)	- 1.336 (ns)	- 0.524 (ns)
Interfacet breadth	(11,13)	- 1.366 (ns)	- 0.985 (ns)	- 1.102 (ns)	- 1.798 (ns)	- 1.770 (ns)	- 0.962 (ns)	0.029 (ns)	0.058 (ns)	- 1.394 (ns)	-
Sacral body breadth	(11,13)	-	-	-	-	-	-	-	-	-	- **2.464**

1 Two-tailed test of significance. M, male; F, female; ns, P > 0.05.

Bold faced type indicates original significance of *P* < 0.05. Asterisks indicate significance reached sequential Bonferroni adjustment.

ns = non significance

Table 4.17. *Alouatta seniculus* lumbopelvic sexual dimorphism: magnitude and results of Wilcoxon Rank Sums test [1] on size adjusted variates

		Magnitude of sexual dimorphism (probability)							
	(n)	Lumbar Level		Lumbar vertebrea			Lumbar Level		Sacrum
Variable	(M,F)	1	2	3	4	5	6	7	
Centrum wedging	(4,5)	1.022 (ns)	1.022 (ns)	**2.307**	**2.307***	1.225 (ns)	1.225 (ns)	0.612 (ns)	-
Centrum surface area	(4,5)	1.347 (ns)	1.225 (ns)	- 0.612 (ns)	0.857 (ns)	1.022 (ns)	1.347 (ns)	1.225 (ns)	0.857 (ns)
Centrum medio-lateral breadth	(4,5)	1.347 (ns)	- 0.122 (ns)	0.367 (ns)	0.857 (ns)	1.023 (ns)	0.122 (ns)	0.122 (ns)	- 0.492 (ns)
Transverse process angle	(4,5)	rib bearing	rib bearing	- 0.261 (ns)	- 1.476 (ns)	- 0.246 (ns)	0.371 (ns)	- 0.615 (ns)	-
Transverse process length	(4,5)	rib bearing	rib bearing	1.443 (ns)	- 1.620 (ns)	1.491 (ns)	1.591 (ns)	0.000 (ns)	-
Pedicle cross-sectional area	(4,5)	0.123 (ns)	0.612 (ns)	0.857 (ns)	0.612 (ns)	- 0.367 (ns)	- 1.225 (ns)	- 1.225 (ns)	-
Prezygapophyseal surface area	(4,5)	0.123 (ns)	- 0.367 (ns)	1.102 (ns)	- 0.857 (ns)	- 0.159 (ns)	- 0.159 (ns)	- 0.367 (ns)	-
Prezygapophyseal angle	(4,5)	- **2.327**	- **2.337**	- **2.233***	- 0.992 (ns)	- 0.988 (ns)	- 0.372 (ns)	- 0.620 (ns)	1.102 (ns)
Interfacet breadth	(4,5)	- 1.347 (ns)	- 1.837 (ns)	- 1.347(ns)	- 0.367(ns)	- 0.122 (ns)	- 0.612 (ns)	- 0.612 (ns)	-
Sacral body breadth	(4,5)	-	-	-	-	-	-	-	0.612 (ns)

[1] Two-tailed test of significance. M, male; F, female; ns, $P > 0.05$.
Bold faced type indicates original significance of $P < 0.05$. Asterisks indicate significance reached sequential Bonferroni adjustment.
ns = non significance

Table 4.18. Lumbar vertebral wedging by sex for orthograde species: *Hylobates lar, Indri indri* and Propithecus verreauxi. Means reported with (standard deviation) in degrees.

	Female			Male		
Vertebral	*Hylobates lar*	*Indri indri*	*P. verreauxi*	*Hylobates lar*	*Indri indri*	*P. verreauxi*
Level[1]	$n = 15$	$n = 7$	$n = 2$	$n = 16$	$n = 2$	$n = 4$
a		4.56	4.73		4.61	3.49
		(1.35)	(0.03)		(1.11)	(1.07)
b		4.54	0.12		4.58	4.83
		(1.84)	(6.33)		(1.05)	(2.83)
c		4.88	5.35		3.2	3.77
		(1.87)	(1.52)		(2.97)	(1.76)
d		6.19	6.25		2.44	5.01
		(2.54)	(4.93)		(0.46)	(2.55)
e	7.51	4.55	1.81	7.9	3.65	4.49
	(2.80)	(3.39)	(2.62)	(3.25)	(0.72)	(1.81)
f	**6.38***	4.27	1.65	**9.13**	2.79	4.59
	(2.68)	(1.34)	(2.65)	(3.47)	(1.36)	(1.42)
g	7.47	5.33	0.95	8.89	3.77	5.88
	(3.02)	(3.54)	(4.19)	(3.36)	(1.36)	(3.96)
h	5.69	4.26	5.10	7.59	3.57	3.36
	(2.54)	(1.64)	(1.76)	(5.19)	(1.77)	(2.17)
i	**0.97****	4.09	1.18	**4.95**	2.28	3.77
	(4.57)	(2.87)	(3.58)	**(3.04)**	(0.23)	(2.32)

Vertebral Level[1]: levels are listed in order from cranialmost to caudalmost position.

Boldface indicates significant result. Wilcoxon Rank Sums Test, Bonferroni adjusted for multiple tests within taxon.

* indicates $P < 0.05$, ** indicates $P < 0.01$.

Positive angles are kyphotic.

Table 4.19. Lumbar vertebral wedging angle by sex for semi-orthograde species: *Pan troglodytes, Pongo pygmaeus* and *Gorilla gorilla and Ateles geoffroyi. Means reported* with (standard deviation) in degrees.

	Female				Male			
Vertebral	*Pan troglodytes*	*Pongo pygmaeus*	*Gorilla gorilla*	*Ateles geoffroyi*	*Pan troglodytes*	*Pongo pygmaeus*	*Gorilla gorilla*	*Ateles geoffroyi*
Level [1]	*n = 15*	*n = 9*	*n = 6*	*n = 5*	*n = 16*	*n = 8*	*n = 7*	*n = 3*
a				5.04 (2.41)				3.72 (1.93)
b	5.24 (2.13)	5.80 (3.44)		4.60 (3.08)	5.33 (2.99)	3.37 (4.01)		3.13 (3.16)
c	3.91 (2.02)	5.39 (2.26)	1.63 (2.97)	5.62 (1.75)	4.52 (2.23)	5.39 (4.46)	2.20 (1.63)	3.06 (1.11)
d	0.26 (0.14)	4.61 (2.45)	0.88 (0.93)	2.09 (2.66)	0.23 (0.12)	2.81 (4.46)	-1.02 (2.58)	3.03 (2.09)
e	-0.48 (2.08)	1.28 (4.59)	-1.78 (3.81)	7.45 (3.57)	0.24 (1.79)	-1.03 (3.77)	-1.82 (1.20)	4.45 (0.75)

Vertebral Level[1]: levels are listed in order from cranialmost to caudalmost position.

Boldface indicates significant result. Wilcoxon Rank Sums Test, Bonferroni adjusted for multiple tests within taxon.

* indicates $P < 0.01$

Positive angles are kyphotic. Negative angles are lordotic. Vertebrae are transitional, neither kyphotic not lordotic, when -0.5° > angle < 0.5°.

Table 4.20. Lumbar vertebral wedging angle by sex for pronograde species: *Alouatta seniculus* and *Macaca fascicularis. M*eans reported with (standard deviation) in degrees.

	Female		Male	
Vertebral Level [1]	*Macaca fascicularis* *n = 13*	*Alouatta seniculus* *n = 5*	*Macaca fascicularis* *n = 11*	*Alouatta seniculus* *n = 4*
a	11.76 (4.04)		9.28 (5.18)	
b	12.26 (4.54)		9.65 (4.08)	
c	12.67 (3.62)	5.97 (2.14)	14.20 (4.26)	8.32 (2.27)
d	13.97 (2.45)	7.98 (1.38)	12.30 (3.98)	10.21 (2.76)
e	11.36 (6.43)	**6.26*** **(0.92)**	11.45 (2.75)	**8.77** **(0.55)**
f	12.99 (3.23)	**4.39*** **(0.87)**	9.96 (2.70)	**7.19** **(1.02)**
g	7.07 (3.41)	4.17 (1.17)	8.92 (3.34)	5.14 (2.14)
h	6.31 (3.55)	4.13 (1.84)	5.94 (3.37)	4.10 (2.14)
i	3.21 (2.85)	3.25 (1.99)	2.76 (3.86)	3.83 (2.38)

Vertebral Level[1]: levels are listed in order from cranialmost to caudalmost position.

Boldface indicates significant result. Wilcoxon Rank Sums Test, Bonferroni adjusted for multiple tests.

* indicates $P < 0.01$.

Positive angles are kyphotic.

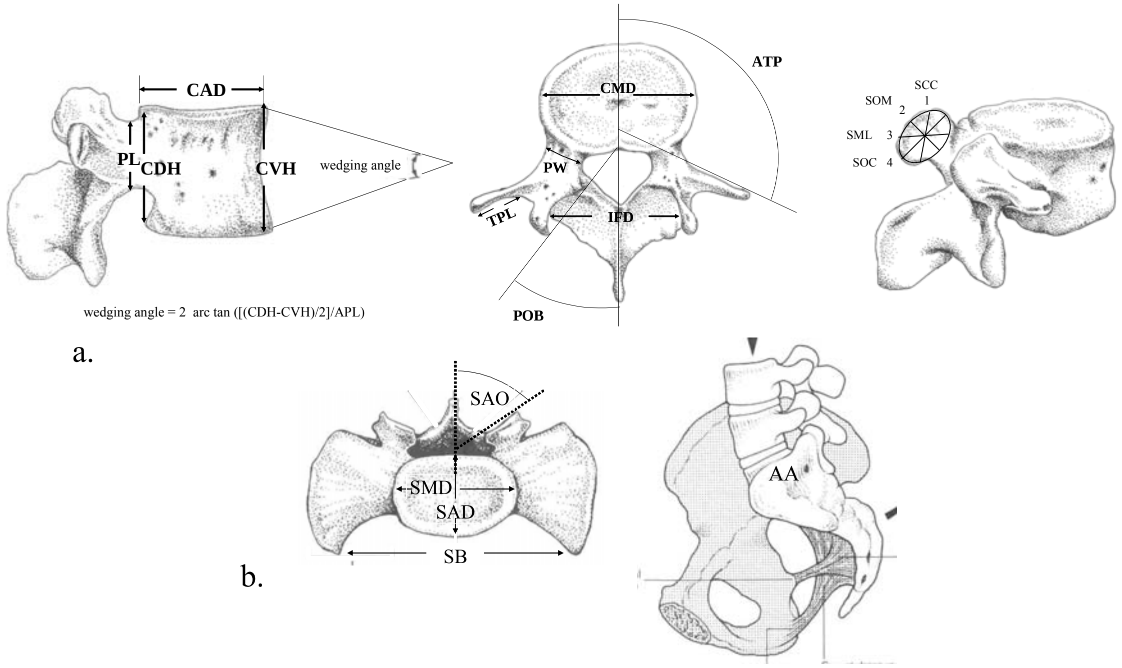


Figure 4.1. Morphometric measurements. a.) Lumbar vertebra. Vertebral body: CAD - Anteroposterior length of centrum cranial surface at midline; CMD - Maximum mediolateral width of centrum cranial surface; CDH - Craniocaudal height of centrum at dorsal midline; CVH - Craniocaudal height of centrum at ventral midline. Pedicle: PL - Minimum craniocaudal length of pedicle; PW - Minimum mediolateral length of pedicle. Transverse process: TPL - Dorsal distance from base of transverse process to process tip; ATP - Angle of transverse process taken from centrum midline to process tip. Zygapophyses: IFD - Linear distance between the most lateral reach of paired prezygapophyses; POB - Angle of prezygapophysis from centrum midline to lateral reach of facet; SCC - Craniocaudal diameter of prezygapophyseal facet; SML - Mediolateral diameter of prezygapophyseal facet; SOC - Oblique craniocaudal diameter of prezygapophyseal facet; SOM - Oblique mediolateral diameter of prezygapophyseal facet. b.) Sacrum: SAD - Anteroposterior length of centrum cranial surface at midline; SMD - Maximum mediolateral width of centrum cranial surface; SB - Maximum mediolateral width on ventral surface; SAO - Angle of sacral prezygapophysis from centrum midline to lateral reach of facet; AA - Area of the auricular surface computed digitally.

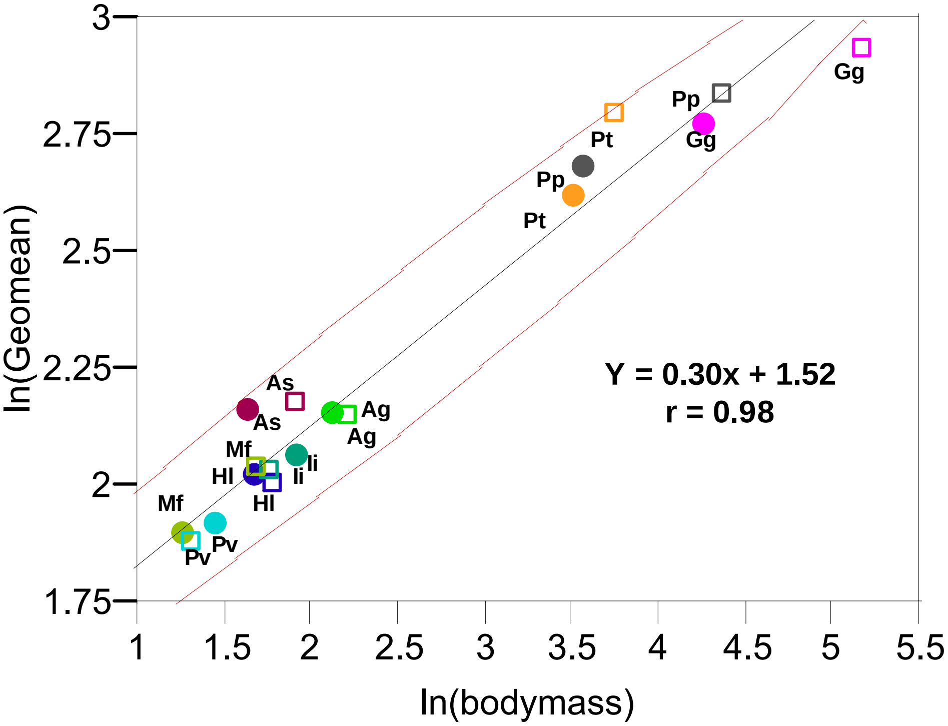


Figure 4.2. Reduced major axis regression of the natural log geometric mean of study species against body mass reported in literature (Smith and Jungers, 1997), transformed to natural log. The regression slope equals isometry (0.30). Density ellipse represents 95% confidence limit. Solid circles female; open squares male.

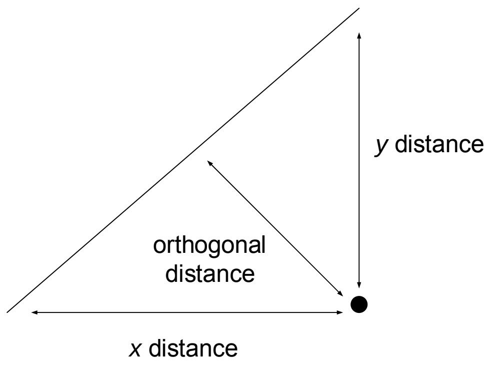
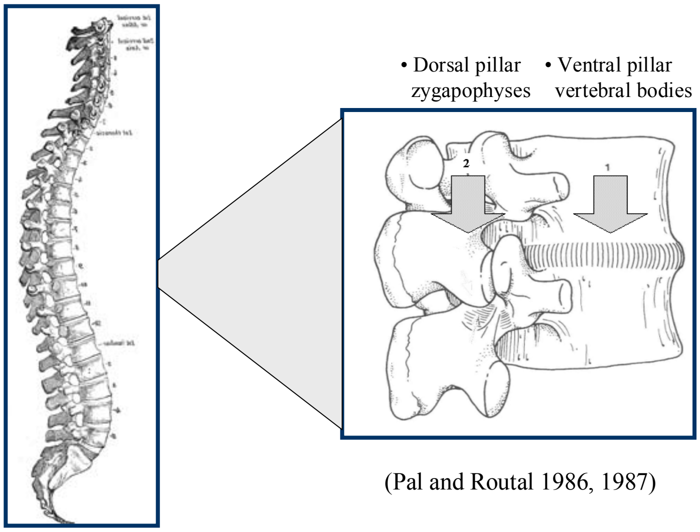


Figure 4.3. Visual representation of Reduced Major Axis (RMA) regression used in the analysis of lumbopelvic variables on the geometric mean as proxy for individual body size. In this case both x and y are assumed to be vulnerable to measurement error.

Two-Pillar Spine Model



(Pal and Routal 1986, 1987)

Figure 4.4. Pair of adjacent lumbar vertebrae, dorsolateral view from right, in anatomical position. Arrows indicate directionality of the two biomechanical pillars. Arrow 1: ventral pillar comprised of vertebral bodies and discs. Arrow 2: dorsal pillar comprised of laminar structures and zygapophyses.

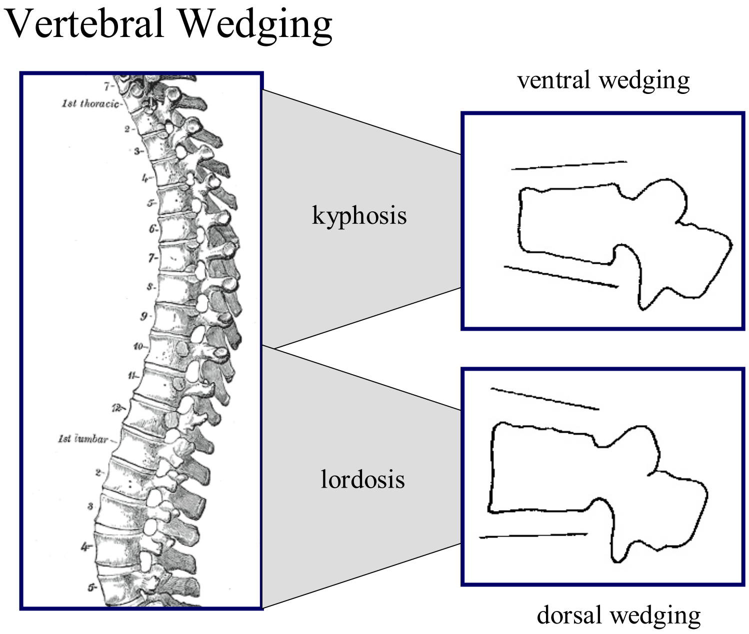


Figure 4.5. Vertebral body wedging results from differing heights of the ventral and dorsal margins of the centrum. Ventral wedging results from reduced ventral length relative to dorsal length and characterizes the thoracic spinal region, generating kyphosis. Dorsal wedging results from increased ventral length relative to dorsal length and characterizes the lordotic region of the spine, generating lumbar lordosis. Proportional loading shifts between the two pillars as a result of both bony morphology and movements initiated along the vertebral column.

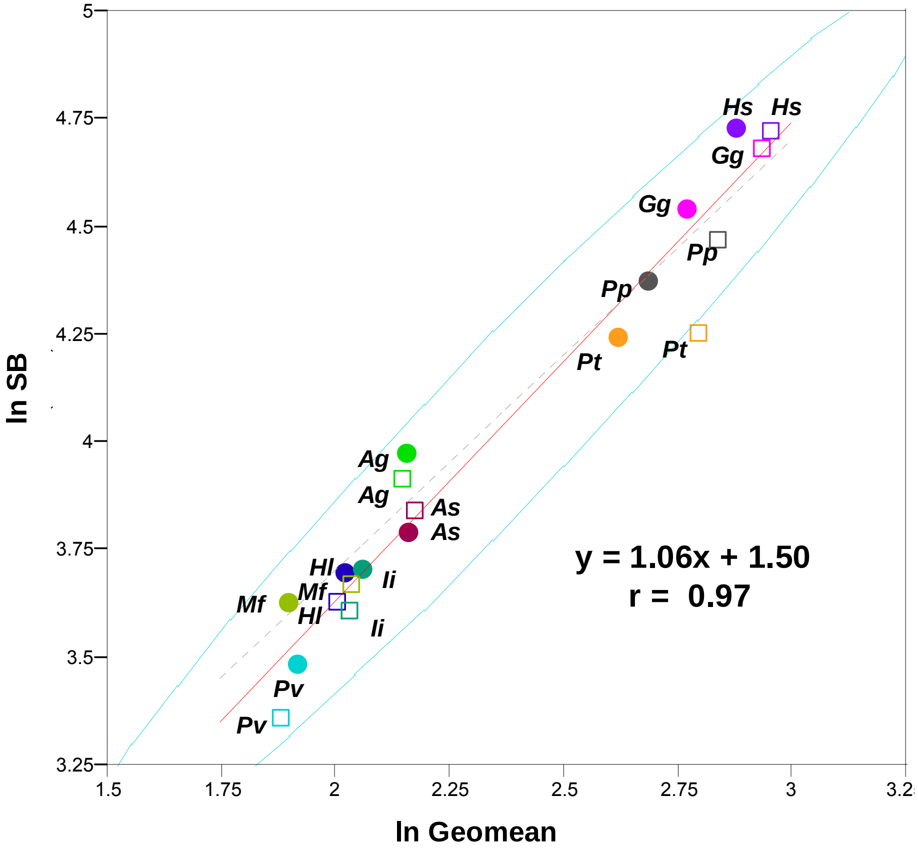


Figure 4.6. Reduced major axis regression of sacral breadth (natural log of raw mean variate) against geomean (natural log). The slope approximates isometry (1.0). Solid line is slope of regression. Dotted line is slope of isometry. Density ellipse represents 95% confidence limit. The slope of isometry lies within the lower (0.932) and upper (1.22) confidence limits of the regression slope. Solid circles female; open squares male. Human values not included in regression; points plotted for comparison. Species labels are defined in Table 4.1.

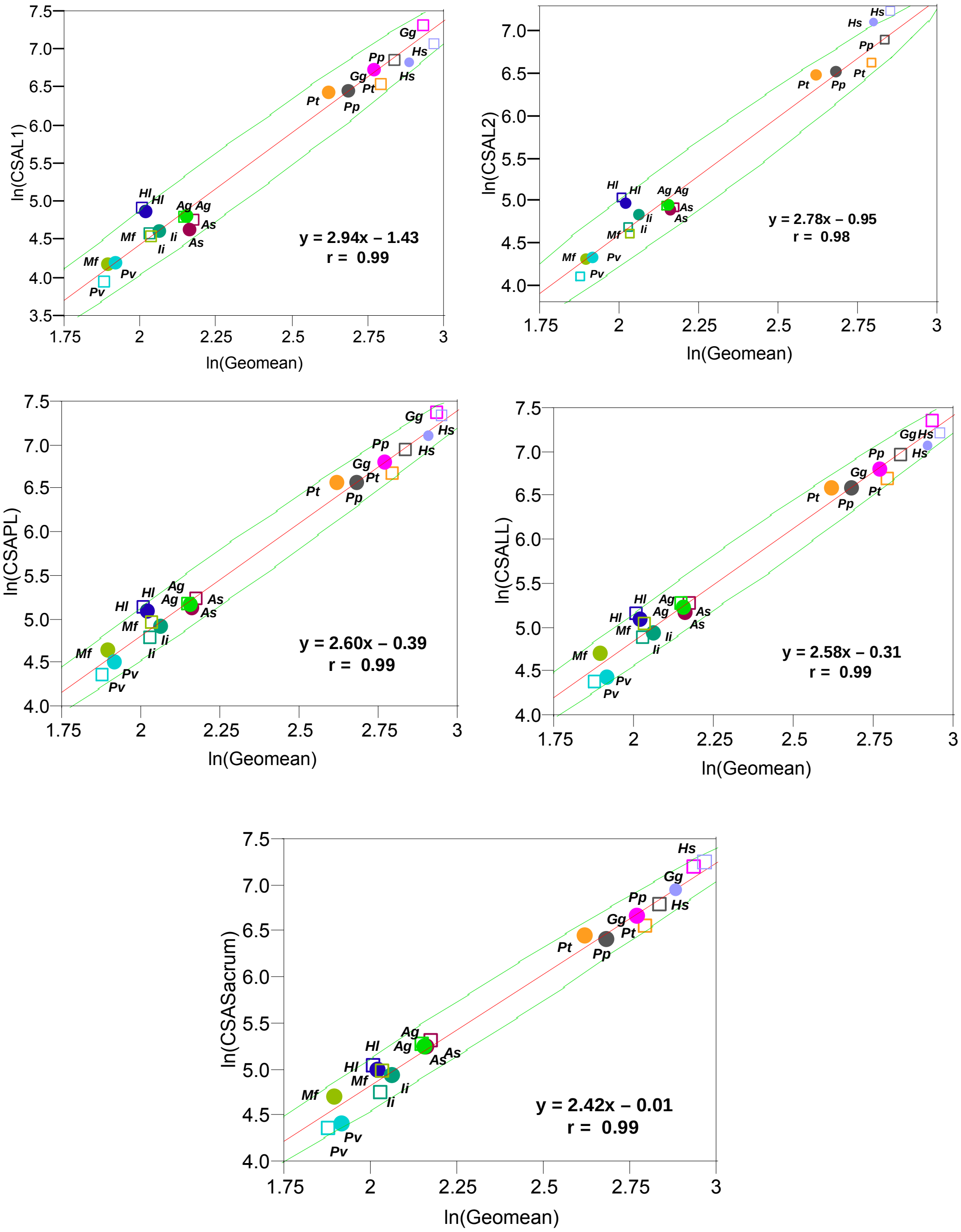


Figure 4.7. Reduced major axis regression of CSA (centrum surface area) against geomean for lumbar vertebral levels L1, L2, PL, LL and sacral vertebra S1. *Gorilla gorilla* levels include L1, PL and LL. Means derived from raw variates and natural log transformed. Slope of isometry = 2.0. The slope of isometry lies below the lower 95% confidence limit of the regression slope at each lumbar and sacral level. Human points plotted after regression, not included in the analysis. Solid circles female; open squares male. Species labels are defined in Table 4.1.

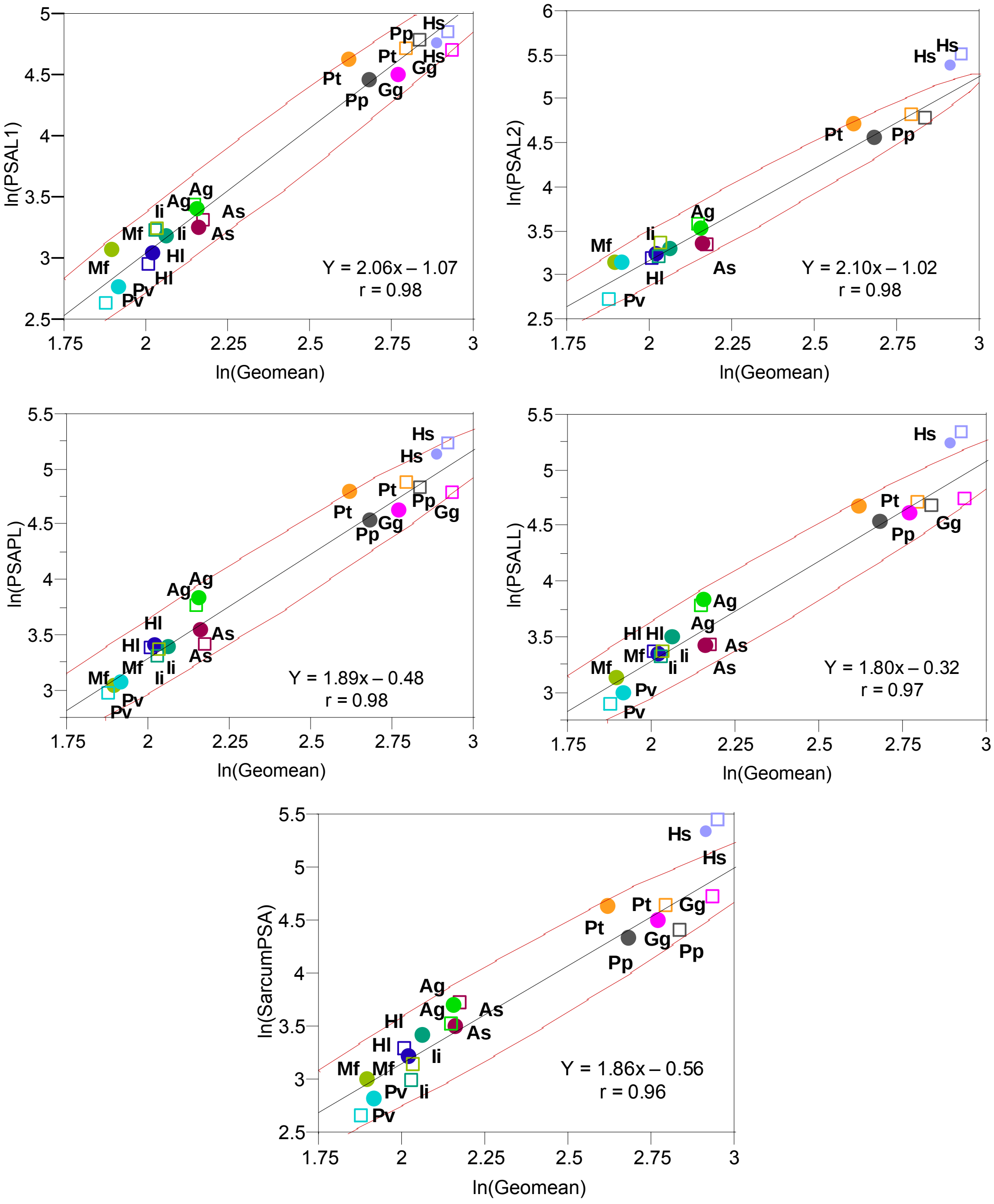


Figure 4.8. Reduced major axis regression of PSA (prezygapophyseal surface area) against geomean for lumbar vertebral levels L1, L2, PL, LL and sacral vertebra S1. *Gorilla gorilla* levels include L1, PL and LL. Means derived from raw variates and natural log transformed. Slope of isometry = 2.0. The slope of isometry lies within the lower and upper 95% confidence limits of the regression slope at each lumbar and sacral level. Human points plotted after regression; not included in the analysis. Solid circles female; open squares male. Species labels are defined in Table 4.1.

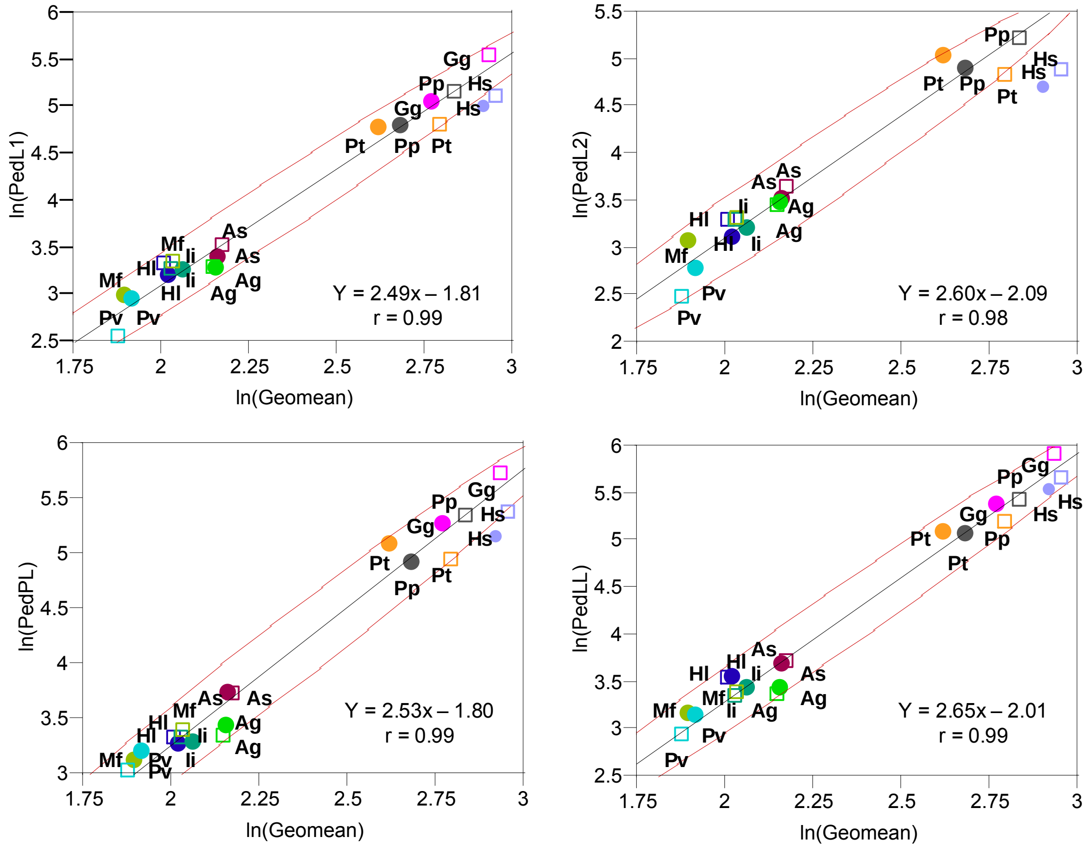


Figure 4.9. Reduced major axis regression of PedXS (pedicle cross-sectional area) against geomean for lumbar vertebral levels L1, L2, PL and LL. *Gorilla gorilla* levels include L1, PL and LL. Points for male and female *Homo sapiens* not included in the regression and were subsequently plotted onto the regression space. Means derived from raw variates and natural log transformed. Slope of isometry = 2.0. Regression slopes at all lumbar levels exhibit significant positive allometry ($p < 0.0000$) as the slope of isometry < lower confidence limits of regression. Solid circles female; open squares male. Species labels are defined in Table 4.1.

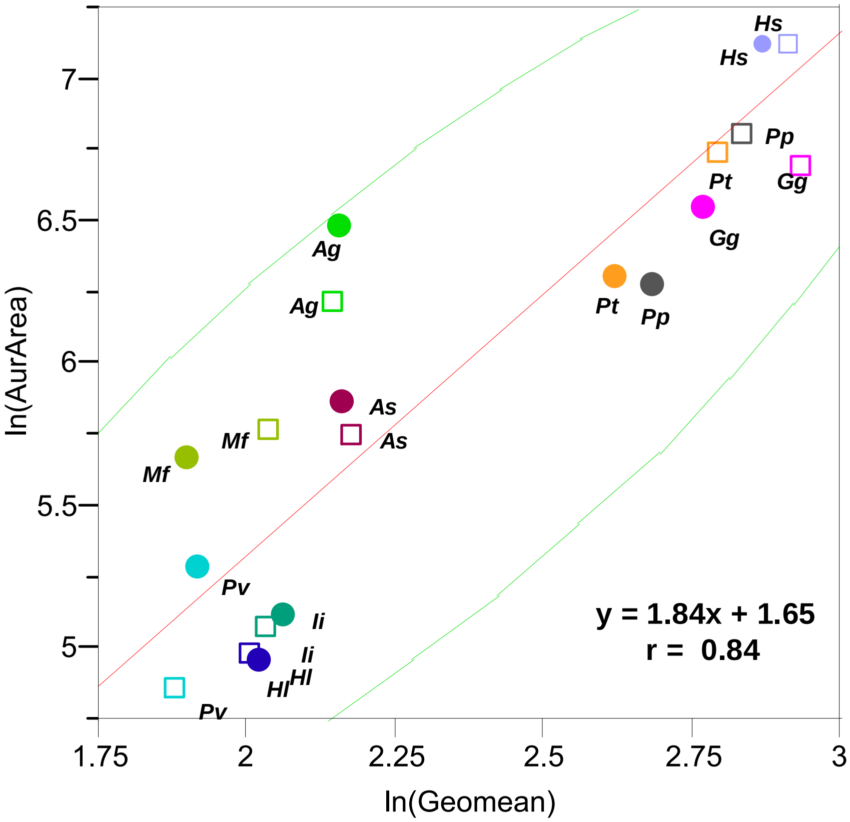


Figure 4.10. Reduced major axis regression of AA (auricular area) against geomean. Means derived from raw variates and natural log transformed. Regression slope (1.84) is negatively allometric ($p = 0.05$). The correlation for auricular area on overall size measure of geomean is not strongly correlated ($r = 0.84$). Points for male and female *Homo sapiens* not included in the regression and were subsequently plotted onto the regression space. Within*Propithecus* (*Pv*), female mean exceeds male mean. This is also the case for the two prehensile-tailed taxa, *Ag* (semi-orthograde) and *As* (pronograde). Solid circles female; open squares male.Species labels are defined in Table 4.1.

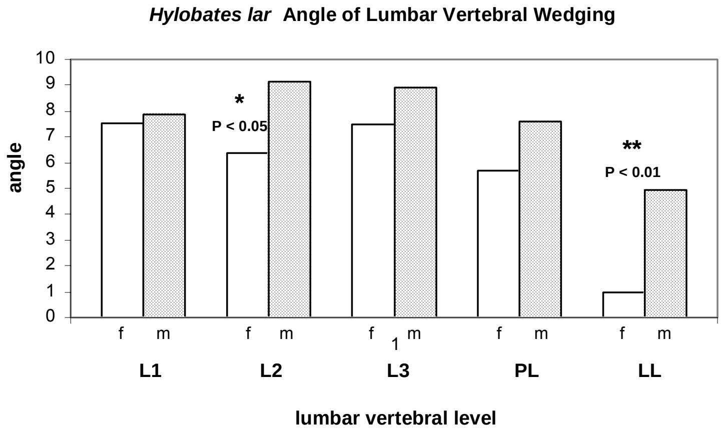


Figure 4.11. Male and female means for lumbar vertebral wedging angle in orthograde *Hylobates lar*. See Table 4.9 for significance test. Female n = 15; male n = 16.

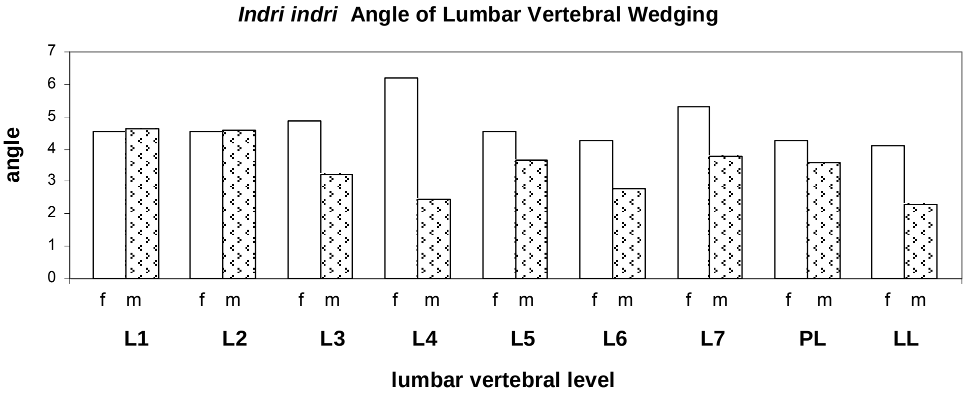


Figure 4.12. Male and female means for lumbar vertebral wedging angle in orthograde *Indri indri*. See Table 4.10 for significance test. Female n = 7; male n = 2.

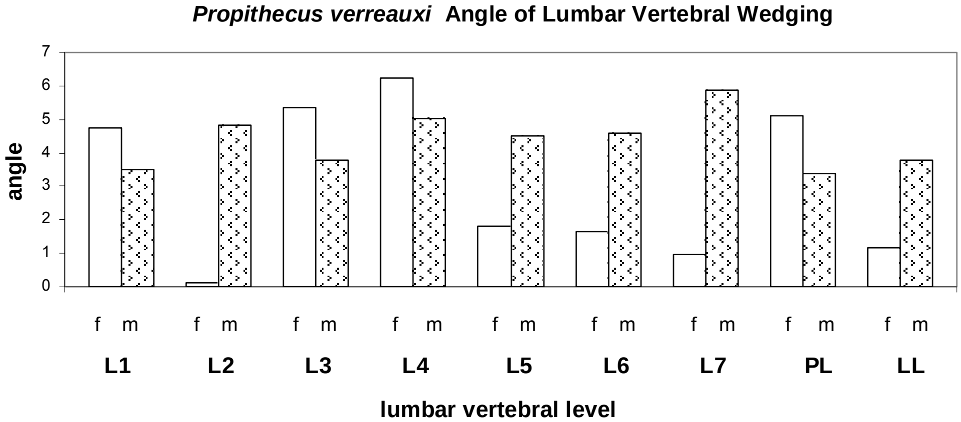


Figure 4.13. Male and female means for lumbar vertebral wedging angle in orthograde *Propithecus verreauxi*. See Table 4.11 for significance test. Female n = 2; male n = 4.

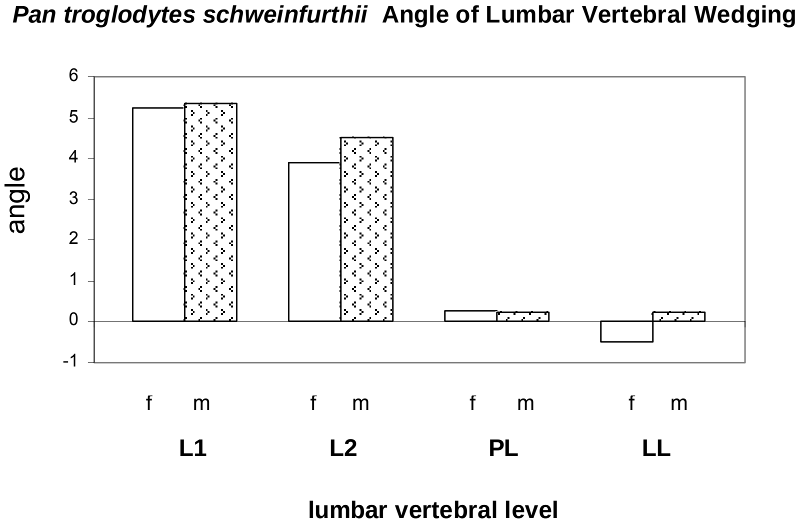


Figure 4.14. Male and female means for lumbar vertebral wedging angle in semi-orthograde *Pan troglodytes*. See Table 4.14 for significance test. Female n = 10; male n = 14.

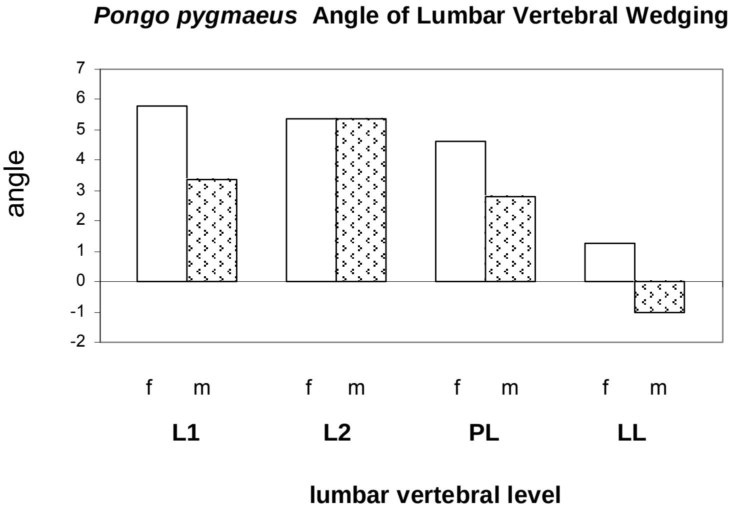


Figure 4.15. Male and female means for lumbar vertebral wedging angle in semi-orthograde *Pongo pygmaeus*. See Table 4.13 for significance test. Female n = 9; male n = 8.

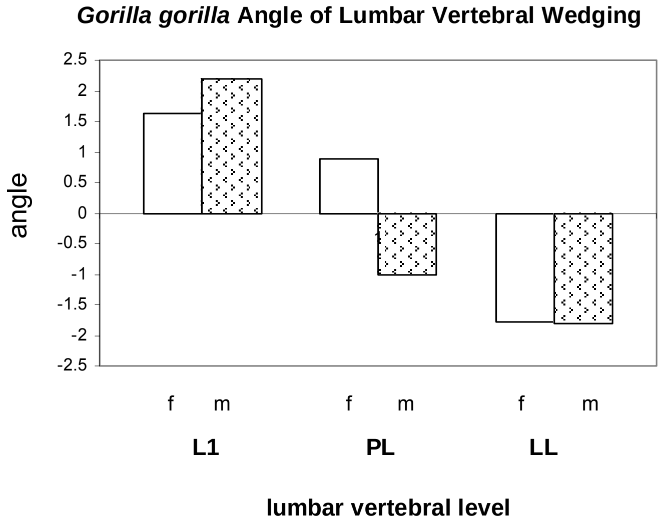


Figure 4.16. Male and female means for lumbar vertebral wedging angle in semi-orthograde *Gorilla gorilla*. See Table 4.12 for significance test. Female n = 6; male n = 7.

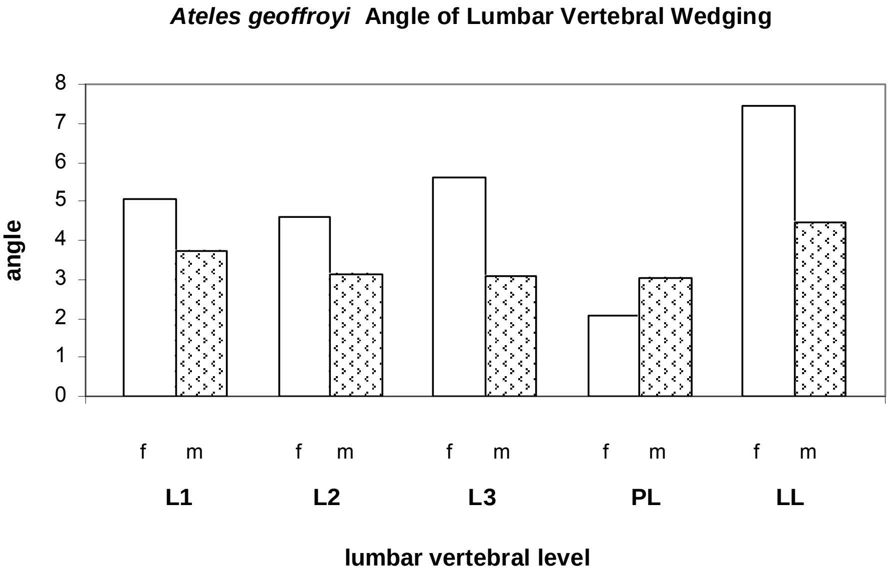


Figure 4.17. Male and female means for lumbar vertebral wedging angle in semi-orthograde *Ateles geoffroyi*. See Table 4.15 for significance test. Female n = 5; male n = 3.

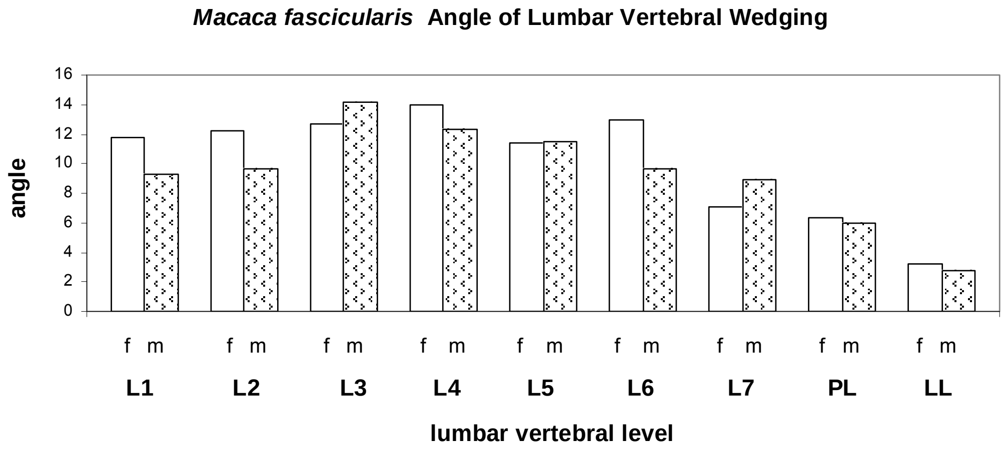


Figure 4.18. Male and female means for lumbar vertebral wedging angle in pronograde *Macaca fascicularis*. See Table 4.16 for significance test. Female n = 13; male n = 11.

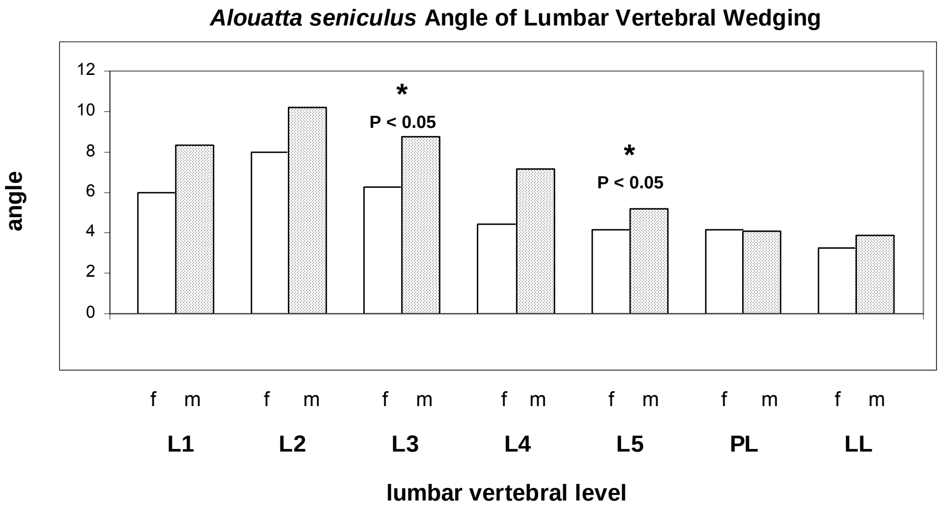


Figure 4.19. Male and female means for lumbar vertebral wedging angle in pronograde *Alouatta seniculus*. See Table 4.17 for significance test. Female n = 5; male n = 4.

REFERENCES

Abitbol M. 1987. Obstetrics and posture in pelvic anatomy. J Hum Evol 16:243-256.

Abitbol MM. 1993. Growth of the fetus in the abdominal cavity. Am J Phys Anthropol 91:367-378.

Abitbol M. 1996. Birth and human evolution: anatomical and obstetrical mechanics in primates. Westport, Conn: Bergin and Garvey.

Altmann SA. 1959. Field observations on a howling monkey society. J Mammal 40:317-330.

Ankel F. 1972. Vertebral morphology of fossil and extant primates. In: Tuttle R, editor. The Functional and Evolutionary Biology of Primates. Chicago: Aldine Atherton pp 223-240.

Ardito G. 1976. Checklist of data on gestation length of primates. J Hum Evol 5:213-222.

Badoux DM. 1974. An introduction to biomechanical principles in primate locomotion and structure. In Jenkins Jr FA (ed). Primate Locomotion. New York, Academic Press. pp 1-44.

Bartlett TQ. 2003. Intragroup and intergroup social interactions in white-handed gibbons. Int J Primatol 24:239-259.

Benton R. 1967. Structural patterns in the Pongidae and Cercopithecidae. Yrbk Phys Anthropol 18:65-88.

Berge C. 1984. Multivariate analysis of the pelvis for hominids and other extant primates: Implications for the locomotion and systematics of the different species of australopithecines. J Hum Evol 13:555-562.

Berge C. 1990. Size and locomotion-related aspects of hominid and anthropoid pelves: an osteometrical multivariate analysis. In: FK Jouffroy, MH Stack, C Niemitz, editors.

Bergeson D. 1996. The positional behavior and prehensile tail use of *Alouatta palliata*, *Ateles geoffroyi*, and *Cebus capucinus*. PhD dissertation, Washington University, St. Louis.

Black E. 1970. Sexual dimorphism of the ischium and pubis of three species of South American monkeys. J Mammal 51*:*794-796.

Bogduk N. 2005. Clinical anatomy of the lumbar spine and sacrum. 3rd edition. New York:Churchill Livingstone.

Canavez FC, Moreira MAM, Ladasky JJ, Pissinatti A, Parham P, Seuanez HN. 1999. Molecular phylogeny of New World primates (Platyrrini) based on beta(s)-microglobulin DNA sequences. Mol Phylo Evol 12:74-82.

Cannon CH, Leighton M. 1994. Comparative locomotor ecology of gibbons and macaques: selection of canopy elements for crossing gaps. Am J Phys Anthropol 93:505-524.

Cant JGH. 1986. Locomotion and feeding postures of spider and howling monkeys: Field study and evolutionary interpretation. Fol Primatol 46:1-14.

Cant JGH. 1987. Positional behavior of female Bornean orangutans (*Pongo pygmaeus*). Am J Primatol 12:71-90.

Cant JGH. 1988. Positional behavior of long-tailed macaques (*Macaca fascicularis*) in Northern Sumatra. Am J Phys Anthropol 76:29-37.

Cant JGH, Youlatos D, Rose MD. 2001. Locomotor behavior of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador: General patterns and nonsuspensory modes. J Hum Evol. 41:141-166.

Carpenter CR. 1964. A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). In Naturalistic Behavior of Nonhuman Primates (ed. Carpenter CR), pp. 145–271. University Park: The Pennsylvania State University Press.

Chen XM, Milne N, O'Higgins P. 2005. Morphological variation of the thoracolumbar vertebrae in Macropodidae and its functional relevance. J Morph 266:167-181.

Clauser DA. 1980. Functional and comparative anatomy of the primate spinal column: Some locomotor and postural adaptations. PhD dissertation. The University of Wisconsin, Milwaukee.

Collins AC. 2004. Atelinae phylogenetic relationships: The trichotomy revived? Amer J Phys Anthropol 124:285-296.

Connour JR, Glandel K, Vincent F. 2000. Postcranial adaptations for leaping in primates J Zool 251: 79-103.

Dagosto M. 1995. Seasonal variation in positional behavior of Malagasy lemurs. Int J Primatol 16:807-833.

Darroch J, Mosimman J. 1985. Canonical and principal components of shape. Biometrika 72:241-252.

Davis PR. 1961. Human lower lumbar vertebrae: some mechanical and osteological considerations. J Anat 95:337-344.

Demes B, Fleagle JG, Jungers WL .1999. Takeoff and landing forces of leaping strepsirhine primates. J Hum Evol 37:279-292.

Demes B, Franz TM, Carlson KJ. 2005. External forces on the limbs of jumping lemurs at takeoff and landing. Am J Phys Anthropol 128:348-358.

Digiovanni B, Scoles P, Latimer B. 1989. Anterior extension of the thoracic vertebral bodies in Scheuermann's kyphosis: an anatomic study. Spine 14(7): 712-716.

Doran DM. 1992. Comparison of instantaneous and locomotor bout sampling methods: A case study of adult male chimpanzee locomotor behavior and substrate use. Am J Phys Anthropol 89:85-99.

Doran DM. 1993. Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion. Am J Phys Anthropol 91: 83–98.

Doran DM, Hunt KD. 1994. Comparative locomotor behavior of chimpanzees and bonobos: species and habitat differences. In Chimpanzee Cultures (eds Wrangham RW, McGrew WC, de Waal FBM, et al.), pp. 93–108. Cambridge:Harvard University Press.

Ellefson JO. 1967. A natural history of gibbons in the Malay Peninsula. PhD thesis, University of California, Berkeley.

Elftman HO. 1932. The evolution of the pelvic floor of primates. J Anat 51:307-346.

Fleagle JG. 1976. Locomotion and posture of the Malayan siamang and implications for hominid evolution. Folia Primatol 26:245–269.

Fleagle JG, Mittermeier RA. 1980. Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. Am J Phys Anthropol 52:301-314.

Flower WH. 1885. An introduction to the osteology of Mammalia. London:MacMillon and Co.

Fontaine R. 1990. Positional behavior in *Saimiri boliviensis* and *Ateles geoffroyi*. Am J Phys Anthropol 82: 485-508.

Gebo DL. 1987. Locomotor diversity in prosimian primates. Am J Primatol 13:271-281.

Gebo DL, Chapman CA. 1995. Positional behavior in 5 sympatric Old-World monkeys. Am J Phys Anthropol 97:49-76.

Gilleard D, Brown W, Brown JM. 1996. Structure and function of the abdominal muscles in primigravid subjects during pregnancy and the immediate postbirth period. Phys Ther 76: 750-762.

Gingerich PD. 1972. The development of sexual dimorphism in the bony pelvis of the squirrel monkey. Anat Rec 172*:*589-595.

Gittins PS. 1983. Use of forest canopy by the agile gibbon. Fol Primatol 40: 134–144.

Givnish TJ, Sytsma KJ. 1997. Homoplasy in molecular vs. morphological data: The likelihood of correct phylogenetic inference. In Givnish TJ, Sytsam KJ (eds.), Molecular evolution and adaptive radiation. Cambridge University Press, Cambridge. pp 55-101.

Hager LD. 1996. Sex differences in the sciatic notch of great apes and modern humans. Am J Phys Anthropol 99*:*287-300.

Halpert A, Jenkins F, and Franks H. 1987. Structure and scaling of the lumbar vertebrae in African bovids (Mammalia and Artiodactyla). J Zool Lond 211:239-258.

Harcourt AH. 1985. Gorilla. In: MacDonald D (ed), Primates. Torstar Books: New York. pp 136-143.

Hollihn U. 1984. Bimanual suspensory behavior: morphology, selective advantages and phylogeny. In: The lesser apes: evolutionary and behavioral biology. Preuschoft H, Chivers DJ, Brockelman WY, Creel N (eds). Edinburgh: Edinburgh University Press. pp 85-95.

Horovitz I, Zardoya R, Meyer A. 1998. Platyrrhine systematics: A simultaneous analysis of molecular and morphological data. Am J Phys Anthropol 106: 261-281.

Hoyt DF, Wickler SJ, Biewener AA, Cogger EA, DeLa Paz KL. 2005. In vivo muscle function vs speed I. Muscle strain in relation to length change of the muscle-tendon unit. J Exp Biol 208:1175-1190.

Hunt KD. 1996. The postural feeding hypothesis: An ecological model for the evolution of bipedalism. S Af J Sci 92:127-151.

Isler K. 2005. 3D-kinematics of vertical climbing in hominoids. Am J Phys Anthropol 126: 66-81.

Johnson SE, Shapiro LJ.1998. Positional behavior and vertebral morphology in atelines and cebines. Am J Phys Anthropol 105:333-354.

Jungers WL, Susman RL. 1984. Body size and skeleton allometry in African apes. In (R. L. Susman, ed.) The Pygmy Chimpanzee. New York: Plenum Press. pp131–177.

Kapandji IA. 1982. Physiology of the joints: The trunk and the vertebral column. Edinburg: Churchill Livingstone.

Kiltie RA. 1982. Intraspecific variation in the mammalian gestation period. J Mammal 63: 646-652.

Knott CJ. 1999. Orangutan behavior and ecology. In Dolhinow P and FuentesA (eds.) The nonhuman primates. Mayfield Press, Mountain View CA pp 50-57.

Lague MR. 2003. Patterns of joint size dimorphism in the elbow and knee of catarrhine primates. Am J Phys Anthropol 120:278-297.

Latimer B, Ward C. 1993. The thoracic and lumbar vertebrae. In: Walker A, Leakey REF, editors. The Nariokotome *Homo Erectus* Skeleton. Cambridge: Harvard University Press p 266-293.

LaVelle M. 1995. Natural selection and developmental sexual variation in the human pelvis. Am J Phys Anthropol 98*:*39-72.

Leutenegger W. 1973. Sexual dimorphism in the pelves of African lorises. Am J Phys Anthropol 38*:*251-254.

Leutenegger W. 1974. Functional aspects of pelvic morphology in simian primates. J Hum Evol 3*:*207-222.

Leutenegger W. 1987. Neonatal brain size and neural cranial dimensions on Pliocene hominids: implications for obstetrics. J Hum Evol 16:291-296.

Leutenegger W, Larson S. 1985. Sexual dimorphism in the postcranial skeleton of New World primates. Folia Primatol 44:82–95.

Little BB. 1989. Gestation length, metabolic-rate, and body and brain weights in primates: epigenetic effects. Am J Phys Anthropol 80: 213-218.

Lindberg D. 1982. Primate obstetrics: The biology of birth. Am J Primatol Supp 1:93-99.

Meder, A. 1993. Gorillas. Okologie und Verhalten. Heidelberg: Springer.

Mittermeier RA. 1978. Locomotion and posture in *Ateles geoffroyi* and *Ateles paniscus.* Fol Primatol 30:161-193.

Mittermeier RA, Fleagle JG. 1976. Locomotor and postural repertoires of *Ateles geoffroyi* and *Colobus guereza* and a re-evaluation of locomotor category semibrachiation. Am J Phys Anthropol 45:235-255.

Mosimann J. 1970. Size allometry: Size and shape variables with characterizations of the log normal and gamma distributions. J Am Stat Assoc 56:930-945.

Odgers P. 1933. The lumbar and lumbosacral diarthrodial joints. J Anat 67:301-317.

Pal GP. 1989. Weight transmission through the sacrum in man. J Anat 162:9-17.

Pal GP, Routal RV. 1986. A study of weight transmission through the cervical and upper thoracic regions of the vertebral column in man. J Anat 148:245-261.

Pal GP, Routal RV. 1987. Transmission of weight through the lower thoracic and lumbar regions of the vertebral column in man. J Anat 152:93-105.

Petter JJ. 1962. Recherches sur l'ecologie et l'ethologie des lemuriens Malgaches. Paris: Editions du Museum.

Pissinatti A, DaSilva EC, Coimbra AF, Bertolazzo W, DaCruz JB. 1992. Sexual dimorphism of the pelvis in *Leontopithecus* (Lesson, 1840). Fol Primatol 58:204-209.

Plavcan J, van Schaik C. 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. Am J Phys Anthropol 103:37–68.

Preuschoft H, Fritz M, Niemitz C. 1979. Biomechanics of the trunk in primates and problems of leaping in *Tarsius*. In: M Morbeck, H Preuschoft, N Gomberg, editors. Environment, behavior and morphology: dynamic interactions in primates. New York: Gustov Fischer. p 327-345.

Rae TC, Koppe T. 2000. Isometric scaling of maxillary sinus volume in hominoids. J Hum Evol 38:411-423.

Reichard U, Sommer V. 2005. Group encounters in wild gibbons (*Hylobates lar*): Agonism, affiliation, and the concept of infanticide. Behav 134: 1135-1174. Part 15-16.

Remis M. 1995. Effects of body size on social context on the arboreal activities of lowland gorillas in the Central African Republic. Am J Phys Anthropol 97:413-433.

Richard A.1970. A comparative study of the activity patterns and behavior of *Alouatta villosa* and *Ateles geoffroyi.* Fol Primatol 12:241-263.

Rockwell H, Gaynor Evans F, Pheasant H. 1938. The comparative morphology of the vertebrate spinal column: its form as related to function. J Morphol 63:87-117.

Rodman PS. 1979. Individual activity patterns and the solitary nature of orangutans. In Perspectives On Human Evolution: The Great Apes. Hamburg DA, McCown ER (eds). Menlo Park, CA:Benjamin/Cummings Publishing Co. pp 235-255.

Rose MD. 1975. Functional proportions of primate lumbar vertebral bodies. J Hum Evol 4:21-38.

Rosenberg KR. 1988. The functional significance of Neanderthal pubic length. Cur Anthropol 29: 595-607.

Rosenberg KR. 1992. The evolution of modern human childbirth. Yrbk Phys Anthropol 35*:*89-124.

Rosenberg KR, Trevathan W. 1996. Bipedalism and human birth: the obstetrical dilemma revisited. Evol Anthropol 4*:*161-168.

Rosenberg KR, Trevathan W. 2002. Birth, obstetrics and human evolution. BJOG – Internat J Obstet Gynecol 109: 1199-1206.

Ruff CB. 1995. Biomechanics of the hip and birth in early *Homo*. Am J Phys Anthropol 98*:*527-574.

Ruiz-Garcia M, Alvarez D. 2003. RFLP analysis of mtDNA from six platyrrhine genera: Phylogenetic inferences. Fol Primatol 74:59-70.

Ruvolo M. 1997. Molecular phylogeny of the hominoids: Inferences from multiple independent DNA sequence data sets. Mol Bio Evol 14:248-265.

Sanders WJ. 1995. Function, allometry, and evolution of the australopithecine lower precaudal spine. PhD dissertation, New York University.

Sanders WJ. 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. J Hum Evol 34:249-302.

Sanders WJ, Bodenbender BE. 1994. Morphometric analysis of lumbar vertebra UMP 67-28: Implications for spinal function and phylogeny of the Miocene Moroto Hominoid. J Hum Evol 26:203-237.

Satie JP, Alfred JRB. 2002. Locomotion and posture in Hoolock gibbon. Ann. For. 10, 298–306.

Schultz AH. 1930. The skeleton of the trunk and limbs of higher primates. Hum Biol 2:303-409.

Schultz AH. 1949. Sex differences in the pelves of primates. Am J Phys Anthropol 7:401-423.

Schultz AH. 1953. The relative thickness of the long bones and the vertebrae in primates. Am J Phys Anthropol 11:277-311.

Shapiro LJ. 1991. Functional morphology of the primate spine with special reference to orthograde posture and bipedal locomotion. PhD Dissertation. State University of New York at Stony Brook.

Shapiro LJ. 1993a. Evaluation of “unique” aspects of human vertebral bodies and pedicles with a consideration of *Australopithecus africanus.* J Hum Evol 25:433-470.

Shapiro LJ. 1993b. Functional morphology of the vertebral column on primates. In: Gebo DL, editor. Postcranial Adaptation in Nonhuman Primates. DeKalb: Northern Illinois University Press p 121-149.

Shapiro LJ. 1995. Functional morphology of indrid lumbar vertebrae. Am J Phys Anthropol 98:323-342.

Shapiro LJ, Simons VM. 2002. Functional aspects of strepsirrhine lumbar vertebral bodies and spinous processes. J Hum Evol 42:753-783.

Slijper EJ. 1946. Comparative biologic-anatomical investigations of the vertebral column and spinal musculature in mammals. Amsterdam: Verhandelingen der Koninklijke Nederlandsche Akadamie van Wetenschappen, Tweedie Sectie 42 (5):1-128.

Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. J Hum Evol 32:523-529.

Stanford CB.2006. Arboreal bipedalism in wild chimpanzees: Implications for the evolution of hominid posture and locomotion. Am J Phys Anthropol 129:225-231.

Steiper ME, Ruvolo M. 2003. New World monkey phylogeny based on X-linked G6PD DNA sequences. Mol Phyl Evol 27:121-130.

Stern JT Jr. 1975. Before bipedality. Yrbk Phys Anthropol 19:59-68.

Steudel K. 1981a. Sexual dimorphism and allometry in primate *os coxae*. Am J Phys Anthropol 55:209-215.

Steudel K. 1981b. Functional aspects of primate pelvic structure: a multivariate approach. Am J Phys Anthropol 55:399-410.

Stoller M. 1995. The obstetric pelvis and mechanism of labor in nonhuman primates. PhD dissertation, University of Chicago, Chicago, Illinois.

Straus WL. 1927. The human ilium: Sex and stock. Am J Phys Anthropol 11:1-28.

Tague RG. 1986. Obstetric adaptations of the human bony pelvis. PhD dissertation, Kent State University.

Tague RG. 1989. Variation in pelvic size between males and females. Am J Phys Anthropol 80:59-71.

Tague RG. 1990. Morphology of the pubis and preauricular area in relation to parity and age at death in *Macaca mulatta*. Am J Phys Anthropol 82*:*517-525.

Tague RG. 1991. Commonalities in dimorphism and variability in the anthropoid pelvis, with implications for the fossil record. J Hum Evol 21:153-176.

Tague RG. 1993. Pubis symphyseal synostosis and sexual dimorphism of the pelvis in *Presbytis cristata* and *Presbytis rubicunda*. Int J Primatol 14*:*637-654.

Tague RG. 1995. Variation in pelvic size between males and females in nonhuman anthropoids. Am J Phys Anthropol 97:213-233.

Tague RG, Lovejoy CO. 1986. The obstetric pelvis of A.L. 288-1 (Lucy). J Hum Evol 15:237-255.

Tan CY, Inglewicz B. 1999. Measurement methods comparisons and linear statistical relationship. Technometrics 41:192-201.

Terranova CJ. 1995. Leaping behaviors and the functional morphology of strepsirhine primate long bones. Fol Primatol 65:181-201.

Terranova CJ. 1996. Variation in the leaping of lemurs. Am J Primatol 40: 145-165.

Tobias PV. 1998. Ape-like *Australopithecus* after seventy years. Was it a hominid? Roy Anthropol Inst 4:283-308.

Trevathan WR. 1987. Human Birth: An Evolutionary Perspective. New York: Aldine de Gruyter.

Trevathan W. 1988. Fetal emergence patterns in evolutionary perspective. Am Anthropol 90*:*19-26.

Trevathan W. 1996. The evolution of bipedalism and assisted birth. Med Anthropol Q 10*:*287-290.

Trinkaus E. 1984. Neandertal pubic morphology and gestation length. Cur Anthropol 25:509-514.

Vereecke EE, D'Août, K, Payne R, Aerts P. 2005. Functional analysis of the foot and ankle myology of gibbons and bonobos. J Anat 206:453–476.

Walker A.1979. Prosimian locomotor behavior. In: The study of prosimian behavior. Doyle GA, Martin RD (eds). Academic Press: New York.

Walker SE, Ayres JM. 1996. Positional behavior of the white uakari (*Cacajao calvus calvus*). Am J Phys Anthropol 101:161-172.

Walrath D, Glantz M. 1996. Sexual dimorphism in the pelvic midplane and its relationship to Neandertal reproductive patterns. Am J Phys Anthropol 100*:*89-100.

Warren RD, Crompton RH. 1997. Locomotor ecology of *Lepilemur edwardsi* and *Avahi occidentalis*. Am J Phys Anthropol 104:471-486.

Washburn SL. 1948. Sex differences in the pubic bone. Am J Phys Anthropol 6:199-207.

Washburn SL, Buettner-Janusch J. 1952. The definition of thoracic and lumbar vertebrae. Am J Phys Anthropol 10:251.

Whitcome KK. 1999. Sexual dimorphism of the human lumbar spine. Am J Phys Anthropol 276-276 Suppl. 28.

Whitcome KK. 2000. Functional morphology of human lumbar vertebral sexual dimorphism. Masters Thesis. Southern Illinois University.

Whitcome KK. 2001. Postural adaptations and sexual dimorphism in the primate pelvis. Am J Phys Anthropol 164. Supp 32.

Wrangham RW. 1980. Bipedal locomotion as feeding adaptation in gelada baboons and its implications for hominid evolution. J Hum Evol 9:329-331.

Youlatos D. 1999. Positional behavior of *Cebuella pygmaea* in Yasuni National Park, Ecuador. Primates 40: 543-550.

Zuckerman S, Ashton EH, Flinn RM, Oxnard CE, Spence TF. 1973. Some locomotor features of the pelvic girdle in primates. Symp Zool Soc Lond 33:71-165.

Chapter 5: Summary and Conclusions

SUMMARY

This study presents the first hypothesis to quantitatively test the prediction that human lumbopelvic sexual dimorphism results in part from obstetric adaptation to structural risks associated with bipedality. Earlier chapters explored two independent lines of inquiry related to the major hypothesis. Chapter 2 investigated the biomechanical link between human fetal load and female positional behavior. The analysis confirmed adult spinal loading patterns associated with fetal growth and maternal shape change, supporting the principal hypothesis. Results provided an obstetric biomechanical context in which the morphological components of human lumbopelvic sexual dimorphism were subsequently examined. Chapters 3 and 4 investigated the osteological evidence for human lumbopelvic sexual dimorphism and placed it in a comparative evolutionary framework for broader evaluation within primates. Unique characteristics of human lumbopelvic sexual dimorphism were thereby identified and further examined for functional relevance to habitual bipedalism, in accordance with the spinal loading patterns identified in Chapter 2. The specific questions addressed in preceding chapters are now considered in culmination.

1) To what extent does sexual dimorphism of the lumbopelvic complex in humans differ from that of other extant primates?

Human lumbopelvic sexual dimorphism is distinct among primates. This human form of shape sexual dimorphism (independent of vertebral size) is related to lumbar lordosis, a key adaptation to bipedalism. Human female vertebrae are dorsally wedged, contributing to the bony lordosis at lumbar levels L3, L4 and L5. At these lordotic levels, female vertebrae bear markedly oblique prezygapophyses. Conversely, lordotic wedging in human males is less extensive along the lumbar column, occurring at the lumbar levels L4 and L5. Female vertebral bodies are less heavily loaded, proportionally, than those of males at any one level in the lumbar region. The greater obliquity of the prezygapophyses in the female lumbar spine is functionally consistent with a more dorsally directed spinal loading pattern, as resistance to an increase in shear stress with dorsal wedging. Furthermore, the relatively large centrum surface areas in males from L1 through L4 and S1 suggest that males bear more of their axial load along the ventral pillar centra than do females.

Where sexual dimorphism of the lumbopelvic variables was identified in the nonhuman primates, the relatively larger values of measure characterized males. There is no pattern of pillar-specific loading by sex, either along the lumbar levels or within them for any of the nonhuman primate species examined. The positional grouping of taxa as orthograde, semi-orthograde and pronograde did not reveal any pattern of shared sexual dimorphism. Although humans and other orthograde primates compressively load their vertebral columns more often than do non-orthograde primates, there appears to be no loading difference between sexes, consistent with positional behavior.

2) Do kinematic adjustments in lumbar lordosis and sagittal pelvic tilt during human pregnancy mediate risk associated with obstetric spinal loading?

Results of the kinematic analyses indicate that under conditions of increasing fetal load, human females positionally adjust their lower back and pelvic segments in association with anterior translation of maternal center of mass. In doing so, the effective fore-aft position of maternal center of mass is biomechanically recovered and its displacement throughout pregnancy restricted within a narrow window of efficiency relative to the supporting joints of the lower body. These positional mechanisms of lumbar lordosis and pelvic tilt occur in both quiet stance and natural gait, signaling a consistent biomechanical strategy in the bipedal behavior of gravid human females.

While the introduction of a reference posture served to constrain body segment alignment to target center of mass resulting from segmental mass change, an alternative posture of natural stance allowed subjects to self-select the positional alignment of body segments. It was in natural stance that the balance mechanisms of lordosis and pelvic tilt were expected to realign the center of mass into a more favorable biomechanical position. When translation in center of mass was contrasted between conditions, stable positioning in natural stance was evident. The positional rigidity imposed by the reference posture revealed a 3.2 cm anterior translation of center of mass. Yet, when subjects self-positioned in natural stance, center of mass during pregnancy changed just -0.3 cm. Although the absolute distance of a 3.2 cm migration in reference posture center of mass may seem minor in linear terms, the effective change in fore-aft location of center of mass relative to the biacetabular axis asserts marked biomechanic effect. The obstetric load-induced position of maternal center of mass shifted anterior to all of the major supporting joints, not only the hips (hip position was held constant by the reference posture), but also the knees and ankles, triggering the postural mechanisms of lumbar lordosis and pelvic tilt. In this manner, pregnant females avoid both the fatigue and energy cost of muscle recruitment that would otherwise be needed to stabilize the torso against the force of gravity acting anterior to the hips. Sustained recruitment of muscle effort throughout the second and third trimesters of human pregnancy would further inflate the risks of back and hip injury to women.

While changes in lumbar lordosis and pelvic tilt during pregnancy have been previously recorded, the results presented in this work clearly demonstrate a biomechanical relationship between maternal center of mass and positional adjustments.

3) Which aspects of human lumbopelvic sexual dimorphism are associated with fetal load?

With an obstetric spinal loading regime identified, the most immediate question is whether lumbopelvic characteristics present in females and absent in males are functionally related to fetal load.

The most prevalent expression of human lumbar sexual dimorphism occurs in the mid lumbar region, levels L2 and L3. This area is the transitional zone of vertebral body wedging where kyphotic vertebral bodies reach their caudal limit. Lumbar level two is the neutral or transitional level in females while lumbar level three is the level of wedge transition in males. Vertebral body wedging in the lumbar region is both less kyphotic cranially and more lordotic caudally in females than in males. Female vertebral bodies therefore are less heavily loaded, proportionally, than those of males at any one level in the lumbar region. The large centrum surface areas, relative to vertebral size, in males from L1 through L4 and S1 also indicate that males bear more of their axial load along the ventral pillar centra. The greater obliquity of the prezygapophyses in the female lumbar spine is functionally consistent with a more dorsally directed spinal loading pattern, enhancing resistance to an increase in shear stress augmented by dorsal wedging. The smaller radius of curvature expressed in females produces a tighter curve relative to males. Although female lumbar lordosis is more acute than that of males, it is distributed across a greater number of vertebrae. By distributing the proportionally larger dorsal pillar load across a longer expanse of vertebrae, the female lumbar spine gains additional structural safety within a vertebral column subjected to obstetric load.

4) To what extent is sexual dimorphism in the human lumbopelvic complex an evolutionary solution to the bipedal challenge of hominin fetal load?

Results of these analyses suggest that the challenge of bipedal obstetric load was cast once early hominins committed to bipedalism and effectively stabilized the upper body via lumbar lordosis. Regardless of the relative size of the early neonate or the gestation time it required, fetal body mass borne anteriorly to the bipedal maternal body increased spinal load and joint torque. Whether early hominin females enacted the positional coping mechanisms of modern human females or recruited sustained muscle effort to counter the instability of obstetric load is uncertain. The evolution of lumbopelvic specialization in the modern human female suggests that early hominins were at minimum subject to selection pressure for vertebral resistance to reproductive load.

The obstetric spinal loading patterns newly identified for human females provide a model that can be applied to the fossil record. This novel tool for interpretation of the hominin fossil record is not simply relevant to the functional role of fossil vertebrae and pelves but to the broader context in which reproductive selection pressures operate. Regardless of the single or myriad as yet undetermined selection pressures favoring hominin bipedality, anatomical commitment to bipedal locomotion constrains other functions. Physical anthropologists have long known that human pelvic shape is a compromise solution to the challenges of bipedal locomotion and pelvic parturition (e.g., Berge et al., 1984; Tague and Lovejoy, 1986; Rosenberg, 1988, 1992; Ruff, 1995). We now add to that complexity of selection pressures the biomechanics of stable bipedal postures and locomotion during pregnancy.

Of the ten comparative primate species examined here, only humans (*Homo sapiens*) are characterized by true lordotic curvature in the lumbar region. Within modal humans, individuals with five lumbar vertebrae, lordosis typically begins at either the L3 or L4 level. The cranialmost region of the lumbar spine is kyphotic, either at the L1 level alone or along two levels inclusive of L1 and L2. The kyphotic span is followed by a neutral, non-wedged level, either L2 or L3, depending on the number of kyphotic vertebrae preceding. Ultimately the lordotic region is terminated by a caudally lordotic series of two or three dorsally wedged vertebrae. The mean cumulative angle of dorsal wedging in females is 9.88°. In contrast, the mean cumulative lordosis in males is less, 8.25°. Notably, the sexes differ not only in total angular lordosis, but also in the distribution by vertebral level of the angular change. In males bony lordosis extends across just two lumbar vertebral levels, while in females vertebral lordosis extends across a greater length of the lumbar column, three lumbar vertebral levels.

Similarly, results of the analysis demonstrate that within the non modal groups, both the L6 variant and the L4 variant, the lordotic sequence of dorsally wedged lumbar vertebrae in females exceeds by one vertebral level the sequence in males. Regardless of the overall number of vertebrae within the lumbar region, four, five or six, the female sequence of dorsally wedged lumbar vertebrae tends to be longer than that of males, within type. The fact that this pattern of sexual dimorphism holds across human numeric types indicates it is a species-wide phenomenon, independent of variation in lumbar vertebral number.

Unlike the human groups investigated here, the nine nonhuman primate species in the analysis express no lumbar lordotic curvature, at least not in the human sense. Not only are the initial cranial levels in the lumbar region of nonhuman primates kyphotic (as in humans), the more caudal levels are kyphotic as well (unlike humans). No transitional level of neutral, non-wedging occurs. In seven of the nine comparative taxa, (exceptions includes *Ateles* and *Alouatta*, prehensile-tailed genera), the final caudal level is infrequently lordotic, dorsally wedged. However, the only primate to demonstrate a mean dorsal angle of the last lumbar vertebra is the gorilla. In all others, the mean remains kyphotic. This nonhuman ventrally wedged pattern is not specific to any one positional group, whether pronograde, semi-orthograde or orthograde, and there are no meaningful patterns of sex difference among them.

IMPLICATIONS FOR EARLY HOMININ EVOLUTION

At what point in the evolution of the human lineage did obstetric load adaptation emerge? As the findings of this study demonstrate, sexual dimorphism of this nature does not occur among other extant primates. In particular, the lack of sex differences in *Pan* suggests that the evolution of human obstetric load sexual dimorphism arose after divergence from the last common ancestor of *Pan* and *Homo*.

Was this a basal adaptation of the hominins or a later adaptation coincident with hominins of modern human limb proportion and pelvic dimension? Although not directly testable given the current hominin fossil record, three indirect lines of evidence point to an early emergence of obstetric load adaptation.

First, bony lumbar lordosis is a key hominin mechanism for upper body stability over a bipedal support base. Early hominins as evidenced by *Australopithecus* specimens A.L. 288-1 and Sts-14 had both large lumbar zygapophyses and massive sacral superior facets relative to vertebral body dimensions (Sanders, 1998), suggesting increased resistance to dorsal pillar loading. Dorsal pillar load was most likely generated by lordotic wedging of the vertebral bodies. Morphological evidence of early homimin vertebral body shape is preserved in the presumed second lumbar and first sacral vertebrae of A.L. 288-1 (*Australopithecus afarensis).* Wide inter-prezygapophyseal distance between the two preserved vertebral elements is inferred to indicate dorsal wedging of the lumbar of the lumbar spine (Ward and Latimer, 1991; Ward, 2002). Further support of basal lumbar lordosis is evidenced in the complete lumbar series of Sts-14 (*Australopithecus africanus)* evidencing a series of four dorsally wedged lumbar vertebrae at levels L3-L6 (Robinson, 1972; Sanders, 1995, 1998).

Given behavioral bipedalism (Leakey and Hay, 1979; Feibel et al., 1996) and morphological lumbar lordosis (e.g., Robinson, 1972; Ward and Latimer, 1991; Sanders, 1995, 1998) in australopithecines, the resultant orthograde compartment of fetal load would have challenged early hominins in ostensibly the exact biomechanical context as modern humans. If the A.L. 288-1 and Sts-14 individuals were female, as is generally inferred from body size and pelvic dimensions (Tague and Lovejoy, 1986; McHenry, 1992; Wood and Quinney, 1996), their robust dorsal pillar facets exemplify a basal sex-specific morphology related to obstetric load. This interpretation will ultimately gain support or correction through the acquisition of additional fossil evidence, namely a range of male and female specimens. The expectation of obstetric load sexual dimorphism is independent of the uncertain modal number of lumbar vertebrae in early hominins, as the modern human pattern demonstrated in this analysis is consistent across modal number and variant groups.

Another relevant point is that to otherwise resist torque generated by the anterior load of the fetus during maternal bipedal posture and locomotion, sustained extensor muscle recruitment would be required. Muscles and the joints they cross are vulnerable to injury when fatigued by sustained effort. Fatigue alone is a sufficient stressor to compromise individual mobility. For early hominins erector spinae fatigue could easily have limited foraging efficiency and predator avoidance, leaving the gravid female vulnerable to nutritional stress and injury or death. These negative consequences hold a high potential to reduce reproductive success. In this sense, postural and locomotor adaptation to obstetric load would be under relatively strong selection pressure in bipeds.

Finally, the complex obstetric role of the pelvis is fundamental to both delivery of the fetus at parturition (e.g., Abitbol, 1987, 1996a, 1996b; Rosenberg, 1992; Hager, 1996; Trevathan and Rosenberg, 2001), and as findings of this study indicate, during gestational growth. Clearly, cephalopelvic proportions of fetus and adult, respectively, are critical for successful fetal descent through the birth canal. Now evident from this analysis, adult female lumbopelvic proportions are important in the sacral transfer of load between the upper body and lower support base. In contrast to that of males, the first sacral centrum of females is small relative to vertebral size and its prezygapophyses relatively large (L6 variant), suggesting that at the lumbosacral junction, females continue to carry more of their vertebral load in the dorsal pillar. The auricular area that is the sacrum's contribution to the articulation of the sacroiliac joint is larger relative to vertebral size in females than in males. Earlier studies report that male auricular area (raw size) exceeds female area (Solonen, 1957; Vleeming et al., 1990a). Vleeming et al. (1990b) suggest the functional role of increased male auricular size is resistance to greater torque related to a more anterior position of upper body center or mass in males (Bellamy et al., 1983). Importantly, once male-female comparison is made using relative size, as in this analysis, female auricular area (relative to vertebral size) exceeds that of male area. Current findings suggest that the functional significance of relatively large female auricular area may be related to the anterior translation of maternal center of mass under conditions of obstetric load and the torque it asserts on pelvic joints.

Considered in sum, these factors strongly indicate that obstetric load was a significant selection factor in the evolution of lumbopelvic sexual dimorphism and the evidence points to an early, basal emergence of obstetric load adaptation in hominins.

CONCLUSION

The goal of this research was to better understand biomechanical change in human pregnancy, particularly, to identify the role that increasing obstetric load plays in the position of maternal center of mass and to accurately characterize the context-specific spinal loading patterns of bipedal pregnancy. Ultimately, with these phenomena clearly understood, we gain mechanistic tools necessary to better reconstruct the evolution of lumbopelvic sexual dimorphism in modern humans and to further identify an adaptive suite of traits that enhance the reproductive success of females.

Human lumbopelvic sexual dimorphism as identified in this study is morphologically distinct compared to a broad range of primate taxa with varying positional behaviors and is functionally tied to bipedal lumbar lordosis. The morphometric portions of the analysis revealed unique vertebral morphology in human females that is well adapted to resist obstetric spinal loading. Evidence of the stabilization mechanisms restricting displacement of the maternal center of mass under conditions of fetal load was provided by kinematic increase in lumbar lordosis and pelvic tilt, adjustments that exacerbate dorsal pillar loading in females. In conclusion, reproductive factors other than the immediate mechanisms of birth, namely bipedal obstetric load, played a role in the evolution of the lumbopelvic complex in modern humans and earlier hominins.

REFERENCES

Abitbol M. 1987. Obstetrics and posture in pelvic anatomy. J Hum Evol 16:243-256.

Abitbol M. 1996a. The shape of the female pelvis: contributing factors. J Rep Med 41:242-250.

Abitbol M. 1996b. Birth and human evolution: anatomical and obstetrical mechanics in primates. Westport, Conn: Bergin and Garvey.

Bellamy N, Park W, Rooney PJ. 1983. What do we know about the sacroiliac joint? Sem Arth Rheu 12:282-313.

Berge C, Orban-Segebarth R, Schmid P. 1984. Obstetric interpretation of the australopithecine pelvic cavity. J Hum Evol 13:573-587.

Feibel C, Agnew N, Latimer B, Demas M, Marshall F, Waane SAC, and Schmid P. 1996. The Laetoli hominid footprints: A preliminary report on the conservation and scientific restudy. Evol Anthropol 4:149–154.

Hager LD. 1996. Sex differences in the sciatic notch of great apes and modern humans. Am J Phys Anthropol 99:287-300.

Leakey MD, Hay RL. 1979. Pliocene footprints in the Laetoli Beds at Laetoli, northern Tanzania. Nature 27:317-323.

McHenry HM. 1992. Body size and proportions in early hominids. Am J Phys Anthropol 87:407-431

Robinson J. 1972. Early Hominid Posture and Locomotion. Chicago: The University of Chicago Press.

Rosenberg KR. 1988. The functional significance of Neanderthal pubic length. Cur Anthropol 29: 595-607.

Rosenberg KR. 1992. The evolution of modern human childbirth. Yrbk Phys Anthropol 35:89-124.

Ruff CB. 1995. Biomechanics of the hip and birth in early *Homo*. Am J Phys Anthropol 98:527-574.

Sanders WJ. 1995. Function, allometry, and evolution of the australopithecine lower precaudal spine. PhD dissertation, New York University.

Sanders WJ. 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. J Hum Evol 34:249-302.

Solonen KA. 1957. The sacroiliac joint in light of anatomical roentgenological and clinical studies. Act Orthop Scand Suppl 27:1-127.

Tague RG, Lovejoy CO. 1986. The obstetric pelvis of AL 288-1 (Lucy). J Hum Evol 15:237-255.

Trevathan W, Rosenberg K. 2001. The evolution of human birth. Scientific American 285:72-77.

Vleeming A, Volkers ACW, Snijders CJ, Stoeckart R. 1990a. Relation between form and function in the sacroiliac joint. Part 1: Clinical anatomical aspects. Spine 15:133-135.

Vleeming A, Volkers ACW, Snijders CJ, Stoeckart R. 1990b. Relation between form and function in the sacroiliac joint. Part 2: Biomechanical aspects. Spine 15:133-135.

Ward CV. 2002. Early hominin posture and locomotion: Where do we stand? Yrbk Phys Anthropol 45:185-215.

Ward CV & B Latimer. 1991. The vertebral column of *Australopithecus*. Am J Phys Anthropol Suppl 12:180.

Wood BA and Quinney PS. 1996. Assessing the pelvis of AL 288-1. J Hum Evol 31:563-568.

Appendices

APPENDIX A: SUBJECT RECRUITMENT FLIER 1

Interested in tracking your posture and gait changes during pregnancy?

Join us in a research study. Your contribution will advance our understanding of the impact the pre-natal baby has on a mother's natural stance and walking stride.

$200 compensation provided to volunteers.

- **Among the many changes a pregnant woman experiences are an increase and redistribution of body mass as her baby develops and grows. Mechanisms for balance of the torso are challenged as the orientation and mass of the baby change with advancing pregnancy. Women manage very well through successive trimesters via subtle adjustments in their posture and walking gait.**
- **The purpose of this study is twofold: to document changes in the standing posture and walking behavior of women through the parous period and to apply a biomechanical model the observations generate to investigate the unique size and shape of the lower back and pelvis of women in contrast to those of men.**
- **Your participation in the study will involve six brief sessions held in a Gait Lab at the University of Texas at Austin. Volunteers perform two routine activities, natural standing and comfortable walking. Compensation for study participation is given in the amount of $200 and on-site no fee parking is provided.**
- **If you are interested in volunteering and you are 24 weeks pregnant or less, please contact us directly or complete and mail this questionnaire. Your privacy is important. This information will only be used in conjunction with participating in this study at the University of Texas at Austin. Your information will not be shared with anyone for any other reason. Responding to this questionnaire in no way obligates you. If you wish to join the study or would like further information, please call Katherine Whitcome, project coordinator, at (512) 471-4206, email kwhitcome@mail.utexas.edu or return flier by mail. Thanks!**

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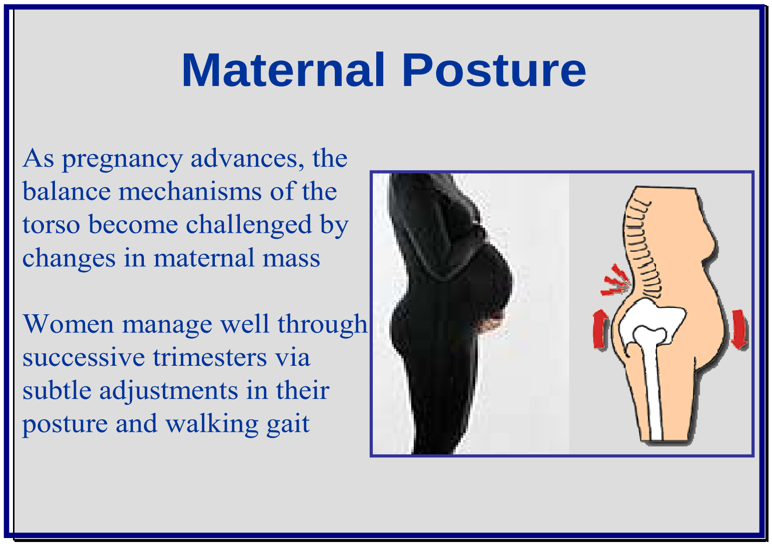

Maternal Posture

As pregnancy advances, the balance mechanisms of the torso become challenged by changes in maternal mass

Women manage well through successive trimesters via subtle adjustments in their posture and walking gait

(fold here)

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To: Katherine Whitcome

Doctoral Candidate
Department of Anthropology

University of Texas at Austin

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APPENDIX B: SUBJECT RECRUITMENT FLIER 2

Interested in tracking your posture and gait changes during pregnancy?

Join us in a research study. Your contribution will advance our understanding of the impact the pre-natal baby has on a mother's natural stance and walking stride.

$200 compensation provided to volunteers.

- Among the many changes a pregnant woman experiences are an increase and redistribution of body mass as her baby develops and grows. Mechanisms for balance of the torso are challenged as the orientation and mass of the baby change with advancing pregnancy. Women manage very well through successive trimesters via subtle adjustments in their posture and walking gait.

- The purpose of this study is twofold: to document changes in the standing posture and walking behavior of women through the parous period and to apply a biomechanical model the observations generate to investigate the unique size and shape of the lower back and pelvis of women in contrast to those of men.

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- If you wish to join the study or would like further information, please call Katherine Whitcome, project coordinator at (512) 471-4206, email kwhitcome@mail.utexas.edu, or visit our study web site:

http://webspace.utexas.edu/whitcome/www/ppgstudy

Reproductive Experiences of Women

Posture and Gait Changes in Pregnancy

- One of the ways you can help improve our understanding of the reproductive experiences of women is by volunteering for a research study at the University of Texas at Austin.
- A posture and gait study of pregnant women is presently recruiting participants.
- For their generosity of interest and time, participants are given financial compensation.
- Any information you provide is strictly confidential and will not be used for any purpose other than contacting you in regard to the study.

If you wish to join the study or would like further information
please call Katherine Whitcome, project coordinator at
(512) 471-4206, email kwhitcome@mail.utexas.edu,
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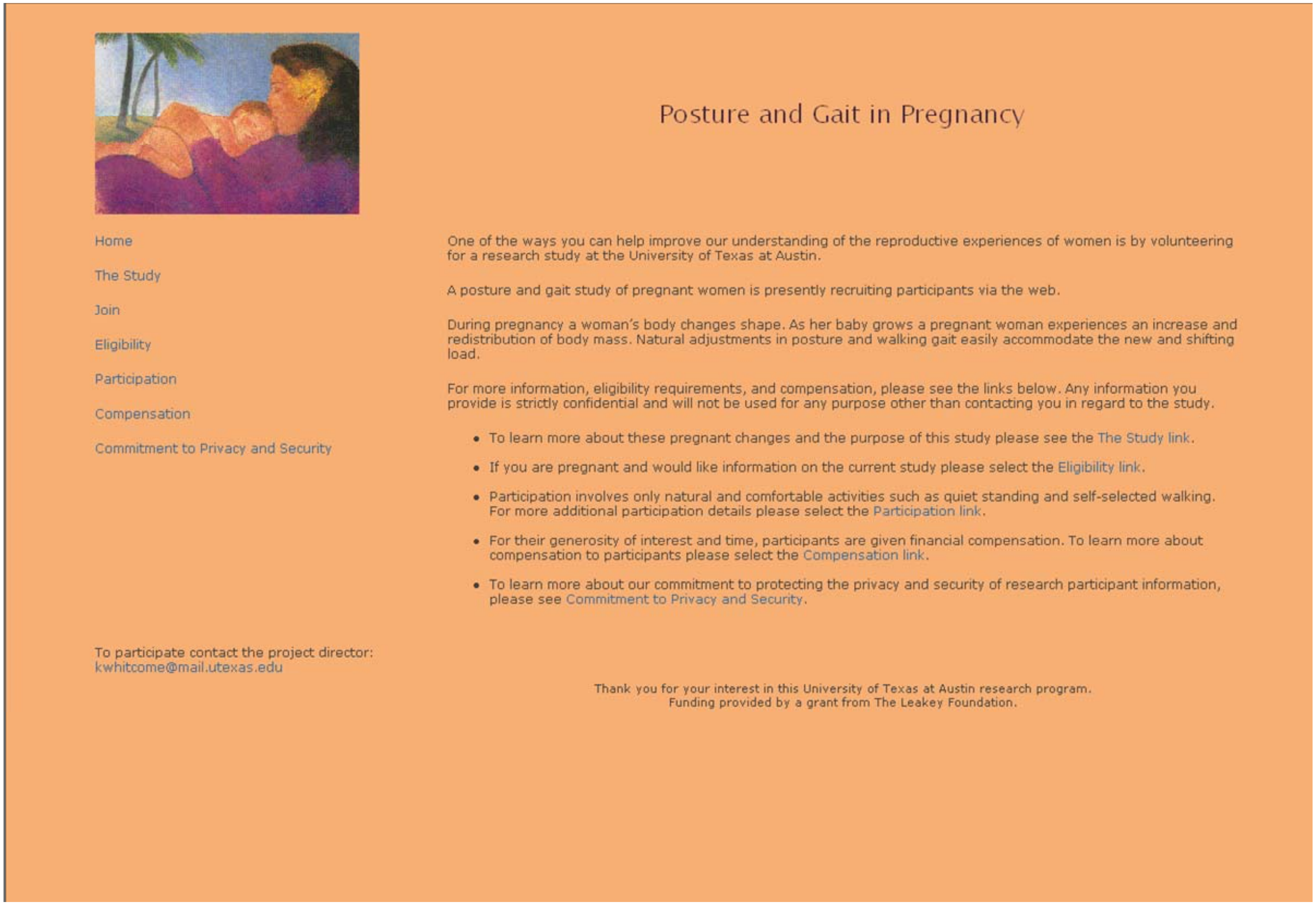
APPENDIX C: SUBJECT RECRUITMENT WEB SITE



Posture and Gait in Pregnancy

One of the ways you can help improve our understanding of the reproductive experiences of women is by volunteering for a research study at the University of Texas at Austin.

A posture and gait study of pregnant women is presently recruiting participants via the web.

During pregnancy a woman's body changes shape. As her baby grows a pregnant woman experiences an increase and redistribution of body mass. Natural adjustments in posture and walking gait easily accommodate the new and shifting load.

For more information, eligibility requirements, and compensation, please see the links below. Any information you provide is strictly confidential and will not be used for any purpose other than contacting you in regard to the study.

- To learn more about these pregnant changes and the purpose of this study please see the The Study link.
- If you are pregnant and would like information on the current study please select the Eligibility link.
- Participation involves only natural and comfortable activities such as quiet standing and self-selected walking. For more additional participation details please select the Participation link.
- For their generosity of interest and time, participants are given financial compensation. To learn more about compensation to participants please select the Compensation link.
- To learn more about our commitment to protecting the privacy and security of research participant information, please see Commitment to Privacy and Security.

To participate contact the project director:
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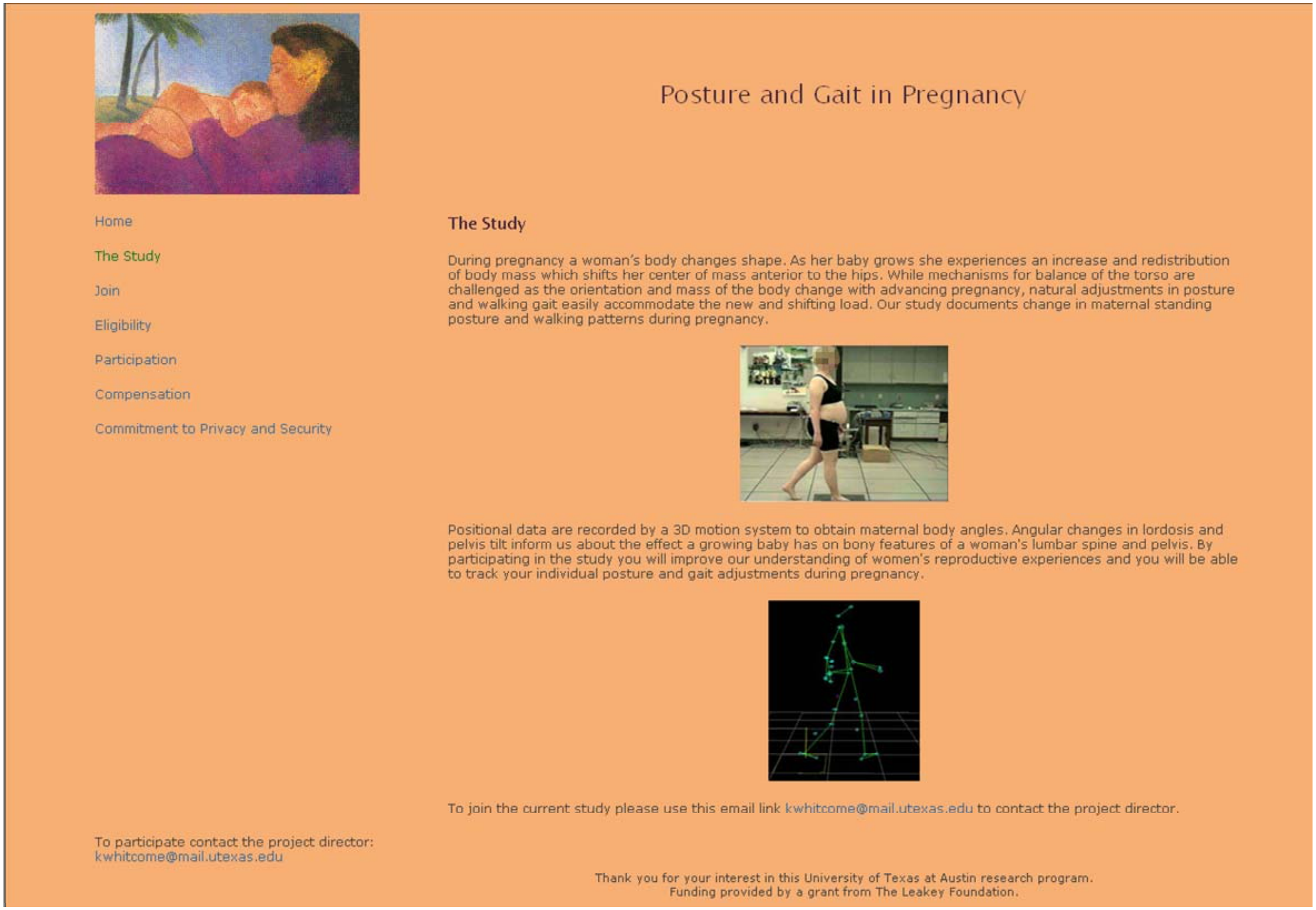

Posture and Gait in Pregnancy

The Study

During pregnancy a woman's body changes shape. As her baby grows she experiences an increase and redistribution of body mass which shifts her center of mass anterior to the hips. While mechanisms for balance of the torso are challenged as the orientation and mass of the body change with advancing pregnancy, natural adjustments in posture and walking gait easily accommodate the new and shifting load. Our study documents change in maternal standing posture and walking patterns during pregnancy.

Positional data are recorded by a 3D motion system to obtain maternal body angles. Angular changes in lordosis and pelvis tilt inform us about the effect a growing baby has on bony features of a woman's lumbar spine and pelvis. By participating in the study you will improve our understanding of women's reproductive experiences and you will be able to track your individual posture and gait adjustments during pregnancy.

To join the current study please use this email link kwhitcome@mail.utexas.edu to contact the project director.

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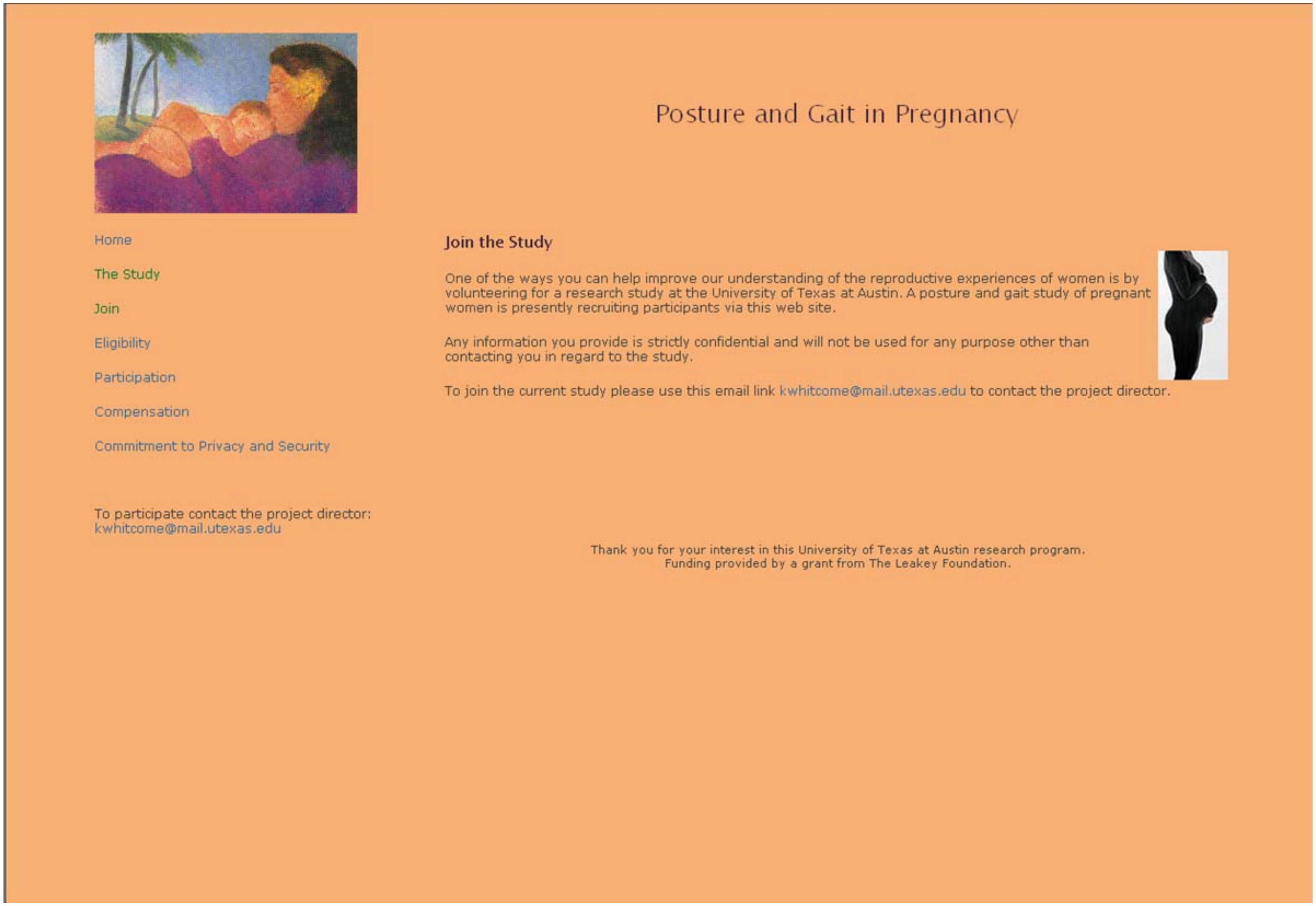

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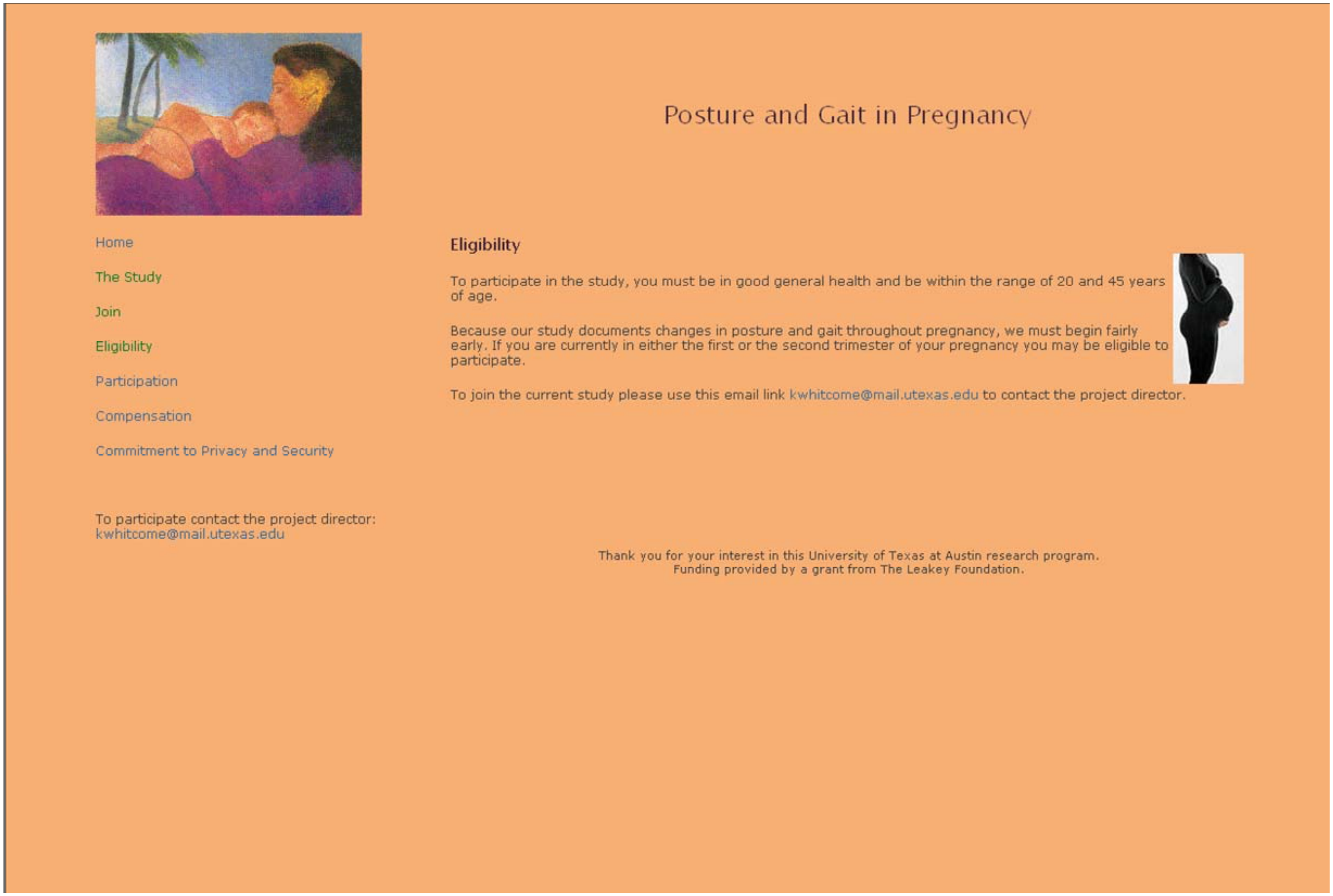
Thank you for your interest in this University of Texas at Austin research program.
Funding provided by a grant from The Leakey Foundation.



Posture and Gait in Pregnancy

Eligibility

To participate in the study, you must be in good general health and be within the range of 20 and 45 years of age.

Because our study documents changes in posture and gait throughout pregnancy, we must begin fairly early. If you are currently in either the first or the second trimester of your pregnancy you may be eligible to participate.

To join the current study please use this email link kwhitcome@mail.utexas.edu to contact the project director.

To participate contact the project director:
kwhitcome@mail.utexas.edu

Thank you for your interest in this University of Texas at Austin research program.
Funding provided by a grant from The Leakey Foundation.

To participate contact the project director:
kwhitcome@mail.utexas.edu

Posture and Gait in Pregnancy

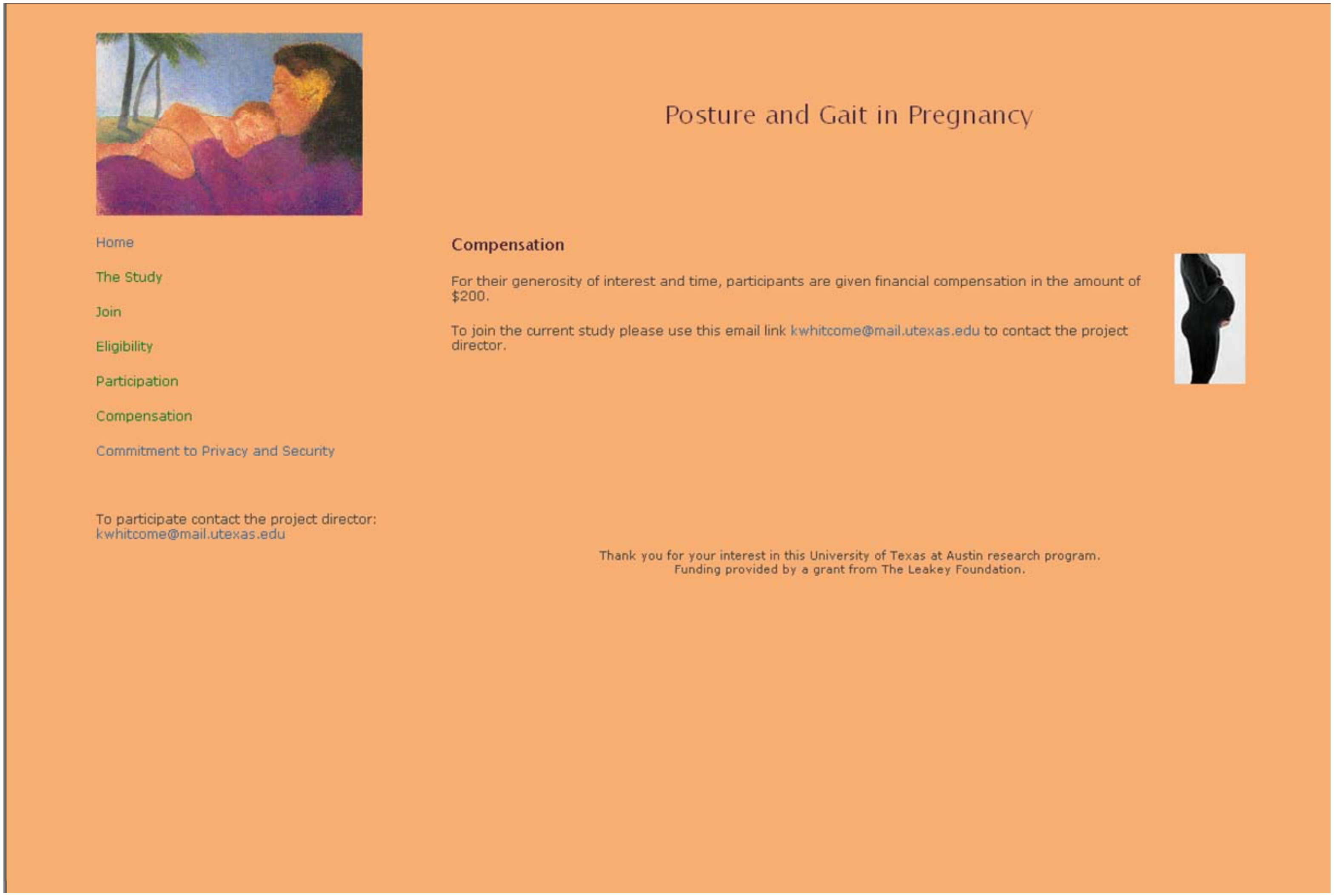
Participation

Participants perform the every day activities of natural stance and comfortable walking during brief sessions within the lab.

The research lab is located at the University of Texas at Austin. Convenient and no-fee parking is provided adjacent to the lab.

To join the current study please use this email link kwhitcome@mail.utexas.edu to contact the project director.

Thank you for your interest in this University of Texas at Austin research program.
Funding provided by a grant from The Leakey Foundation.



Posture and Gait in Pregnancy

Compensation

For their generosity of interest and time, participants are given financial compensation in the amount of $200.

To join the current study please use this email link kwhitcome@mail.utexas.edu to contact the project director.

To participate contact the project director:
kwhitcome@mail.utexas.edu

Thank you for your interest in this University of Texas at Austin research program.
Funding provided by a grant from The Leakey Foundation.

Posture and Gait in Pregnancy

To participate contact the project director:
kwhitcome@mail.utexas.edu

Privacy and Security

The researchers and the University of Texas at Austin will protect the confidentiality of the participants.

Confidentiality is protected by law, Section 308(d) of the Public Health Service Act (42USC242m) and the Privacy Act of 1974 (5USC552a).

To join the current study please use this email link kwhitcome@mail.utexas.edu to contact the project director.

Thank you for your interest in this University of Texas at Austin research program.
Funding provided by a grant from The Leakey Foundation.

APPENDIX D: SCREENING QUESTIONNAIRE

Participant Telephone Screening Questionnaire

Name________________________________

Contact Number________________________

Date ________________________

When is your baby due? ____

How many weeks pregnant are you? ____

Are you expecting a single birth? ____

What is your general state of health? ____

What is your age? ____

What is your approximate height? ____

approximate weight? ____

Do you have any current medical conditions? ________________________________

____

Have you ever injured your back, hip, leg, foot? ________________________________

____

Have you been pregnant before? ____

Did you carry the pregnancy to term? ____

Did you experience any physical discomfort? ________________________________

____

Did you experience any restriction in your physical activity? ____________________

____

Are you able to participate one day each month over a ten-month period from December 2003 to August 2004?

____

Are you able to travel to the University of Texas at Austin for each session?

____

Will you be able to continue the study in the final months of your pregnancy?

____

Will you be able to continue the study in the three months following the birth of your baby?

____

How did you hear about our study? ______________________________________

Do you have any questions? __________________________________

____

____

____

Your participation requires formal consent. When we meet I will request you read and sign a voluntary consent form. If you have additional questions we can discuss them at that meeting. In the meantime, you may reach me by phone at 512-232-3905 or email at kwhitcome@mail.utexas.edu

APPENDIX E: CONSENT FORM

IRB# 2002050067

Informed Consent to Participate in Research

The University of Texas at Austin

You are being asked to participate in a research study. This form provides you with information about the study. The Principal Investigator (the person in charge of this research) or his/her representative will also describe this study to you and answer all of your questions. Please read the information below and ask questions about anything you don't understand before deciding whether or not to take part. Your participation is entirely voluntary and you can refuse to participate without penalty or loss of benefits to which you are otherwise entitled.

Title of Research Study: Posture and Gait Changes in Pregnancy, **in association with the study: Bipedal Obstetric Load and the Evolution of Human Lumbopelvic Sexual Dimorphism**

Principal Investigator(s) (include faculty sponsor), UT affiliation, and Telephone Number(s):

Katherine K Whitcome, MA, Principal Investigator, University of Texas at Austin, 512-232-3905
Liza Shapiro, PhD, Faculty Sponsor, University of Texas at Austin, 512-471-7533

Funding source:

Current Funding provided by:	The Leakey Foundation
Funding pending:	National Science Foundation (notification expected by February 2004)

What is the purpose of this study?

Among the many changes a pregnant woman experiences are an increase and redistribution of body mass as her baby develops and grows. Mechanisms for balance of the torso are challenged as the orientation and mass of the baby change with advancing pregnancy. Women manage very well through successive trimesters via subtle adjustments in their posture and walking gait.

The purpose of this study is twofold: to document changes in the standing posture and walking behavior of women through the parous period and to apply a biomechanical model the observations generate to investigate the unique size and shape of the lower back and pelvis of women in contrast to those of men.

What will be done if you take part in this research study?

Participants will perform natural postural and locomotor activities in one-hour sessions at the University of Texas at Austin Motor Development Lab. The protocol for each of the six data sessions will proceed in the following manner. Volunteers will simply stand and walk comfortably providing positional data via small reflective markers recorded by a motional analysis system. Participants will be asked to wear a spandex gait suit during each session. Suit design is similar to popular exercise attire and will ensure comfort through all stages of pregnancy. In the first few minutes of each data session, preliminary information will be recorded, including weight, height, and torso circumference. An additional ten minutes of preparation will follow while the reflective markers are placed on major joints of the body.

Over a twenty to thirty minute period, participants will routinely stand and walk about the laboratory during which time the position of the makers will be identified by their reflective properties. The data session will conclude at the end of the scheduled hour. The changing and restroom facility is conveniently located adjacent to the lab, and participants are free to request a session intermission at any time.

What are the possible discomforts and risks?

Small lightweight markers will be gently applied by removable double-sided tape to the torso, arms, and legs. Participants will be asked to stand comfortably and walk at normal speed within the lab. No discomfort or injury is anticipated as all activities are routine and performed with ease. Proper placement of markers on the body will require painless palpation of body joints.

What are the possible benefits to you or to others?

Participants are expected to gain modest intellectual and financial benefit from the study. Increased awareness of physical changes associated with pregnant biomechanical load may serve to alleviate possible concerns women have as a result of postural and locomotor adjustments during pregnancy. Monetary compensation in the amount of $20 per data session will provide participants with a total financial reward of $200.

If you choose to take part in this study, will it cost you anything?

No costs will be incurred by participants. Complementary campus parking will be provided.

Will you receive compensation for your participation in this study?

Monetary compensation in the amount of $20 per data session will provide participants with a total financial reward of $200.

What if you are injured because of the study?

Injury is unlikely as a result of this study. Should a participant require medical attention during a study session, no medical treatment will be provided, and the affected participant will be directed to consult a medical provider. No payment can be issued in the event of a medical problem.

If you do not want to take part in this study, what other options are available to you?

Participation in this study is entirely voluntary. You are free to refuse to be in the study, and your refusal will not influence current or future relationships with The University of Texas at Austin.

How can you withdraw from this research study?

If you wish to end your participation in this research study for any reason, you should contact: Katherine Whitcome at (512) 232-3905. You are free to withdraw your consent and stop participation in this research study at any time without penalty or loss of benefits for which you may be entitled. Throughout the study, the researchers will notify you of new information that may become available and that might affect your decision to remain in the study.

In addition, if you have questions about your rights as a research participant, please contact Clarke A. Burnham, Ph.D., Chair, The University of Texas at Austin Institutional Review Board for the Protection of Human Subjects, 512/232-4383.

How will your privacy and the confidentiality of your research records be protected?

Authorized persons from The University of Texas at Austin and the Institutional Review Board have the legal right to review your research records and will protect the confidentiality of those records to the extent permitted by law. If the research project is sponsored then the sponsor also has the legal right to review your research records. Otherwise, your research records will not be released without your consent unless required by law or a court order.

If the results of this research are published or presented at scientific meetings, your identity will not be disclosed.

Will the researchers benefit from your participation in this study beyond publishing or presenting the results?

No

IRB# 2002050067

Signatures:

As a representative of this study, I have explained the purpose, the procedures, the benefits, and the risks that are involved in this research study:

____

Signature and printed name of person obtaining consent
Date

You have been informed about this study's purpose, procedures, possible benefits and risks, and you have received a copy of this Form. You have been given the opportunity to ask questions before you sign, and you have been told that you can ask other questions at any time. You voluntarily agree to participate in this study. By signing this form, you are not waiving any of your legal rights.

____

Printed Name of Subject **Date**

____

Signature of Subject **Date**

____

Signature of Principal Investigator **Date**

Sessions will be videotaped in accordance with the lab protocol to provide time frame information for gait events. The cassettes will be coded so that no personally identifying information is visible. They will be kept in a secure locked file cabinet in the investigator's office. They will be heard or viewed only for research purposes by the investigator and his or her associates.

We may wish to present some of the tapes from this study at scientific conferences or as demonstrations in classrooms. Please sign below if you are willing to allow us to do so with the tape of your performance.

I hereby give permission for the video tape made for this research study to be also used for educational purposes

Signatures:

As a representative of this study, I have explained the purpose, the procedures, the benefits, and the risks that are involved in this research study:

Signature and printed name of person obtaining consent

Date

You have been informed about this study's purpose, procedures, possible benefits and risks, and you have received a copy of this Form. You have been given the opportunity to ask questions before you sign, and you have been told that you can ask other questions at any time. You voluntarily agree to participate in this study. By signing this form, you are not waiving any of your legal rights.

Printed Name of Subject **Date**

Signature of Subject **Date**

Signature of Principal Investigator Date

APPENDIX F: CONSENT FORM AMENDMENT

IRB# 2002050067
The University of Texas at Austin

Informed Consent to Participate in Research
Consent Amendment

Title of Research Study:

Posture and Gait Changes in Pregnancy, in association with the study: Bipedal Obstetric Load and the Evolution of Human Lumbopelvic Sexual Dimorphism

Principal Investigators:
Katherine K Whitcome, MA, Principal Investigator, University of Texas at Austin, 512-232-3905
Liza Shapiro, PhD, Faculty Sponsor, University of Texas at Austin, 512-471-7533

In order that we may track the changes in maternal posture and gait associated with the growth of your baby, we schedule six sessions during your pregnancy. Each session is timed to correspond with average patterns of fetal growth and is therefore planned by the calendar according to your weeks of pregnancy. At the close of each session we confer with you to confirm a date for the subsequent meeting.

Please feel free to contact us to reschedule a planned session at your discretion. Each stage of your baby's fetal growth is framed by a two week window of time during which we hope to see you. Should you wish to reschedule an appointment, we will gladly identify an alternate date and time.

While pregnancy is a natural life experience and most women feel well and remain active, the prolonged period from early pregnancy to full delivery may find a woman with occasional discomforts either related to or independent of her pregnancy. Your health and well-being are a priority to us and we understand that pregnancy is a busy and demanding time. Should a scheduled session appear inconvenient for you, we can easily reschedule.

If illness or injury, no matter how minor it may seem, results in a need to either reschedule or cancel a session, we ask your permission to follow-up on your condition with a phone call in the days immediately following the schedule change.

Participation in this study is entirely voluntary. If you wish to end your participation in this research study for any reason, you should contact: Katherine Whitcome at (512) 232-3905. You are free to withdraw your consent and stop participation in this research study at any time without penalty or loss of benefits for which you may be entitled. In addition, if you have questions about your rights as a research participant, please contact Clarke A. Burnham, Ph.D., Chair, The University of Texas at Austin Institutional Review Board for the Protection of Human Subjects, 512/232-4383.

IRB# 2002050067

Signatures:

As a representative of this study, I have explained the purpose, the procedures, the benefits, and the risks that are involved in this research study:

____

Signature and printed name of person obtaining consent

Date

By signing this form, you are not waiving any of your legal rights.

____

Printed Name of Subject **Date**

____

Signature of Subject **Date**

____

Signature of Principal Investigator **Date**

APPENDIX G: ANGLE MODEL

```
{*VICON BodyLanguage*}

{*copyright Oxford Metrics 1997*}


{*FETALLOAD.MOD, for use with FETALLOAD.MP parameter file*}


{* Angle Outputs *}
{* ============= *}


Pelvis = [SACR, LUML-SACR, LUMF-LUML, zyx]
Lumbar = [LUML, LUMF-LUML, SACR-LUML, zyx]
Lumbarangle = <Pelvis, Lumbar>
Pelvicsegment = [RPSI, (RASI-RPSI), (SACR-RPSI), 1]
pelvicangle = <pelvicsegment, 1>
```

APPENDIX H: MATLAB SCRIPT FOR CENTER OF MASS POSITION

```
function Tfxzero=FindFxZero(startIndex,Fx)

n=length(Fx);
Tfxzero=-1;
if (Fx(startIndex)>0)
      sign=1;
  else
      sign=-1;
  end
for i=startIndex+1:n
   if (Fx(i)>0)
      sign1=1;
  else
      sign1=-1;
  end
  if sign1~=sign
      Tfxzero=i;
      break;
  end
end
Tfxzero;

function Xglp_t1=zpz(Fx,m, T,Xcop_t0, Xcop_t1)

%T is the time vector from tn to tnplus1
%Fx is the Fx(t) vector from tn to tnplus1
F=(0.1*Fx)/(0.1*m);
part1=trapz(T,F);
%assume xdeta_0=0
part2=0;
Xglp_t1=part1+part2+Xcop_t0;
%step 3
t0=T(1);
t1=T(length(T));
Xdelta_t0=(Xglp_t1-Xcop_t1)/(t1-t0);
part2=Xdelta_t0*(t1-t0);
%Repeat step 2
Xglp_t1=part1+part2+Xcop_t0

data=xlsread('testdata1.xls');
m=10;
T=data(:,1)';
Xcop=data(:,2)';
```

```
F=data(:,3)';

Xglp(1)=Xcop(1);
k=2;
startIndex=FindFxZero(1, F);
endIndex=FindFxZero(startIndex, F);
while(endIndex>startIndex)
   Fx=F(startIndex:endIndex);
   Tx=T(startIndex:endIndex);
   Xcop_t0=Xcop(startIndex);
   Xcop_t1=Xcop(endIndex);
   Xglp(k)=zpz(Fx,m, Tx,Xcop_t0, Xcop_t1);
   k=k+1;
   startIndex=endIndex;
   endIndex=FindFxZero(startIndex, F);

end
Xglp
average_Xglp=mean(Xglp)
```

COM method following Zatsiorsky and King (1998).
MatLab scripts written in consultation with Dr. Tim Eakin and Shu Wang, UT ITS Research Consultants.

APPENDIX I: MATLAB PROGRAM FOR RADIUS OF CURVATURE

```
% determine radius of curvature for fused quadrilateral polygons
(vertebrae)
% test script for just two bones
% assign dorsal lengths, ventral lengths, and width for each polygon
% d = dorsal length, v = ventral length, w = width
d(1) = 26.8; % supply the mean dorsal length of first vertebra
d(2) = 27.0; % supply the mean dorsal length of second vertebra
d(3) = 26.2; % etc.
d(4) = 24.6;
v(1) = 26.7;
v(2) = 27.7;
v(3) = 28.0;
v(4) = 27.7;
w(1) = 30.7;
w(2) = 31.8;
w(3) = 32.3;
w(4) = 32.2;

%bones = length(d); % determines how many vertebrae are being
considered
% prototype with only 2 bones
bones = length(d);

% determine wedge angles
% assume line of symmetry, same wedge angle at bottom as at top
for i = 1:bones
    theta(i) = atan(((v(i) - d(i))/2)/w(i));
end;

% determine vertex and midpoints of all bone polygons
    % c1 = top left vertex, c2 = top right vertex
    % c3 = bottom right vertex, c4 = bottom left vertex
    % m1 = midpoint of top line, m2 = midpoint of ventral line
    % m3 = midpoint of bottom line, m4 = midpoint of dorsal line
for i = 1:bones
    c1(i,1) = 0;% arbitrarily choose top left vertex horizontal
position at 0
    c1(i,2) = 0; % arbitrarily choose top left vertex vertical position
at 0
    c2(i,1) = c1(i,1) + w(i);
    c2(i,2) = (v(i)-d(i))/2;
    c3(i,2) = -d(i) - (v(i)-d(i))/2;
    c3(i,1) = c2(i,1);
    c4(i,1) = 0;
    c4(i,2) = -d(i);
end;
for i = 1:bones
    for j = 1:2
        m1(i,j) = (c1(i,j)+c2(i,j))/2;
        m2(i,j) = (c2(i,j)+c3(i,j))/2;
```

```
        m3(i,j) = (c3(i,j)+c4(i,j))/2;
        m4(i,j) = (c4(i,j)+c1(i,j))/2;
    end;
end;

for i = 1:bones
    cx(i,:) = [c1(i,1) c2(i,1) c3(i,1) c4(i,1) c1(i,1)];
    cy(i,:) = [c1(i,2) c2(i,2) c3(i,2) c4(i,2) c1(i,2)];
    mx(i,:) = [m1(i,1) m2(i,1) m3(i,1) m4(i,1)];
    my(i,:) = [m1(i,2) m2(i,2) m3(i,2) m4(i,2)];
end;

% fuse the bones together with a common graph origin
% bottom side of bone i flush with top side of bone i+1
% midpoint of a bone's bottom side coincides with midpoint of adjacent
top side

% first rotate the bones by the needed angle (sum current and previous
thetas)
for i = 1:bones
    rot(i) = 0;
    for j = 1:i
        for k = 1:j
            rot(i) = rot(i) - (theta(k));
        end;
    end;
    rotmatrix = [cos(rot(i)) -sin(rot(i)); sin(rot(i)) cos(rot(i))];
    rotc1(i,1:2) = (rotmatrix*[c1(i,1);c1(i,2)])';
    rotc2(i,1:2) = (rotmatrix*[c2(i,1);c2(i,2)])';
    rotc3(i,1:2) = (rotmatrix*[c3(i,1);c3(i,2)])';
    rotc4(i,1:2) = (rotmatrix*[c4(i,1);c4(i,2)])';
    rotm1(i,1:2) = (rotmatrix*[m1(i,1);m1(i,2)])';
    rotm2(i,1:2) = (rotmatrix*[m2(i,1);m2(i,2)])';
    rotm3(i,1:2) = (rotmatrix*[m3(i,1);m3(i,2)])';
    rotm4(i,1:2) = (rotmatrix*[m4(i,1);m4(i,2)])';
end;

for i = 1:bones
    rcx(i,:) = [rotc1(i,1) rotc2(i,1) rotc3(i,1) rotc4(i,1)
rotc1(i,1)];
    rcy(i,:) = [rotc1(i,2) rotc2(i,2) rotc3(i,2) rotc4(i,2)
rotc1(i,2)];
    rmx(i,:) = [rotm1(i,1) rotm2(i,1) rotm3(i,1) rotm4(i,1)];
    rmy(i,:) = [rotm1(i,2) rotm2(i,2) rotm3(i,2) rotm4(i,2)];
end;

% next translate everything in the x,y directions for the midpoint
junctions
% no translation for first bone
xdiff(1) = 0;
ydiff(1) = 0;
trcx(1,:) = rcx(1,:);
```

```
trcy(1,:) = rcy(1,:);
trmx(1,:) = rmx(1,:);
trmy(1,:) = rmy(1,:);

% align top midpoint of other bones with bottom midpoint of previous
bone
for i = 2:bones
    xdiff(i) = rmx(i,1) - rmx(i-1,3);
    ydiff(i) = rmy(i,1) - rmy(i-1,3);
    cumxdiff(i) = 0;
    cumydiff(i) = 0;
    for j = 1:i
        cumxdiff(i) = cumxdiff(i) + xdiff(j);
        cumydiff(i) = cumydiff(i) + ydiff(j);
    end;
    trcx(i,:) = rcx(i,:) - cumxdiff(i);
    trcy(i,:) = rcy(i,:) - cumydiff(i);
    trmx(i,:) = rmx(i,:) - cumxdiff(i);
    trmy(i,:) = rmy(i,:) - cumydiff(i);
end;

% plot the rotated and translated bones
hold off;
plot(trcx(1,:),trcy(1,:),'m');
hold on;
plot(trcx(2,:),trcy(2,:),'b');
plot(trcx(3,:),trcy(3,:),'r');
plot(trcx(4,:),trcy(4,:),'g');

%make a column vector of all top midpoints plus bottom midpoint of
final bone
xmid = trmx(:,1)';
ymid = trmy(:,1)';
xmid(bones+1) = trmx(bones,3);
ymid(bones+1) = trmy(bones,3);
midpoints = [xmid' ymid'];

% make small ircles around the midpoints to be used for finding a best
fit
plot(midpoints(:,1),midpoints(:,2),'ko');

% find best fit to a circle through the midpoints
% minimize least squares
% choose the origin as a starting guess for center of circle
xcen(1) = 0;
ycen(1) = 0;
% determine mean x and y positions of midpoints
xmean = sqrt(sum(xmid.^2));
ymean = sqrt(sum(ymid.^2));
rad(1) = sqrt(xmean^2 + ymean^2);
```

```
%construct an error measurement from the initial guess

for i = 1:length(xmid)
    guess(i) = sqrt((xmid(i)- xcen(1)).^2 + (ymid(i) - ycen(1)).^2);
end;
errorsq = sum((guess  - rad(1)).^2 );

% adjust xcen, ycen, rad until stable
% select testing incements
xinc = 0.01*rad(1);
yinc = 0.01*rad(1);
rinc = 0.01*rad(1);
%initalize new values
newxcen = 0;
newycen = 0;
newrad = 1;
% change values until minimum error is reached
count = 0;
while(((xcen(1)~=newxcen) | (ycen(1)~=newycen) | (rad(1)~=newrad)) &
count <80)
    count = count + 1;
    xcen(1) = newxcen;
    ycen(1) = newycen;
    rad(1) = newrad;
    xcen(2) = xcen(1) + xinc;
    xcen(3) = xcen(1) - xinc;
    ycen(2) = ycen(1) + yinc;
    ycen(3) = ycen(1) - yinc;
    rad(2) = rad(1) + rinc;
    if rad(1) > rinc
        rad(3) = rad(1) - rinc;
    else
        rad(3) = rad(1)/2;
    end;
    for i = 1:3
        for j = 1:3
            for k = 1:3
                for m = 1:length(xmid)
                    xlen(m) = xmid(m)- xcen(i);
                    ylen(m) = ymid(m)- ycen(j);
                    rlen(m) = sqrt(xlen(m)^2 + ylen(m)^2);
                    rdiff(m) = rlen(m) - rad(k);
                    rdiffsq(m) = (rdiff(m)).^2;
                end;
                newerrorsq = sum(rdiffsq);
                if newerrorsq < errorsq
                    xmin = i;
                    ymin = j;
                    rmin = k;
                    errorsq = newerrorsq;
                end;
            end;
```

```
        end;
    end;
    newxcen = xcen(xmin);
    newycen = ycen(ymin);
    newrad = rad(rmin);
    for k = 1:360
        phi(k) = k/(2*pi);
        xnew(k) = xcen(xmin) + rad(rmin)*cos(phi(k));
        ynew(k) = ycen(ymin) + rad(rmin)*sin(phi(k));
    end;
end;
plot(xnew,ynew,'k');
xcenter = xcen(1)
ycenter = ycen(1)
radiusofcurvature = rad(1)
```

Bibliography

Abitbol M. 1987. Obstetrics and posture in pelvic anatomy. J Hum Evol 16:243-256.

Abitbol M. 1993. Growth of the fetus in the abdominal cavity. Am J Phys Anthropol 91:367-378.

Abitbol M. 1996a. The shape of the female pelvis: contributing factors. J Rep Med 41:242-250.

Abitbol M. 1996b. Birth and human evolution: anatomical and obstetrical mechanics in primates. Westport, Conn: Bergin and Garvey.

Adams MA, Hutton WC. 1980. The effect of posture on the role of the apophyseal joints in resisting intervertebral compressive forces. J Bone Joint Surg 62B:358-362.

Adams MA, Hutton WC. 1983. The mechanical function of lumbar apophyseal joints. Spine 8:327-330.

Alexander GR, Himes JH, Kaufman RB, Mor J, Kogan M. 1996. A United States national reference for fetal growth. Obstet Gyn 87:163-168.

Altmann SA. 1959. Field observations on a howling monkey society. J Mammal 40:317-330.

Ankel F. 1972. Vertebral morphology of fossil and extant primates. In: Tuttle R, editor. The Functional and Evolutionary Biology of Primates. Chicago: Aldine Atherton pp 223-240.

Ardito G. 1976. Checklist of data on gestation length of primates. J Hum Evol 5:213-222.

Badoux DM. 1974. An introduction to biomechanical principles in primate locomotion and structure. In Jenkins Jr FA (ed). Primate Locomotion. New York, Academic Press. pp 1-44.

Bartlett TQ. 2003. Intragroup and intergroup social interactions in white-handed gibbons. Int J Primatol 24:239-259.

Baskett TF, Nagele F. 2000. Naegele's rule: a reappraisal. British J Obstet Gyn 107:1433-1435.

Begun D, Walker A. 1993. The endocast. In: Walker A, Leakey R, editors. The Nariokotome *Homo erectus* skeleton. Cambridge, MA:Harvard University Press. P 326-358.

Bellamy N, Park W, Rooney PJ. 1983. What do we know about the sacroiliac joint? Sem Arth Rheu 12:282-313.

Benton R. 1967. Structural patterns in the Pongidae and Cercopithecidae. Yrbk Phys Anthropol 18:65-88.

Berge C. 1984. Multivariate analysis of the pelvis for hominids and other extant primates: Implications for the locomotion and systematics of the different species of australopithecines. J Hum Evol 13:555-562.

Berge C. 1990. Size and locomotion-related aspects of hominid and anthropoid pelves: an osteometrical multivariate analysis. In: FK Jouffroy, MH Stack, C Niemitz, editors. Gravity, Posture and Locomotion in Primates. Firenze: Il Sedicesimo. p 97-108.

Berge C, Orban-Segebarth R, Schmid P. 1984. Obstetric interpretation of the australopithecine pelvic cavity. J Hum Evol 13:573-587.

Bergeson D. 1996. The positional behavior and prehensile tail use of *Alouatta palliata*, *Ateles geoffroyi*, and *Cebus capucinus*. PhD dissertation, Washington University, St. Louis.

Bird AR, Menz HB, Hyde CC. 1999. The effect of pregnancy on footprint parameters: a prospective investigation. Journal of the American Podiatric Medical Association 89:405-409.

Bjorntorp P. 1996. The regulation of adipose tissue distribution in humans. Int J Obesity 20:291-302.

Black E. 1970. Sexual dimorphism of the ischium and pubis of three species of South American monkeys. J Mammal 51*:*794-796.

Blacke SP, Connors AM. 2004. Sacral insufficiency fracture. Brit J Radiol 77:891-896.

Blackith R, Reyment RA. 1971. Multivariate morphometrics. Academic Press, New York.

Block RA, Hess LA, Timpano EV, Serlo C. 1985. Physiologic changes in the foot during pregnancy. J Amer Pod Med Assoc 75:297-299

Bogduk N. 2005. Clinical anatomy of the lumbar spine and sacrum. 3rd edition. New York:Churchill Livingstone.

Bornstein P, Peterson R. 1966. Numerical variation of the presacral vertebral column in three population groups in North America. Am J Phys Anthropol 25:139-146.

Bullock J, Jull G, Bullock M.1987. The relationship of low back pain to postural changes during pregnancy. Aust J Phys 33:10-17.

Bullock-Saxton J. 1993. Postural alignment in standing: a repeatability study. Aust. J Physiother 39:25-29.

Canavez FC, Moreira MAM, Ladasky JJ, Pissinatti A, Parham P, Seuanez HN. 1999. Molecular phylogeny of New World primates (Platyrrini) based on beta(s)-microglobulin DNA sequences. Mol Phylo Evol 12:74-82.

Cannon CH, Leighton M. 1994. Comparative locomotor ecology of gibbons and macaques: selection of canopy elements for crossing gaps. Am J Phys Anthropol 93:505-524.

Cant JGH. 1986. Locomotion and feeding postures of spider and howling monkeys: Field study and evolutionary interpretation. Fol Primatol 46:1-14.

Cant JGH. 1987. Positional behavior of female Bornean orangutans (*Pongo pygmaeus*). Am J Primatol 12:71-90.

Cant JGH. 1988. Positional behavior of long-tailed macaques (*Macaca fascicularis*) in Northern Sumatra. Am J Phys Anthropol 76:29-37.

Cant JGH, Youlatos D, Rose MD. 2001. Locomotor behavior of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador: General patterns and nonsuspensory modes. J Hum Evol. 41:141-166.

Cappozzo A. 1981. The forces and couples in the human trunk during level walking. J Biomech 265-277.

Carpenter CR. 1964. A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). In Naturalistic Behavior of Nonhuman Primates (ed. Carpenter CR), pp. 145–271. University Park: The Pennsylvania State University Press.

Chen XM, Milne N, O'Higgins P. 2005. Morphological variation of the thoracolumbar vertebrae in Macropodidae and its functional relevance. J Morph 266:167-181.

Clauser DA. 1980. Functional and comparative anatomy of the primate spinal column: Some locomotor and postural adaptations. PhD dissertation. The University of Wisconsin, Milwaukee.

Collins AC. 2004. Atelinae phylogenetic relationships: The trichotomy revived? Amer J Phys Anthropol 124:285-296.

Connour JR, Glandel K, Vincent F. 2000. Postcranial adaptations for leaping in primates J Zool 251: 79-103

Corruccini RS. 1987. Shape in morphometrics: comparative analyses. Am J Phys Anthropol 73: 289-303.

Crosbie J. 1995. Interrupted time series analysis with short series: why it is problematic; how it can be improved. In: The analysis of change, Gottman JM (ed). Mahwah, NJ: L Erlbaum Associates.

Crosbie J, Vachalathiti R, Smith R. 1997. Patterns of spinal motion during walking Gait Post 5: 6-12.

Culver CC, Viano DC. 1990. Anthropometry of seated women during pregnancy. Defining a fetal region for crash protection research. Hum Factors 32:625-636.

Cunningham DJ. 1886. Cunningham's manual of practical anatomy. Oxford, NY: Oxford University Press.

Cunningham D. 1889. The proportion of bone and cartilage in the lumbar section of the vertebral column of the ape and several races of men. J Anat 24:117-126.

Dagosto M. 1995. Seasonal variation in positional behavior of Malagasy lemurs. Int J Primatol 16:807-833.

Danforth CH. 1930. Numerical variation and homologies in vertebrae. Am J Phys Anthropol 14:463-481.

Darroch J, Mosimman J. 1985. Canonical and principal components of shape. Biometrika 72:241-252.

Davis PR. 1961. Human lower lumbar vertebrae: some mechanical and osteological considerations. J Anat 95:337-344.

Day MH, Wickens EH. 1980. Laetoli Pleiocene hominid footprints and bipedalism. Nature 286:385-387.

DeBeer Kaufmann P. 1974. Variation in the number of presacral vertebrae in Bantu-speaking South African Negroes. Am J Phys Anthropol 40:369-374.

Department of Health and Human Services. 1983. Obese and overweight adults in the United States. Publication No (PHS) 83-1680.

Demes B, Fleagle JG, Jungers WL .1999. Takeoff and landing forces of leaping strepsirhine primates. J Hum Evol 37:279-292.

Demes B, Franz TM, Carlson KJ. 2005. External forces on the limbs of jumping lemurs at takeoff and landing. Am J Phys Anthropol 128:348-358.

Demes B, Jungers WL, Fleagle JG, Wunderlich RE, Richmond BG, Lemelin P. 1996. Body size and leaping kinematics in Malagasy vertical clingers and leapers. J Hum Evol 31:367-388.

Derry DE. 1912. The influence of sex on the position and composition of the human sacrum. J Anat Physiol 46:184-192.

Digiovanni B, Scoles P, Latimer B. 1989. Anterior extension of the thoracic vertebral bodies in Scheuermann's kyphosis: an anatomic study. Spine 14(7): 712-716.

Doran DM. 1992. Comparison of instantaneous and locomotor bout sampling methods: A case study of adult male chimpanzee locomotor behavior and substrate use. Am J Phys Anthropol 89:85-99.

Doran DM. 1993. Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion. Am J Phys Anthropol 91: 83–98.

Doran DM, Hunt KD. 1994. Comparative locomotor behavior of chimpanzees and bonobos: species and habitat differences. In Chimpanzee Cultures (eds Wrangham RW, McGrew WC, de Waal FBM, et al.), pp. 93–108. Cambridge:Harvard University Press.

Dumas GA, Reid JG, Griffin MP, McGrath MJ. 1995. Exercise, posture, and back pain during pregnancy. Clin Biom 10(2):98-105.

Eames MHA, Cosgrove A, Baker R. 1999. Comparing methods of estimating total body center of mass in three-dimensions in normal and pathological gait. Hum Move Sci 18: 637-646.

Elftman HO. 1932. The evolution of the pelvic floor of primates. Am J Anat 51*:*307-346.

Ellefson JO. 1967. A natural history of gibbons in the Malay Peninsula. PhD thesis, University of California, Berkeley.

Fajardo RJ, Müller R. 2001. Three-dimensional analysis of nonhuman primate trabecular architecture using micro-computed tomography. Am J Phys Anthrop 115: 327–336.

Falsetti AB, Jungers WL, Cole TM. 1993. Morphometrics of the callitrichid forelimb: A case study in size and shape. Int J Primatol 14(4):551-572.

Feibel C, Agnew N, Latimer B, Demas M, Marshall F, Waane SAC, and Schmid P. 1996. The Laetoli hominid footprints: A preliminary report on the conservation and scientific restudy. Evol Anthropol 4:149–154.

Fleagle JG. 1976. Locomotion and posture of the Malayan siamang and implications for hominid evolution. Folia Primatol 26:245–269.

Fleagle JG, Mittermeier RA. 1980. Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. Am J Phys Anthropol 52:301-314.

Flower WH. 1885. An introduction to the osteology of Mammalia. London:MacMillon and Co.

Fontaine R. 1990. Positional behavior in *Saimiri boliviensis* and *Ateles geoffroyi*. Am J Phys Anthropol 82: 485-508.

Foti T, Davids J, Bagley A. 2000. A biomechanical analysis of gait during pregnancy. J Bone Joint Surg 82A:625-632.

Franklin M, Conner-Kerr T. 1998. An analysis of posture and back pain in the first and third trimesters of pregnancy. J Ortho Sports Phys Ther 28:133-138.

Galik K, Senut B, Pickford M. 2004. External and internal morphology of the BAR 1002’00 *Orrorin tugenensis* femur. Science 305:1450-1453.

Gebo DL. 1987. Locomotor diversity in prosimian primates. Am J Primatol 13:271-281.

Gebo DL, Chapman CA. 1995. Positional behavior in 5 sympatric Old-World monkeys. Am J Phys Anthropol 97:49-76.

Gilad I, Nissan M. 1985. Sagittal evaluation of elemental geometric dimensions of human vertebrae. J Anat 143:115-120.

Gilleard D, Brown W, Brown JM. 1996. Structure and function of the abdominal muscles in primigravid subjects during pregnancy and the immediate postbirth period. Phys Ther 76: 750-762.

Gingerich PD. 1972. The development of sexual dimorphism in the bony pelvis of the squirrel monkey. Anat Rec 172:589-595.

Gittins PS. 1983. Use of forest canopy by the agile gibbon. Fol Primatol 40: 134–144.

Givnish TJ, Sytsma KJ. 1997. Homoplasy in molecular vs. morphological data: The likelihood of correct phylogenetic inference. In Givnish TJ, Sytsam KJ (eds.), Molecular evolution and adaptive radiation. Cambridge University Press, Cambridge. pp 55-101.

Gracovetsky S. 1985. A hypothesis for the role of the spine in human locomotion: a challenge to current thinking. J Biomed Eng 7:205-216.

Granata KP, Sanford AH. 2000. Lumbar-pelvic coordination is influenced by lifting task parameters. Spine 25:1413-1418.

Haeusler, M., Martelli, S., Boeni, T., 2002. Vertebrae numbers of the early hominid lumbar spine. J Hum Evol 43, 621-643.

Hager LD. 1989. The evolution of sex differences in the hominid bony pelvis. Ph.D. dissertation, University of California at Berkeley, Berkeley, California.

Hager LD. 1996. Sex differences in the sciatic notch of great apes and modern humans. Am J Phys Anthropol 99*:*287-300.

Halpert A, Jenkins F, and Franks H. 1987. Structure and scaling of the lumbar vertebrae in African bovids (Mammalia and Artiodactyla). J Zool Lond 211:239-258.

Harcourt AH. 1985. Gorilla. In: MacDonald D (ed), Primates. Torstar Books: New York. pp 136-143.

Hart DL, Rose SJ. 1986. Reliability of a noninvasive method for measuring the lumbar curve. J Orthop Sports Phys Ther 8:180-184.

Hollihn U. 1984. Bimanual suspensory behavior: morphology, selective advantages and phylogeny. In: The lesser apes: evolutionary and behavioral biology. Preuschoft H, Chivers DJ, Brockelman WY, Creel N (eds). Edinburgh: Edinburgh University Press. pp 85-95.

Horovitz I, Zardoya R, Meyer A. 1998. Platyrrhine systematics: A simultaneous analysis of molecular and morphological data. Am J Phys Anthropol 106: 261-281.

Hoyt DF, Wickler SJ, Biewener AA, Cogger EA, DeLa Paz KL. 2005. In vivo muscle function vs speed I. Muscle strain in relation to length change of the muscle-tendon unit. J Exp Biol 208:1175-1190.

Huiskes R, Ruimerman R, Van Lenthe GH, Janssen JD. 2000. Effects of mechanical forces on maintenance and adaptation of form in trabecular bone. Nature 405: 704–706.

Hunt KD. 1996. The postural feeding hypothesis: An ecological model for the evolution of bipedalism. S Af J Sci 92:127-151.

Institute of Medicine of the National Academies. 1990. Nutrition during pregnancy. Part1. Weight gain. Washington DC: National Academy Press.

Isler K. 2005. 3D-kinematics of vertical climbing in hominoids. Am J Phys Anthropol 126: 66-81.

Jaccard J, Wan CK. 1996. LISREL approaches to interaction effects in multiple regression. Thousand Oaks, CA: Sage Publications.

Jenkins FA. Jr. 1974. Tree shrew locomotion and the origins of primate arborealism. In Jenkins FA Jr. (ed), Primate locomotion. New York: Academic Press. pp 85-115.

Jensen R, Doucet S, Treitz T. 1996. Changes in segment mass and mass distribution during pregnancy. J Bio 29:251-256.

Jensen RK, Treitz T, Doucet S. 1996b. Prediction of human segment inertias during pregnancy. J Appl Biom 12:15-30.

Johnson SE, Shapiro LJ. 1998. Positional behavior and vertebral morphology in atelines and cebines. Am J Phys Anthropol 105:333-354.

Jones WP. 2003. Single-case times series with Bayesian analysis: a practitioner's guide. Measurement and Evaluation in Counseling and Development 36:28-35.

Jorgensen MJ, Marras WS, Granata KP, Wiand JW. 2001. MRI-derived moment-arms of the female and male spinal loading muscles. Clin Biom 16:182-193.

Jorgensen MJ, Marras WS, Gupta P, Waters TR. 2003. Effect of torso flexion of the lumbar torso extensor muscle sagittal plane moment arms. Spine J 3:363-369

Jungers W. 1984. Aspects of size and scaling in primate biology with special reference to the locomotor skeleton. Yrbk Phys Anthropol 27:73-97.

Jungers WL, Falsetti AB, Wall CE. 1995. Shape, relative size, and size-adjustments in morphometrics. Yrbk Phys Anthropol 38:137-161.

Jungers WL, Susman RL. 1984. Body size and skeleton allometry in African apes. In (R. L. Susman, ed.) The Pygmy Chimpanzee. New York: Plenum Press. pp131–177.

Kapandji IA. 1982. Physiology of the joints: The trunk and the vertebral column. Edinburg: Churchill Livingstone.

Kappelman, J. 1996. The evolution of body mass and relative brain size in fossil hominids. J Hum Evol 30:243-276.

Keith A. 1923. Man's posture and its evolution and disorders. II. The evolution of the orthograde spine. Brit Med J 1:499-502.

Kiltie RA. 1982. Intraspecific variation in the mammalian gestation period. J Mammal 63: 646-652.

Klingenberg CP. 1996. Multivariate allometry. In Marcus LF, Corti M, Loy A, Naylor G, Slice D (eds) Advances in morphometrics. Plenum Press: New York. Pp 23-49.

Knussman R, Finke E. 1980. Studies on the sex-specificity of the human spinal profile. J Hum Evol 9:615-620.

Knott CJ. 1999. Orangutan behavior and ecology. In Dolhinow P and FuentesA (eds.) The nonhuman primates. Mayfield Press, Mountain View CA pp 50-57.

Koo WWK, Walters JC, Hockman EM. 2004. Body composition in neonates: relationship between measured and derived anthropometry with dual-energy x-ray absorptiometry measurements. Pediat Res 56:694-700

Krogman WM. 1951. The scars of human evolution. Sci Am December 1951:54-57.

Lague MR. 2003. Patterns of joint size dimorphism in the elbow and knee of catarrhine primates. Am J Phys Anthropol 120:278-297.

Lamoth CJC, Beek PJ, Meijer OG. 2002. Pelvis-thorax coordination in the transverse plane during gait. Gait Posts 16:101-114.

Latimer B, Lovejoy CO. 1990. Hallucal tarsometatarsal joint in *Australopithecusafarensis*. Am J Phys Anthropol 82:125-133.

Latimer B, Ward C. 1993. The thoracic and lumbar vertebrae. In: Walker A, Leakey REF, editors. The Nariokotome *Homo Erectus* Skeleton. Cambridge: Harvard University Press p 266-293.

LaVelle M. 1995. Natural selection and developmental sexual variation in the human pelvis. Am J Phys Anthropol 98:39-72.

Leakey MD, Hay RL. 1979. Pliocene footprints in the Laetoli Beds at Laetoli, northern Tanzania. Nature 27:317-323.

Leong JCY, Luk KDK, Chow DHK, Woo CW. 1987. The biomechanical functions of the iliolumbar ligament in maintaining stability of the lumbosacral junction. Spine 12, 669–674.

Leutenegger W. 1972. New born size and pelvic dimensions of *Australopithecus*. Nature 240:568-569.

Leutenegger W. 1973. Sexual dimorphism in the pelves of African lorises. Am J Phys Anthropol 38*:*251-254.

Leutenegger W. 1974. Functional aspects of pelvic morphology in simian primates. J Hum Evol 3*:*207-222.

Leutenegger W. 1982a. Sexual dimorphism in nonhuman primates. In: Hall RL, editor. Sexual Dimorphism in *Homo Sapiens*: A Question of Size. New York: Praeger p 11-33.

Leutenegger W. 1982b. Encephalization and obstetrics in primates with particular reference to human evolution. In: Armstrong E, Falk D, editors. Primate Brain Evolution: Methods and Concepts. New York: Plenum Press p 85-95.

Leutenegger W. 1987. Neonatal brain size and neural cranial dimensions on Pliocene hominids: implications for obstetrics. J Hum Evol 16:291-296.

Leutenegger W, Larson S. 1985. Sexual dimorphism in the postcranial skeleton of New World primates. Folia Primatol 44:82–95.

Levine D, Whittle MW. 1996. The effects of pelvic movement on lumbar lordosis in the standing position. J Orthoped Sports Phys Ther 24: 130-135.

Lindberg D. 1982. Primate obstetrics: The biology of birth. Am J Primatol Supp 1:93-99.

Lindsay CA, Huston L, Amini SB, Catalano PM. 1997. Longitudinal changes in the relationship between body mass index and percent body fat in pregnancy. Obs Gyn 89:377-382.

Little BB. 1989. Gestation length, metabolic-rate, and body and brain weights in primates: epigenetic effects. Am J Phys Anthropol 80: 213-218.

Llorens L, Casinos A, Berge C, Majoral M, Jouffroy FK. 2001. A biomechanical study of the long bones in platyrrhines. Fol Primatol 72:201-216.

Lou SZ, Chou YL, Chou PH, Lin CJ, Chen UC, Su FC. 2001. Sit-to-stand at different periods in pregnancy. Clin Biom 16:194-198.

Louis R. 1985. Spinal stability as defined by the three-column spine concept. Anat Clin 7:33-42.

Lovejoy CO. 1979. A reconstruction of the pelvis of AL 288 (Hadar Formation, Ethiopia). Am J Phys Anthropol 50:460.

Lovejoy CO. 1980. Hominid origins: the role of bipedalism. Am J Phys Anthropol 52:250.

Lymbery JK, Gilleard W. 2005. The stance phase of walking during late pregnancy: Temperospatial and ground reaction force variables. J Amer Pod Med Asso 95:247-253.

McHenry HM. 1992. Body size and proportions in early hominids. Am J Phys Anthropol 87:407-431

McKenzie AM, Taylor NF. 1997. Can physiotherapists locate lumbar spinal levels by palpation? Physiother 83:235-239.

Meder, A. 1993. Gorillas. Okologie und Verhalten. Heidelberg: Springer.

Merbs CF. 1983. Patterns of activity-induced pathology in a Canadian Inuit population. Otttawa: National Museum of Man Mercury Series, Archaeological Survey of Canada paper no 199.

Merbs CF. 1996. Spondylolysis and spondylolythesis: A cost of being an erect biped or a clever adaptation? Yrbk Phys Anthropol 39:201-228.

Merbs, CF. 2002. Asymmetrical spondylolysis. Am J Phys Anthropol 119:156-174.

Merbs CF. 2004. Sagittal clefting of the body and other vertebral development errors in Canadian Inuit skeletons. Am J Phys Anthropol 123:236-249.

Mittendorf R, Williams MA, Berkey CS, Lieberman E, Monson RR. 1993. Predictors of human gestational length. Am J Obstet Gynecol 168:480-484.

Mittlemark R, Wiswell R, Drinkwater B. 1991. Exercise in pregnancy. Baltimore: Williams and Wilkins.

Mittermeier RA. 1978. Locomotion and posture in *Ateles geoffroyi* and *Ateles paniscus.* Fol Primatol 30:161-193.

Mittermeier RA, Fleagle JG. 1976. Locomotor and postural repertoires of *Ateles geoffroyi* and *Colobus guereza* and a re-evaluation of locomotor category semibrachiation. Am J Phys Anthropol 45:235-255.

Mongelli MB, Wilcox M, Gardosi J. 1996. Estimating the date of confinement: ultrasonographic biometry versus certain menstrual dates. Amer J Obstet Gynecol 174:278-281.

Moore K, Dumas GA, Reid, JG. 1990. Postural changes with pregnancy and their relationship with low back pain. Clin Bio 5:169-174.

Morinaga Y, Kimura M, Ienaga T, Higuchi K. 1997. Clinical study of pelvic insufficiency fractures. Orthop Sur Tram 40:219-228.

Mosimann J. 1970. Size allometry: Size and shape variables with characterizations of the log normal and gamma distributions. J Am Stat Assoc 56:930-945.

National Institutes of Health. 1998. Clinical guidelines on the identification, evaluation and treatment of overweight and obesity in adults. Bethesda, MD: NIH National Heart, Lung and Blood Institute.

Nourbakhsh MR, Ottenbacher KJ. 1994. The statistical analysis of single-subject data: a comparative examination. Phys Ther 74:768-776.

Odgers P. 1933. The lumbar and lumbosacral diarthrodial joints. J Anat 67:301-317.

Ortengren R, Andersson G. 1977. Electromyographic studies of trunk muscles with special reference to the anatomy of the lumbar spine. Spine 2:44-52.

Ostgaard HC, Andersson GBJ, Schultz AB, Miller JAA. 1993. Influence of some biomechanical factors on low-back pain in pregnancy. Spine 18:61-65.

Pal GP. 1989. Weight transmission through the sacrum in man. J Anat 162:9-17.

Pal GP, Routal RV. 1986. A study of weight transmission through the cervical and upper thoracic regions of the vertebral column in man. J Anat 148:245-261.

Pal GP, Routal RV. 1987. Transmission of weight through the lower thoracic and lumbar regions of the vertebral column in man. J Anat 152:93-105.

Pal GP, Routal RV. 1991. Relationship between the articular surface-area of a bone and the magnitude of stress passing through it. Anat Rec 230:570-574.

Petter JJ. 1962. Recherches sur l'ecologie et l'ethologie des lemuriens Malgaches. Paris: Editions du Museum.

Phenice TW. 1969. A newly developed visual method of sexing in the *Os pubis.* Am J Phys Anthropol 30:297-301.

Pissinatti A, DaSilva EC, Coimbra AF, Bertolazzo W, DaCruz JB. 1992. Sexual dimorphism of the pelvis in *Leontopithecus* (Lesson, 1840). Fol Primatol 58:204-209.

Plavcan J, van Schaik C. 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. Am J Phys Anthropol 103:37–68.

Preuschoft H. 1998. The shape of the pelvis and trunk in primates. Folia Primatol 69*:*187.

Preuschoft H, Fritz M, Niemitz C. 1979. Biomechanics of the trunk in primates and problems of leaping in *Tarsius*. In Morbeck ME, Preuschoft H, Gomberg M, Eds., Environment, behavior and morphology: dynamic interactions in primates, pp. 327-345. New York: Fischer Verlag.

Rae TC, Koppe T. 2000. Isometric scaling of maxillary sinus volume in hominoids. J Hum Evol 38:411-423.

Rasband WS, ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://rsb.info.nih.gov/ij/, 1997-2006.

Reichard U, Sommer V. 2005. Group encounters in wild gibbons (*Hylobates lar*): Agonism, affiliation, and the concept of infanticide. Behav 134: 1135-1174. Part 15-16.

Remis M. 1995. Effects of body size on social context on the arboreal activities of lowland gorillas in the Central African Republic. Am J Phys Anthropol 97:413-433.

Rhodes P. 1958. Orthopaedic conditions associated with childbearing. Practitioner 181:304-312.

Richard A.1970. A comparative study of the activity patterns and behavior of *Alouatta villosa* and *Ateles geoffroyi.* Fol Primatol 12:241-263.

Rightmire GP. 1990. Variation in early *Homo* from eastern Africa. Am J Phys Anthropol 81:286-286.

Robinson J. 1972. Early Hominid Posture and Locomotion. Chicago: The University of Chicago Press.

Rockwell H, Gaynor Evans F, Pheasant H. 1938. The comparative morphology of the vertebrate spinal column: its form as related to function. J Morphol 63:87-117.

Rodman PS. 1979. Individual activity patterns and the solitary nature of orangutans. In Perspectives On Human Evolution: The Great Apes. Hamburg DA, McCown ER (eds). Menlo Park, CA:Benjamin/Cummings Publishing Co. pp 235-255.

Rose MD. 1975. Functional proportions of primate lumbar vertebral bodies. J Hum Evol 4:21-38.

Rosenberg KR. 1988. The functional significance of Neanderthal pubic length. Cur Anthropol 29: 595-607.

Rosenberg KR. 1992. The evolution of modern human childbirth. Yrbk Phys Anthropol 35*:*89-124.

Rosenberg K, Trevathan W. 1996. Bipedalism and human birth: the obstetrical dilemma revisited. Evol Anthropol 4*:*161-168.

Rosenberg K, Trevathan W. 2002. Birth, obstetrics and human evolution. BJOG – Internat J Obstet Gynecol 109: 1199-1206.

Ruff CB. 1995. Biomechanics of the hip and birth in early *Homo*. Am J Phys Anthropol 98*:*527-574.

Ruff C, Niskanen M, Junno J-A, Jamison P. 2005. Body mass prediction from stature and bi-iliac breadth in two high latitude populations, with application to earlier higher altitude humans. J Hum Evol 48:381-392

Ruff CB, Runestead JA. 1992. Primate limb bone adaptations. Ann Rev Anthropol 21:407-433.

Ruff C, Trinkaus E, Holliday TW. 1997. Body mass and encephalization in Pleistocene *Homo*. Nature 387:173-176.

Ruiz-Garcia M, Alvarez D. 2003. RFLP analysis of mtDNA from six platyrrhine genera: Phylogenetic inferences. Fol Primatol 74:59-70.

Ruvolo M. 1997. Molecular phylogeny of the hominoids: Inferences from multiple independent DNA sequence data sets. Mol Bio Evol 14:248-265.

Sanders WJ. 1990. Weight transmission through the lumbar vertebrae and sacrum in australopithecines. Am J Phys Anthropol Annual Mtg Issue 81:2 Abstract.

Sanders WJ. 1995. Function, allometry, and evolution of the australopithecine lower precaudal spine. PhD dissertation, New York University.

Sanders WJ. 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. J Hum Evol 34:249-302.

Sanders WJ, Bodenbender BE. 1994. Morphometric analysis of lumbar vertebra UMP 67-28: Implications for spinal function and phylogeny of the Miocene Moroto Hominoid. J Hum Evol 26:203-237.

Satie JP, Alfred JRB. 2002. Locomotion and posture in Hoolock gibbon. Ann. For. 10, 298–306.

Scholl TO, Hediger ML, Schall JI, Ances IG, Smith WK. 1995. Gestational weight gain, pregnancy outcome, and postpartum weight retention. Obstet Gyn 86:423–427.

Schultz AH. 1930. The skeleton of the trunk and limbs of higher primates. Hum Biol 2:303-409.

Schultz AH. 1949. Sex differences in the pelves of primates. Am J Phys Anthropol 7:401-423.

Schultz AH. 1953. The relative thickness of the long bones and the vertebrae in primates. Am J Phys Anthropol 11:277-311.

Schultz AH. 1961. Vertebral column and thorax. Primatol 4:1-66.

Shapiro LJ. 1991. Functional morphology of the primate spine with special reference to orthograde posture and bipedal locomotion. PhD Dissertation. State University of New York at Stony Brook.

Shapiro LJ. 1993a. Evaluation of "unique" aspects of human vertebral bodies and pedicles with a consideration of *Australopithecus africanus.* J Hum Evol 25:433-470.

Shapiro LJ. 1993b. Functional morphology of the vertebral column on primates. In: Gebo DL, editor. Postcranial Adaptation in Nonhuman Primates. DeKalb: Northern Illinois University Press p 121-149.

Shapiro LJ. 1995. Functional morphology of Indrid lumbar vertebrae. Am J Phys Anthropol 98:323-342.

Shapiro LJ, Simons CVM. 2002. Functional aspects of strepsirrhine lumbar vertebral bodies and spinous processes. J Hum Evol 42:753-783.

Slijper EJ. 1946. Comparative biolog-anatomical investigations on the vertebral column and spinal musculature of mammals. Verh K Ned Akad Wet 42: 1-128.

Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. J Hum Evol 32:523-529.

Snijders C, Seroo J, Snijders J, Hoedt H. 1976. Changes in form of the spine as a consequence of pregnancy. Digest of the 11th International Conference on Medical and Biological Engineering 1:670-671.

Snijders CJ, Vleeming A, Stoeckart R. 1993. Transfer of lumbosacral load to iliac bones and leg. Part 1. Biomechanics of self-bracing of the sacroiliac joints and its significance for treatment and exercise. Clin Biom 8:285-294.

Sokal RR, Rohlf FJ. 2004. Biometry: the principles and practice of statistics in biological research. New York: WH Freeman.

Solonen KA. 1957. The sacroiliac joint in light of anatomical roentgenological and clinical studies. Act Orthop Scand Suppl 27:1-127.

Stanford CB.2006. Arboreal bipedalism in wild chimpanzees: Implications for the evolution of hominid posture and locomotion. Am J Phys Anthropol 129:225-231.

Steiper ME, Ruvolo M. 2003. New World monkey phylogeny based on X-linked G6PD DNA sequences. Mol Phyl Evol 27:121-130.

Stern JT Jr. 1975. Before bipedality. Yrbk Phys Anthropol 19:59-68.

Stern JT Jr. 2000. Climbing to the top: A personal memoir of *Australopithecus afarensis*. Evol Anthropol 9:113-133.

Stern, JT Jr, Susman RL. 1983. The locomotor anatomy of *Australopithecus afarensis*. Am J Phys Anthropol. 60:279–317.

Steudal K. 1981a. Sexual dimorphism and allometry in primate *os coxae*. Am J Phys Anthropol 55:209-215.

Steudel K. 1981b. Functional aspects of primate pelvic structure: a multivariate approach. Am J Phys Anthropol 55:399-410.

Stokes V, Andersson C, Forssberg H. 1989. Rotational and translational movement features of the pelvis and thorax during adult human locomotion. J Biom 22:43-50.

Stoller M. 1995. The obstetric pelvis and mechanism of labor in nonhuman primates. PhD dissertation, University of Chicago, Chicago, Illinois.

Straus WL. 1927. The human ilium: Sex and stock. Am J Phys Anthropol 11:1-28.

Sturesson B, Uden A, Vleeming A. 2000. A radiostereometric analysis of movements of the sacroiliac joint during the standing hip flexion test. Spine 25:364-368.

Susman RL, Stern JT Jr, Jungers WL.1984. Arboreality and bipedality in the Hadar hominids. Fol Primatol 43: 113–156.

Tague RG. 1986. Obstetric adaptations of the human bony pelvis. PhD dissertation, Kent State University.

Tague RG. 1989. Variation in pelvic size between males and females. Am J Phys Anthropol 80:59-71.

Tague RG. 1990. Morphology of the pubis and preauricular area in relation to parity and age at death in *Macaca mulatta*. Am J Phys Anthropol 82:517-525.

Tague RG. 1991. Commonalities in dimorphism and variability in the anthropoid pelvis, with implications for the fossil record. J Hum Evol 21:153-176.

Tague RG. 1992. Sexual dimorphism in the human bony pelvis with a consideration of the Neanderthal pelvis from Kebara Cave, Israel. Am J Phys Anthropol 88:1-21.

Tague RG. 1993. Pubis symphyseal synostosis and sexual dimorphism of the pelvis in *Presbytis cristata* and *Presbytis rubicunda*. Int J Primatol 14:637-654.

Tague RG. 1995. Variation in pelvic size between males and females in nonhuman anthropoids. Am J Phys Anthropol 97:213-233.

Tague RG, Lovejoy CO. 1986. The obstetric pelvis of AL 288-1 (Lucy). J Hum Evol 15*:*237-255.

Tague RG, Lovejoy CO. 1998. AL 288-1 - Lucy or Lucifer: gender confusion in the Pliocene. J Hum Evol 35*:*75-94.

Tan CY, Inglewicz B. 1999. Measurement methods comparisons and linear statistical relationship. Technometrics 41:192-201.

Taves C, Charteris J, Wall JC. 1982. The kinematics of treadmill walking during pregnancy. Physiother Canada 34:321-323.

Taylor J, Twomey L. 1984. Sexual dimorphism in human vertebral body shape. J Anat 138:281-286.

Terranova CJ. 1995. Leaping behaviors and the functional morphology of strepsirhine primate long bones. Fol Primatol 65:181-201.Terranova CJ. 1996. Variation in the leaping of lemurs. Am J Primatol 40: 145-165.

Thompson E. 1995. Introduction to maternity and pediatric nursing, 2nd ed., Philadelphia: WB Saunders Company.

Thurston AJ, Harris JD. 1983. Normal kinematics of the lumbar spine and pelvis. Spine 8: 199-205.

Tobias, P.V., 1998. Ape-like *Australopithecus* after seventy years. Was it a hominid? J. Roy. Anthropol. Inst. 4, 283-308.

Toussaint M, Macho GA, Tobias PV. 2003. The third partial skeleton of a late Pliocene hominin (Stw 431) from Sterkfontein, South Africa. S Afr J Sci 99:215-223.

Trevathan WR. 1987. Human Birth: An Evolutionary Perspective. New York: Aldine de Gruyter.

Trevathan W. 1988. Fetal emergence patterns in evolutionary perspective. Am Anthropol 90*:*19-26.

Trevathan W. 1996. The evolution of bipedalism and assisted birth. Med Anthropol Q 10*:*287-290.

Trevathan W, Rosenberg K. 2001. The evolution of human birth. Scientific American 285:72-77.

Trinkaus E. 1984. Neandertal pubic morphology and gestation length. Cur Anthropol 25:509-514.

Trinkaus E, Wolpoff M. 1992. Brain size in post-habiline archaic *Homo*. Am J Phys Anthropol Supp 14:163.

Trotter M. 1929. The vertebral column in whites and in American negroes. Am J Phys Anthropol 9(4):95-107.

Tryon W. 1982. A simplified time-series analysis for evaluating treatment interventions. J Appl Beh Anal 15:432-429.

Tveit P, Daggfeldt K, Hetland S, Thorstensson A. 1994. Erector spinae level arm length variations with changes in spinal curvature. Spine 19:199-204.

Ubelaker DH, Volk CG. 2002. A test of the Phenice method for the estimation of sex. J Foren Sci 47:19-24.

Vereecke EE, D'Aoȗt, K, Payne R, Aerts P. 2005. Functional analysis of the foot and ankle myology of gibbons and bonobos. J Anat 206:453–476.

Vleeming A, Volkers ACW, Snijders CJ, Stoeckart R. 1990a. Relation between form and function in the sacroiliac joint. Part 1: Clinical anatomical aspects. Spine 15:133-135.

Vleeming A, Volkers ACW, Snijders CJ, Stoeckart R. 1990b. Relation between form and function in the sacroiliac joint. Part 2: Biomechanical aspects. Spine 15:133-135.

von Lackum HL. 1924. The lumbosacral region. An anatomic study and some clinical observations. J Am Med Assoc. 82:1109-1114.

Walker A.1979. Prosimian locomotor behavior. In: The study of prosimian behavior. Doyle GA, Martin RD (eds). Academic Press: New York.

Walker SE, Ayres JM. 1996. Positional behavior of the white uakari (*Cacajao calvus calvus*). Am J Phys Anthropol 101:161-172.

Walrath D, Glantz M. 1996. Sexual dimorphism in the pelvic midplane and its relationship to Neandertal reproductive patterns. Am J Phys Anthropol 100:89-100.

Wang M, Dumas GA. 1998. Mechanical behavior of the female sacroiliac joint and influence of the anterior and posterior sacroiliac ligaments under sagittal loads. Clin Biom 13:293-299.

Ward CV. 1993. Torso morphology and locomotion in *Proconsul nyanzae.* Am J Phys Anthropol 92:291-328.

Ward CV. 1994. Locomotor and obstetric constraints in hominoid pelvic evolution. Am J Phys Anthropol Supplement 18:204.

Ward CV. 2002. Early hominin posture and locomotion: Where do we stand? Yrbk Phys Anthropol 45:185-215.

Ward CV, B Latimer. 1991. The vertebral column of *Australopithecus*. Am J Phys Anthropol Suppl 12:180.

Ward CV, Latimer B. 2005. Human evolution and the development of spondylolysis. Spine 30:1808-1814.

Warren RD, Crompton RH. 1997. Locomotor ecology of *Lepilemur edwardsi* and *Avahi occidentalis*. Am J Phys Anthropol 104:471-486.

Washburn SL. 1948. Sex differences in the pubic bone. Am J Phys Anthropol 6:199-207.

Washburn SL. 1950. The analysis of primate evolution with particular reference to the origin of man. Cold Spring Harb Symp Quant Biol 15:67-78.

Washburn SL, Buettner-Janusch J. 1952. The definition of thoracic and lumbar vertebrae. Am J Phys Anthropol 10:251.

Whitcome KK. 1999. Sexual dimorphism of the human lumbar spine. Am J Phys Anthropol 276-276 Suppl. 28.

Whitcome KK. 2000. A functional examination of sexual dimorphism in human lumbar vertebrae. Masters thesis. Southern Illinois University, Carbondale.

Whitcome KK. 2001. Postural adaptations and sexual dimorphism in the primate pelvis. Am J Phys Anthropol 164. Supp 32.

White AA. 2006. Clinical biomechanics of the spine. Williams and Wilkins:

Whittle MW, Levine D. 1997. Measurement of lumbar lordosis as a component of clinical gait analysis. Gait and Posture 5:101-107.

Whittle MW, Levine D. 1999. Three-dimensional relationships between the movements of the pelvis and lumbar spine during normal gait. Hum Move Sci 18:681-692.

Wilson SE, Granata KP. 2003. Reposition sense of lumbar curvature with flexed and asymmetric lifting postures. Spine 28: 513-518.

Woollard H. 1925. The anatomy of *Tarsius spectrum.* Proc Zool Soc Lond 70:1071 -1184.

Wood BA and Quinney PS. 1996. Assessing the pelvis of AL 288-1. J Hum Evol 31:563-568.

Wrangham RW. 1980. Bipedal locomotion as feeding adaptation in gelada baboons and its implications for hominid evolution. J Hum Evol 9:329-331.

Wu WH, Meijer OG, Lamoth CJC, Uegaki K, van Dieen JH, Wuisman PIJM, de Vries JIP, Beek PJ. 2004. Gait coordination in pregnancy: Transverse pelvic and thoracic rotations and their relative phase. Clin Bio 19:480-488.

Youlatos D. 1999. Positional behavior of *Cebuella pygmaea* in Yasuni National Park, Ecuador. Primates 40: 543-550.

Zatsiorsky V, King D. 1998. An algorithm for determining gravity line location from posturographic recordings. J Biom. 31:161-164.

Zollikofer CPE, Ponce de Leon MS, Lieberman DE, Guy F, Pilbeam D, Likius A, Mackaye HT, Vignaud P, Brunet M. 2005. Virtual cranial reconstruction of *Sahelanthropus tchadensis*. Nature 434 (7034):755-759.

Zuckerman S, Ashton EH, Flinn RM, Oxnard CE, Spence TF. 1973. Some locomotor features of the pelvic girdle in primates. Symp Zool Soc Lond 33:71-165.

Vita

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