A new examination of childbirth-related pelvic anatomy in Neandertal females

by

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Dedication

to my family

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Abstract

Morphological differences between Neandertal and recent human pelves have been explained as relating to birth, though there are few recognizably female pelvic remains in the Neandertal record. Birth hypotheses depend on the most complete Neandertal pelvis, a male unlikely to be informative about birth, or the most complete female partial pelvis, which has been reconstructed differently based on different assumptions. The aim of this project is to systematically compare the female pelvic morphology of Neandertals and a large cold adapted sample of recent humans to assess how differences in birth-related pelvic anatomy might affect the birth process. This study tests the null hypothesis that there are no significant morphological differences between these samples.

Based on two reliably sexually dimorphic pelvic features in Neandertals, seven female Neandertal individuals were identified. This sample was used to develop a suite of 30 measurements that could be taken on at least two female Neandertals and that potentially related to the birth process. A bootstrap resampling algorithm compared the small Neandertal sample to the larger recent human sample for all measurements, by calculating the probability of finding the Neandertal mean in a recent human subsample of identical size. The null hypothesis was rejected for 15 of 30 birth-related measurements, with Neandertals being significantly larger than the recent humans for eight of those measurements and smaller for seven.

These findings demonstrate that there are significant differences between the samples that cannot be explained by differences in body size. The differences that did not reflect changes in joint size fit the Neandertal pelvic model predicted by the male Kebara 2 pelvis, suggesting that for pelvic morphology, Neandertal females more closely resemble Neandertal males than they do females today. Based on these findings, I hypothesize how the differences quantified in this study relate to birth. I suggest that

Neandertal pelvic morphology is best explained by posture differences that require further exploration, but that the Neandertal bony birth canal may have also adapted to birth neonates that were differently shaped than those of recent humans.

Chapter 1: Introduction

Much has previously been hypothesized about Neandertal childbirth, but the sample of female Neandertal pelves available and the traditional methods of assessing this sample have limited paleoanthropologists' abilities to test these hypotheses. This dissertation aims to address Neandertal childbirth by systematically comparing female pelvic morphology in Neandertals and recent humans. While previous studies have shown that pelvic morphology differs between Neandertal and recent human males, I questioned whether the same is true of females. I reason that if female pelves also differ, differences in the birth process might also be expected. Birth in recent humans is sometimes associated with high risks of maternal or infant mortality, which may be caused by evolutionary compromises in pelvic morphology. Neandertals represent a relatively recent hominin population made up of large-brained bipeds whose males had different pelvic morphology than humans today. I am therefore interested to know whether the evolutionary compromises in pelvic morphology that cause birth challenges in recent humans also applied to this ancient population. In this chapter, I provide a detailed outline of the research conducted for this dissertation.

In Chapter 2, I describe the recent human birth process in general. I recount the cardinal movements of labor and the resulting fetal rotations associated with them. I provide evidence of the risks associated with recent human birth, and discuss how these risks are intensified or relieved by variation in maternal pelvic morphology and neonate brain and body size. I end this chapter by defining three models of the evolution of hominin birth, each of which can be used to explain recent human female pelvic morphology in a different light. Pelvic morphology is thought to be the result of bipedal locomotion and encephalization under the obstetrical dilemma model; environmental factors such as climate or nutrition under the ecological variation model; and neonate size reflecting maternal energy production under the energetics of gestation and growth model.

In Chapter 3, I introduce Neandertals as an anatomically distinct population of ancient humans living in Europe and West Asia during the Late Pleistocene and describe the fossil sites that are most relevant to this project. I then assess the previous hypotheses that have been made about Neandertal childbirth, including those based on male pelvic anatomy and those based on reconstructed female pelvic anatomy. I discuss the limitations of each hypothesis and then go on to propose a systematic study of female Neandertal pelvic morphology that will identify any differences in female pelvic anatomy that can be assessed from the fossil record and use it to discuss potential differences in the birth process. My project tests the null hypothesis that there are no significant differences in female pelvic morphology between Neandertals and a cold adapted recent human female sample.

In Chapter 4, I explain how I test this null hypothesis. First, I determine the sex of the Neandertal pelvic fossils, to establish a sample of female Neandertal fossils. I describe the measurements I develop based on the parts preserved in the female Neandertal sample. I relate these measurements to the size and shape of the true pelvis. I establish an algorithm to compare the small Neandertal sample to a larger cold adapted recent human sample using a bootstrap resampling approach. This algorithm provides the conditions necessary to reject the null hypothesis.

In Chapter 5, I describe the sample of Neandertal female pelvic fossils and the most complete Neandertal pelvis, which happens to be male. I also describe the context and makeup of the recent human comparative sample.

In Chapter 6, I present the results of the statistical analysis comparing the female Neandertal and recent human samples for each of the measurements. I indicate which measurements are significantly different between the samples, and in those cases whether the Neandertal females are larger or smaller than the recent humans.

In Chapter 7, I discuss the implications of this study's findings and whether or not the null hypothesis was rejected. I relate the results of the pelvic morphology analysis back to the evolutionary models of birth presented in Chapter 2. Using these models as a base, I discuss the possible conclusions that could be drawn from these results, including new hypotheses developed based on this study's findings.

In Chapter 8, I summarize the project, emphasizing the conclusions drawn from it. I also set up the requirements for future work on this subject.

This study aims to test the null hypothesis that based on the evidence available from the fossil record, there are no significant differences in pelvic dimensions between Neandertal females and a sample of cold-adapted recent human females. A rejected null hypothesis would provide evidence of differences in female pelvic morphology, which may relate to obstetrical differences between these populations.

Chapter 2: Human birth

Introduction

The recent human birth process has historically been associated with challenges of obstructed labor as a result of cephalopelvic disproportion (Marieskind 1979; Oxorn and Foote 1975; World Health Organization 2005). One of the aims of this study is to determine whether this was also the case for Neandertals. As described in Chapter 3, Neandertals were humans living in the Late Pleistocene who were bipedal and large brained, similar to recent humans, but at least in males had different pelvic morphology. This suggests that they would have had similar selective pressures for obstetrics as recent humans and raises the question of why their pelvic morphology is so different. Before exploring Neandertal birth in the next chapter, I will first use this chapter to characterize the human birth process, discuss anatomical factors that have been predicted to affect birth, and explore three models used to interpret the evolution of hominin birth in general.

I begin by describing the birth process of recent humans. The mechanical process of birth in recent humans typically entails the fetus rotating three times to fit through and exit the birth canal. While most births follow a predictable pattern, there is some variation between individuals. Much of the variation in birth process observed in recent humans is associated with an increased risk to mother and offspring, which may have damaging or deadly consequences if left unchecked.

The recent human birth process can be altered and affected by maternal pelvic morphology and fetal body and head size (Greulich and Thoms 1938; MacDonell 1913; Oxorn and Foote 1975; Stålberg et al. 2006). I describe each of these factors in terms of how much variation there is in each, and how each can potentially lead to negative birth outcomes under certain circumstances. Female pelvis shape can vary greatly while still allowing for successful birth. Increased fetal size can cause problems for the birth process if not matched by a complementary increase in maternal pelvic dimensions (DeSilva 2011; Edmonds 2012; Tague 1992).

Evolutionary models, presented in the form of hypotheses, seek to explain why the recent human birth process is so complex. Most anthropologists accept that adaptations for bipedal locomotion constrained the birth canal, which when paired with a large-brained fetus cause the birth complications known as the obstetrical dilemma (Franciscus 2009; Krogman 1951; Rosenberg 1992; Rosenberg and Trevathan 2002; Schultz 1949; Trevathan 1988; Trevathan 2011; Walsh 2008; Washburn 1960). In response to this dilemma, they suggest that recent humans adopted rotational birth, offspring helplessness at birth, and the use of birth attendants (Franciscus 2009; Krogman 1951; Rosenberg 1992; Rosenberg and Trevathan 2002; Schultz 1949; Trevathan 1988; Trevathan 2011; Walsh 2008; Washburn 1960). Wells et al. (2012) argue that the combination of bipedalism and encephalization is not sufficient for explaining difficulties in birth seen today and thought to have occurred in ancient hominins. Instead, they propose that more recent, variable ecological factors have a stronger affect on the birth process today than these early adaptations for bipedal locomotion. Finally, Dunsworth et al. (2012) argue that maternal energy production falling short of fetal energy needs drives the timing of birth and therefore the size of the fetus at birth. In this scenario, pelvis shape does not constrain birth, but instead adapts to fetal size.

Human birth process

In this section, I detail the course the fetus typically takes to pass through the mother's birth canal and introduce how it connects to the evolutionary models presented in the next section. The recent human birth process generally involves the fetus rotating three times in order for the head and then the shoulders to progress through the differently shaped planes of the birth canal. This results in the neonate's head exiting the mother facing posteriorly in response to the constraints from the shape of the maternal pelvis, and then turning to face laterally as postcranial body is birthed. In some cases, the process differs and results in neonates being born in different presentations, some of which are associated with severe risks (Trevathan 2011). For example, when the fetus is born in occiput posterior presentation or in any breech presentation, it increases the probability of maternal injury and infant mortality (Trevathan 2011).

While the birth canal includes soft tissue in the form of musculature supporting the cervix and the vagina, these do not preserve in the fossil record. Therefore, the study here will focus on the bony birth canal, represented by the true pelvis, and its impact on the birth process. The bony birth canal includes and is defined by results summary: the inlet, midplane, and outlet (Scott et

al. 1999; see also Walrath 2003). These planes represent where the bony birth canal changes shape in cross-section, constricting the passage of the fetus. The pectineal and arcuate lines along with the border of the sacral promontory define the pelvic inlet; its anteroposterior diameter stretches from the superior portion of the pubic symphysis to the midpoint of the sacral promontory. In many females, the inlet is slightly more transversely wide than its anteroposterior dimension (Gibbs et al. 2008; Trevathan 2011). The pelvic midplane is defined as the middle region of the obstetric pelvis; its anteroposterior diameter stretches from the inferosuperior midpoint of the pubic symphysis to the inferosuperior midpoint of the sacrum, while its mediolateral diameter is taken between the ischial spines. The midplane is constrained by the ischial spines such that it is not as broad mediolaterally as the inlet. Furthermore, the mediolateral diameter of the midplane separates this cross-section into anterior and posterior spaces; in the majority of female pelves the anterior space is more spacious than the posterior (Trevathan 2011, based on statistics from Oxorn and Foote 1975). Finally, the ischiopubic rami, ischial tuberosities, and inferior tip of the coccyx define the pelvic outlet; its anteroposterior diameter stretches from the inferior portion of the pubic symphysis to the apex of the coccyx. In many females, the outlet narrows even more, resulting in a shape that is longer anteroposteriorly than it is mediolaterally (Gibbs et al. 2008; Trevathan 2011).

The fetus traversing this birth canal has a head that is anteroposteriorly long and mediolaterally narrow, creating an oval shape when viewed superiorly. Although the unfused sutures of the cranium allow for some flexibility between the cranial bones during birth, the sagittally long dimension will typically not fit through the birth canal without rotation (Trevathan 2011). Perpendicular to the head, the already-starting-to-ossify clavicles make the shoulders a mediolaterally longer dimension than the head, which also must fit through the birth canal. As discussed below, the typical human female pelvis has a rounded and slightly transversely wide inlet, paired with a midplane and outlet that both tend to be larger for their anteroposterior diameters. The shapes of the pelvic planes define the birth canal and influence how the fetus rotates during the birth process.

The recent human birth mechanism has been broken down into cardinal movements of labor that typically facilitate three rotations of the fetus. These movements include: engagement, flexion, descent, internal rotation, extension, external rotation, and expulsion (Dutton et al. 2009; Edmonds 2012; Gibbs et al. 2008; Trevathan 2011). Based on the descriptions given by these

authors, I will describe when the fetus rotates during these cardinal movements. The first rotation occurs during engagement, when the fetal head rotates so that its long sagittal diameter lines up with the largest diameter of the maternal pelvic inlet. This typically involves the fetus rotating so that it is facing somewhat laterally relative to the mother, because the transverse diameter is usually the largest for the inlet (Trevathan 2011). Engagement can occur days before the rest of labor occurs (Edmonds 2012; Gibbs et al. 2008). The second rotation occurs during internal rotation. The fetal head rotates within the birth canal so that its long sagittal diameter can pass through the typically mediolaterally shortened but anteroposteriorly lengthened midplane and outlet. Complicating this process is the fact that the fetal cranium is widest posteriorly at the bi-parietal length, and is narrower anteriorly. This egg-like shape influences which direction the fetal head rotates during internal rotation. As described above, the anterior space of the midplane tends to be more spacious, which makes it geometrically advantageous for the fetal head to rotate so that the wider parietal and occipital bones are anterior relative to the maternal midplane, and so that the relatively narrower frontal bone is facing the mother's sacrum in the posterior space of the midplane. This leads to the fetal head exiting the birth canal facing posteriorly, in what is called "occiput anterior" presentation. Occiput anterior presentation is the most common presentation for non-breech births, likely because of midplane and fetal head shape (Trevathan 2011). During this same stage, the broad and relatively inflexible shoulders rotate so that their coronal width matches the slightly mediolaterally longer diameter of the pelvic inlet. The final rotation occurs during external rotation, which is sometimes called restitution. Occurring after the neonatal head has exited the mother's body, this is when the fetal body rotates so that the shoulders can pass through the mediolaterally constrained midplane and outlet, typically resulting in a neonate who is facing laterally relative to the mother. Thus, the recent human birth process is characterized by the fact that the fetus usually rotates three times as it traverses the birth canal, typically being born with occiput anterior presentation (Edmonds 2012; Gibbs et al. 2008; Oxorn and Foote 1975; Scott et al. 1999).

A small percentage of births result in a neonate being born either cephalically (head-first) in occiput posterior presentation or breech (postcrania-first) presentation. These are both associated with greater health risks for both neonate and mother, explaining their relatively low incident rate. The direction of fetal rotations depends somewhat on the dimensions of the maternal birth canal, as demonstrated by midplane dimensions leading to occiput anterior

presentation. While a neonate may be born facing anteriorly, posteriorly, left laterally, or right laterally (Dutton et al. 2009), facing anteriorly (i.e., occiput posterior presentation) generates the most risk in recent humans. The fetus rotating internally to face anteriorly instead of posteriorly has been known to lead to perineal lacerations, prolonged delivery, arrest at the perineum, and intensified molding of the fetal cranium during birth (Edmonds 2012; Gibbs et al. 2008). These all result because, according to Trevathan (2011), an occiput posterior presentation requires the mother to push a larger dimension of the fetus through a more constricted part of the maternal pelvis, due to size differences between the anterior and posterior spaces of the birth canal. Such a mismatch can injure both the mother and the fetus, and can even lead to increased risk of mortality for one or both.

However, this situation only arises when occiput posterior presentation is associated with a typical maternal pelvis; in females with less common pelvis shapes, it is possible for occiput posterior presentation to be more beneficial than occiput anterior presentation (Trevathan 2011). Many studies have shown that occiput posterior presentations are more often associated with narrower midplane and/or outlets, which also have larger posterior relative to anterior spaces, the opposite of the typical female pelvis described above (Baragi et al. 2002; Floberg et al. 1987; Oxorn and Foote 1975). Floberg et al. (1987) found that 5.1 percent of first-time mothers delivered in occiput posterior position and that the prevalence of occiput posterior births was related to the decreased area of the pelvic outlet. This suggests that females who have a smaller pelvic floor, i.e., those whose ischial tuberosities are oriented more medially and/or whose sacral apex is located more anteriorly, face greater risks during delivery. Oxorn and Foote (1975) report that occiput posterior presentations were more common in females whose pelvic inlets were narrower anteriorly. Walrath (2003) describes occiput posterior positioning as a "failure of spontaneous anterior rotation prior to complete dilation" (p13, citing Phillips and Freeman 1974). Consequently, the occiput posterior position may be more common when the mother has a small anterior space that encourages rotation in the opposite direction of what is typically observed.

Breech births, where some part of the postcrania presents before the head, make up approximately 3-4 percent of singleton births (Dutton et al. 2009). Breech births come in many forms, including fetuses born feet-first, buttocks-first, knee-first, or shoulder-first (Dutton et al. 2009; Oxorn and Foote 1975; Trevathan 2011). Breech births are associated with prematurity, hydrocephaly, excess amniotic fluid, or multiple births. Oxorn and Foote (1975) found no

association between breech births and maternal pelvic types, though they did recognize that females who previously had breech births were more likely to do so again. Trevathan (2011) suggests that this may signify some genetic predisposition to breech births. I would speculate that it could just as easily be associated with a mother's behavior (perhaps her activity level, diet, or preparation for birth) repeating between pregnancies.

According to data from Oxorn and Foote (1975) and Marieskind (1979), Trevathan (2011) reports that infant mortality from breech births is high even in countries with access to good medical care today: 10-20 percent of breech births result in infant mortality, perhaps explaining why 60-90 percent of breech births are delivered by Caesarean section. However, the latter may be a function of medical school education no longer including training on delivering breech births vaginally (Marieskind 1979; Trevathan 2011; Walrath 2003). In breech presentations, the portion of the fetus pushing against the cervix is smaller than in cephalic presentations; this results in slow dilation that can lead to the mother pushing before the cervix is ready (Trevathan 2011). Additional complications caused by breech presentation include the fetal head being caught in the cervix for too long and suffering asphyxiation, early membrane ruptures, or prolapsed umbilical cords. With assistance, it is possible for a mother to successfully birth a neonate in breech position, but there is a greater risk of complications than a cephalic presentation (Dutton et al. 2009; Trevathan 2011).

In summary, recent human births typically involve the fetus rotating three times to fit through the various planes of the mother's birth canal, which change in cross-sectional shape, resulting in a neonate who is born facing first posteriorly (occiput anterior presentation), then laterally. As explained above, there are instances where the fetus is born either in occiput posterior or breech presentation, though these birth processes are less common, probably due to the higher risk of complications associated with them.

Factors affecting the human birth process

Despite the typical birth process described above, there are complications that have the potential to challenge the success of this process. In this section, I establish the risks associated with birth, and then assess how maternal pelvic morphology and neonate size may intensify those risks.

The average age of death for females in many historical cemetery samples is significantly lower than the average age of death for males from the same sample (MacDonell 1913; Wells 1975). Wells et al. (2012) interpret these data as demonstrating that females were at a greater risk for death caused by parturition than anything facing the males in these populations. Similarly, Wells et al. (2012) suggest that birth challenges are more severe in countries with fewer medical resources, based on data showing that certain countries continue to have high infant and maternal mortality rates even as global rates decrease (see data in Hogan et al. 2010). Though both the lower average age of death in females in the archaeological record and the continued high maternal mortality seen in some countries today suggest parturition is associated with maternal deaths, neither statistic clarifies the cause of deaths. Wells et al. (2012) speculate that there is a link between lack of medical care and high maternal mortality, but fail to address whether this could also be caused by a combination of poverty, hunger, and/or lack of hygiene. Without separating these factors, these data are circumstantial at best, as the former list of factors are most certainly affecting lifespans in some of the regions considered. However, some data do indicate a clear risk associated with the recent human birth process. According to the World Health Organization (2005), obstructed labor accounts for ~8 percent of maternal deaths globally, suggesting that the birth process itself poses risks to females giving birth. The possible causes of obstructed labor are discussed below.

While the above establishes that birth may pose some risks to the mother, the birth process is more hazardous for neonates. Every year, approximately 1.1 million stillbirths occur due to complications from the delivery process (World Health Organization 2006). There is also some archaeological evidence for infant (and maternal) mortality. In archaeological samples, there are occasional instances of a female being uncovered with a fetus in her pelvis, which is termed "obstetric death" (Arriaza et al. 1988; Elliot-Smith and Wood-Jones 1910; Hawkes and Wells 1975; Liston and Papadopoulos 2004; Owsley and Bradtmiller 1983; Roberts and Cox 2003; Willis and Oxenham 2013). However, these deaths may be the result of infection or other causes rather than being the direct result of difficult labor (Wells 1975). Wells et al. (2012) emphasize that even though fetal skeletal material is less likely to preserve than other skeletal remains, obstetric deaths are shockingly absent from the archaeological record. They take this to

mean that deaths from birthing complications occurred less frequently in the past (see the description of their ecological variation model below).

Constraints on the birth process caused by maternal pelvic morphology

The shape and size of the maternal pelvis has the potential to constrain the birth canal, affecting birth (Baragi et al. 2002; Greulich and Thoms 1938; MacDonell 1913; Oxorn and Foote 1975; Stålberg et al. 2006; Trevathan 2011; Wells 1975; Wells et al. 2012). The evidence presented here demonstrates that recent human females vary in pelvis form, despite all presumably being under similar selective pressures for successful parturition. The bony structure of the birth canal determines what sized fetus can pass through it (or according to Dunsworth et al. 2012, neonate size determines the size and shape of the maternal pelvis; see discussion below) and whether rotations will be necessary for that fetus to fit through the planes of the birth canal.

Despite predictions that the female pelvis would be less variable than males because it is under greater selection for obstetrical requirements, Tague (1989) found that there was just as much variability in male pelves as in female pelves for dimensions of the true pelvis. Multiple studies show that recent human females within and between populations vary in pelvis shape, which is typically defined by the relationship between the anteroposterior and mediolateral diameters of the birth canal (Caldwell et al. 1934; Emmons 1913; Greulich and Thoms 1938; Oxorn and Foote 1975; Williams 1922). While Emmons (1913) described maternal pelvic variation as continuous, later authors categorized it into discrete pelvic types (Caldwell et al. 1934; Greulich and Thoms 1938; Oxorn and Foote 1975; Williams 1922). Emmons' model is most likely the more accurate, as those attempting to define discrete types are unable to agree on the number and definition of types. Still, their research clearly indicates female pelvic variability.

While variability is present, it is not evenly distributed. Regardless of what the authors call a particular pelvic shape (e.g., what Caldwell et al. 1934 call "gynaecoid", Greulich and Thoms 1938 call "mesatipellic"), nearly 50 percent of females may have a more circular inlet (Oxorn and Foote 1975) with nearly equal dimensions for anteroposterior and mediolateral diameters (see Table 2.1). Other birth canal forms are less common, but include having the anteroposterior diameter be longer than the mediolateral diameter (called anthropoid or dolichopellic), or having the mediolateral diameter be longer than the anteroposterior diameter (called platypelloid or brachypellic). The frequency for these other forms is more variable, with 25 percent of females having the anthropoid form according to Oxorn and Foote (1975; though

see sample variation for this frequency in see Table 2.1). Extremely platypellic pelvis forms are rare in recent humans; they vary between 0 and 8.3 percent in some recent human samples (Greulich and Thoms 1938; Oxorn and Foote 1975; see Table 2.1). In his analysis of variability in pelvic brim dimensions between male and female humans, Tague (1992) found that while the mediolateral diameter of the inlet was not statistically different between females and males, circumference of the inlet was significantly larger in females. He suggested that this meant that diameters of the birth canal are less affected by selection for obstetrics than the circumference of the birth canal.

Table 2.1. Frequency of pelvic types and birth interventions. Data from Greulich and Thoms (1938). This table summarizes four studies of false pelvis shape in different samples of American White females. The first three studies reported the frequency of variation in pelvis shape among the samples considered. The last study explored the potential correlation between pelvis shape and the frequency of interventions during birth.

	Definition[A]	Incidence of pelvis shape[B]			Intervention frequency[B,C]
		N=100	N=132	N=450	N=600
Dolichopellic	AP > ML	37.0%	13.6%	15.5%	16.3%
Mesatipellic	AP = ML	46.0%	43.9%	45.1%	18.0%
Brachypellic	AP < ML	17.0%	34.1%	34.5%	19.5%
Platypellic	AP << ML	0.0%	8.3%	4.9%	30.7%

[A]Each pelvic type is defined based on how the anteroposterior (AP) and mediolateral (ML) dimensions of the false pelvis compare. Since this study was done on living females, these dimensions do not reflect the diameters of the inlet, but instead the palpable dimensions of the false pelvis, which may not directly reflect inlet shape.
[B]These percentages reflect what percent of the total sample in each of these three studies has the particular pelvis shape. In some cases, there were additional pelvic types identified that were not reported.
[C]Interventions include Caesarean section, version extraction, or use of forceps.

Connecting pelvic morphological variability directly to birth is more difficult than establishing that variability exists in the first place. Using birth interventions, such as Caesarean section, version extraction, and the use of forceps, as a proxy for birth complications, Greulich and Thoms (1938) associated birth complications with pelvis types (see Table 2.1). They were surprised to find that the form that was least often associated with birth interventions was not the form that was most common in recent humans. Stålberg et al. (2006) found that Caesarean sections are more common in females with narrow pelves, though it is unclear if this is caused by obstetric necessity or assumptions by doctors that females with narrow pelves will have more

trouble giving birth vaginally. Baragi et al. (2002) found that a sample of African American females had a 5 percent smaller pelvic outlet area than a contemporary sample of European females. They did not offer an explanation for this finding, except to suggest that it would be beneficial in preventing pelvic prolapse in the African American females. In any case, the data presented here illustrate that there is some variability in pelvic morphology between recent human females, though most forms are associated with successful births. This may suggest that selective pressures other than those relating to obstetrics are acting on female pelvic shape.

Wells et al. (2012) briefly explored the possibility that pelvic morphology may be genetic, but were unable to find conclusive evidence demonstrating heredity of specific pelvic features. Sharma (2002) suggest that 60-80 percent of pelvic variation may be genetic, but Wells and Stock (2011) point out that their results were based on the study of twins, which notoriously overestimates genetic heritability. Additionally, there are studies that attempt to demonstrate a genetic link to challenging birth by linking being born with some sort of birth intervention (Caesarean section, cephalopelvic disproportions, shoulder dystocia) to giving birth with some sort of complication (Berg-Lekås et al. 1998; Shy et al. 2000; Tollånes et al. 2008; Varner et al. 1996). However, these studies are limited in size and scope, and are far from conclusive. Caesarean births can be elective, and factors such as birthing position and intervention use can affect birthing complications as well. Until a study distinguishes these other factors from heritable factors, the heredity of pelvis types that cause labor complications will remain unknown.

Constraints on the birth process caused by neonatal brain and body size

Increased fetal size has the potential to exacerbate birth challenges by disrupting the fit of the fetus through the birth canal (DeSilva 2011; Trevathan 1988; Wells et al. 2012). Complicating the issue of fetal size, the mammalian fetus benefits from an extended *in utero* period where growth can occur with fewer risks from the outside world (Trevathan 2011). Cranial size at birth experiences little variation across recent humans, while body size varies significantly (Trevathan 2011; Wells et al. 2012). The breadth of the fetal shoulders also constrains how well the fetus will fit through the birth canal; this, like differing neonate presentations at birth mentioned in the previous section, may support early use of birth attendants in the hominin lineage.

Compared with other hominoids, recent human neonates are born at an earlier stage of development; in a state some call "secondary altriciality" (Portmann 1990). At birth, recent human neonates have grown only 28.0 percent of their adult brain size, while chimpanzees have already grown 40.1 percent (DeSilva and Lesnik 2008). These percentages reflect the overall large size of recent human adult brains, because even with relatively less of their brain developed at birth, recent human neonates have absolutely larger crania than chimpanzee neonates (DeSilva 2011). When neonatal *body* size is considered in place of brain size, recent humans are born more developed relative to maternal body size than chimpanzees (6.1 percent versus 3.3 percent; DeSilva 2011). This suggests that despite their early developmental stage for cognitive abilities, recent human neonates actually are born relatively large in size compared to chimpanzee neonates (DeSilva 2011; Dunsworth et al. 2012; Leutenegger 1972; Wells et al. 2012).

During birth, the recent human fetus has unfused cranial sutures that allow for some flexibility in cranial shape and size as it traverses the birth canal (Pu et al. 2011; Schultz 1926; Sorbe and Dahlgren 1983; Trevathan 2011), though excessive cranial molding may lead to brain injury (Kriewall and McPherson 1981; McPherson and Kriewall 1980a,b). In general, cranial dimensions vary less for recent human neonates compared with the variation seen in the female pelvis, regardless of the mother's body size or nutritional status (Wells et al. 2012). Even among undernourished mothers whose offspring are otherwise born small (Leary et al. 2006), head size at birth is similar to that of populations where undernutrition is not a problem. This suggests that growing approximately 30 percent of the human brain *in utero* is selected for at the expense of growing the rest of the fetal body.

Unlike neonatal brain size, recent humans do vary considerably for other neonatal body dimensions at birth, including body weight, skinfold thickness, girth, and length (Leary et al. 2006; Wells and Cole 2002). Larger fetuses have been associated with higher risks for Caesarean section, shoulder dystocia, and neonatal asphyxia (Bérard et al. 1998; Ezegwui et al. 2011; Gehrman et al. 2006; Ju et al. 2009; Vidarsdottir et al. 2011). In the other direction, undernutrition can lead to smaller neonates at birth, however fetal head size is still protected (Hales and Barker 1992). Indian neonates suffering undernutrition were 24 percent smaller for birth weight but only 6 percent smaller for head circumference when compared to nutritionally stable European neonates (Yajnik et al. 2003). Wells et al. (2012) conclude based on these data

that while there seems to be selective pressure to grow the fetal brain to a certain size, there is less pressure on fetal body size.

In summary, the size and shape of both the maternal pelvis and the fetal cranium influence the process of birth in recent humans. While there is variation in female pelvic morphology among recent humans, changes to the birth canal that result in the fetus rotating in a non-typical direction during birth are associated with higher risks of infant and/or maternal mortality. Fetal cranium size affects the birth process in terms of overall fit through the birth canal, and by influencing the direction the fetus rotates in response to the shape of the birth canal. However, fetal brain size at birth varies very little across recent human populations, while fetal body size may vary significantly. This suggests that recent human females are under selective pressure to birth neonates of a certain brain size.

Evolutionary framework of birth

Here I will discuss the background for birth-related pelvic evolution in hominins, and explore factors that affect the recent human rotational birth process, including the risks tenuously associated with it based on maternal pelvic morphology and neonatal brain and body size. I first describe the current thinking of obstetrics for australopithecines and early *Homo*. I then characterize three evolutionary hypothesis-based models that seek to explain the evolution of the human birth process. All three models interpret the pelvic and cranial factors characterized above, but do so in ways that result in different evolutionary interpretations of this anatomy.

Tague and Lovejoy (1986) reconstructed the pelvis of a female *Australopithecus afarensis* (AL 288-1, or Lucy; see Tague and Lovejoy 1998 for discussion of why this individual is female). Their reconstruction showed that her pelvis was extremely wide (based on bi-iliac breadth; similar to the width of a recent human pelvis, despite being a much smaller individual), with a mediolaterally wide and anteroposteriorly short birth canal (an extreme platypellic shape at the inlet, midplane, and outlet). They conclude that this shape means the birth process in *Australopithecus afarensis* would have had the fetus being born facing the mother's side as it passed through the inlet, midplane, and outlet. In short, they claim that the mediolaterally wide birth canal would have made internal rotation during birth unnecessary. Leutenegger (1972) reconstructed the female *Australopithecus afarensis* pelvis, Sts 14, and found that the birth canal in this species was more circular than that of Lucy. Tague and Lovejoy (1986) took issue with this reconstruction because part of the Sts 14 fossil was taphonomically warped, influencing the

shape of the pelvis. Overall, Tague and Lovejoy (1986) claimed that the australopithecine pelvic shape in general would have limited the area of the birth canal at each of the three planes, which would have coincided with selection for more "altricial" neonates relative to other primates. Ruff (1995) predicted that the early *Homo* pelvis would have had similar obstetric dimensions to Lucy, which he interprets as meaning early *Homo* had a non-rotational birth process. Simpson et al. (2008) introduced a female hominin pelvis from later in time, the Gona BSN49/P27 pelvis. They associated this pelvis with *Homo erectus,* though this has been challenged by Ruff (2010) who suggested this pelvis actually belongs to *Paranthropus* based on its small body size. In any case, this individual represented a change in birth canal shape from Lucy. The Gona BSN49/P27 pelvis had a spacious birth canal relative to the individual's overall body size. It was also spacious relative to the adult brain size of both *Homo erectus* (Simpson et al. 2008) or especially *Paranthropus* (Ruff 2010). Unlike the australopithecine pelvis that Tague and Lovejoy (1986) suggested required selection for smaller neonates (in both brain and body size), the Gona pelvis indicated that some hominins were adapted to birth relatively small neonates through spacious birth canals. It matters whether the evolutionary trend went from a Lucy-like pelvis, to a Gona-like pelvis, to a recent human shaped pelvis. If this evolutionary trend occurred, then it seems that the australopithecine pelvis was most constrained among hominins, and that the birth canal became more spacious prior to significant encephalization that occurred in later *Homo*. This evidence can be interpreted under various evolutionary models of birth. Here, I will describe three key models that seek to explain female hominin pelvic morphology and neonatal dimensions at birth.

The first model is the most commonly accepted by anthropologists: the obstetrical dilemma, which hypothesizes that adapting to bipedal locomotion changed hominin pelvic morphology dramatically, placing obstetric constraints on the birth of large neonates that we still experience today. Initially, this hypothesis emphasized the complications caused by birthing large-brained neonates (Washburn 1960), but it was later expanded to explain complications in birthing large-bodied or broad-shouldered neonates as well (Trevathan 1988). A hypothesis related to this model is the midwifery hypothesis, which suggests that because of these obstetrical constraints, the behavior of having a birth attendant was strongly selected for (Trevathan 1988).

The second model is based on what I call the ecological variation hypothesis, presented by Wells et al. (2012). The ecological variation model is similar to the obstetrical dilemma in that they both predict that pelvis shape directly affects the birth process. Whereas the obstetrical dilemma hypothesized that the pelvic changes constraining birth were caused by bipedal locomotion and encephalization, the ecological variation model suggests that the factors influencing birth outcomes are the result of relatively recent environmental conditions, including adaptations to climate changes and response to undernutrition. Because these factors are influenced by local environment, they do not affect birth across all recent humans, but may impact pelvic morphology and neonatal size in individual populations. Unlike the obstetrical dilemma, the ecological variation model introduces factors that cause birth-related changes to pelvic shape that are more recent than the constraints placed on the recent human pelvis by bipedalism.

Finally, the third model is based on the energetics of gestation and growth hypothesis, which flips the assumptions of the first two hypotheses by suggesting that pelvis shape is an adaptation to neonatal size, not a constraint on that size (Dunsworth et al. 2012). Specifically, it predicts that a mother's ability to produce energy is the most important constraining factor for birth. Therefore, the energetics of gestation and growth model suggests that when a fetus requires more energy than a mother can produce (i.e., when it reaches a particular size), labor begins. Maternal pelvic dimensions, in turn, have adapted to accommodate the size of the fetus when this "cross-over" occurs, but have no reason to adapt to be larger.

Obstetrical dilemma

Many studies have suggested, based on pelvic dimensions and neonate size, that birth in other great apes is a short, relatively easy process that may not require fetal rotations (Krogman 1951; Schultz 1949; Trevathan 1988; Washburn 1960; however, see Hirata et al. 2011). Anthropologists have hypothesized that the reason recent human birth is more complex is because of evolutionary compromises between walking bipedally and birthing large brained neonates (Franciscus 2009; Krogman 1951; Rosenberg 1992; Rosenberg and Trevathan 1995, 2002; Trevathan 1988; Walsh 2008; Washburn 1960; Wittman and Wall 2007). The obstetrical dilemma model asserts that when hominins became bipedal, the size of the true pelvis reduced, constricting the size of the birth canal; while later, when hominin brain size increased, the larger fetus further impeded the birth process. This model was initially developed based on the

assumption that the last common ancestor between recent humans and chimpanzees had a chimpanzee-like pelvis and was not bipedal (Washburn 1960; see Table 2.2 for a comparison of chimpanzee and recent human obstetrical dimensions; midplane and outlet dimensions were unavailable for chimpanzees). As such, it focused on how a chimpanzee-shaped pelvis would change into a recent human-shaped pelvis in response to bipedalism, and how such a pelvis would adapt to birth neonates that are larger on average than chimpanzee neonates.

Table 2.2: Neonatal cranium and maternal inlet in chimpanzees and humans.

	Chimpanzee	**Human**
Neonate brain mass (g)	152.8 ± 16.6 [A]	373.8 ± 100.6 [A]
Neonate cranium circumference (mm)	203 [B]	283 [B]
Adult female inlet anteroposterior diameter (mm)	143 ± 9.5 [B]	109 ± 13.1 [B]
Adult female inlet mediolateral diameter (mm)	105 ± 6.2 [B]	131 ± 8.8 [B]
Adult female inlet circumference (mm)	374 [B]	384 [B]

[A] Data from DeSilva (2011).
[B] Data from Tague (1991).

The obstetrical dilemma model was developed to explain recent human neonates being born less developed compared with other primates. The phrase "obstetrical dilemma" applied in this context was coined by Washburn (1960), who proposed that being born less developed was how recent humans resolved the dilemma posed by potential cephalopelvic disproportion. Trevathan (2011) hypothesized that assisted birth developed as a cultural adaptation to reduce the risk of obstructed labor (see also Rosenberg 1992, 1998; Rosenberg and Trevathan 1995, 2002; Trevathan 1988, 1993, 1996, 2011; Trevathan and Rosenberg 2000). She argued that in light of the risks associated with occiput posterior birth in recent humans as a result of the locomotor shift to bipedalism, occiput anterior birth has been selected for, which is a change from the presentation observed in some nonhuman primates. Trevathan (2011) suggested that a female monkey giving birth can reach down and guide the neonate out of the birth canal in part because that neonate is facing anteriorly. She therefore postulated that if recent humans birthing

neonates in occiput anterior presentation attempted such a maneuver, they would risk damaging the neonate's spinal cord. She further hypothesized that it would have been beneficial to birthing outcomes for recent human females to give birth accompanied by an attendant who could guide the neonate out when the positioning was too awkward for the mother to do it herself. While this hypothesis is difficult to test, Trevathan (2011) described evidence that cross-culturally among recent humans there are very few instances where labor is planned to occur alone.

The obstetrical dilemma originally focused on the importance of encephalization, but it is possible this aspect of the model needs further explanation in light of newer fossil discoveries and a better understanding of early hominin evolution. DeSilva (2011) proposed that neonatal body size may add constraints to the obstetrical dilemma model of birth evolution in addition to those from neonatal brain size. Similarly, Trevathan (1988) argued that shoulder breadth also may constrain birth by increasing the risk of shoulder dystocia due to the relatively inflexible and broad shoulders in neonates (see also Rosenberg and Trevathan 1995; Trevathan 1988; Trevathan and Rosenberg 2000). Rosenberg and Trevathan (1995; Trevathan 1988; Trevathan and Rosenberg 2000) argued that if large shoulders, associated with an ancestry that included brachiating or suspensory locomotion, were present in early bipedal adapters, then they would have experienced obstetrical distress even before larger crania from encephalization evolved. The *Australopithecus afarensis* partial skeleton KSD-VP-1/1 from Woranso-Mille, Ethiopia confirms part of this prediction. The Woranso-Mille skeleton, dated to 3.58 Ma, has a recent human-sized clavicle while being attributed to a species whose adult brain size was closer to a chimpanzee (Haile-Selassie et al. 2010). Both of these body size related additions to the obstetrical dilemma model account for the possibility that it may have affected hominin birth to some degree even before encephalization; either in response to large-bodied neonates or broad-shouldered neonates.

Overall, the obstetrical dilemma model predicts that evolving to be bipedal constrained the size of the hominin birth canal, which in turn led to an increase in risks associated with birth when neonatal cranium size increased, which may have been accommodated by a reduction in development at birth compared to other primates. Trevathan (1988, 2011) argued that risks would have increased during the initial evolution of bipedalism, because while cranium size was still small in early hominins, shoulder dimensions would likely have been large. She hypothesized that one way hominins may have dealt with the birth challenges they faced as a

result of becoming bipedal is to have there be selection for having an attendant present during birth, to aid with the labor by catching the neonate as it is born in a presentation that differs from other primates.

Ecological variation model

The ecological variation model is what I have named the model proposed by Wells et al. (2012). This model is similar to the obstetrical dilemma model, in that it, too, predicts that changes to maternal pelvis shape affect recent human birth. Where it differs is that instead of advocating that the current recent human birth process is solely a response to bipedal adaptations that affect all recent humans (and hominins), the ecological variation model suggests that birth has been affected more recently by ecological factors that change female pelvic morphology in some recent humans but not others. Wells et al. (2012) suggested that adaptations to living in an extreme climate and consequences of having poor nutritional health have a significant impact on pelvic morphology in groups experiencing these ecological factors. Wells et al. (2012) asserted that hominins have been bipedal for so long that any obstetrical compromises required would have evolved long ago; in this way, their model does not completely refute the importance of the obstetrical dilemma hypothesis. However, they suggested that ecological factors have a more recent effect on pelvic morphology, and that these factors explain the current instances of obstructed labor in recent humans better than the obstetrical dilemma model.

First, Wells et al. (2012) argued that recent human females are not compromised in their ability to walk efficiently compared with males. They suggested that variation in the size of the female pelvis in recent humans demonstrates that pelvic morphology changes in response to factors that are unrelated to locomotion. Using data from Leary et al. (2006), they showed that there is more variation in pelvic dimensions than there is in neonatal head size. Dunsworth et al. (2012; see also Warrener 2011) and Lewton (2012) also addressed this issue by testing for biomechanical penalties to obstetric adaptations in recent humans. These studies compared walking efficiency in males and females, and found that despite there being musculature differences reflecting pelvic dimorphism, the measured locomotive efficiency of individuals with different pelvic types did not differ significantly. Both Dunsworth et al. (2012) and Lewton (2012) suggested that their results indicates no locomotive differences in efficiency between recent human males and females, though they allowed that differences in other aspects of locomotion may still exist. These studies looked at American shoe-wearing individuals who were

able to walk or run for the limited distances used in each study. It is possible that differences in locomotor efficiency would not be observable in such a sample, but may be more evident in samples where the individuals regularly walk long distances, such as nomadic hunter-gatherers. However, both Wells et al. (2012; based on the Lewton 2012 study) and Dunsworth et al. (2012) concluded that the absence of locomotor efficiency differences relative to pelvic morphology in these studies means that birthing constraints that differentiate male and female pelvic morphology require an explanation unrelated to differences in locomotor efficiency. Wells et al. (2012), as stated above, proposed that birthing constraints in recent humans are found only when ecological factors are present to cause them. Here I will describe their argument that climate and undernutrition are two such ecological factors.

Wells et al. (2012) reviewed how thermal environment and maternal shape are related according to Bergmann's and Allen's rules (Allen 1877; Bergmann 1847). These rules predict that in mammals in general, thermal environment affects body proportions and predicts that mammals in hot climates will adapt to maximize heat loss by increasing their body's surface area, resulting in long (tall) narrow bodies and limbs, while mammals in cold climates will adapt to maximize their body's ability to retain heat by minimizing surface area, resulting in short thick bodies and limbs (Allen 1877; Bergmann 1847; Katzmarzyk and Leonard 1998; Paterson 1996; Ruff 1994). This model has been tested and supported for humans by numerous studies (Crognier 1981; Hiernaux 1968; Hiernaux and Froment 1976; Roberts 1953, 1973; Ruff 1994; Wells 2012). Wells et al. (2012) argued that in a hot climate, where people are adapted to a long and narrow *Bauplan*, pregnancy increases the stress caused by heat (Wells 2002). In addition to producing energy for fetal growth, pregnant females in hot environments also must produce energy to dissipate excess heat. Wells et al. (2012) therefore suggested that hot climates may exacerbate the obstetrical dilemma by challenging maternal energy requirements. In addition to this energetic constraint, pelvis shape in response to thermoregulatory adaptations may impede (or ease) the birth process, though the data on this affect are in disagreement (Kurki 2007; Kurki et al. 2008).

Another ecological factor Wells et al. (2012) predicted affects pelvis shape and birth outcomes is undernutrition. Undernutrition, either in terms of mineral or caloric deficiencies, causes a flattened, platypellic pelvis. As discussed at the beginning of the chapter, platypelloid pelves are extremely wide transversely, and extremely short anteroposteriorly. Tague and

Lovejoy (1986) observed this pelvis shape in *Australopithecus afarensis*, and hypothesized that it would have made rotational birth impossible even for this small-brained hominin. While recent humans have a different pelvic morphology than australopithecines, the platypellic shaped recent human pelvis is associated with the large brains found in recent human fetuses, meaning recent humans face even greater risks associated with obstetric fit (Wells et al. 2012, based on data from Caldwell and Moloy 1933). Rickets, the condition caused by long term vitamin D deficiency during growth and frequently associated with undernutrition, likewise results in a severely compromised pelvis that greatly increases the risk of maternal or infant mortality or of needing Caesarean delivery (Merewood et al. 2009; Skippen 2009; Wells 1975; but see Brunvand et al. 1998). Rickets was the most common cause of obstructed labor from the 1600s to 1900s (Wells 1975).

The difficulty with assessing the obstetrical consequences of undernutrition in the past is that undernutrition also makes one more susceptible to diseases that could lead to infant or maternal mortality via mechanisms unrelated to obstructed labor. Furthermore, the evidence provided by Wells et al. (2012) focuses on flattened birth canals that mostly result from vitamin D deficiency, even when the population studied is suffering more generalized undernutrition. This calls into question whether undernutrition in instances where vitamin D is still readily available but calories are not would have the same obstetrical results.

Having provided arguments that the ecological factors of climate and nutritional health affect birth, Wells et al. (2012) argued that the emergence of agriculture and its corresponding health consequences had a severe and direct impact on birth. Generally, the emergence of agriculture in a population is associated with poorer health and greater population size (Bocquet-Appel 2002; Cohen 1989; Larsen 1995; Steckel and Rose 2002). The dietary changes associated with agriculture likely affected maternal stature and fetal growth (Wells et al. 2012). Childhood growth and adult stature are both associated with protein intake (Galvin 1992; Hoppe et al. 2004a,b; Rolland-Cachera et al. 1995; Stein et al. 2003), which was probably typically higher in many hunter-gatherer diets compared with the newly adopted agricultural diets (Colagiuri and Brand Miller 2002; McMichael 2001; Milton 2000). The reduction in protein availability may explain why people became shorter in stature with the emergence of agriculture. High glycemic diets tend to increase birth weight (Moses et al. 2006; Scholl et al. 2004), while high protein diets reduce birth weight (Andreasyan et al. 2007; Campbell et al. 1996; Godfrey et al. 1996; Kramer

and Kakuma 2003; Sloan et al. 2001; but see Mathews et al. 1999 and Moore et al. 2004). According to Wells et al. (2012), these data suggest that the dietary changes associated with the emergence of agriculture would have led to short mothers giving birth to large-bodied neonates. Since short stature is somewhat associated with narrower or smaller birth canals (Baird 1949; Illsley 1966), it is plausible that this scenario would increase birth complications.

Wells et al. (2012) compared their own data on hunger-gatherer populations to agricultural populations (data from Owsley and Bradtmiller 1983; Storey 1986; Tocheri et al. 2005) to examine perinatal mortality rates. They found that hunter-gatherer skeletal samples had a much lower incidence of perinatal or infant skeletons compared to the agricultural samples (0-6.5 percent compared to 31.3-35.5 percent, respectively). They argued that these data demonstrated greater obstetric risks in agricultural populations relative to the hunter-gatherers. They briefly acknowledged, though did not adequately justify, that all samples were archaeological and therefore subject to taphonomic preservation complications. They suggested these were of no concern because the presence of some perinatal and infant skeletons in all populations demonstrated that taphonomy did not prevent the preservation of such skeletons overall, possibly due to burial practices observed. They therefore felt justified in using the percentage of skeletons in each sample from each age range as representative. I am concerned by this method, as it assumes that the samples are representative of not only perinatal and infant deaths, but also the number of deaths and people in the population overall. Furthermore, they assert that infant deaths were likely not caused by obstructed labor, but instead were probably the result of infectious disease since the neonate had time to grow into an infant. In contrast, they propose that perinatal deaths were the result of obstructed labor. Yet, other than age at death, they give no evidence for this and dismiss the possibility that perinatal deaths also may have been caused by disease. They claim that these data support their hypothesis that agriculture was an ecological factor that changed the recent human birth process.

Wells et al. (2012) identify various ways recent humans have responded to the birth complications caused by climate and nutrition. Nutrition affects maternal pelvis shape and neonate size, which combined can lead to cephalopelvic disproportion or shorter gestation periods to compensate for the limited pelvic dimensions (Borja and Adair 2003; Brabin and Brabin 1992; Brabin et al. 2002; Larsson and Svanberg 1983; Nkwabong and Fomulu 2009). The position the mother is in also affects the birth process, as squatting or kneeling can increase the

size of the birth canal by 28 percent, yet is rarely used in industrialized societies where the preference is for the mother to lie on her back to make the neonate more accessible to medical professionals when it is born (De Jonge et al. 2004; Dundes 1987; Engelmann 1882; Jarcho 1934; Michel et al. 2002; Naroll et al. 1961; Rosenberg and Trevathan 2002; Russell 1982; Walrath 2003; Wertz and Wertz 1977). There is some evidence that decreasing nutritional intake toward the end of pregnancy will reduce fetal size, as a compensation for mothers with small outlets (Brems and Berg 1988; Choudhry 1997; Christian et al. 2006; Pan 1929; van Steijn et al. 2009; Yajnik et al. 2003). As predicted by the hypothesis proposed by Wells et al. (2012), the earliest recorded Caesarean section was observed in Uganda in 1879 (Sewell 1993), suggesting that there has been a history of needing to birth this way in response to ecological factors affecting pelvic shape.

Overall, the ecological variation model predicts that ecological factors that affect particular populations in the short-term have a greater chance of affecting pelvic morphology in ways that increase the risk of birth than long-term evolutionary responses to bipedal locomotion that affect the entire human species. Here, I have highlighted the negative effects on the pelvis associated with climatic adaptations and poor nutrition. Wells et al. (2012) argue that hominins have been bipedal long enough that this should no longer be a significant influencer of birth success.

Energetics of gestation and growth model

The energetics of gestation and growth hypothesis, proposed by Dunsworth et al. (2012), differs completely from the obstetrical dilemma and ecological variation models. Unlike the others, it predicts that the timing of birth is determined by when the pregnant female stops being able to produce enough energy to satisfy the needs of the growing fetus, and that birth is not constrained by maternal pelvic dimensions. Under the energetics of gestation and growth model, maternal pelvic dimensions are adapted to the size of the fetus when energetic constraints cause labor to induce, and are not reflective of locomotor, climate, or nutritional constraints on birth. This model would completely invalidate the obstetrical dilemma and ecological variation models because it denies the possibility of pelvic constraints affecting birth.

In mammals, gestation is influenced by fetal size, maternal size, fetal growth rate, brain weight, litter size, and placenta type (Trevathan 2011); of these factors, brain weight and development may be the most important (Sacher and Staffeldt 1974). Even within a species,

gestation length may vary; e.g., Jukic et al. (2013) found that in recent human females where the date of ovulation was known, pregnancy length varied from 208 to 284 days. According to Trevathan (2011), great apes birth small neonates who have highly developed brains relative to their body size, explaining their long gestation period and precocial neonates. In comparison, human neonates are born underdeveloped compared to other apes, having only reached 30 percent of their adult brain size instead of the 40 percent observed in chimpanzees (DeSilva and Lesnik 2006). Furthermore, human neonates do not reach the motor and cognitive developmental stage that other primates are born at until 6-9 months after birth (Gould 1977; Montagu 1961; Portmann 1990; Trevathan 2011). However, as demonstrated above, human neonates are large in terms of absolute body and brain size at birth relative to other primates and relative to maternal body size, suggesting that it may be inappropriate to label recent humans "less developed". Dunsworth et al. (2012) argue that recent human gestation length is longer than expected based on their maternal body size and comparisons across primates. Using data from Charnov and Ernest (2006) and Martin (1990), they found that human gestation length relative to human maternal body size is longer than gestation length in chimpanzees or gorillas; overall, average human gestation is 37 days longer than predicted for average human body size, though still shorter than predicted for adult brain size (see also Leutenegger 1972; Martin 1996; Schultz 1926; Trinkaus 1984). Having established that human gestation length is longer than expected for body size, Dunsworth et al. (2012) propose an alternative hypothesis that has nothing to do with pelvis dimensions, but instead is based on energetics.

The energetics of gestation and growth model is based on the fact that during gestation, a mother must meet both her own metabolic needs and those of the growing fetus (Martin 1981, 1983, 1996, 1998; Sacher and Staffeldt 1974; Wood 1994). Dunsworth et al. (2012) propose that energetic constraints on both mother and child are the determining factor for when labor initiates, not just in recent humans, but across mammalian species (see also Ellison 2001). It predicts that labor begins when the energy needs of the fetus are greater than the energy the mother is able to produce. The resulting metabolic stress triggers labor via hormonal signaling.

While the obstetrical dilemma hypothesis proposes that there is a limitation to how large a fetus can grow before they will no longer fit through the bony birth canal, which is constrained in size by the requirements of bipedal locomotion, the energetics of gestation and growth hypothesis suggests that there is a limitation to how much energy the mother can invest in the

fetus before the fetal energy requirements exceed what the mother can produce. Under the energetics of gestation and growth hypothesis, the size of the bony birth canal is a *response* to this energetic constraint, not a *cause* of the timing of birth. Dunsworth et al. (2012) demonstrate this by showing that variation in recent human pelvic dimensions could accommodate a larger fetus, whereas there is a limit to the metabolic expense a mother's body can handle that corresponds to approximately nine months of gestation. Under both the obstetrical dilemma and energetics of gestation and growth models, hominins evolved to have larger brains, which made the fit through the birth canal challenging for fetuses; they differ in whether that challenge was caused by the maximum brain size of a neonate being limited by the size of the maternal birth canal (the obstetrical dilemma model) or by the size of the maternal birth canal adapting to the size of a fetus that required more energy than the mother's body could provide (energetics of gestation and growth hypothesis).

Conclusion

In this chapter, I have reviewed the evidence for the process of birth as humans today experience it. This includes the more common three-rotation birth mechanism that results in an occiput anterior presentation, as well as variations such as occiput posterior or breech presentations that are associated with greater risk for most pelvic types. I also described when and how recent human female pelvis shape varies, and the potential impacts on birth of those pelvic types. I will revisit this variation in Chapter 7 to aid in the interpretation of female Neandertal pelvic shape.

This chapter also describes three evolutionary models used by paleoanthropologists to interpret the evolution of the human birth process. The obstetrical dilemma model predicts that adaptations for bipedal locomotion affected maternal pelvis shape, and that increases in neonatal brain and body size ultimately affected birth as a result. The ecological variation model predicts that pelvic morphology and neonate size are affected by environmental factors like climate and nutrition, which change the birth process in particular local groups experiencing those factors. The energetics of gestation and growth model dispenses with the idea that pelvic morphology constrains the birth process and instead proposes that maternal energy production affects fetal size and determines the timing of birth. In Chapter 7, I will discuss how female Neandertal pelvic morphology, based on the findings of the present study, can be interpreted under each of these models. While none of these models can be tested directly, it will be possible to theorize, based

on the framework established here, which model or models most plausibly explain female Neandertal pelvic morphology and therefore Neandertal birth.

Chapter 3: Neandertal birth

Introduction

Neandertals were a population of humans that lived during the Late Pleistocene in Europe and West Asia. They can be distinguished as a population by morphological features that separate them from humans today and some humans living elsewhere during the Late Pleistocene. Neandertals were the first hominin fossils discovered, which means that they have been studied longer than any other hominin. Recent genetic studies have provided evidence that humans today share genes with Neandertals (Green et al. 2010). This has been interpreted by some to mean that Neandertals are direct ancestors of recent humans (Caspari and Wolpoff 2013, but see Stringer 2014). Yet, paleoanthropologists have previously noted that one of the features that distinguishes Neandertals as a population is the bony pelvis (Rak 1990, 1991; Rak and Arensburg 1987; Rosenberg 1988; Trinkaus 1984). The reason for this distinction requires further explanation. Paleoanthropologists suggest that the major selective pressures acting on the hominin pelvis are either related to locomotion or obstetrics (Dean et al. 1986; Friedlander and Jordan 1994; Ponce de León et al. 2008; Rak 1990, 1991; Rak and Arensburg 1987; Rosenberg 1988; Trinkaus 1984; Weaver and Hublin 2009). As a result, numerous hypotheses have been proposed to explain Neandertal pelvic shape in terms of birth differences.

Here, I provide a context for discussing Neandertal birth before outlining the hypotheses tested in this study. I begin by generally describing Neandertals in place and time, providing more details for the sites relevant to the present study. I then describe the hypotheses that explain Neandertal pelvic morphology by linking it to obstetrics. Some of these hypotheses consider only the most complete (but male) Neandertal pelvis, Kebara 2 (Rak and Arensburg 1987; Rak 1990, 1991; Tague 1992). Others consider a more complete portion of the Neandertal pelvic fossil record, focusing on the long iliopubic ramus observed in multiple Neandertal individuals (Dean et al. 1986; Friedlander and Jordan 1994; Rosenberg 1988; Trinkaus 1984). I examine the different reconstructions of the most complete female Neandertal pelvis, Tabūn C1, and what each has suggested about her birth process (McCown and Keith 1939; Ponce de León et al. 2008;

Weaver and Hublin 2009). I end by stating the null hypothesis tested in this study and explaining how it differs from these previous attempts to characterize Neandertal birth.

Neandertals in context

The human population living in Late Pleistocene Europe and Western Asia had anatomical traits that distinguished them from humans living elsewhere (Hawks and Wolpoff 2001). This population, named Neandertals, remained sufficiently distinct to identify from the fossil record until 30,000 years ago. Admixture between contemporaneous populations, coupled with a small population size that could be significantly affected by genetic drift, have been proposed to explain why characteristics attributed to the Neandertals became less frequent (Caspari and Wolpoff 2013; though see Stringer 2014 for an alternate interpretation).

The suite of features distinctive to Neandertals included both cranial and postcranial traits (Harvati 2007). Examples of Neandertal cranial features include midfacial prognathism, presence of an occipital bun, a small mastoid process, an asymmetric mandibular notch, and a horizontal-oval shape of the mandibular foramen. Postcranial features include curved femora and radii, thick cortical bones, robust muscle attachments, short stature, broad ribcage, short distal limbs, and large articular surfaces of the tibia and femur. The average height estimated for Neandertals was ~169 cm for males and ~160 cm for females. The average body mass estimated for Neandertals was ~78 kg for males and ~66 kg for females (summarized in Harvati 2007). One plausible explanation for Neandertal anatomy that has been presented is that they were adapted to surviving the glacial environment found in Europe during the Late Pleistocene (Churchill 1998; Ruff 1991).

The Neandertal fossil record is vast compared with other hominins. The first hominin fossils ever discovered were found in 1829, though they were not named as Neandertals until the Feldhofer 1 skeleton was discovered in the Neander Valley (Germany) in 1856 (Henke 2007). As the first fossil hominin discovered, Neandertals have been studied the longest, and have the largest fossil record of any fossil hominin known today, spanning multiple sites and time periods. Males are overrepresented in the record, largely due to the fact that most of the burials that have been excavated have preserved male skeletons, whereas the female Neandertal record comes mostly from non-burial sites that result in less-well preserved individuals. Even with the inclusion of the recent finds from Palomas, Spain, which reportedly include a female Neandertal skeleton, there are still many more males than females among the Neandertal fossils for which

sex can be determined. This means that while Neandertals in general are well studied, Neandertal females are not.

Below I describe the Neandertal sites that are relevant to the current study. The fossils from these sites will be described in Chapter 5. The key individuals from all of the following sites have been identified as female, with the exception of the male Kebara 2 skeleton. This represents the Neandertal skeleton that preserves the most complete pelvis in the fossil record. Since my exploration of Neandertal birth focuses on interpreting pelvic morphology, it is important to consider the most complete Neandertal pelvis, even if it is male. Additionally, comparing the Kebara 2 pelvis to the most complete female Neandertal pelvis in the fossil record, Tabūn C1, provides the opportunity to characterize sexual dimorphism in the Neandertal pelvis. Below I will describe the sites of Kebara (Israel), Tabūn (Israel), Krapina (Croatia), La Ferrassie (France), and Palomas (Spain).

Kebara

Kebara Cave (Mugharet el-Kebara or Me'arat Kabara) is located on the western slope of Mt. Carmel in Israel (Bar-Yosef 1991). Although excavations started in 1930 by Dorothy Garrod and later by Francis Turville-Petre and C.A. Baynes (Garrod 1954; Turville-Petre 1932), the relevant Neandertal material was not discovered until 1983 (Bar-Yosef 1991). The upper layers of the excavated cave had Aurignacian assemblages, while the lower layers were associated with Levalloiso-Mousterian artifacts (Garrod 1954). In the 1950s, Moshe Stekelis started excavating and uncovered hearths in the Mousterian layers (Schick and Stekelis 1977). In 1983, a burial of a skeleton of a young male was discovered (Tillier et al. 1991). It is described by Bar-Yosef and Vandermeersch (1991). Based on thermoluminescence and electron spin resonance dating, the skeleton was dated to 60,000 BP (Grün and Stringer 1991; Tillier et al. 1991; Valladas et al. 1987).

The skeleton, Kebara 2, is missing the cranium and parts of the lower limbs. Based on its position, completeness, and surrounding sediment, and the presence of a pit, it is considered a burial (Bar-Yosef et al. 1992). The articulation of the skeleton suggests that the cranium, except for some fragmentary upper molars, was removed by humans after some decomposition had occurred, leading to this skeleton being described as "the first clear-cut case recorded in a Mousterian context for later human intervention in a primary burial" (Bar-Yosef et al. 1992: 529). This skeleton is identified as a male adult 25-35 years old using dental, rib, and pelvic

morphology (Bar-Yosef et al. 1992). This individual's stature was estimated to be 1.74 m (Bar-Yosef et al. 1992).

Tabūn

Tabūn Cave (Mugharet et-Tabūn), also located on the western slope of Mt. Carmel in Israel, but to the north of Kebara (for map, see Figure 1 in Bar-Yosef et al. 1992), was excavated by a team of women led by Dorothy Garrod in 1929-1934 (Garrod and Bate 1937; McCown and Keith 1939; Weaver and Hublin 2009). Yusra (surname unknown) spotted a hominin tooth that was part of the Tabūn C1 cranium, which led to the discovery of the Tabūn C1 skeleton. This skeleton, which was very complete compared to any other female Neandertal, was found near a poorly preserved infant skeleton that was later lost during processing (Bar-Yosef and Callander 1999). Garrod wrote that since the skeleton was found near the top of Layer C, it may actually be a burial from Layer B (Bar-Yosef and Callander 1999; Garrod and Bate 1937; Weaver and Hublin 2009). This makes dating this skeleton challenging; however Layer C has been dated to 165±16 Ka by thermoluminescence and to 143±37 Ka by electron spin resonance (Grün and Stringer 2000; Mercier et al. 1995). The site, including its fauna and artifacts, is described in Garrod and Bate (1937) while the Tabūn woman (Tabūn C1 skeleton) and other hominin fossils are described in McCown and Keith (1939).

Krapina

The Krapina rock shelter, located in the mountains of northern Croatia, was excavated by Dragutin Gorjanović-Kramberger in 1899-1905 (Radovčić 1988; Radovčić 2011). The Neandertal remains found at this site included over 70 individuals, representing different ages and sexes and made up of ~900 elements (Gorjanović-Kramberger 1906; Radovčić 1988; Radovčić 2011; Radovčić et al. 1988; Simek and Smith 1997; Smith 1976; Wolpoff 1979). On the one hand, this allows variation within a population to be studied; on the other hand, the Krapina remains were taphonomically disassociated postmortem so that individual elements of bone cannot confidently be associated with other elements from the same site. The remains were dated to 130 Ka using electron spin resonance and U-series analyses (Rink et al. 1995). The Krapina site and remains were originally described in Gorjanović-Kramberger (1906).

La Ferrassie

La Ferrassie is a rock shelter in Dordogne, France that was excavated in the early 1900s and yielded hominin fossils and Mousterian artifacts (Heim 1976). The layer where the hominins were found has been dated to 72 Ka based on a comparison of its stratigraphy to the site Le Moustier (Heim 1982, cited in Holliday 1997). The La Ferrassie hominins, most notably skeletons 1 and 2, are described by Heim (1976, 1982).

Sima de las Palomas

The Sima de las Palomas site is a vertical cave system in southeast Spain (Walker et al. 2012). In 1991, Juan Carlos Blanco-Gago discovered Neandertal cranial fossils in the cave. The layer containing three breccia-encased hominin skeletons has been dated to 55-50 Ka (Walker et al. 2012). They were found with Mousterian artifacts nearby, and what skeletal morphologies are visible suggest the skeletons are Neandertals. The Palomas 96 (SP-96) skeleton, which is 85% complete, was excavated in 2007 and called a female based on the morphology of its *os coxae* and sacrum (Walker et al. 2012). This skeleton is still being cleaned and described, and consequentially, it is not included in the analysis of this study despite being a female Neandertal pelvic remain.

Neandertal pelvic morphology and birth

Neandertal pelvic morphology has been explained in terms of obstetrics by many previous studies, which are described in this section. I have separated them based on the evidence used in each study. Generally, there is good evidence showing that male Neandertal pelves had a different pelvic morphology than recent humans, though the same differences are less well established for *female* Neandertal pelvic morphology, which complicates predicting the Neandertal birth process.

First, I describe studies that are based on the morphology of the mostly complete male Neandertal pelvis Kebara 2. Rak and Arensburg (1987; also see Rak 1990) used this fossil to reconstruct a model of overall Neandertal pelvic shape, which they suggested would not have led to birth differences in Neandertals. Based on his study of sexual dimorphism in the true pelvis, Tague (1992) used the Kebara 2 pelvis to hypothesize potential obstetrical complications in Neandertals.

Following these descriptions are studies that refer to multiple Neandertal pelvic fossils to predict a larger birth canal in Neandertals. Trinkaus (1984) explained the larger birth canal as meaning Neandertals has a longer gestation period, and therefore larger neonates, than recent humans. Dean et al. (1986) argued that Neandertal pelvic morphology indicated that their neonates were larger than recent human neonates because they found that the Devil Tower, Gibraltar Neandertal infant had a faster growth rate than recent humans. Rosenberg (1988) suggested that Neandertal neonate size was proportional to their body size, and that the maternal pelvic dimensions adapted to this neonate size. Friedlander and Jordan (1994) proposed that Neandertal neonates were similarly sized to those of recent humans, but that an increase in bone density in Neandertals compared with humans today made the maternal pelvis less flexible during birth, which in turn required a larger birth canal to accommodate the neonate.

Finally, I discuss studies that focused on drawing birth conclusions based on reconstructing the most complete female Neandertal pelvis, Tabūn C1. McCown and Keith (1939) partially reconstructed the pubis and partial ilium of Tabūn C1 to demonstrate that her longer iliopubic ramus would have resulted in a mediolaterally narrower inlet than in recent humans. Ponce de León et al. (2008) virtually reconstructed Tabūn C1 to show how she could have had a birth canal similar to that of recent humans. In contrast, Weaver and Hublin (2009) virtually reconstructed Tabūn C1 to find that she had a platypellic shaped pelvis that was so short anteroposteriorly it would have complicated the birth of large-brained neonates.

Neandertal pelvic morphology based on Kebara 2

The most complete Neandertal pelvis so far discovered is that of Kebara 2. This pelvis is male, and preserved parts of both *ossa coxae* and the sacrum. Rak and Arensburg (1987) reconstructed the pelvis to show what a mostly complete Neandertal pelvis looked like (see also Rak 1990, 1991). They found that the Kebara 2 pelvis differs from that of a recent human in that it has a long iliopubic ramus combined with flat, posteriorly oriented iliac blades. The iliopubic ramus of Kebara 2 was longer than what is seen in recent human females, and the iliac blades were oriented differently than what is seen in recent humans of either sex. The pelvic anatomy of Kebara 2 is described in greater detail in Chapter 5; however, based on these pelvic differences between Kebara 2 and recent humans, Rak and Arensburg (1987) hypothesized that these differences result from the *ossa coxae* being rotated relative to the recent human orientation. Positioning the pelvic aperture anteriorly relative to its position in recent humans would require a

longer iliopubic ramus, and may explain iliac blades that are oriented more posteriorly than in recent humans. Such differences would result in a Neandertal pelvis with laterally oriented acetabula and an anteriorly positioned sacrum, which combined with the long pubis would yield a pelvic aperture similar in size to that of a recent human.

Rak and Arensburg (1987) argued that this difference in morphology (which they describe as being from the human form to the Neandertal form, though it was more likely the reverse) reflected a difference in posture and locomotion, and not an adaptation for a different birth process. They suggested that this means obstetrical demands did not drive the selection of the late *Homo* pelvis, but they neither discuss how this change in orientation and posture may have affected birth nor specify what the locomotor changes might have been. Their hypothesis that bipedal locomotion may have differed between Neandertals and humans today raised the question of whether differences in posture impact the birth process, as would be predicted by the obstetrical dilemma model discussed in Chapter 2. Furthermore, while this established a plausible model for interpreting pelvic morphology differences in males, potential pelvic sexual dimorphism in Neandertals raises the question of whether Kebara 2 is an accurate model for understanding female Neandertal anatomy, which was presumably adapted for giving birth. Female Neandertals also appear to have had long iliopubic rami and somewhat flared iliac blades, but the rest of their pelvic anatomy is too poorly preserved to be directly compared with Kebara 2.

Although Rak and Arensburg (1987) did not go into great detail of the obstetric consequences of the Kebara 2 pelvic morphology, Tague (1992) used this male pelvis to discuss the Neandertal birth process. Tague (1992) compared male and female recent human pelves and found that true pelvic dimensions related to birth in recent human females were not significantly different in males from the same population. While diameters were not sexually dimorphic, he found that recent human females had a more consistent inlet *area*, compared to males in the same population. He suggested that this meant male pelves could reasonably used to assess linear dimensions related to birth within a population, and that overall the area of the inlet affected the birth process more than any particular linear dimension. Based on his findings, Tague (1992) analyzed Kebara 2 to investigate Neandertal birth, assuming that birth-related pelvic dimensions were similarly not sexually dimorphic in this Late Pleistocene population. He found that while Neandertals had a larger pelvic inlet than recent humans, they had a smaller pelvic outlet. Based

on the "funneled" shaped birth canal, he predicted that Neandertal females, compared to recent humans, either birthed smaller neonates or had more difficulty birthing similar-sized neonates.

Thus, based on Kebara 2, researchers have suggested that Neandertals and recent humans shared a similar birth process (Rak 1990, 1991; Rak and Arensburg 1987) or that they may have birthed smaller neonates or had more difficulty with birth compared to recent humans (Tague 1992). However, the argument for using Kebara 2 as an appropriate pelvis to model Neandertal birth is problematic, as it assumes similar sexual dimorphism in Neandertals and recent humans, which has not been demonstrated (see Chapter 4 for further discussion). Furthermore, while Tague (1992) focused on the similarity of linear measurements between male and female recent humans, he demonstrated that the area of the inlet is sexually dimorphic. This would indicate that sexually dimorphic differences in the true pelvis do exist in recent humans, and must be considered before using a male Neandertal pelvis as a proxy for understanding birth in the past.

Neandertal pelvic morphology based on multiple fossils

Although there are few recognizably female pelvic remains in the Neandertal fossil record, the overall pelvic sample for Neandertals is relatively large (approaching 30 specimens). Here I describe previous studies that have used many of these individuals, both male and female, to draw conclusions about how Neandertal pelvic morphology affected Neandertal birth.

Trinkaus (1984) proposed a hypothesis related to timing of birth and gestation length based on the long iliopubic ramus observed in multiple Neandertal individuals. He predicted that neonatal size would have been larger in Neandertals, which would have meant they had a longer gestation period than humans. He hypothesized that the longer iliopubic ramus meant they had a larger birth canal area (but see Rak and Arensburg 1987 for dissent). Trinkaus (1984) reasoned that if all other parts of the Neandertal pelvis were similar to humans, then a longer pubis would result in a larger birth canal area. This led him to his hypothesis that Neandertals had a longer gestation period than humans (12 months vs. 9 months, respectively). If Neandertals had a significantly larger birth canal than humans (by 15 to 25 percent), then it would be possible for them to birth a 15 to 25 percent larger neonate than a human neonate at birth. Trinkaus assumed that Neandertals and recent humans had the same growth rate, and calculated that the recent human brain size grows 15 to 25 percent larger in the first 2-3 postnatal months. Based on this, he calculated that Neandertals gestated for 12 months. Trinkaus (1984) supported his hypothesis with the observation that human neonates are relatively helpless at birth, due in part to the

shortened gestation period they have relative to the gestation length their brain size would predict. Trinkaus (1984) argued that human offspring survive postnatally due to cultural adaptations, such as non-mother caregivers and monogamous mating systems. He hypothesized that Neandertals, who he thought did not possess these cultural adaptations, would have needed their neonates to be less dependent on others at birth, which could have been accomplished by spending more time gestating. Criticisms of Trinkaus' theory have suggested that Neandertal pelvic shape is explained not by a longer gestation period, but instead by a large body size (Rosenberg 1988) or a different posture than that of recent humans (Rak and Arensburg 1987).

Dean et al. (1986) explained Neandertal pelvic proportions based on a large neonate; however they predicted large neonatal size from an increased growth rate for Neandertal fetuses based on Devil Tower, Gibraltar Neandertal child's dental age versus development. They found that this three year old had a larger cranium than expected for its age, suggesting that Neandertals grew faster than humans today. Based on this premise, they hypothesized that Neandertal offspring grew faster prenatally, and therefore were larger than human offspring at birth even after the same gestation time (see also Smith 1991). These authors based their hypothesis on the observation that Neandertals have long pubic bones, which implies a larger birth canal, which they take to mean a larger neonate.

Rosenberg (1988) compared Neandertal true pelvis dimensions across Neandertal individuals to differently sized and differently proportioned recent human populations to show that in Neandertal and recent human populations, neonate size is proportional to maternal body size. Assuming that the Neandertal birth canal was adapted to birthing proportional neonates, she tested her prediction by comparing maternal pelvic dimensions to overall body dimensions in different populations. Rosenberg (1988) found that the apparent differences in Neandertal pelvic dimensions, such as iliopubic ramus length, compared with recent human populations could be explained by differences in measurements that indicated body size and height. She demonstrated that iliopubic ramus length varies between populations of humans in response to body mass, and to a lesser degree, height. Populations with small body masses (represented by samples of Andaman Islanders, Philippine Negritos, and African Pygmies for short individuals and Kerma for tall individuals) tended to all have short pubic bones, with the tall sample having slightly longer pubes than the short samples. In contrast, populations with large body masses (represented by samples of Zuni and Kodiak for short individuals and Norse and Hamann-Todd

Whites for tall individuals) all tended to have relatively longer pubic bones, again with relatively longer bones in the taller individuals. When Neandertals were compared to the varying human samples, Rosenberg (1988) found that the regression predicted their actual pubic size for individuals with their body dimensions (short height and large body mass). From this, she hypothesized that they would have been able to accommodate the large fetuses that were probably also associated with this population's body size.

Friedlander and Jordan (1994) explained the presumed large Neandertal inlet (though see Rak and Arensburg 1987 for an alternate view) as a response to bone density and neonatal size. They argued that Neandertals had higher bone density than recent humans, and that this would have limited the flexibility of both the unfused fetal skull and the maternal pelvis during birth. Since in humans, the fetal cranium is much more plastic during the birth process than the maternal pelvic joints, reducing this flexibility could lead to severe birth complications. Based on this, Friedlander and Jordan (1994) proposed that a larger inlet would make it possible to accommodate a less plastic fetal cranium. Importantly, under their model the cranium size does not differ between Neandertals and humans, rather, its flexibility while maneuvering through the birth canal differs.

The studies discussed here all seek to explain a large pelvic inlet based on Neandertal males and females having long iliopubic rami. However, as discussed above, this is not the only interpretation available for a long iliopubic ramus. It may be possible for iliopubic ramus length to be long without increasing the area of the pelvic inlet compared to recent humans (Rak and Arensburg 1987; Rak 1990, 1991) or that a large inlet may appear with a smaller pelvic outlet than is seen in recent humans (Tague 1992). While the ideas presented here are interesting in terms of how neonatal size could be larger in Neandertals compared with humans today, having a long iliopubic ramus is not enough information to draw conclusions about the Neandertal birth process.

Neandertal pelvic morphology based on Tabūn C1

The most complete female Neandertal pelvis is Tabūn C1, which (as described more fully in Chapter 5) preserves the anterior portion of the pelvis. Multiple researchers have turned to this pelvis as the best evidence for uncovering the Neandertal birth process, as more features than the iliopubic ramus length can be considered. There have been three attempts to reconstruct this incomplete pelvis, which are described here.

McCown and Keith (1939) reconstructed the pubis and part of the ilium of Tabūn C1, and compared it to a recent human European female. They suggested that the increased length of the iliopubic ramus, combined with the morphology of the anterior ilium, would have resulted in an anteroposteriorly long and mediolaterally narrow Neandertal pelvic inlet compared with the inlet of the recent human. However, they did not discuss the implications such a shape could have had on the Neandertal birth process. Tague (1992) suggested that inlet shape is less important to successful birth than inlet area, which would have been similar to that of recent humans in the McCown and Keith (1939) version of Tabūn C1. Alternatively, as discussed in Chapter 2, different shaped maternal pelves may impact how a fetus rotates during birth. This means that if the McCown and Keith (1939) reconstruction is accurate, the Neandertal fetus entered the birth canal facing either anteriorly or posteriorly relative to the mother. It is still not clear if or how the fetus rotated during the rest of labor is unknown, since Tabūn C1 does not preserve ischial spines or a sacrum.

Ponce de León et al. (2008) reconstructed the female Neandertal pelvis Tabūn C1 to be able to birth the reconstructed Neandertal infant cranium from Mezmaiskaya via the same birth process as is seen in recent humans. They virtually reconstructed the Tabūn C1 female pelvis to show how it would have looked if it were able to give birth in three rotations to the Mezmaiskaya infant, who was 1-2 weeks old at death and whose skull they also virtually reconstructed. They found that when they did this, the birth canal was slightly wider in Tabūn C1 compared to recent humans, but that this accommodated a rotational birth process for the Mezmaiskaya infant whose cranium was also elongated relative to that of a recent human. They hypothesized that the wider dimensions of the Neandertal pelvic inlet would not have prevented, and still may have required, rotational birth. They tested the accuracy of the reconstruction two different ways. First, they compared birth canal dimension ratios (e.g., the ratio of the anteroposterior depth of the inlet to the mediolateral width of the inlet) to humans and other hominin fossils. They found that the Tabūn C1 reconstruction's ratios fit the range of both modern humans and other hominin fossils, suggesting that this reconstruction presents a reasonable birth canal. Second, they completed a geometric morphometric analysis of pelvic shape variability for 10 male and 10 female modern humans, Kebara 2, and their Tabūn C1 reconstruction. They found that while Neandertals had wider pelvic brims than recent humans, the difference between the male and female Neandertals was very similar to the difference between the recent human males and females. The limitations

of this study are that while their technique reconstructed pelvic size based on neonatal dimensions, it also assumed a recent human-like pelvic shape and a recent human-like birth mechanism from the start. This exercise was useful in showing that the Tabūn C1 pelvic material can be reconstructed to look like that of a recent human female, but does little to directly test hypotheses about birth.

Weaver and Hublin (2009) also virtually reconstructed the Tabūn C1 pelvis, but did so with the goal of testing a hypothesis about birth. They estimated sacral dimensions for Tabūn C1 based on a sample of human sacra. Once their reconstruction was complete, they checked their work by comparing it to a hypothetical female pelvis generated using the male Kebara 2 as a model and the human pattern of pelvic sexual dimorphism. While their "female" Kebara 2 did not resemble their reconstructed Tabūn C1 for most features, all features of the birth canal were sufficiently similar to support the accuracy of their reconstruction. In their Tabūn C1 reconstruction, the area of the inlet and outlet were similar to that of recent humans. However, the shape of these planes was vastly different: both planes were far more mediolaterally wide in Neandertals than in recent humans, making the Tabūn C1 pelvis extremely platypellic. They suggested that the wide outlet meant no rotations would be required between the neonate's head entering the inlet and exiting the outlet; instead the head would stay in the same position, facing laterally relative to the mother, throughout the birth. This is similar to the pelvic shape of earlier female fossil hominins, including the australopith A.L. 288-1 ("Lucy") and the probable *Homo erectus* from Gona BSN49/P27. Consequently, Weaver and Hublin (2009) hypothesized that a platypellic pelvis is the ancestral condition for hominins. They further suggested that the recent human pelvic form evolved in a hot climate as a derived form distinct from Neandertals. This derived pelvis was narrower compared to the pelvis of earlier hominins, including Neandertals. The narrowness was caused by Bergmann and Allen's rules, which state that a taller and narrower body will increase the skin's surface area, allowing for greater bodily cooling. In order to accommodate birth while changing the shape of the pelvis in response to the hot climate, the birth canal went from being transversely oval at the inlet to being more circular due to an expanded anteroposterior dimension. Weaver and Hublin (2009) proposed that this form spread and remained throughout humanity, even after humans with this pelvic form moved to colder climates. I speculate that if their hypotheses are supported, the potential benefits of a wider, platypellic pelvis for recent humans living in a cold environment were counteracted by cultural

adaptations, such as improved clothing and shelter, that deemed them unnecessary and the added benefits of a circular inlet for birth (see Chapter 2 for discussion of the potential dangers of a platypellic pelvis).

McCown and Keith (1939), Ponce de León et al. (2008), and Weaver and Hublin (2009) all started with the same source material – the pelvic remains of Tabūn C1, but all reached different conclusions about how the female Neandertal pelvis was shaped by using different methodologies. In their reconstruction of Tabūn C1, McCown and Keith (1939) predicted an anteroposteriorly long inlet, Ponce de León et al. (2008) predicted a nearly circular but slightly mediolaterally elongated inlet, and Weaver and Hublin (2009) predicted an extremely mediolaterally wide inlet. As discussed in Chapter 2, these inlets would have all had different implications for childbirth. Overall, these interpretations demonstrate the difficulty with basing conclusions about birth on a single, incomplete pelvis.

Null hypothesis tested here

The study presented here takes a different approach to exploring Neandertal birth. Instead of extrapolating from a male Neandertal pelvis or reconstructing a fragmentary female Neandertal pelvis, this study compares Neandertal pelvic dimensions directly. The full methodology, including how the female Neandertal sample was identified, measurements developed to be taken on this sample, and statistical analysis for comparing it with a relevant recent human sample, is described in Chapter 4.

The overall goal of this project is to test the null hypothesis that there are no significant differences in pelvis dimensions between Neandertal and human females. Establishing whether Neandertal and recent human females differ in size and shape in ways similar to Neandertal and recent human males is required before asking questions about birth. If it turns out that recent human and Neandertal males have different shaped pelves, but females do not, then that would suggest that pelvic morphology and the birth process do not differ much between these groups. If instead my findings establish differences between female pelves for these two groups, this may indicate that there were also birth differences, even if the same differences are known in Neandertal males. I hypothesize that differences in the anatomy of the female true pelvis affect the birth process even if selective pressures related to obstetrics do not drive the differences. I will discuss any pelvic differences by exploring how my results would be interpreted under each of the three evolutionary models discussed here and in Chapter 2.

Conclusion

      Neandertals living in Late Pleistocene Europe and Western Asia had skeletal differences that distinguish them from recent humans. Here I focus on the differences in the pelvis, and specifically how those differences have been related to birth. Differences in male pelvic morphology for Neandertals and recent humans can be explained by Neandertals having a rotated ilium and a lengthened pubis (Rak and Arensburg 1987); however, no female Neandertal pelvis is sufficiently complete to determine whether this explanation applies to females, as well.

      Obstetrical hypotheses have been developed based on male Neandertal pelvic morphology, the limited morphology observed on various incomplete male and female Neandertal pelvic fossils, or the different reconstructions of the same female Neandertal pelvis fossil. However, these hypotheses do not lead to agreement on what female Neandertal pelvic morphology looked like, or how it related to their birth process.

      In the study described in the following chapters, I test the fossil record directly for differences in female pelvic anatomy that may reflect obstetrical adaptations. Regardless of what model is used to explain the cause of differences in pelvic morphology, I establish in Chapter 2 that variation in pelvis shape within recent humans can affect the birth process, providing a context for interpreting any morphological differences found between female Neandertal and recent human pelves. In this study, I compare these two groups for measurements of the true pelvis that I developed based on their obstetrical relevance to test the null hypothesis of no difference. Whether any differences found between Neandertal and recent human females match those predicted by Rak and Arensburg (1987), the existence of pelvic morphological differences between these two female groups likely has an effect on their birth process.

Chapter 4: Methods

Introduction

The null hypothesis that there are no significant differences in the birth related pelvic dimensions of Neandertal and recent human females is challenging to test because of the state of the fossil record. The Neandertal fossil record only includes a very few females, all of which are incomplete. As such, traditional statistical techniques cannot be applied, but rather creative methodologies are required to answer questions about Neandertal birth.

The first step is to identify as many female Neandertal pelvic fossils as possible. Since sites like Krapina consist of unassociated skeletal material, sex assessment can be challenging. However, the pelvis, likely because of its relation to birth, is particularly sexually dimorphic in recent humans, and may be equally useful in identify sex in Neandertals. In this chapter, I describe the features I found to be most reliably sexually dimorphic in the Neandertal sample.

Once a sample of Neandertal female pelvic fossils is established (a sample that will be described more thoroughly in Chapter 5), measurements were selected or developed based on their preservation. For a measurement to be useful for testing the null hypothesis, it must be both potentially related to birth and measurable on at least two Neandertal females. The latter requirement greatly reduced the number of relevant standard measurements that could be used, so new measurements were developed specifically for this project. They are defined and illustrated here.

Finally, once a sample of Neandertal females had been identified, and relevant measurements taken, those same measurements were taken on a cold adapted female recent human comparative sample, and the samples were compared. Since sample sizes for all of the measurements were small, traditional methods of comparing samples, such as a *t*-test were not valid. Instead, bootstrap resampling was used to develop a methodology for comparing the small Neandertal sample to the larger recent human sample. This methodology made it possible to assess the probability of finding the Neandertal pattern, characterized by its mean, in the larger comparative recent human sample, taking the small size of the Neandertal sample into account.

The goal of this chapter is to ascertain both the advantages and limitations of the approaches used to assess sex in the Neandertal sample, describe the metric approaches that maximize the comparisons that can be made given the incomplete natures of the remains, and discuss the analyses that directly address the null hypothesis.

Assessing sex from the *os coxae*

Though the Neandertal fossil record is fairly large compared to other fossil hominins, when sex is identifiable, the record is skewed toward having more male individuals than females. In some cases, it is difficult to assess sex from the skeleton at all, especially if the fossil fragment in question is unassociated with the rest of its body. However, the pelvis is the most useful skeletal element for determining sex in recent humans, and as such many techniques have been developed to use it to assess sex (Brůžek 2002; Genovés 1954; Klales et al. 2012; Meindl et al. 1985; Murail et al. 1999; Novotný 1975; Phenice 1969; Rogers and Saunders 1994; Schulter-Ellis et al. 1985; Tague 1992, 2007; Walker 2005; Washburn 1948). Here I describe the two techniques I used to ascertain sex in the Neandertal sample and explain why they were more reliable than other techniques that are commonly used on recent humans.

Unlike the rest of the body, where sexual dimorphism manifests as males being larger for a particular feature than females, females are larger than males for many of the sexually dimorphic pelvic traits. These differences emphasize the expanded birth canal in females (Rosenberg 2002; Tague 1992). Features that are generally absolutely larger in female recent humans include the length of the iliopubic ramus, the width of the subpubic concavity, the size (both diameter and circumference) of the inlet, and the width of the greater sciatic notch (Brůžek 2002; Genovés 1954; Murail et al. 1999; Novotný 1975; Rogers and Saunders 1994; Walker 2005; Washburn 1948).

Importantly, the sexually dimorphic features of the recent human pelvis vary across populations (Genovés 1954; Hager 1989; Murail et al. 2005; Novotný 1986; Rosenberg 1988, 2002; Tague 1989, 1992; Walker 2005; Washburn 1948). For instance, Rosenberg (2002) quantified the shape of the greater sciatic notch in multiple populations while accounting for sex. She found that the average width associated with female Australian Aborigines (after Davivongs 1963) was similar to the average width associated with male Chinese (i.e., Han Chinese; after Wu et al. 1982). These data suggest that while female sciatic notches are wider than male sciatic

notches within the same population, the possibility of population variation must be considered when assessing sex.

In addition to population variation, another complication to testing the null hypothesis is the poor preservation of the fossil record. Often, not enough of a fossil skeleton is preserved to use the features mentioned above, let alone compare it to other fossils to see whether and how specific traits are sexually dimorphic within a population. For example, the Phenice (1969; see also Klales et al. 2012) method is widely accepted as an accurate means of assessing sex in recent humans (Meindl et al. 1985). However, few fossils preserve the portions of the pubis required to use this test. Of the Neandertals considered in this study, only the male form of the Phenice technique is observed. Since no female Neandertals preserve the medial pubis, it is unknown if Neandertals were dimorphic for ventral arc, subpubic concavity, and ischiopubic ramus ridge form in the way that Phenice described. While it can reasonably be predicted that they were since these features appear in australopithecines, the lack of a female Neandertal example makes this technique impractical for use on this fossil sample.

When sex has been estimated for Neandertal fossils previously, it has been based on well-preserved *ossa coxae* using techniques developed for humans, or has been corroborated based on sexually dimorphic non-pelvic regions of the skeleton closely associated with the more fragmentary pelvis (e.g., Kebara 2, La Ferrassie 1). Yet, for other Neandertal fossils there are no associated skeletal elements, and the *os coxae* was so poorly preserved that many techniques typically used on recent humans could not be applied (e.g., Krapina 255.1, Krapina 255.10). I therefore compared Neandertals for features that were considered sexually dimorphic in humans, focusing on features that were frequently preserved in the Neandertal sample.

While iliopubic ramus length is longer in female humans than it is in males, the unusually long ramus observed on Kebara 2 and other male Neandertals, whose sex was determined from multiple skeletal elements, called the pattern of sexual dimorphism of this feature into question for Neandertals. A seriation of Neandertal iliopubic lengths, which included very few individuals, confirmed that this trait was typically long relative to ischium height regardless of the estimated sex of the individual. I therefore excluded iliopubic ramus length from my selection of features to be used in determining sex in Neandertals.

Absent that feature, and with the incomplete preservation of the pubic bone, when it was preserved at all, I found that only two features unambiguously demonstrated Neandertal sexual

dimorphism across the Neandertal sample. These were the width of the greater sciatic notch and the height of the acetabulum. I describe these two features below.

I establish that the Neandertal sample can be seriated for each of these traits to demonstrate sexual dimorphism. In Chapter 5, I demonstrate that both of these techniques accurately assess the sex of the most complete male (Kebara 2) and most complete female (Tabūn C1) Neandertal pelves, both of which have had their sex estimated from other skeletal elements in addition to pelvic ones. In this way, I determine that within the context of the Neandertal sample in general and these two individuals in particular, the width of the greater sciatic notch and the diameter of the acetabulum can be used to assess the sex of Neandertals. The sample of female Neandertal *ossa coxae* described in Chapter 5 are selected based on the methods described here.

Greater sciatic notch width

The width of the greater sciatic notch can be used to assess sex in recent humans. Within a population, females tend to have a wider and more U-shaped notch while males have a narrower or more J-shaped notch that is consequently narrower at its opening than the U-shaped form (Brůžek 2002; Rogers and Saunders 1994; Walker 2005). It is likely that this trait is sexually dimorphic in recent humans because it is related to females having an expanded anteroposterior dimension of the birth canal created by the sacrum being angled further away from the acetabulum, resulting in a wide notch. There have been numerous attempts to quantify this feature by measuring the width of the opening, measuring the height of the notch, or calculating an index from the anterior and posterior portions of the opening based on splitting the notch opening at the line of the apex (Brůžek 2002; Davivongs 1963).

It is difficult to accurately measure the width of the complete notch or the anterior and posterior portions required to calculate an index when the posterior inferior iliac spine and the ischial spine are not preserved. To quantify the angle itself, a significant portion of both the anterior and posterior legs of the greater sciatic notch is required. These features are rarely preserved in archaeological or fossil remains, and are absent from most of the Neandertal fossils. To overcome this difficulty, I assessed the greater sciatic notch as a nonmetric binomial trait, describing two conditions: wide (when the notch expands outward from the apex at an obtuse angle) and narrow (when the notch expands outward from the apex at an acute angle). The former were characterized as female, while the latter were characterized as male. This technique

is not ideal, as it obscures many of the subtleties of notch shape that have been established in recent humans; however, it was the only way to score the maximum number of Neandertal individuals. When all of the Neandertal fossils preserving the apex of the greater sciatic notch were lined up from widest to narrowest, it became clear that there was a distinct difference between these two conditions; i.e., the male Neandertals have particularly narrow greater sciatic notches compared to the female Neandertals. The results of this scoring are recorded in Table 4.1. The Neandertal individuals that preserve enough of the greater sciatic notch to be assessed for this feature are Amud 1, Kebara 2, Krapina 207, Krapina 209/212, Krapina 211, Krapina 255.8, La Chapelle-aux-Saints, La Ferrassie 1, La Ferrassie 2, Neanderthal 1, and Tabūn C1.

Acetabulum height

Acetabulum height tends to be larger in males than in females, and for some human populations is the best single indicator of sex from the pelvis (Patriquin et al. 2005; Rogers and Saunders 1994; Steyn and Işcan 2008). This joint surface reflects both the biomechanical aspects of pelvic shape that influence joint pressure, and the weight and robusticity of the individual (McHenry 1992; Ruff 1991; Ruff et al. 1997).

This feature was additionally useful for this study because of the large number of Neandertals preservations. When acetabulum height could not be taken reliably on a fossil, occasionally it was possible to estimate the height based on femoral head height, which further increased the Neandertal sample. Using a multi-sample dataset representing a number of recent human populations and including data on over 1,269 individuals (Auerbach 2014), I calculated a regression formula to predict acetabulum height from femoral head diameter. The resulting formula calculates acetabulum height in mm:

$$AcetabulumHeight = 0.9854(FemurHead) + 6.1202$$

$$(r = 0.96, \text{SEE} = 1.129 \text{ mm}).$$

I tested the accuracy of this regression formula on Neandertals by comparing the measured acetabulum height for La Ferrassie 1 to the acetabulum height predicted by this equation. For La Ferrassie 1, I compared the actual acetabulum height of 59 mm (Wolpoff personal communication, July 2014) to the acetabulum height predicted from the femoral head height of 54.0 mm (Trinkaus 2011). The regression formula predicts an acetabulum height of 59.3 mm. This indicates that the calculated regression equation is applicable to predicting Neandertal acetabular diameters, and does so with a precision of approximately ± 0.03 mm (at

Table 4.1: Results of sex estimation techniques applied to Neandertal fossils.

	Greater sciatic notch width	Acetabulum height (mm)	Sex estimate
Palomas 96	Wide	(48.5)[A]	Female
Tabūn C1	Wide	(50.0)[A]	Female
Krapina 209/212	Wide	50.9[B]	Female
La Ferrassie 2	Wide	(51.4)[A]	Female
Krapina 208	--	52.7[B]	Female
Krapina 211	Wide	--	Female
Krapina 255.5	Wide	--	Female
Krapina 255.8	Wide	--	Female
La Ferrassie 1	Narrow	59[C]	Male
Kebara 2	Narrow	60.5	Male
Amud 1	Narrow	61.0	Male
Neanderthal 1	Narrow	62.8	Male
Krapina 255.3	Narrow	--	Male
La Chapelle-aux-Saints	Narrow	--	Male
Regourdou	Narrow	--	Male
Krapina 255.1	--	--	Unknown
Krapina 255.4	--	--	Unknown
Krapina 255.6	--	--	Unknown
Krapina 255.7	--	--	Unknown
Krapina 255.9	--	--	Unknown
Krapina 255.10	--	--	Unknown

[A] Data from Trinkaus (2011).
[B] Data from Rosenberg (1986).
[C] Data from Wolpoff (personal communication, July 2014).
( ) indicate that acetabulum height was calculated from femoral head diameter, using the calculated regression equation: $AcetabulumHeight = 0.9854(FemurHead) + 6.1202$ (r = 0.96, SEE = 1.129 mm), as described in the text.

least for this one individual). Using the reported femoral head diameter for Tabūn C1, Palomas 96, and La Ferrassie 2, I calculated their predicted acetabular diameters and used these values to assess their sex (see Table 4.1).

Seriating the Neandertals by acetabulum size demonstrated a gap between 52.7 mm and 59 mm. This suggests that the largest adult female acetabulum was 52.7 mm (Krapina 208), while the smallest male acetabulum was 59 mm (La Ferrassie 1) (see Table 4.1). The gap between 52.7 mm and 59 mm confirms that in Neandertals, like in recent humans, females tend to be smaller and males tend to be larger for acetabulum height. The Neandertal individuals that can be assessed for the this feature, either using measured acetabulum height or predicted acetabulum height based on the regression formula, are Amud 1, Kebara 2, Krapina 207, Krapina 208, Krapina 209/212, La Ferrassie 1, La Ferrassie 2, Palomas 96, Neanderthal 1, and Tabūn C1.

Together, both of these features – greater sciatic notch width and acetabulum height – separate the Neandertal fossil sample into two groups. The predicted sex based on these two features also agrees with the sex previously estimated for many of the Neandertal fossils that have more complete skeletons. All of this supports the validity of using these techniques for assessing the sex of the more poorly preserved fossil remains.

Pelvimetrics

As discussed in Chapter 2, changes to the size or shape of the birth canal have potential obstetrical implications. When only a very small part of the pelvis is preserved, shape becomes difficult to assess. Here, I explore the size of different pelvic measurements that reflect overall pelvis size as well as describing the orientation of different pelvic features to each other. The latter is the best approximation for shape that can be compared. Here, I define the measurements taken and how they potentially relate to childbirth by first defining the pelvic landmarks that are commonly present in the Neandertal sample.

The fossil record for female Neandertal pelvic remains is extremely limited and consists solely of incomplete *ossa coxae*. This makes it impossible to take standard or commonly used measurements of the birth canal on one, let alone more than one individual. The statistical analysis used for this study is designed to compare a small sample to a large sample, however its strength requires a sample size of at least two individuals. Therefore, new measurements were developed based on landmarks (standard and newly developed) that are frequently preserved in the female Neandertal pelvic sample. All measurements were selected because they could be

taken on at least two Neandertal females. In total, 22 landmarks were identified to form 30 measurements. The landmarks are illustrated in Figure 4.1 and described in Table 4.2; the measurements are illustrated in Figure 4.1 as well, and their relevance described in Table 4.3. As many measurements as possible were taken on each Neandertal fossil. All measurements were taken with sliding calipers: plastic-tipped for fossils to prevent damaging the fragile specimens and metal-tipped digital for the human sample.

The measurements were selected based on two criteria: 1) it was possible to take the measurement on at least two female Neandertal individuals; and 2) the measurement was relevant to the birth process. For a measurement to be considered relevant, it needed to reflect the size or shape of the true pelvis (i.e., the birth canal) by describing a size dimension or giving the orientation of two features on the true pelvis. I also included measurements that reflected the robusticity and overall size of the pelvis. While having a narrow maximum pubis breadth is not immediately informative for obstetrics, it would indicate that this portion of the pelvis is gracile compared to individuals with thicker iliopubic rami. This gracility may relate to the previously proposed Neandertal birth hypotheses described in Chapter 3. The relevance of each measurement is described below, and the outcomes discussed in Chapter 7. The intra-observer error for these measurements ranged between 0-10 percent, with a mean error of 4 percent.

Figure 4.1: Illustrations of landmarks and measurements. Figures traced and modified from White et al. (2012). Lateral view: A and B; medial view: C and D; superior view: E and F.
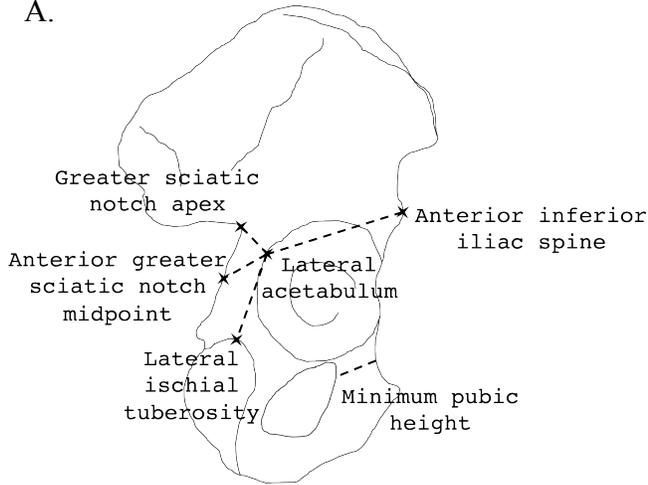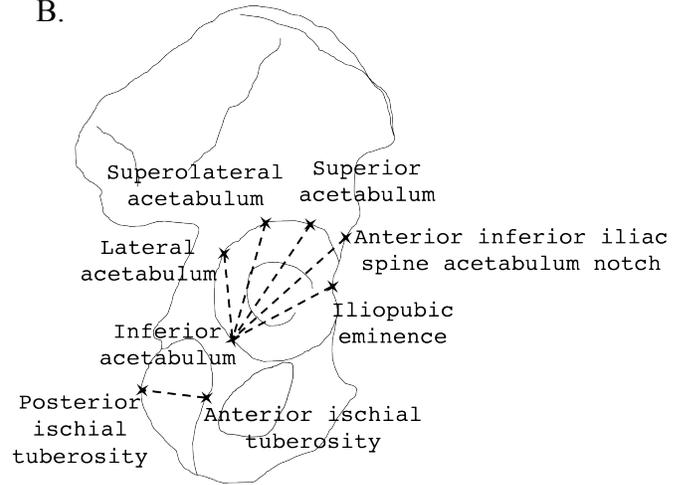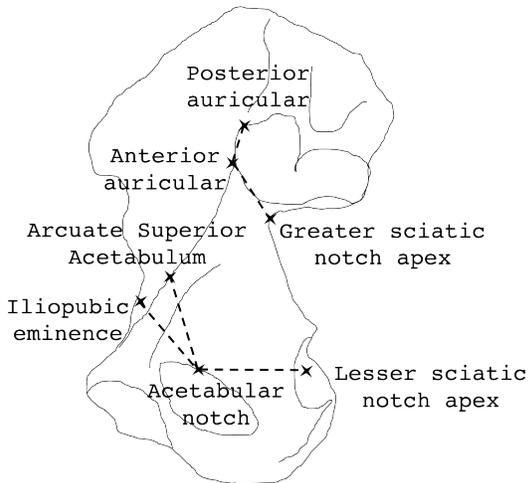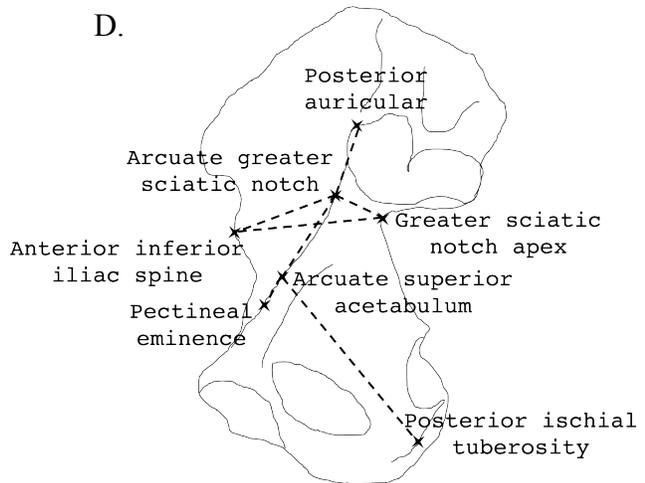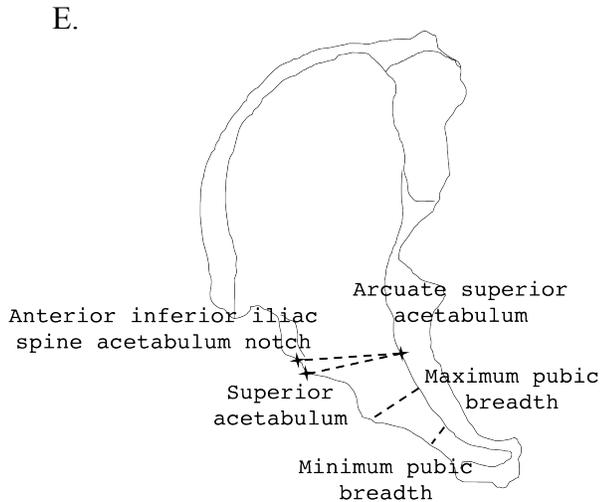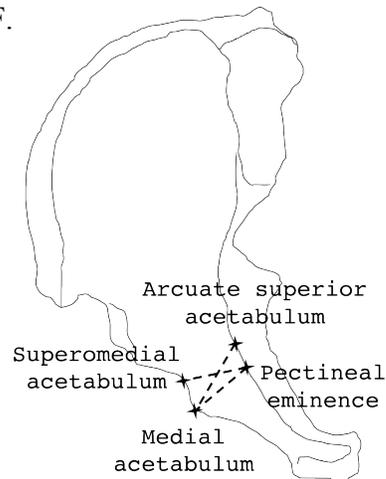
Table 4.2: List of landmarks used to define measurements (see Table 4.3). Unless otherwise noted, the pelvis was oriented so that the plane of the inlet was parallel to the table. In incomplete fossils, the arcuate and/or pectineal lines were used to define the plane. Landmarks are listed in alphabetical order by name.

Landmark	Description
Acetabular notch	Midpoint of the acetabular notch along the acetabular margin: the acetabular notch is the portion of the acetabular margin between the legs of the lunate surface; this point is the midpoint between those extremities. This point also falls on the lateral margin of the obturator foramen.
Anterior auricular	Point where the arcuate line and the anterior margin of the auricular surface intersect: because the auricular surface is curved and variably shaped, its anterior point is difficult to identify on incomplete specimens. This point, defined by an intersection of the arcuate line (which sometimes appears to split as it approaches the auricular surface; in those cases the superior most line was used) and the most anterior portion of the auricular surface that it meets.
Anterior greater sciatic notch midpoint	Midpoint on the anterior leg of the greater sciatic notch (or best approximation when ischial spine is absent). The anterior leg of the greater sciatic notch is the margin formed from the apex of the notch to the ischial spine. This point is the approximate midpoint, which may not be the closest point on the anterior leg to the lateral acetabulum margin.
Anterior inferior iliac spine	Anterior inferior iliac spine: this is a standard landmark. However, this feature is often rounded such that a specific point is difficult to identify. In those cases, the point that was most anterior (this time in true anatomical position) and inferior was used.
Anterior inferior iliac spine acetabulum notch	Midpoint between the anterior inferior iliac spine and the nearest point on the acetabular margin. In some individuals, this point falls at the apex of a notch, while in others the border between these two features is straight and the midpoint must be estimated.
Anterior ischial tuberosity	Midpoint on the anterior margin of the ischial tuberosity: in anterior view, the mediolateral midpoint of the ischial tuberosity. This point will be very near, but not necessarily directly underneath, the inferior margin of the obturator foramen.

Arcuate greater sciatic notch	Point on the arcuate line closest to the greater sciatic notch: this point was found by identifying the shortest distance from the apex of the greater sciatic notch to the arcuate line.
Arcuate superior acetabulum	Point on the arcuate line closest to the superior acetabular margin: this point was found by first identifying the superior acetabular margin, and then finding the closest point on the arcuate line. This point is always lateral to the landmark pectineal eminence. In cases where the arcuate line is oriented such that the nearest point could be in multiple places, the more anteromedial point was used.
Greater sciatic notch apex	Point on the greater sciatic notch closest to the arcuate line (apex of the greater sciatic notch). This is the highest point on the curve, identified as such because it is the part of the greater sciatic notch that is closest to the arcuate line.
Iliopubic eminence	The bump left when the ilium and the pubis fuse. When this eminence is rounded or difficult to identify, it is the most superior portion of the iliopubic ramus directly above the acetabulum.
Inferior acetabulum	Inferior acetabular margin: the most inferior point on the acetabular margin. This point falls on the inferior leg of the lunate surface, but is not the apex of the leg. This point forms a diameter with landmark superior acetabulum.
Lateral acetabulum	Lateral acetabular margin: the most lateral point on the acetabular margin. This point forms a diameter with the medial acetabulum.
Lateral ischial tuberosity	Lateral (and often superior) point on the ischial tuberosity that is closest to the acetabulum. Note that this is not the point closest to the acetabulum because that point is typically more anterior than lateral. Because there is great variation in ischial tuberosity shape, this point is sometimes not the most superior point of the margin, which will sometimes also appear on the anterior side.
Lesser sciatic notch apex	Apex of the lesser sciatic notch: midway between the ischial spine (or its close approximation) and the ischial tuberosity, this is the part of the notch closest to the acetabulum. In some individuals, the curve will be obscured by ischial tuberosity-like roughness, in which case it must be estimated as a midpoint of a line and not a curve.

Medial acetabulum	Medial acetabular margin: the point along the acetabular margin that is closest to the pubic symphysis.
Pectineal eminence	Point on the pectineal line closest to the center of the iliopubic eminence. When the pectineal line had a spine at this point from excess muscle attachment, this landmark was defined as the point on the spine closest to the iliopubic eminence landmark.
Posterior auricular	Point where the *spina limitans* and the superior margin of the auricular surface intersect: this landmark is where the line forming the superior margin of the auricular surface separates from that surface to extend toward the iliac crest; this line is known as the *spina limitans*. Where that line and the auricular surface margin separate is the location of this point.
Posterior ischial tuberosity	Point on posterior margin of ischial tuberosity: this point is defined as the maximum distance from the midpoint on the anterior margin that is still on the posterior margin of the ischial tuberosity.
Superior acetabulum	Superior acetabular margin: the point on the acetabular margin that is closest to the anterior inferior iliac spine. It should form a diameter with the inferior acetabular margin.
Superolateral acetabulum	Acetabular margin midpoint between the superior and lateral acetabular margins. This landmark forms a diameter with the acetabular notch.
Superomedial acetabulum	Acetabular margin midpoint between the superior and medial acetabular margins. This landmark would form a diameter with the midpoint of the lateral and inferior acetabular margins. This point is likely the point on the acetabular margin that is closest to the iliopubic eminence landmark.

Table 4.3: List of measurements and their relevance. Listed in alphabetical order by name. Names are taken from the landmarks listed in Table 4.2. The relevance column describes the potential importance of this measurement to either obstetrics or overall robusticity (which reflects muscle attachments, bone density, and overall body size). The last column refers to the figure illustrating the measurement.

Measurement	Relevance	Figure
Acetabular notch to arcuate superior acetabulum	Dimension of the acetabulum. Reflects height of the true pelvis and birth canal.	4.1 C.
Acetabular notch to iliopubic eminence	Dimension of the acetabulum. Reflects robusticity and height of true pelvis, relating to the birth canal.	4.1 C.
Acetabular notch to lesser sciatic notch apex	Orientation of the ischium. Reflects orientation and potential size of midplane and outlet.	4.1 C.
Anterior auricular to greater sciatic notch apex	Orientation of the auricular surface to the greater sciatic notch. Reflects orientation of sacrum.	4.1 C.
Anterior auricular to posterior auricular	Breadth of auricular surface. Reflects robusticity at this joint.	4.1 C.
Anterior inferior iliac spine acetabulum notch to arcuate superior acetabulum	Breadth of the ilium. Reflects robusticity.	4.1 E.
Anterior inferior iliac spine acetabulum notch to inferior acetabulum	Orientation of acetabulum to anterior inferior iliac spine. Reflects relative placement of the birth canal.	4.1 B.
Anterior inferior iliac spine to arcuate greater sciatic notch	Orientation of ilium. Reflects whether the ilium is anteriorly or posteriorly oriented relative to the greater sciatic notch.	4.1 D.
Anterior inferior iliac spine to greater sciatic notch apex	Orientation of ilium. Reflects whether the ilium is anteriorly or posteriorly oriented relative to the greater sciatic notch.	4.1 D.
Anterior ischial tuberosity to posterior ischial tuberosity	Breadth of the ischial tuberosity. Reflects robusticity.	4.1 B.
Arcuate greater sciatic notch to greater sciatic notch apex	Height of the true pelvis at the greater sciatic notch. Reflects height of the birth canal.	4.1 D.

Arcuate greater sciatic notch to posterior auricular	Dimension of the posterior space. Reflects posterior pelvic inlet size.	4.1 D.
Arcuate superior acetabulum to arcuate greater sciatic notch	Dimension of the pelvic inlet. Reflects birth canal size at this plane.	4.1 D.
Inferior acetabulum to iliopubic eminence	Dimension of the acetabulum. Reflects the height of the birth canal and robusticity at this joint.	4.1 B.
Lateral acetabulum to anterior greater sciatic notch midpoint	Dimension of the acetabulum. Reflects acetabular depth, which signifies orientation and robusticity.	4.1 A.
Lateral acetabulum to anterior inferior iliac spine	Orientation of acetabulum to anterior inferior iliac spine. Reflects relative placement of the birth canal.	4.1 A.
Lateral acetabulum to greater sciatic notch apex	Orientation of acetabulum to greater sciatic notch. Reflects relative placement of the birth canal.	4.1 A.
Lateral acetabulum to inferior acetabulum	Dimension of the acetabulum. Reflects robusticity.	4.1 B.
Lateral acetabulum to lateral ischial tuberosity	Height of the true pelvis. Reflects height of birth canal.	4.1 A.
Maximum pubic breadth	Breadth of the pubis. Reflects robusticity.	4.1 E.
Medial acetabulum to arcuate superior acetabulum	Breadth of the pubis. Reflects robusticity.	4.1 F.
Medial acetabulum to pectineal eminence	Breadth of the pubis. Reflects robusticity.	4.1 F.
Minimum pubic breadth	Breadth of the pubis. Reflects robusticity.	4.1 E.
Minimum pubic height	Height of the pubis. Reflects robusticity.	4.1 A.
Pectineal eminence to arcuate superior acetabulum	Dimension of the pelvic inlet. Reflects birth canal size at this plane.	4.1 D.
Posterior ischial tuberosity to arcuate superior acetabulum	Height of the true pelvis. Reflects height of the birth canal.	4.1 D.
Superior acetabulum to	Breadth of iliopubic region. Reflects	4.1 E.

arcuate superior acetabulum	robusticity.	
Superior acetabulum to inferior acetabulum	Acetabulum height. Reflects robusticity and is potentially related to body size.	4.1 B.
Superolateral acetabulum to inferior acetabulum	Dimension of the acetabulum. Reflects robusticity at this joint.	4.1 B.
Superomedial acetabulum to pectineal eminence	Breadth of the pubis. Reflects robusticity.	4.1 F.

Statistical analyses

In this section I describe the statistical analyses used to compare the Neandertal and recent human female samples, with the goal of trying to reject the hull hypothesis. To begin, I describe the bootstrap resampling approach and how it can be used to test hypotheses involving small fossil samples. Next, I demonstrate that the human comparative sample used in this analysis meets the criteria required by the bootstrap resampling approach. Finally, I describe the specific analyses used in this study that compare Neandertal and human samples. The samples, both recent human and Neandertal, are described in Chapter 5. All coding scripts can be found in Appendix 1. All raw data can be found in Appendix 2. Results are found in Chapter 6.

Bootstrap resampling is a statistical approach that can be used to compare small sample sizes, such as those found in the fossil record, to larger comparative samples (Lee 2001). Unlike assumption-dependent traditional statistical tests, the only assumption in bootstrap resampling is that the larger sample to be resampled is representative of the true population. As long as this assumption is met, the data from this sample can be used to generate a distribution of subsamples identical in size to the smaller sample. This makes it possible to statistically test the probability of finding the smaller sample's values in the larger comparative sample. In paleoanthropology, this technique can be applied by using fossil observations for the small sample and observations from a relevant extant species for the large sample.

As described by Manly (2006), bootstrap resampling predicts whether an observed result can be explained by sampling bias. When comparing two differently sized samples directly, it is unknown if the results are due to the samples being different or the sample sizes being different, since small samples do not always accurately reflect the mean of the population from which they were drawn. Bootstrap resampling overcomes this by generating a distribution based on samples equal in number to the fossil sample in question. This allows the assessment of likelihood of

equivalence for the fossil sample, based on its distance from the mean of the resampled distribution in units of standard deviation (Cofran 2012; Lee 2001; Manly 2006).

While any test statistic can be used to characterize the central tendency of the initial small sample and each of the generated subsamples, for this project I will be using the arithmetic mean. As described in Chapter 3, my null hypothesis is that there are no demonstrable differences in the size of each of the pelvic measurements examined between Neandertal and Ipiutak human females. Therefore, comparing the average magnitude and not the variance or range of each small sample or subsample is most relevant for this hypothesis.

Table 4.4 presents the algorithm used to test the general null hypothesis that there are no differences between two differently sized samples using a bootstrap resampling approach. This algorithm clarifies the R code found in Appendix 1. All statistical analyses were done using the computing package R and the integrative development environment (IDE) RStudio (R Core Team 2013; RStudio 2014).

Table 4.4. Algorithm for bootstrap resampling analysis.

1. If *n* is the sample size for the fossil metric, randomly select a subsample size *n* from the larger comparative sample and record its mean in distribution *D*.
2. Repeat Step 1 10,000 times.
3. Calculate the sampling statistic, *z*, by taking the difference of the mean of the Neandertal sample and the mean of the recent human distribution *D*, and dividing by the standard deviation of the recent human distribution *D*:
$$z = \frac{\bar{x}_N - \bar{x}_D}{SD_D}$$
4. Convert *z* into a percentage based on a normal distribution by referring to a *z*-table. This demonstrates what percentage of the recent human distribution *D* is less than the Neandertal mean.
5. Compare the resulting *z* percentage to the two-sided 95 percent confidence interval surrounding the human distribution mean. If the percentage is less than 2.5 percent or greater than 97.5 percent, the null hypothesis is rejected. A rejected null hypothesis signifies that 95 percent of the recent human distribution subsamples have means different than the Neandertal mean.

Before comparing Neandertals and recent humans, I first must demonstrate that the recent human sample used adequately meets the criterion implicit in bootstrap resampling; i.e., I must show that the sample is large enough to accurately represent the amount of variability found in the true population. There is no set sample size that is universally considered large enough to be

representative of the true pelvis. Instead, the appropriate sample size is determined by the amount of variability for a measure within a particular population; when the standard deviation for a sample approaches the true standard deviation of the population, variation is considered low.

For this study, the female *ossa coxae* from the Ipiutak collection at the American Museum of Natural History in New York, NY were used as the larger comparative sample. The justification for using this sample, as well as details about the historical context of the sample, are provided in Chapter 5. Here, the concern is whether the sample is sufficiently large to represent pelvic variation in the original population. In this collection, 23 pelvic remains could be confidently identified as female. If the variation for the measurements considered is low in these 23 individuals, then this sample size is adequate for bootstrap resampling.

To statistically demonstrate that variation is low within this sample for the measurements considered, I compared the standard deviation of generated recent human distributions. Using the bootstrap resampling algorithm described above, I generated a recent human distribution of subsamples consisting of two randomly selected individuals and calculated its standard deviation. This distribution was pulled from the original Ipiutak sample; I then removed one individual from that sample at random and repeated the procedure. I repeated this for every sized Ipiutak sample possible. I plotted the sample size on which each distribution was based versus the corresponding calculated standard distribution (see Appendix 3). When sample size was very small, standard distribution differed greatly between samples. However, as the samples approached the maximum size available, the standard deviation approached a single variable. This indicates that adding more individuals to the sample for any of the measurements would not dramatically change the standard deviation. In other words, for each measurement, the sample size available from the Ipiutak collection is sufficient to have representative variability, and therefore meets the criterion for conducting a bootstrap resampling analysis.

To test the null hypothesis that there is no significant difference between the Neandertal female and Ipiutak human female samples for these measurements, I applied the algorithm defined in Table 4.4 to the data described in the Pelvimetrics section of this chapter. The measurements taken on the female Neandertal *ossa coxae* were compared to the measurements taken on the female Ipiutak human *ossa coxae*. If the measurements were different in one direction (e.g., if the Neandertal values were always significantly larger than the recent human

values), I would repeat the analysis comparing ratios of the raw measurements with acetabulum height, which can be used as a proxy for body size (Ruff 1994). I discuss the effects of body size more thoroughly in Chapter 7. Each sample is described more fully in Chapter 5, and the results of the comparison for each measurement are given in Chapter 6.

Conclusion

This chapter describes the procedure used in this study. First, I described how methods of assessing sex from the bony pelvis can and cannot be applied to Neandertals. I discovered two features that were demonstrably sexually dimorphic in Neandertals, and explained how they were used to estimate sex. This defined the sample of Neandertal females to be used when testing the null hypothesis of no difference.

Next, I justified the development of new measurements to be taken on the pelvis. The fragmentary nature of the Neandertal record makes it difficult to take standard measurements on even one individual, let alone on all of them. For a measurement to be useful in my analysis, it needed to be present on at least two Neandertal females. Since the female Neandertal sample was so small, and was made up of bones that were mostly incomplete, many standard pelvic measurements did not meet this criterion. I therefore developed new measurements that reflected the preservation of the female Neandertal sample.

Finally, I described how these measurements would be used to compare Neandertal and recent human female *ossa coxae*, to test the hypothesis that there are no significant differences between these two groups. The small size of the female Neandertal sample makes it impossible to use traditional statistical techniques, such as the t-test, to compare these samples. I therefore employ a bootstrap resampling approach that accounts for the small Neandertal sample size by comparing it to distributions of similarly sized subsamples of recent humans. I justify the size of the recent human sample used for comparison is sufficiently large by demonstrating that the addition of more individuals does not significantly alter the standard deviation of the resampled distribution.

Chapter 5: Materials

Introduction

      The methodology described in Chapter 4 was used to assemble the largest sample of Neandertal female pelvic remains available from the fossil record. The sex determination techniques used on the larger Neandertal sample resulted in a total of eight female Neandertals being identified based on their pelvic morphology. In this chapter, I fully describe these female pelvic fossils based on my personal study of them.

      I start by describing Kebara 2. Though this pelvis is male, it is the most complete Neandertal pelvis in the fossil record, providing an adequate model for interpreting pelvic morphology on more fragmentary remains. I use it to establish general Neandertal pelvic morphology, and as a male counterpoint when considering the form of sexually dimorphic features in the female sample.

      Next, I describe the eight Neandertal female pelvic remains selected based on their acetabulum diameter and greater sciatic notch width. Although I studied all eight personally, and all are described here, it should be noted that at the time of study, the Palomas 96 pelvic remains were encrusted in breccia, making it impossible to take measurements on them. Therefore, it is not included in the statistical analysis done here.

      Finally, I describe the context and makeup of the cold adapted recent human comparative sample used in this study. Because climate adaptations have such a strong potential to impact pelvis form, and because Neandertals lived in northern latitudes during an ice age, I found it appropriate to compare them to a cold-adapted recent human sample that might have the same selective forces acting on them. I chose the Ipiutak who are from a higher latitude than the Kodiak Island Koniag individuals that previous researchers have used, but which are no longer available for study.

Neandertal pelvis shape based on Kebara 2

Kebara 2 (also known as Kebara Mousterian Hominid 2) is a skeleton found in the Mousterian section of the Mugharet el-Kebara cave at Mt. Carmel in Israel, as described in Chapter 3. The pelvis is the most complete in the Neandertal fossil record. It includes a mostly complete right *os coxae* and sacrum, as well as portions of the left *os coxae* (personal observation). Bar-Yosef et al. (1992) noted that diagenetic processes affected the entire left side of the skeleton, including the left *os coxae*. Based on my personal observations, the right *os coxae* is complete except for a few cracks, a crushed posterior superior iliac spine, and a missing superior portion of the pubic symphysis. The left *os coxae* is crushed, leading to an oval-shaped acetabulum and a flattened morphology overall. It is completely missing the pubis, the anterior iliac spines, the obturator foramen, and most of the ischial tuberosity. The sacrum is mostly complete except for some cracks and breaks on the posterior side. It is sufficiently complete to articulate well with both *ossa coxae*. Here I describe the morphology of the sacrum, ilium, ischium, and pubis before considering how this pelvis compares to male recent humans.

The morphology of the Kebara 2 pelvis suggests that relative to the recent human male form, Kebara 2 had a false pelvis (characterized by the iliac blades) that was rotated posteriorly and a true pelvis (characterized by the pelvic brim and all pelvic portions inferior to it) that is pushed anteriorly (also described in Rak and Arensburg 1987). This results in the following specific morphological differences between recent human males and the Kebara 2 pelvis.

In Kebara 2 (see Figure 5.1), the more anterior position of the sacrum causes a very narrow greater sciatic notch due to its closeness to the ischial body, as well as creating a larger post-auricular space. In the lateral view of the iliac blade, the highest point on the iliac crest is near the center instead of being anteriorly placed as it is in recent humans (making recent humans look "beretlike", with the highest portion of the iliac crest being offset anteriorly compared to its placement in Kebara 2) (Rak 1991; Rak and Arensburg 1987). This morphology balances the muscles connecting the torso to the false pelvis while still permitting the true pelvis to be located more anteriorly than it is in humans. The iliac blade posterior to the iliac pillar is rotated so that it orients closer to the coronal plane than in recent humans (Rak 1991), which probably further reflects the anterior position of the sacrum. The iliopubic ramus is long in Kebara 2 (Rak 1991), reflecting the anteriorly positioned true pelvis and marking a main difference between Kebara 2 and human males today. The long pubis observed in Kebara 2

affects other aspects of the pelvis: it creates a wider sub-pubic angle, extends the pelvic brim anteriorly, and rotates the acetabula laterally compared with male recent humans (Rak 1990, 1991; Rak and Arensburg 1987). When viewed superiorly, the iliopubic ramus of Kebara 2 angles anteriorly from the bi-acetabular line more so than what is seen in recent humans. A short summary of data from the literature that includes measurements of Kebara 2 is found in Table 5.2.

Figure 5.1: Kebara 2. A. Right os coxae, approximate pelvic view. B. Right os coxae, approximate superior view. C. Sacrum, anterior view.
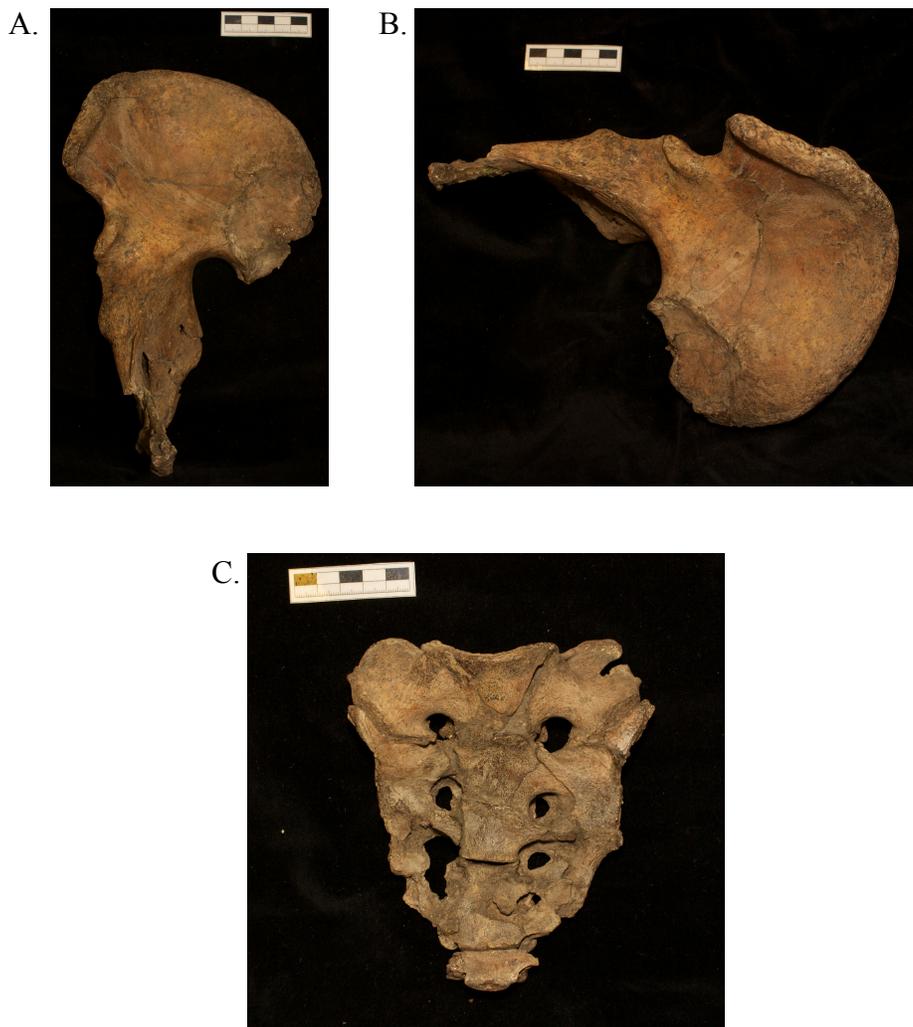
Table 5.2. Data from Kebara 2. When it was given, an average for recent humans was also included. When noted, the measurement was taken on the reconstructed pelvis where the right os coxae *was mirrored.*

	Kebara 2	Recent human mean
Minimum iliac breadth	57.5 mm[1]	
Iliac flare	33.9° [1]	31° [2]
Iliac height	137 mm [1]	
Obturator foramen region height	92 mm [3]	98.5 mm (SD = 4.5) [3]
Iliopubic ramus length	89 mm [1]	
Iliopubic ramus minimum height	8 mm [1]	
Maximum width of pelvis (reconstructed)	313 mm [1]	
Interacetabular distance (reconstructed)	129 mm [1]	
Transverse diameter of pelvic brim (reconstructed)	141 mm [1]	
Anteroposterior diameter of pelvic brim (reconstructed)	117 mm [1]	

[1]Data from Rak and Arensburg 1987.
[2]Data from Lovejoy 1975.
[3]Data from Rak 1990.

Kebara 2 has a few key signs of robusticity. First, it has a strong iliac pillar and cristal tubercle. Second, there are discernible gluteal lines. Finally, the ischial tuberosity extends to the ischial spine, obscuring the internal obturator groove (or lesser sciatic notch). This feature is seen in other Neandertal ischia (Neanderthal 1 and Tabūn C1 are identified by Rak 1990). Rak (1990) did not see this feature in 71 recent humans examined. However, I was able to find this in particularly robust recent human males and females.

The pelvis has been identified as a male, largely due to the narrow greater sciatic notch and robusticity (Rak and Arensburg 1987). Here, I recognize it as male based on the narrow greater sciatic notch and the large acetabulum diameter (see Table 4.1). The overall morphology of the pelvis is best observed when the right side has been mirrored, as done by Rak and Arensburg (1987). As described above, the iliac blades are rotated so that they are more flared, less parallel, and more posteriorly positioned than in recent humans. Transversely, the true pelvis is simultaneously pushed forward, as indicated by the location of the auricular surfaces, the

orientation of the acetabula, the length of the iliopubic rami, and the width of the sub-pubic angle.

Female Neandertal *ossa coxae*

Here, I describe the preservation and morphology of the eight female Neandertal pelvic fossils identified based on their small acetabulum diameter and/or wide greater sciatic notch relative to the Kebara 2 specimen. Although Palomas 96 was studied and is described here, this fossil was not included in the statistical analyses of this project, as at the time of study not enough breccia had been removed to permit accurate measurement. The Shanidar pelvic remains were unavailable for study and are therefore not described; see Trinkaus (1983) for information on these Neandertal pelvic remains.

Tabūn C1

The Tabūn C1 skeleton was found at the top of Layer C of the Mugharet et-Tabūn cave at Mt. Carmel in Israel, as described in Chapter 3. The pelvis is the most complete female in the Neandertal fossil record. It includes portions of two *ossa coxae* that are both attached to portions of the associated femora (see Figure 5.2). The left ilium (NHMUK PA EM 3717/78) preserves both anterior iliac spines, most of the anterior portion of the iliac crest, the cristal tubercle, the iliac pillar, a very crushed portion of the superior acetabulum, the anterior portion of the greater sciatic notch, and the arcuate line above it. Posteriorly, the ilium is mostly crushed, obscuring any sign of the auricular surface, and is missing the posterior-most portion of the iliac crest. The left pubis (NHMUK PA EM 3718/79) preserves portions of the iliopubic ramus that while broken clearly articulate and include the ramus from the acetabulum to the symphyseal face, though parts are missing superiorly and anteriorly. The acetabulum is not complete and suffers from having the femoral head crushed into it, as demonstrated by the non-anatomical orientation of the femoral shaft. No portion of the left ischium preserves.

Figure 5.2: Tabūn C1. A. Left os coxae, *lateral ilium (NHMUK PA EM 3717/78). B. Left* os coxae, *anterior pubis (NHMUK PA EM 3718/79). C. Right* os coxae, *lateral view (NHMUK PA EM 3739/100).*

A.

B.

C.
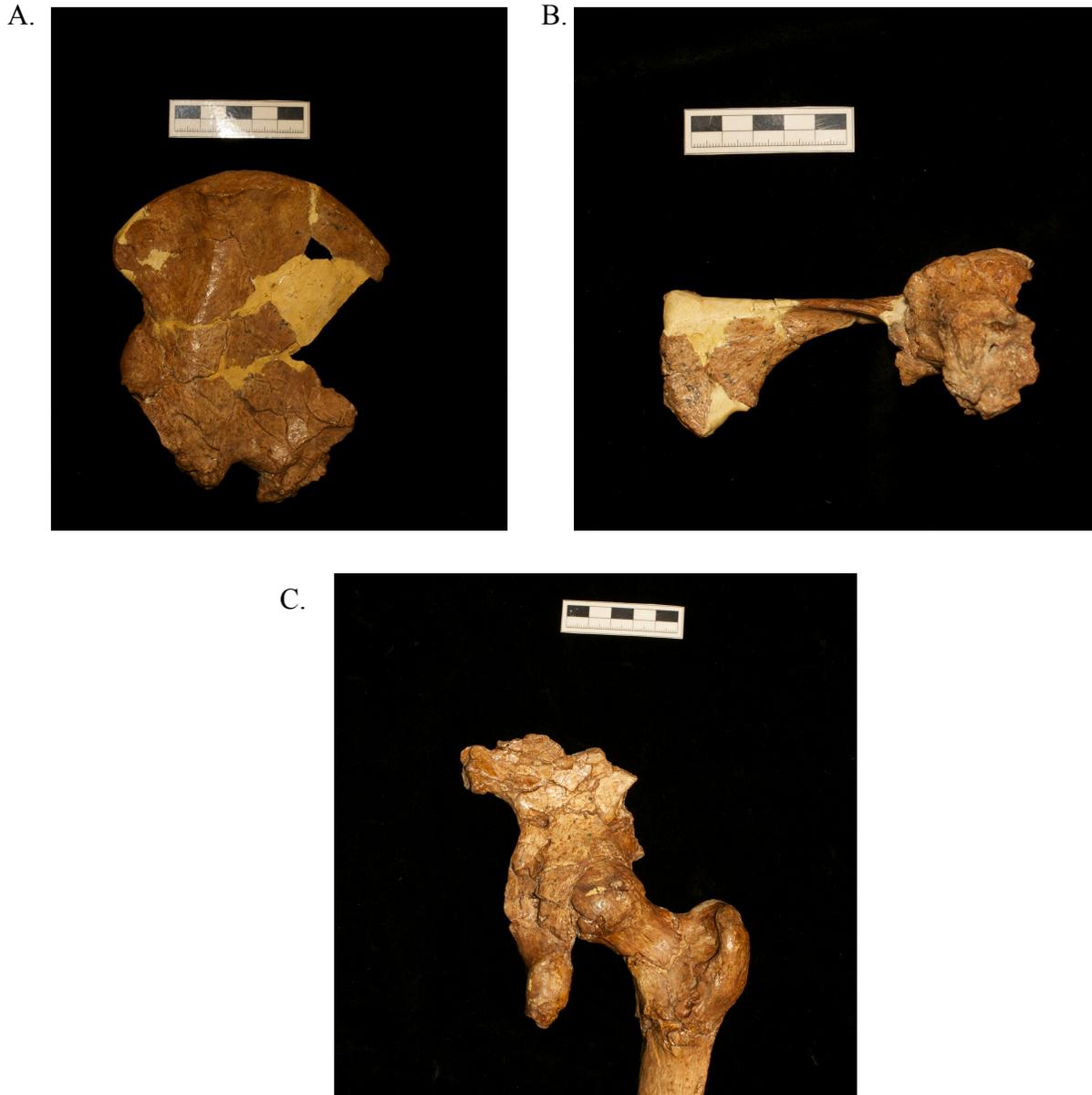
The right pubis (NHMUK PA EM 3719/80) preserves the symphyseal face except for the most superior portion. Inferiorly, a small portion of the ischiopubic ramus ridge is preserved. The surrounding portion of the pubic body is separated by plaster from the iliopubic ramus. The iliopubic ramus preserves in pieces that roughly articulate and preserve the arcuate line, but is missing some of the anterior surface. The iliopubic ramus is broken just as it is starting to widen

anteroposteriorly, signifying the start of the medial acetabulum. The acetabulum itself is not preserved on this piece. The final Tabūn C1 fossil consists of portions of the right ischium, acetabulum, ilium, and femur (NHMUK PA EM 3739/100). Unlike the left side, this fossil is attached to the entire proximal femur. The portion of the *os coxae* that is preserved includes the greater sciatic notch, the acetabulum, and portions of the ischial body and tuberosity. While the greater sciatic notch is clearly preserved, the bone posterior and superior to it is crushed and quickly breaks off so that none of the auricular surface preserves, and most of the iliac blade is missing as well. Due to its attachment to the femur, the acetabulum is highly crushed, making it impossible to measure its diameter. The femoral head diameter can be measured, and Rosenberg (1986) found it to be 42.3 mm at its largest. See Table 4.1 for how I transformed this measurement into an acetabulum diameter of 50.0 mm.

The Tabūn C1 pelvis has a strong iliac pillar. The right greater sciatic notch, which is the less crushed of the two, is very wide. The femoral head diameter suggests a small acetabulum and therefore body size. Both iliopubic rami appear to be very long compared to the ischium height, and became very flat and thin in the middle. While this would be an indication of being female in recent humans, Kebara 2 has a longer iliopubic ramus, suggesting that this is not a good trait on which to base sex assessment of Neandertals. The right pubis suggests that the ischiopubic ramus ridge would have been narrow and sharp were it complete. I assessed this individual as female based on the greater sciatic notch width and the acetabulum diameter calculated from the femoral head diameter. These features are in contrast with the morphologies observed on Kebara 2. This somewhat confirms their use for assessing sex in Neandertals, especially when combined with the seriation shown in Table 4.1.

La Ferrassie 2

La Ferrassie 2 preserves the following parts of the right *os coxae*: iliac blade, top of the greater sciatic notch, posterior portion of the arcuate line, inferior acetabulum, and lateral portion of the obturator foramen. The left *os coxae* preserves parts of the iliac blade, top of the greater sciatic notch, posterior portion of the arcuate line, some of the auricular surface, the inferior acetabulum, lateral obturator foramen, and lesser sciatic notch.

The greater sciatic notch is wide (see Figure 5.3), suggesting that this is a female individual. Heim (1976) determined this skeleton was female based on its body size relative to the much larger La Ferrassie 1 skeleton.

Figure 5.3: La Ferrassie 2. A. Left os coxae, *medial view. B. Right* os coxae, *medial view. Both display the top of the greater sciatic notch and portions of the iliac blades.*

A.

B.
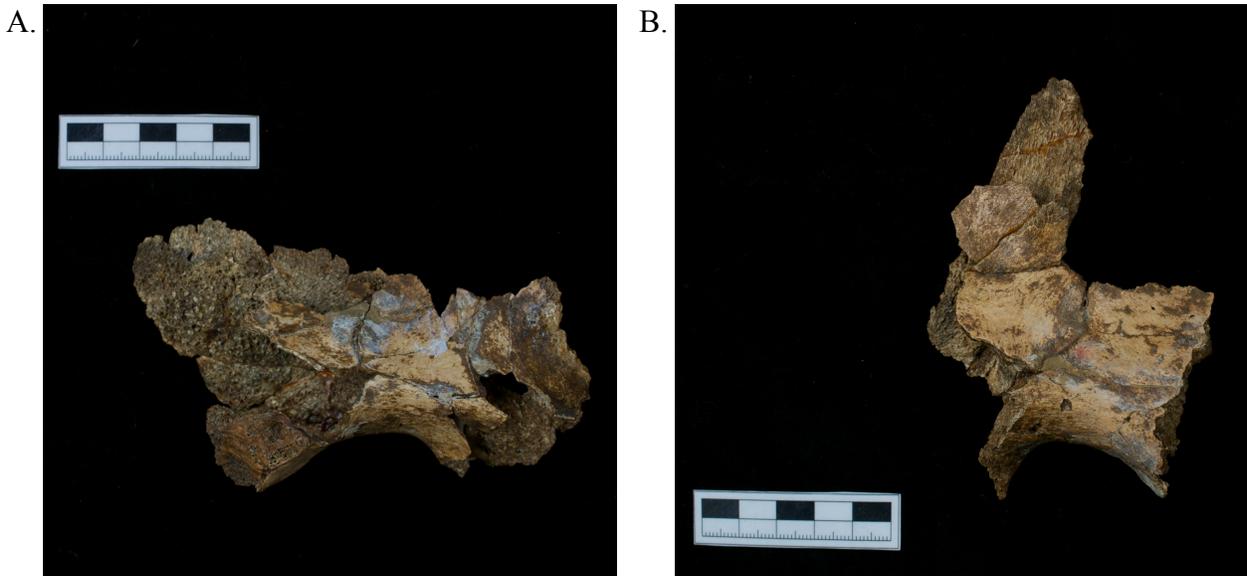
Krapina 209/212

Krapina 209 and 212 are part of the same partial right *os coxae* that have been glued together, with the former including the anterior portion of the *os coxae* and the latter including the posterior ilium (see Figure 5.4). This individual is female based on the width of the greater sciatic notch, length of the iliopubic ramus, and size of the acetabulum.

Figure 5.4: Krapina 209/212 (Cx 3/9). A. Anterior view. B. Pelvic view.

A.

B.
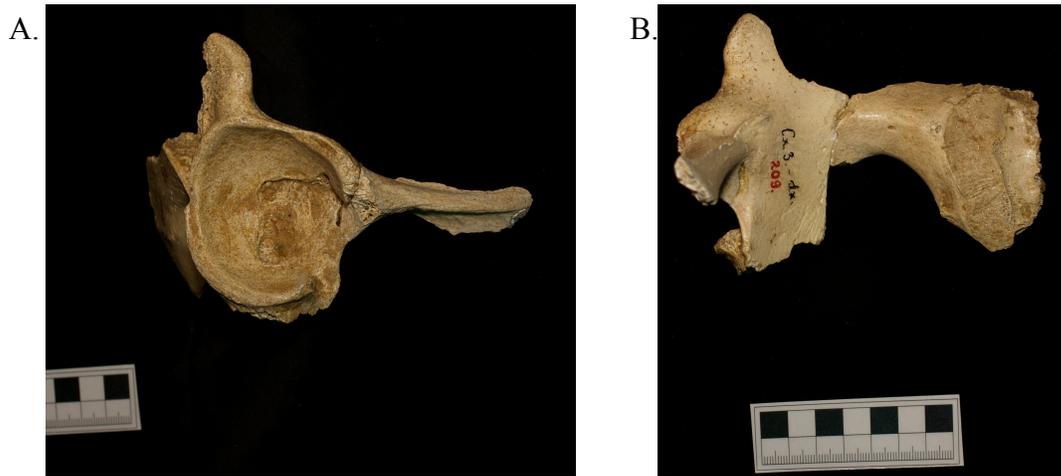
Krapina 209 preserves the acetabulum, the surrounding anterior ilium, a small portion of the ischium, and most of the iliopubic ramus of the pubis. The acetabulum preserves the entire margin, lunar surface, and notch. The anterior inferior iliac spine, iliac eminence, and the portion of bone posterior to the lateral acetabulum are all preserved as well. The bone is broken posteriorly before reaching the greater sciatic notch, and immediately inferior to the acetabulum so that none of the ischial body preserves. The pelvic side of the ilium is complete for the parts described here. The pubis is made up of a piece that articulates directly and is glued into place (and is also numbered 209). The pubis extends medially past the highest point of the obturator foramen by about 40 mm. The bone is broken on the inferior surface at the most medial end, which is probably part of the pubic corpus.

Krapina 212 preserves the posterior ilium beginning with the superior portion of the greater sciatic notch. On the pelvic surface, Krapina 209 and 212 articulate closely; the gluteal side of the bone is more eroded, so the fit is not perfect. Krapina 212 consists of the arcuate line above the greater sciatic notch, a portion of the greater sciatic notch, and the auricular surface. The posterior and superior portion of the greater sciatic notch is preserved. The posterior inferior iliac spine is preserved, as is the complete auricular surface. While there is a slight break in the arcuate line where Krapina 209 meets 212, it is otherwise continuous from the pubis to the auricular surface. The superior posterior portion of the iliac blade is missing.

The lunate surface is wide laterally but narrow medially, which makes it uncertain what the joint surface area would have been. The acetabulum maximum diameter is 56.4 mm, making this individual larger than some recent human females and the immature male Krapina 207 (whose greatest acetabulum diameter is 54.0 mm), but smaller than Neandertal males Kebara 2 (60.5 mm) and Amud 1 (61.0 mm). The iliopubic ramus is long, even if the break point is assumed to be the start of the pubic body. However, since the ischium is not fully preserved, pubis length cannot be considered relative to ischial height. At the highest point of the obturator foramen, the sagittal cross section of the iliopubic ramus is a horizontal rectangle. Further on medially, it twists to a vertical diamond. Where it breaks, the bone is very thin anteroposteriorly. This makes it very similar to the long iliopubic ramus seen in Tabūn C1. The ridge along the pectineal line is well developed. The greater sciatic notch is very wide and U-shaped. On the lateral surface of Krapina 212, the posterior gluteal line is visible and fairly robust. The auricular surface is very tall and narrow. Posterior to the auricular surface, there is a groove; anterior to the

auricular surface there is a piriform tubercle. The piriform tubercle forms on muscularly robust individuals, which means it has been associated with males in recent humans (Brůžek 2002; Genovés 1959). However, since this feature also has been seen in some robust recent human females (personal observation), it alone does not change the sex assessment of Krapina 209/212.

Krapina 211

Krapina 211 is a right ilium fragment (see Figure 5.5). The posterior section of the ilium is present, preserving the top of the auricular surface, the top of the greater sciatic notch, and part of the blade connecting these sections. On the auricular surface, the upper outline is clear and the center is clearly made up of cortical bone. However, the sides and other edges are broken. The posterior ilium is broken so that no crest or spines are preserved.

Figure 5.5: Krapina 211 (Cx 5). Lateral view.
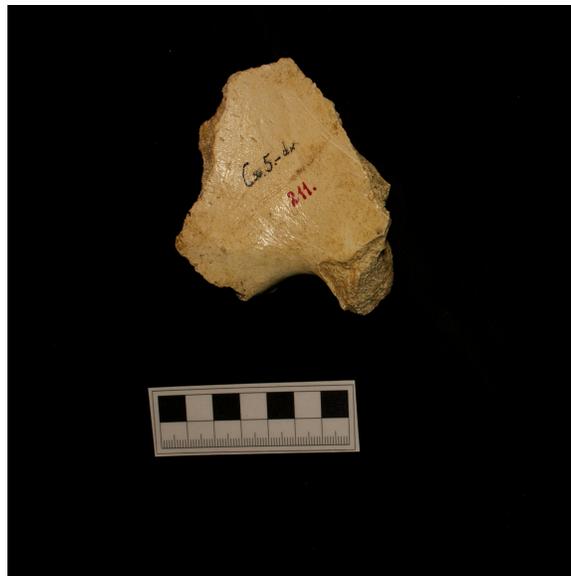
The retroauricular region is grooved and has rugged muscle markings superiorly. The preauricular region has a slight negative relief that is not sufficiently deep to be a pit. It also has some bumps, but no clear pisiform tubercle, possibly because that region is broken. The greater sciatic notch looks like it may have been wide, but since so much is missing it is impossible to confirm. This fragment was previously assessed as being female based on the greater sciatic notch and the pitting in the retroauricular area. In my opinion, the retroauricular area is not well preserved enough to be assessed. Furthermore, since few retroauricular regions preserve in

Neandertals, there is little evidence to support this feature being sexually dimorphic in this population. However, the greater sciatic notch is sufficiently wide to label this individual female.

Krapina 208

Krapina 208 is a partial right *os coxae* that is potentially female based on the length of the iliopubic ramus relative to the height of the ischium. Most of the acetabulum is preserved, along with the part of the ilium, ischium, and pubis as they extend out from the acetabulum (see Figure 5.6). The acetabulum is broken into two pieces. The largest piece consists of the superior part of the lunate surface and part of the notch; this piece includes the pubis and ilium extensions. A smaller piece articulates with the medial side of the acetabulum notch and also preserves the inferior part of the lunate surface. The lunate surface present on each piece does not articulate, and the gap is filled with plaster. The smaller piece includes the extension of the ischial body. Very little of the iliac blade preserves; no iliac spines are present, and the only feature present is the inferior end of the iliac pillar. The greater sciatic notch preserves the top of the curve, the anterior edge, and the area surrounding the ischial spine though the actual spine is broken. The pubis is better preserved. The iliopubic ramus is preserved medially past the highest point of the obturator foramen (distinguished because the superior-inferior height of the pubis starts to increase again medially before the bone breaks off). The pubic tubercle and symphyseal face are not preserved. The ischium preserves the lateral edge of the obturator foramen and most of the ischial tuberosity.

*Figure 5.6: Krapina 208 (Cx 2). Anterior view.*

The greater sciatic notch is not sufficiently preserved to assess its width. The preserved portion of the iliopubic ramus suggests it would have been long when the bone was complete. However, the iliopubic ramus morphology differs from Tabūn C1 in that it does not become overly flat anteroposteriorly. On the lateral pelvic side of the iliopubic ramus, along the pectineal line, there is a significant spine for abdominal muscles to attach. This feature is seen in other Neandertals and some recent humans, both male and female, suggesting it is not of obstetrical importance but likely demonstrates robust muscles. The ischial tuberosity does not cover the lesser sciatic notch in this individual, suggesting less robust musculature than is seen in some recent humans and many Neandertals. The sex of this individual can be estimated to be female from the medium-to-small acetabulum diameter. The acetabulum is 52.7 mm at its maximum diameter.

Krapina 255.5

Krapina 255.5 is a left ilium fragment. It preserves a small part of the arcuate line, the top of the greater sciatic notch, and part of the auricular surface (see Figure 5.7). The greater sciatic notch looks broad and potentially U-shaped. The pre-auricular area has no negative reliefs. Radovčić et al. (1988) lists this individual as being immature, but gives no explanation. This may be due to the small size of this fragment, or to the abraded surface of the auricular surface area, which may have more clearly resembled a growth surface in 1988. Based on what little is preserved, this is potentially female due to its greater sciatic notch morphology.

*Figure 5.7: Krapina 255.5. Pelvic view.*
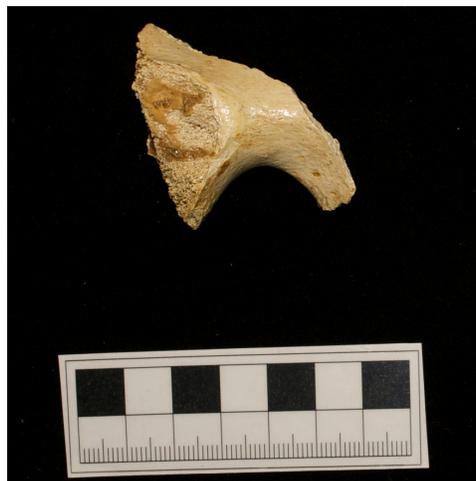
Krapina 255.8 is a left ilium fragment (see Figure 5.8). It preserves the superior part of the acetabulum, but not the margin. The anterior inferior iliac spine and most of the margin between it and the anterior superior iliac spine are present. The iliac blade preserves a triangular portion framed by the anterior iliac margin, the arcuate line, and a break line running from superior to the greater sciatic notch to the superior portion of the iliac margin. The iliac crest is not preserved. The arcuate line from the greater sciatic notch to posterior to the acetabulum is preserved, as is the inferior posterior wall of the acetabulum below the arcuate line. The greater sciatic notch is preserved, but the surface is broken on the lateral side. The auricular surface is not preserved, though it is possible that where the bone broke along the arcuate line posterior to the top of the greater sciatic notch is where the auricular surface would have started.

The joint surface of the acetabulum is completely flat with no sign of a lunate surface. The anterior margin and inferior spine of the iliac blade are both very thick and rounded; neither comes to a sharp margin. The lateral side of the iliac blade is spotted with foramina and overall has a very curved topography. The iliac pillar is broken superiorly, but is detectable inferiorly without being particularly strong. The greater sciatic notch is wider than the male Krapina 207 (Cx. 1), providing weak evidence that this is potentially female. Radovčić et al. (1988) list this individual as male without giving any reasons, despite also acknowledging the broad greater sciatic notch.

Figure 5.8: Krapina 255.8. A. Anterior view. B. Lateral view.
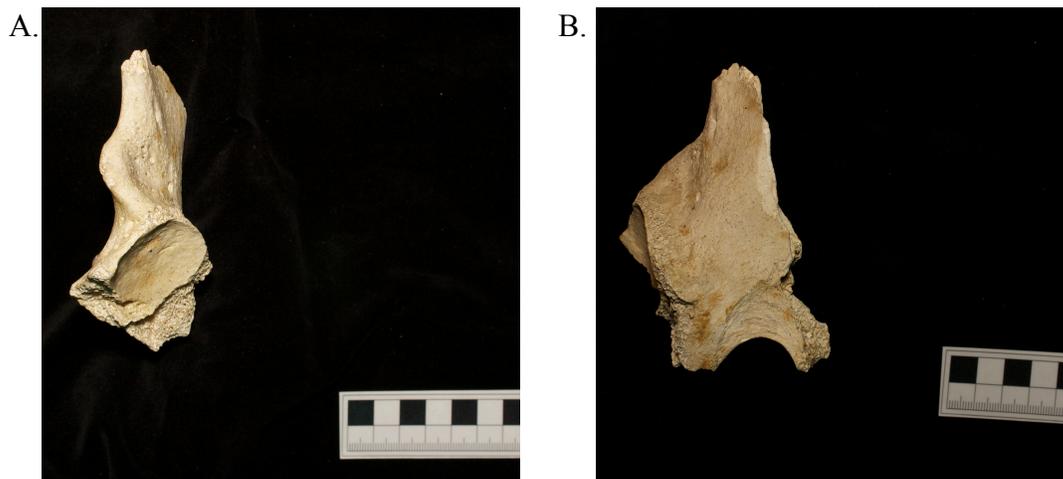
The Palomas 96 pelvis from Sima de las Palomas is mostly complete, preserving parts of the left and right *ossa coxae* and sacrum. This fossil is in the process of being cleaned and fully described by a team at Universidad de Murcia. Here, I describe merely the portions that were visible as of November 2012, when much of it was still covered in sedimentary matrix. Since the Murcia team's work was in progress, no photographs or measurements were taken for the present project. Though this is potentially a female Neandertal pelvis, it is not included in the analyses conducted here.

The left *os coxae* has parts of the lateral sides cleaned, while much of the medial and anterior portions are still encased in matrix. The ilium preserves the cristal tubercle and iliac pillar, though only the lateral side is cleaned of sediment. Also on the lateral side, the upper portion of the greater sciatic notch is preserved and cleaned. The ischium preserves the most complete ischial spine in the Neandertal fossil record. The anterior section of the ischium is imbedded in sediment. The ischiopubic ramus is present, but broken, with the medial surface covered in sediment. The ischium is broken before the acetabulum, and the femoral head is imbedded in sediment with only the lateral edge of the acetabulum visible. The pubis is broken into three pieces that can all be articulated. The medial piece is the pubic corpus, and is mostly in sediment next to the right pubic corpus. The second piece is the iliopubic ramus, which preserves a portion of the arcuate line. The third pubic piece preserves the lateral part of the iliopubic ramus.

The right *os coxae* preserves the anterior iliac spines and the margin between them. The lateral portion of the acetabulum is preserved, however the acetabulum is filled with a sediment-covered femoral head. The iliac blade that includes the iliac pillar and cristal tubercle is also present. A piece of ilium posterior to the portion with the pillar preserves the lateral/gluteal surface including the iliac crest. The superior and anterior edges of the greater sciatic notch are preserved. The ischial spine has some ischial tuberosity ruggedness, unlike the morphology seen on the left ischium. The ischial tuberosity preserves the lateral and inferior sides. The arcuate line is preserved from the area inferior to the iliac pillar to the area posterior to the medial acetabulum margin. The iliopubic ramus is broken in two pieces, but is otherwise preserved.

The sacrum is very complete, preserving five sacral vertebrae that are not fully fused. The right ala is broken and crushed, but the left ala is preserved. A possible piece of the left posterior greater sciatic notch edge may be attached via the auricular surface to the left part of the sacrum.

The relevant morphological features on this pelvis are those that reflect the age or the sex of the individual. The unfused cristal tubercle and sacral bodies suggest this is an immature individual. Walker et al. (2011) state that based on these features and the full eruption of the left M^3, this individual was ~20 years old at death. The pelvis can be considered gracile for its ischial tuberosity morphology, but is robust in its iliac pillar and cristal tubercle presentation, making muscle attachment robusticity unhelpful in assessing sex. The iliopubic ramus is long with a horizontal cross-section near the middle, somewhat resembling Tabūn C1. The greater sciatic notch appears to be wide on the left, but so little preserves this cannot be confirmed; it does not preserve enough on the right side to estimate width. The portion of iliac bone attached to the left side of the sacrum would appear to make the left greater sciatic notch wide. The sacrum is broad mediolaterally and short inferosuperiorly, similar to a recent human female. However, it is also very curved, resembling a recent human male. According to Walker et al. (2011), Palomas 96 has one of the smallest body sizes of all Neandertal individuals, based on a femoral head height of 43.0 mm (which would convert to an acetabulum height of 48.5 mm using the regression formula developed in Chapter 4). Thus, both the greater sciatic notch width and body size point to Palomas 96 being female.

Female recent humans

This study, as described in Chapter 4, compares female Neandertal *ossa coxae* to those of female recent humans. I took into account a number of considerations when deciding which human sample to use for this comparative study. Genetically, European populations tend to have a higher percentage of Neandertal genes than other populations (Green et al. 2010). However, none of those genes have been shown to affect pelvic morphology. Instead, pelvic morphology and especially bi-iliac breadth is highly correlated with climate adaptations (Ruff 1994). Neandertals mostly lived in a cold environment given that they were alive during an ice age. Many have argued that Neandertal skeletons were cold adapted (Anderson 1989; Ruff 1994; Weaver 2002; Weaver and Hublin 2009). Therefore, I prioritized finding a cold adapted population of recent humans to use as my comparative sample. Previously, the Kodiak Island Koniag individuals have been used to make comparisons to Neandertals (Holliday and Hilton

2010; Rosenberg 1986). However, these skeletons more recently have become unavailable for study. Here, I describe the Ipiutak sample used in this study, which is from further north in the arctic than the Koniag. The comparative human sample came from the Ipiutak site at Point Hope, Alaska, from the collection at the American Museum of Natural History in New York, New York. The *ossa coxae* of 23 females were measured to include in this study.

Point Hope, Alaska, located 200 km north of the Arctic Circle, has two sites associated with it: Ipiutak and Tigara. Helge Larsen and Froelich G. Rainey excavated both sites in 1939-1941 (Holliday and Hilton 2010; Larsen and Rainey 1948). The Ipiutak site date from ~100 BC to 500 AD, while the Tigara site dates from 1200 to 1600 AD (Holliday and Hilton 2010). The people from the Ipiutak site do not appear to be ancestors of the Tigara people, based on cranial markers and cultural artifacts (Debetz 1959; Holliday and Hilton 2010; Keenleyside 2006). Both groups subsisted largely on sea mammals, though the Ipiutak ate more caribou than the Tigara (Holliday and Hilton 2010).

Given that Point Hope is 1,360 km north of Kodiak Island, Holliday and Hilton (2010) expected that the Ipiutak and Tigara would be more extreme in their cold adaptations (defined by limb length and body size based on bi-iliac breadth) than the Kodiak, that all three would be more cold adapted than recent Europeans, and that all three groups and the recent Europeans would be more cold adapted than recent Sub-Saharan Africans. They found that while all groups were more cold adapted than recent Sub-Saharan Africans, there were minimal differences between the circumpolar peoples and Europeans, and even fewer differences between the Koniag, Ipiutak, and Tigara samples. Overall, their results did show that that the Ipiutak were more cold adapted than the Tigara or European samples, which were more similar to each other. These results were just not as strong as Holliday and Hilton (2010) originally predicted.

I chose to use Ipiutak only, as they were ultimately the most cold adapted sample available for study. In particular, their pelvic morphology was affected by cold adaptations by being wide relative to their long bone lengths (bi-iliac breadth measurements from Holliday and Hilton, personal communication, March 2014; long bone lengths from Goldman Data Set, Auerbach 2014). This allowed me to compare cold adapted Neandertal pelves to cold adapted recent humans in order to isolate morphological differences that are the result of something other than living in a cold environment.

Conclusion

In this chapter, I described Neandertal pelvic morphology based on the male Kebara 2 pelvis, the most complete pelvic individual available. Following the observations by Rak and Arensburg (1987) and Rak (1990), I noted that the *ossa coxae* of this pelvis were rotated in orientation relative to human males today. This leads to more laterally facing acetabula, longer iliopubic rami, and an anteriorly positioned sacrum relative to the posterior ilium. This pelvis also confirms that a large acetabulum diameter and a narrow greater sciatic notch are found in Neandertal males, per the sex assessment described in Chapter 4.

I next described the eight Neandertals whose pelvic remains I identified as female. These included the most complete Neandertal female, Tabūn C1, which preserves most of the anterior pelvis, though the pieces are crushed and broken. Tabūn C1 confirmed that small acetabulum size and wide greater sciatic notch were associated with female Neandertals, contrasting with the morphology observed in Kebara 2. The other female Neandertal fossils included in this study are: La Ferrassie 2, Krapina 209/212, Krapina 211, Krapina 208, Krapina 255.5, Krapina 255.8, and Palomas 96.

Finally, I provided the justification and context of the comparative human sample used in this analysis. Like the Neandertals, the Ipiutak from Point Hope, Alaska had skeletons adapted for cold environments, an adaptation that typically affects pelvic morphology. This makes it necessary to account for the affects of living in a cold climate when selecting appropriate samples. The collection at the American Museum of Natural History included 23 pelves that were sufficiently complete to measure and that could be reliably identified as female, both according to the museum records and my own assessment. These female Ipiutak pelves were used in the following analysis as the comparative sample for the Neandertal females.

Chapter 6: Results

Introduction

        In this chapter, I present my results of the statistical analyses used to test the null hypothesis that there are no significant differences between the Neandertal and Ipiutak female samples for pelvic morphology. As described in Chapter 4, for each of the 30 measurements, I used a bootstrap resampling approach to compare the female Neandertal sample of *ossa coxae* to the female Ipiutak sample of *ossa coxae*, with the latter representing a large comparative recent human population. I predicted based on my null hypothesis that the Neandertal means for each measurement would fall within a 95 percent confidence interval set around the mean of the recent human subsample distribution. For each measurement, I calculated the probability of finding a recent human subsample with a mean below that of the Neandertal mean, and used this to assess whether or not the Neandertal mean was within the confidence interval. Importantly, if the Neandertal mean fell outside of this confidence interval, I also reported whether it was larger or smaller than the recent human resampled mean.

Bootstrap resampling results

        Below are the results of my statistical analysis. I have included a graph demonstrating where the Neandertal mean falls relative to the recent human female distribution of subsamples, as well as the probability of finding the recent human female subsamples with means less than the Neandertal mean (represented by *z*, which has been converted into a percent). Table 6.1 summarizes these results, for which 15 of the 30 measurements reject the null hypothesis. In the following figures, all measurements are in mm.

Table 6.1: Results of the bootstrap resampling analysis. The Neandertal mean is based on how many female Neandertals had the measurement preserved. The Ipiutak resampled mean is based on the mean of the 10,000 generated subsamples. The z percent is the percent of the Ipiutak distribution that falls below the Neandertal mean. If the z percent is ≤ 2.5 percent or ≥ 97.5 percent, then the null hypothesis of no difference is rejected (denoted by an *). Measurements are listed in alphabetical order.

Measurement	Neandertal mean (mm)	Ipiutak resampled mean (mm)	z %
Acetabular notch to arcuate superior acetabulum	41.0	44.1	6
Acetabular notch to iliopubic eminence	35.8	35.2	59
Acetabular notch to lesser sciatic notch apex	50.6	45.4	99*
Anterior auricular to greater sciatic notch apex	28.7	32.6	5
Anterior auricular to posterior auricular	14.1	27.7	0*
Anterior inferior iliac spine acetabulum notch to arcuate superior acetabulum	31.4	29.1	88
Anterior inferior iliac spine acetabulum notch to inferior acetabulum	52.9	55.1	14
Anterior inferior iliac spine to arcuate greater sciatic notch	63.0	55.8	100*
Anterior inferior iliac spine to greater sciatic notch apex	69.3	68.7	62
Anterior ischial tuberosity to posterior ischial tuberosity	25.3	22.6	94
Arcuate greater sciatic notch to greater sciatic notch apex	16.1	23.2	0*
Arcuate greater sciatic notch to posterior auricular	33.1	46.5	0*
Arcuate superior acetabulum to arcuate greater sciatic notch	33.8	28.4	92
Inferior acetabulum to iliopubic eminence	56.3	51.7	99*
Lateral acetabulum to anterior greater sciatic notch midpoint	29.3	34.6	0*
Lateral acetabulum to anterior inferior iliac spine	43.3	54.6	0*

|			
Lateral acetabulum to greater sciatic notch apex	44.6	42.8	76
Lateral acetabulum to inferior acetabulum	38.8	37.2	79
Lateral acetabulum to lateral ischial tuberosity	45.6	33.6	100*
Maximum pubic breadth	21.8	19.3	97
Medial acetabulum to arcuate superior acetabulum	45.0	38.0	100*
Medial acetabulum to pectineal eminence	32.8	24.7	100*
Minimum pubic breadth	7.4	9.7	1*
Minimum pubic height	7.8	12.8	0*
Pectineal eminence to arcuate superior acetabulum	19.9	21.0	31
Posterior ischial tuberosity to arcuate superior acetabulum	80.2	87.2	5
Superior acetabulum to arcuate superior acetabulum	31.3	32.0	31
Superior acetabulum to inferior acetabulum	56.1	48.8	100*
Superolateral acetabulum to inferior acetabulum	42.5	45.7	5
Superomedial acetabulum to pectineal eminence	32.3	22.1	100*

Below are the results for each measurement. I have grouped the measurements together based on their results. First, I give the results of measurements for which Neandertal females were found to be significantly larger than recent human females, next I give the results of measurements for which Neandertal females were found to be significantly smaller than recent human females, and finally I give the results for which Neandertal females were found to be similar to recent human females based on this analysis. There are 15 measurements in total for which Neandertals are significantly different than the resampled human mean; for eight of these Neandertals are larger than recent humans and for seven they are smaller.

Measurements for which Neandertals are significantly larger than recent humans

        The measurements that reject the null hypothesis and find the Neandertal mean to be larger than the recent human resampled mean are given here. They include: lateral acetabulum to lateral ischial tuberosity; medial acetabulum to arcuate superior acetabulum; superomedial acetabulum to pectineal eminence; inferior acetabulum to iliopubic eminence; medial acetabulum to pectineal eminence; acetabular notch to lesser sciatic notch apex; superior acetabulum to inferior acetabulum; and anterior inferior iliac spine to arcuate greater sciatic notch. The transformed _z_ score percent is given on each figure; this is the percentage of recent human female subsamples that have a mean less than the Neandertal female mean.

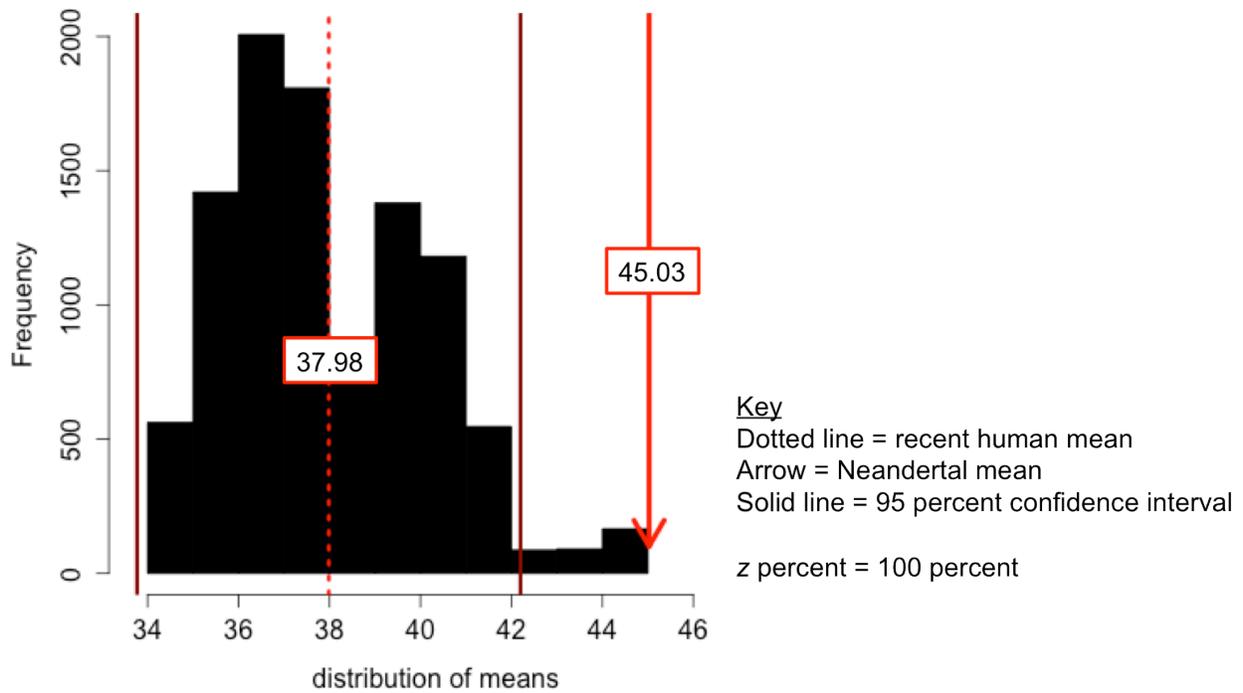   For the measurement lateral acetabulum to lateral ischial tuberosity, the Neandertal female mean is based on two individuals, Krapina 208 and Tabūn C1. The results are illustrated in Figure 6.1. There is a ≥ 95 percent probability that the Neandertal female mean is significantly larger than the recent human female resampled mean.

Figure 6.1: Lateral acetabulum to lateral ischial tuberosity results.
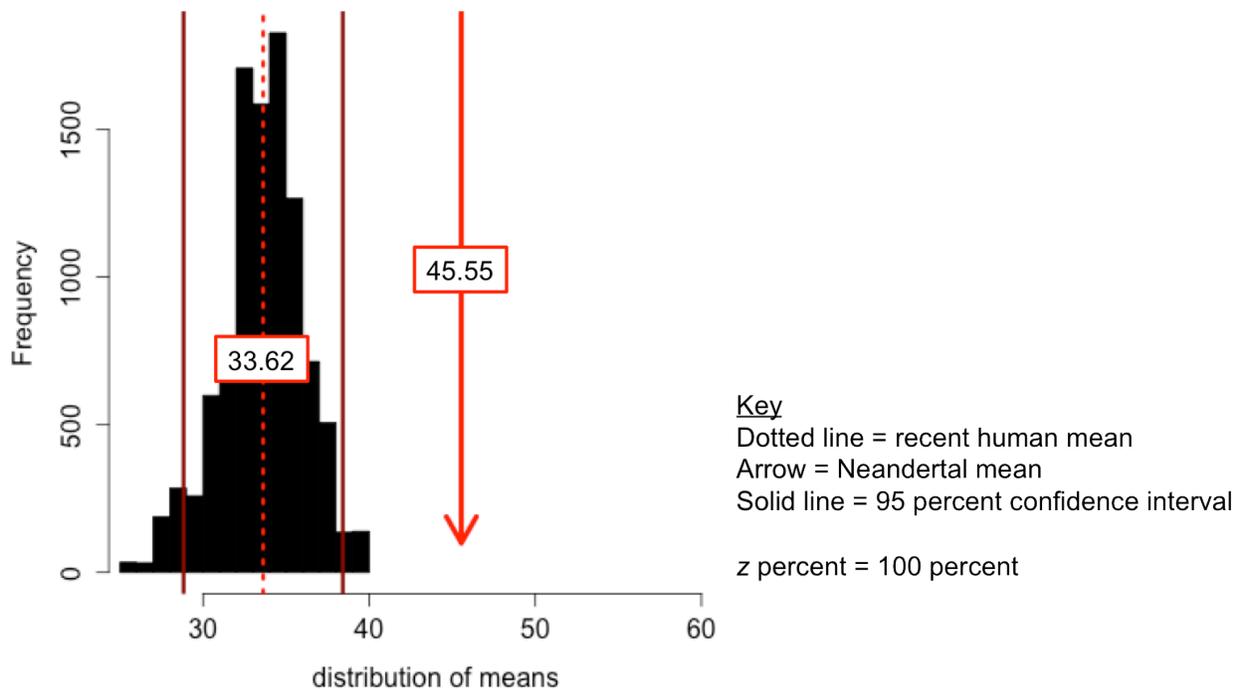
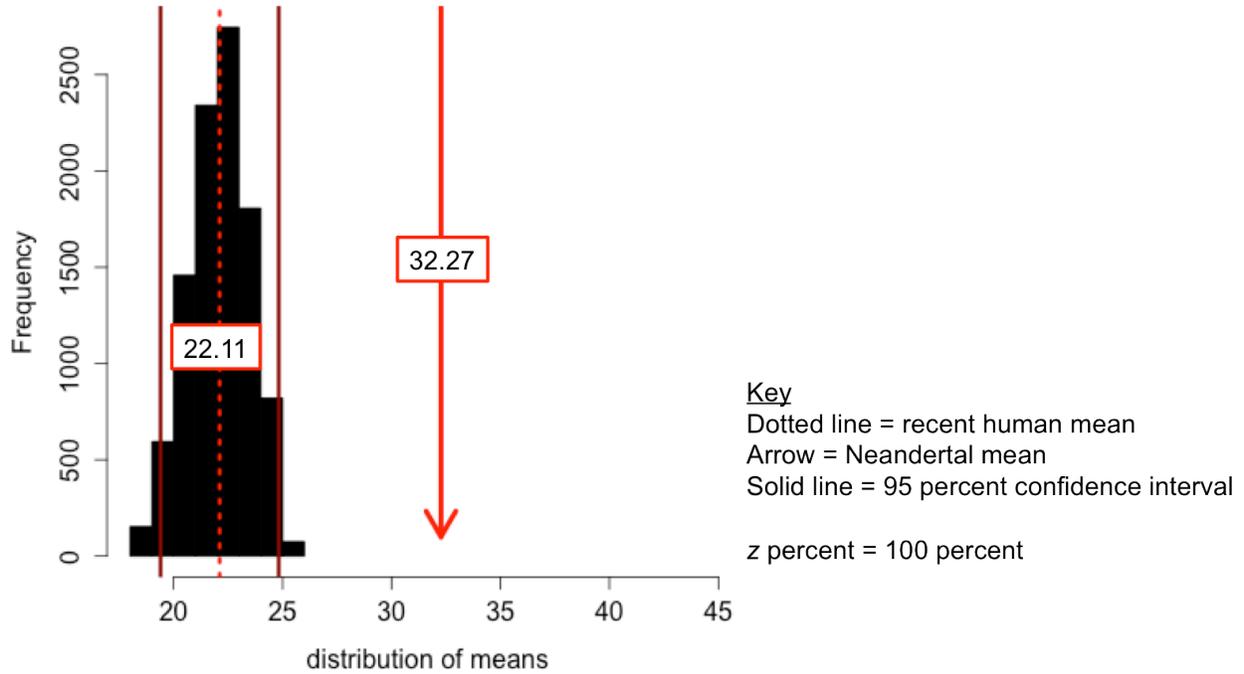For the measurement medial acetabulum to arcuate superior acetabulum, the Neandertal female mean is based on two individuals: Krapina 208 and Krapina 209/212. The results are illustrated in Figure 6.2. There is a ≥ 95 percent probability that the Neandertal female mean is significantly larger than the recent human female resampled mean.

Figure 6.2: Medial acetabulum to arcuate superior acetabulum results.

For the measurement superomedial acetabulum to pectineal eminence, the Neandertal female mean is based on three individuals, Krapina 208, Krapina 209/212, and Tabūn C1. The results are illustrated in Figure 6.3. There is a ≥ 95 percent probability that the Neandertal female mean is significantly larger than the recent human female resampled mean.

Figure 6.3: Superomedial acetabulum to pectineal eminence results.

Key
Dotted line = recent human mean
Arrow = Neandertal mean
Solid line = 95 percent confidence interval

z percent = 100 percent

For the measurement inferior acetabulum to iliopubic eminence, the Neandertal female mean is based on two individuals: Krapina 208 and Krapina 209/212. The results are illustrated in Figure 6.4. There is a ≥ 95 percent probability that the Neandertal female mean is significantly larger than the recent human female resampled mean.

Figure 6.4: Inferior acetabulum to iliopubic eminence results.

Key
Dotted line = recent human mean
Arrow = Neandertal mean
Solid line = 95 percent confidence interval

z percent = 99 percent

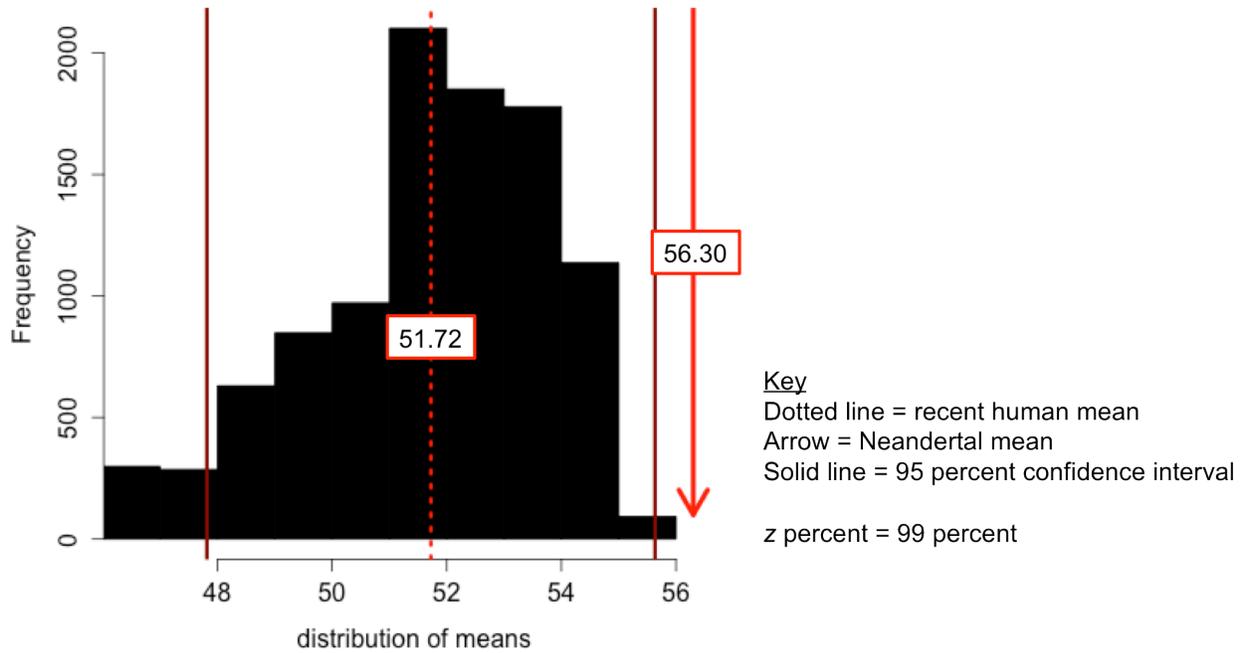For the measurement medial acetabulum to pectineal eminence, the Neandertal female mean is based on three individuals: Krapina 208, Krapina 209/212, and Tabūn C1. The results are illustrated in Figure 6.5. There is a ≥ 95 percent probability that the Neandertal female mean is significantly larger than the recent human female resampled mean.

Figure 6.5: Medial acetabulum to pectineal eminence results.

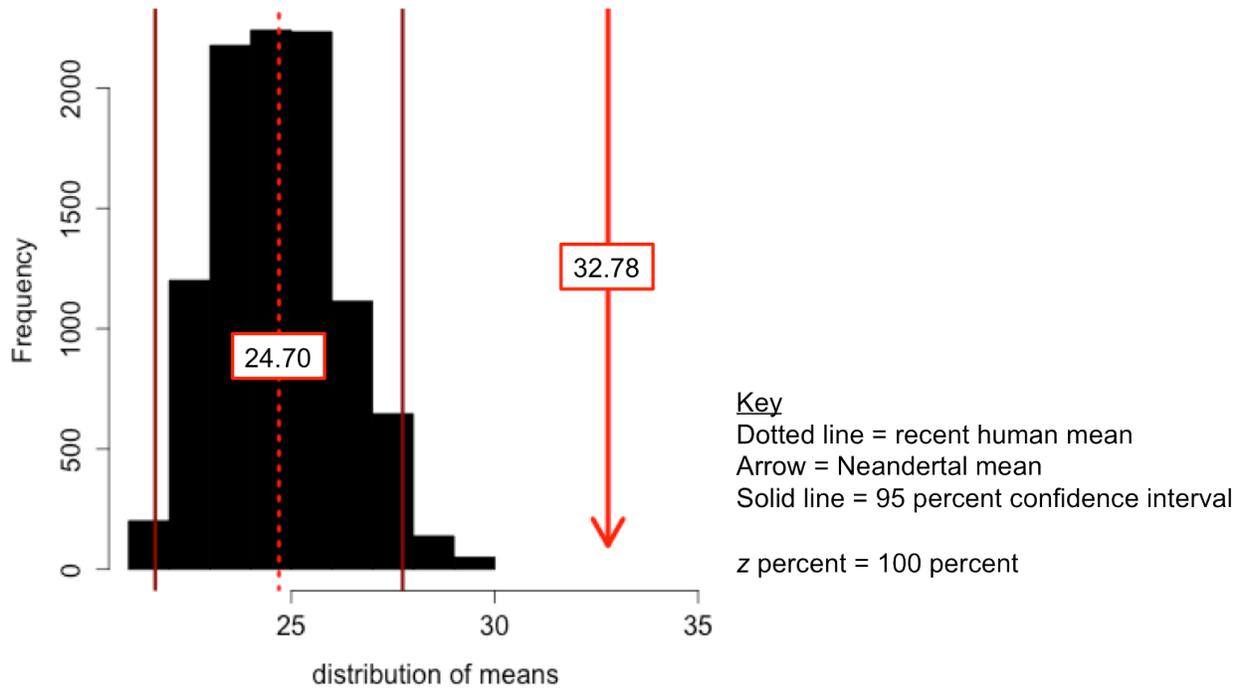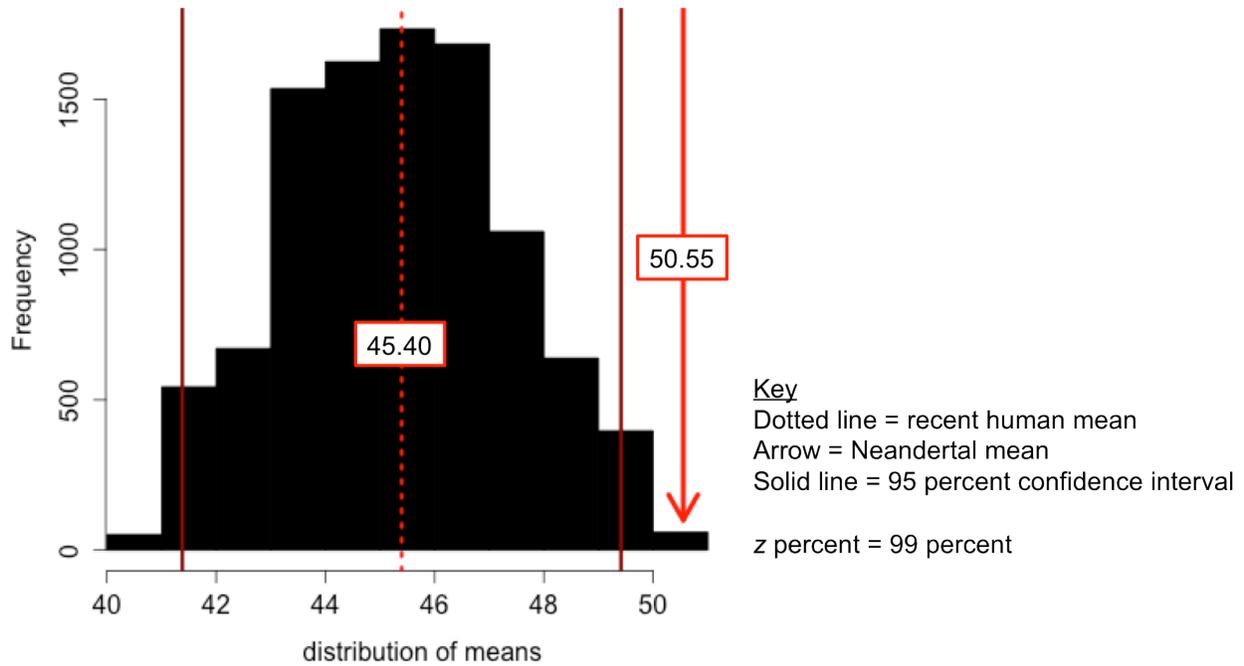For the measurement acetabular notch to lesser sciatic notch apex, the Neandertal female mean is based on two individuals, Krapina 208 and La Ferrassie 2. The results are illustrated in Figure 6.6. There is a ≥ 95 percent probability that the Neandertal female mean is significantly larger than the recent human female resampled mean.

Figure 6.6: Acetabular notch to lesser sciatic notch apex results.

Key
Dotted line = recent human mean
Arrow = Neandertal mean
Solid line = 95 percent confidence interval

z percent = 99 percent

For the measurement superior acetabulum to inferior acetabulum, the Neandertal female mean is based on two individuals: Krapina 208 and Krapina 209/212. The results are illustrated in Figure 6.7. There is a ≥ 95 percent probability that the Neandertal female mean is significantly larger than the recent human female resampled mean.
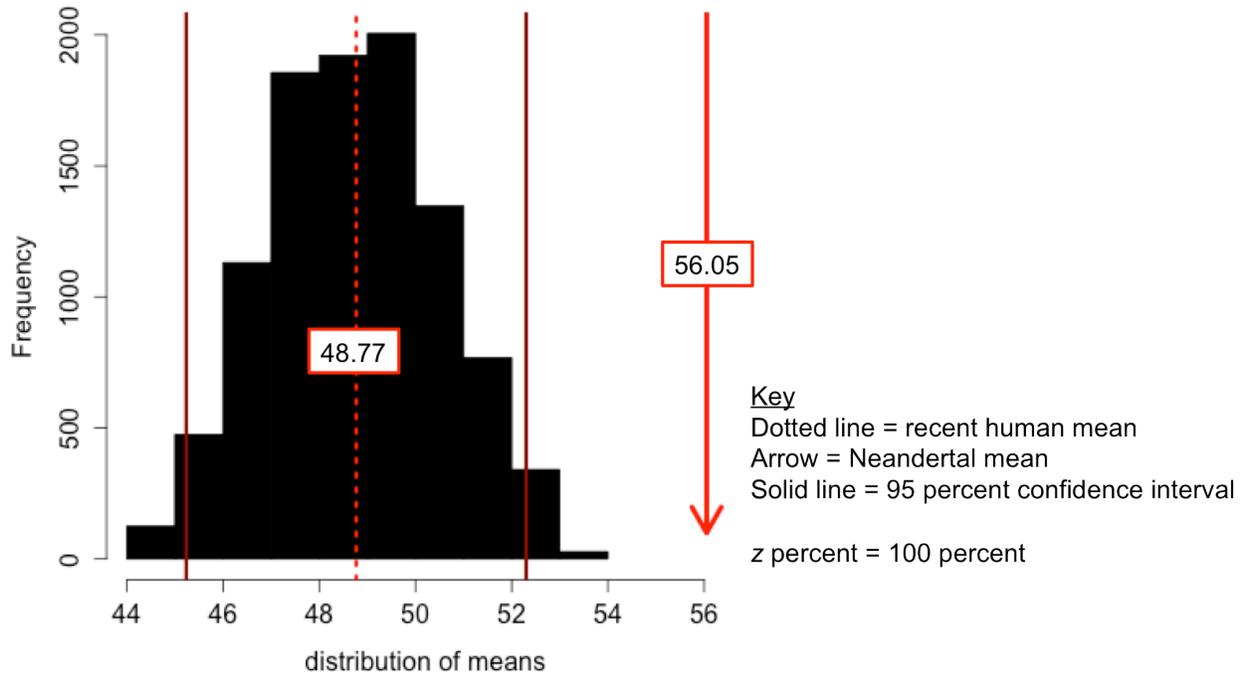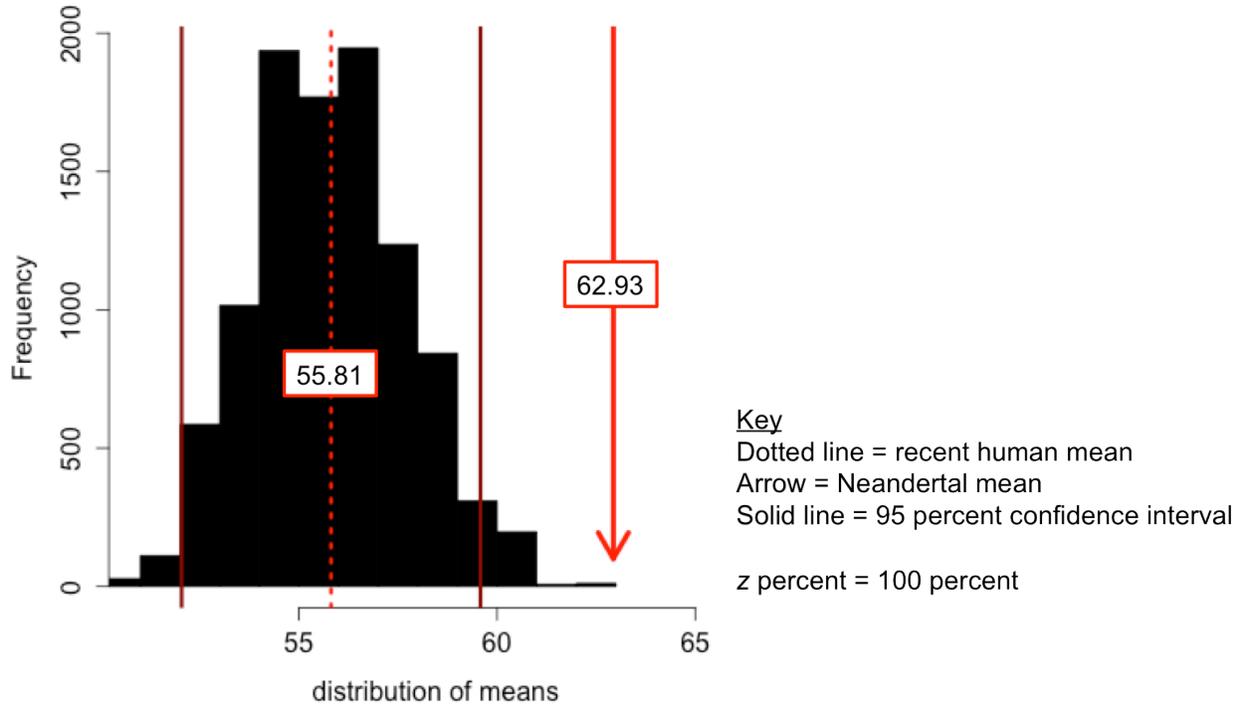
Figure 6.7: Superior acetabulum to inferior acetabulum results.

For the measurement anterior inferior iliac spine to arcuate greater sciatic notch, the Neandertal female mean is based on three individuals: Krapina 209/212, Krapina 255.8, and Tabūn C1. The results are illustrated in Figure 6.8. There is a ≥ 95 percent probability that the Neandertal female mean is significantly larger than the recent human female resampled mean.

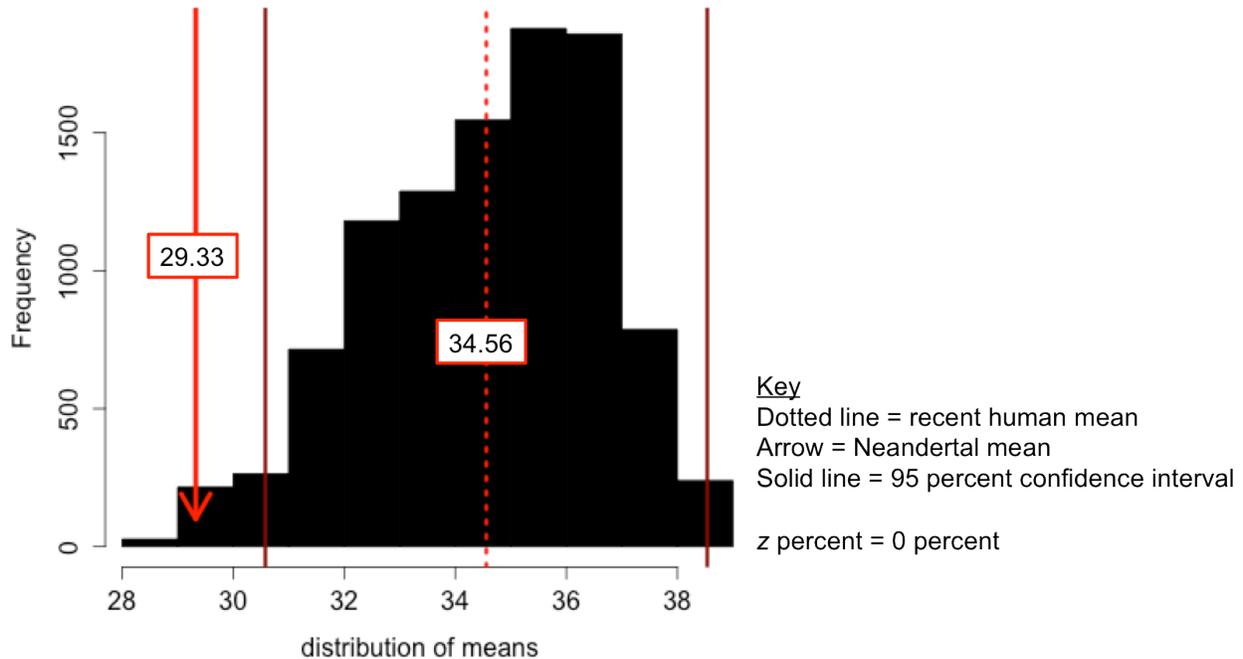Figure 6.8: Anterior inferior iliac spine to arcuate greater sciatic notch results.

Key
Dotted line = recent human mean
Arrow = Neandertal mean
Solid line = 95 percent confidence interval

z percent = 100 percent

The measurements that reject the null hypothesis and find the Neandertal female mean to be smaller than the recent human female resampled mean are given here. They include: lateral acetabulum to anterior greater sciatic notch midpoint; lateral acetabulum to anterior inferior iliac spine; arcuate greater sciatic notch to greater sciatic notch apex; minimum pubic breadth; arcuate greater sciatic notch to posterior auricular; anterior auricular to posterior auricular; and minimum pubic height. The transformed *z* score percent is given on each figure; this is the percentage of recent human subsamples that have a mean less than the Neandertal mean.

For the measurement lateral acetabulum to anterior greater sciatic notch midpoint, the Neandertal female mean is based on two individuals: Krapina 208 and Tabūn C1. The results are illustrated in Figure 6.9. There is a ≥ 95 percent probability that the Neandertal female mean is significantly smaller than the recent human female resampled mean.

Figure 6.9: Lateral acetabulum to anterior greater sciatic notch midpoint results.

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For the measurement lateral acetabulum to anterior inferior iliac spine, the Neandertal female mean is based on two individuals: Krapina 209/212 and Tabūn C1. The results are illustrated in Figure 6.10. There is a ≥ 95 percent probability that the Neandertal female mean is significantly smaller than the recent human female resampled mean.

Figure 6.10: Lateral acetabulum to anterior inferior iliac spine results.
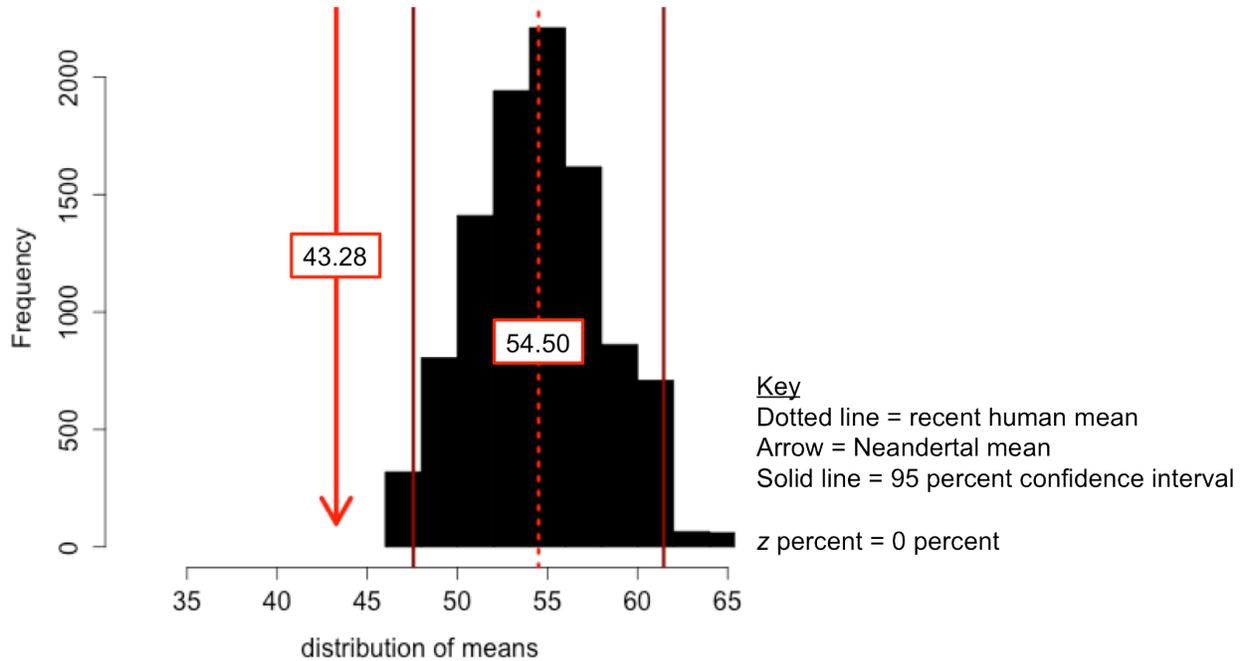
For the measurement arcuate greater sciatic notch to greater sciatic notch apex, the Neandertal female mean is based on six individuals: Krapina 209/212, Krapina 211, Krapina 255.5, Krapina 255.8, La Ferrassie 2, and Tabūn C1. The results are illustrated in Figure 6.11. There is a ≥ 95 percent probability that the Neandertal female mean is significantly smaller than the recent human female resampled mean.

Figure 6.11: Arcuate greater sciatic notch to greater sciatic notch apex results.
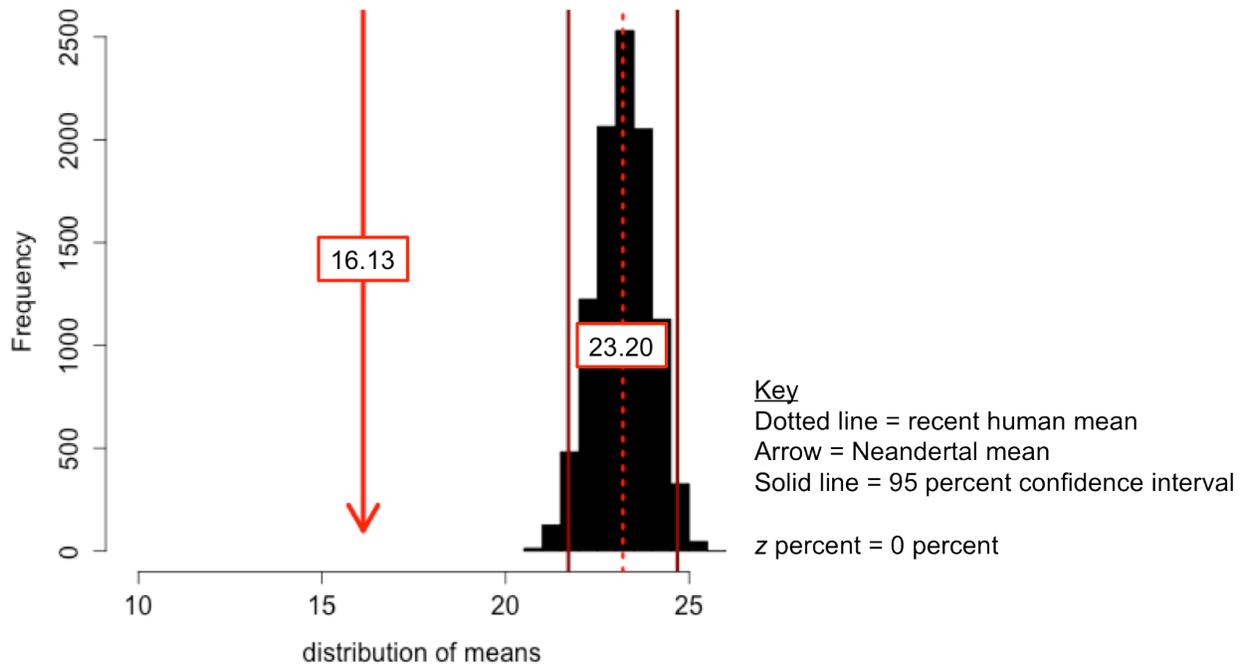
For the measurement minimum pubic breadth, the Neandertal female mean is based on three individuals, Krapina 208, Krapina 209/212, and Tabūn C1. The results are illustrated in Figure 6.12. There is a ≥ 95 percent probability that the Neandertal female mean is significantly smaller than the recent human female resampled mean.

Figure 6.12: Minimum pubic breadth results.
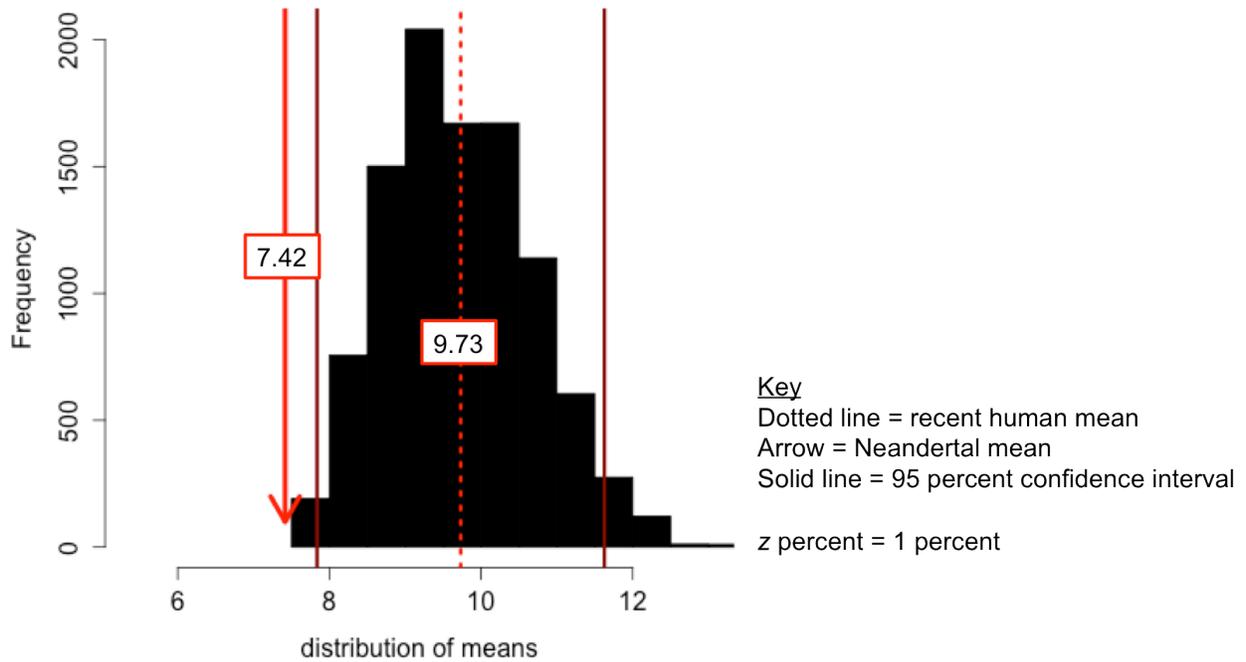
For the measurement arcuate greater sciatic notch to posterior auricular, the Neandertal female mean is based on two individuals, Krapina 209/212 and Krapina 211. The results are illustrated in Figure 6.13. There is a ≥ 95 percent probability that the Neandertal female mean is significantly smaller than the recent human female resampled mean.

Figure 6.13: Arcuate greater sciatic notch to posterior auricular results.

For the measurement anterior auricular to posterior auricular, the Neandertal female mean is based on two individuals, Krapina 209/212 and Krapina 211. The results are illustrated in Figure 6.14. There is a ≥ 95 percent probability that the Neandertal female mean is significantly smaller than the recent human female resampled mean.

Figure 6.14: Anterior auricular to posterior auricular results.

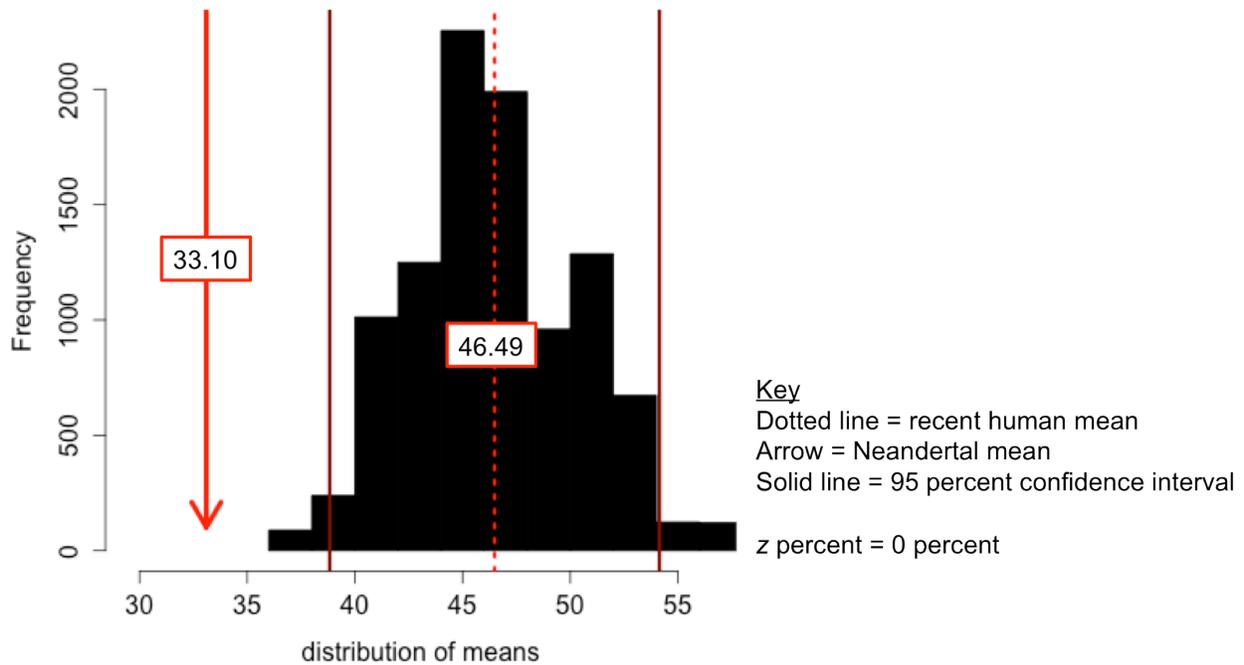For the measurement minimum pubic height, the Neandertal female mean is based on three individuals, Krapina 208, Krapina 209/212, and Tabūn C1. The results are illustrated in Figure 6.15. There is a ≥ 95 percent probability that the Neandertal female mean is significantly smaller than the recent human female resampled mean.

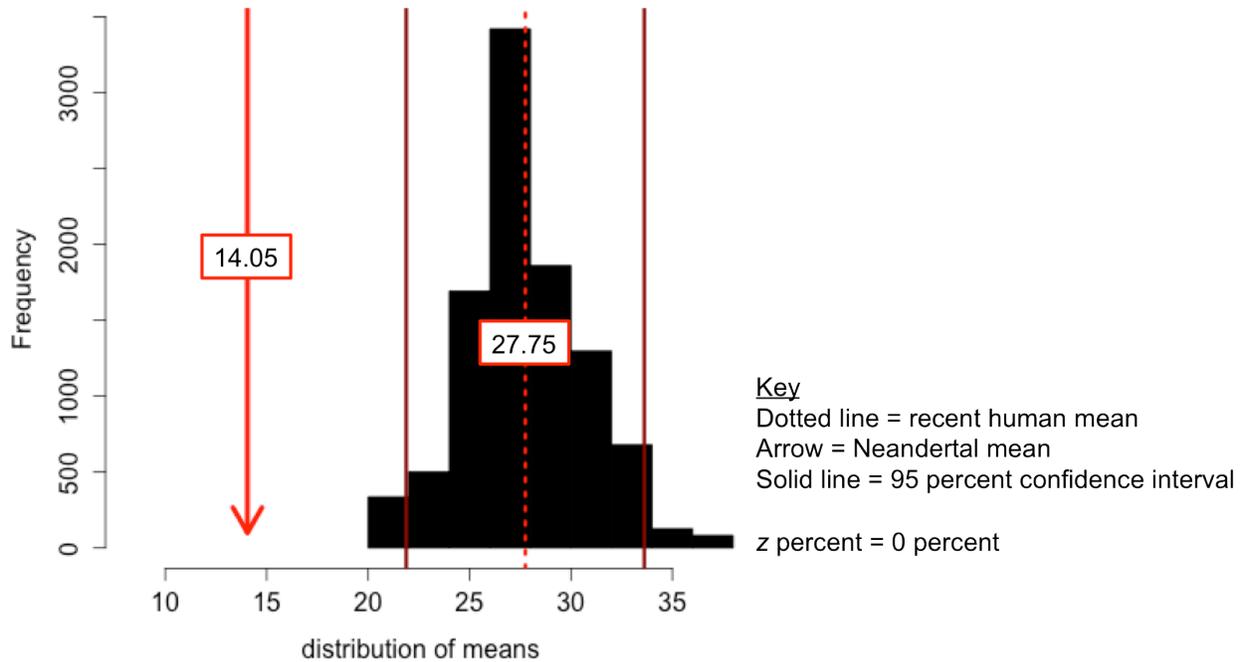*Figure 6.15: Minimum pubic height results.*
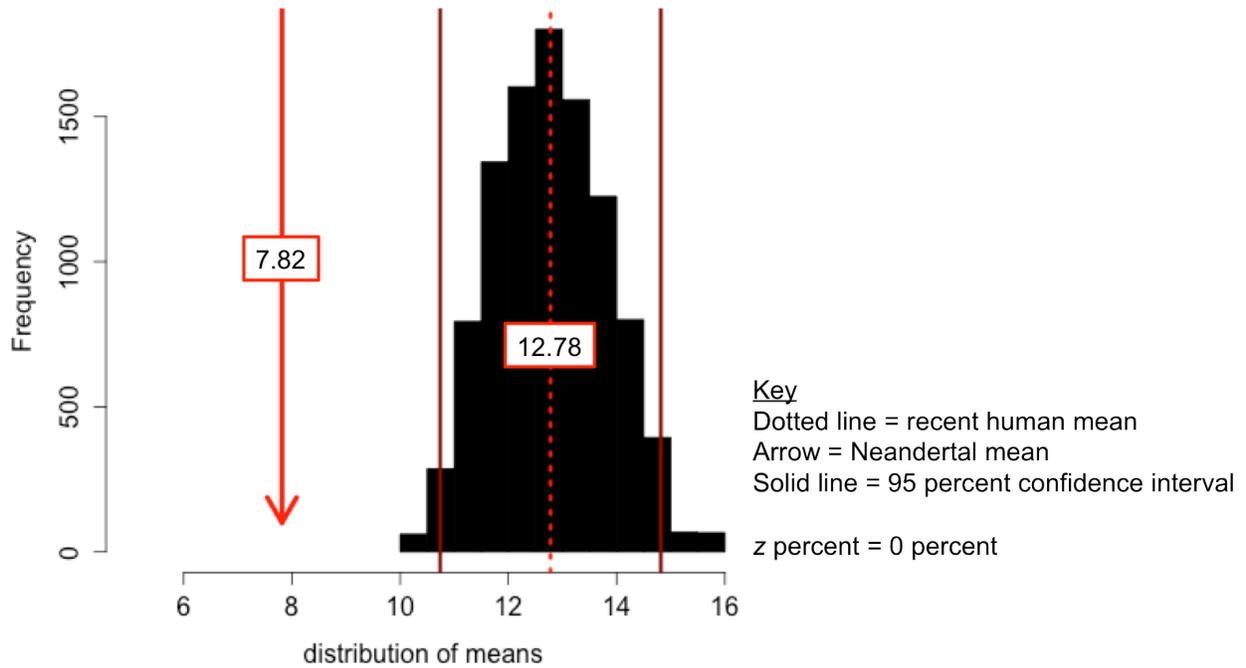
The measurements that fail to reject the null hypothesis because the Neandertal mean falls within the 95 percent confidence interval of the human resampled mean are given here. They include: anterior inferior iliac spine acetabulum notch to arcuate superior acetabulum; superior acetabulum to arcuate superior acetabulum; maximum pubic breadth; acetabular notch to iliopubic eminence; acetabular notch to arcuate superior acetabulum; pectineal eminence to arcuate superior acetabulum; arcuate superior acetabulum to arcuate greater sciatic notch; lateral acetabulum to greater sciatic notch apex; anterior ischial tuberosity to posterior ischial tuberosity; anterior inferior iliac spine to greater sciatic notch apex; posterior ischial tuberosity to arcuate superior acetabulum; anterior auricular to greater sciatic notch apex; anterior inferior iliac spine acetabulum notch to inferior acetabulum; superolateral acetabulum to inferior acetabulum; and lateral acetabulum to inferior acetabulum. The transformed z score percent is given on each figure; this is the percentage of recent human subsamples that have a mean less than the Neandertal mean.

For the measurement anterior inferior iliac spine acetabulum notch to arcuate superior acetabulum, the Neandertal female mean is based on two individuals, Krapina 209/212 and Tabūn C1. The results are illustrated in Figure 6.16. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

Figure 6.16: Anterior inferior iliac spine acetabulum notch to arcuate superior acetabulum results.
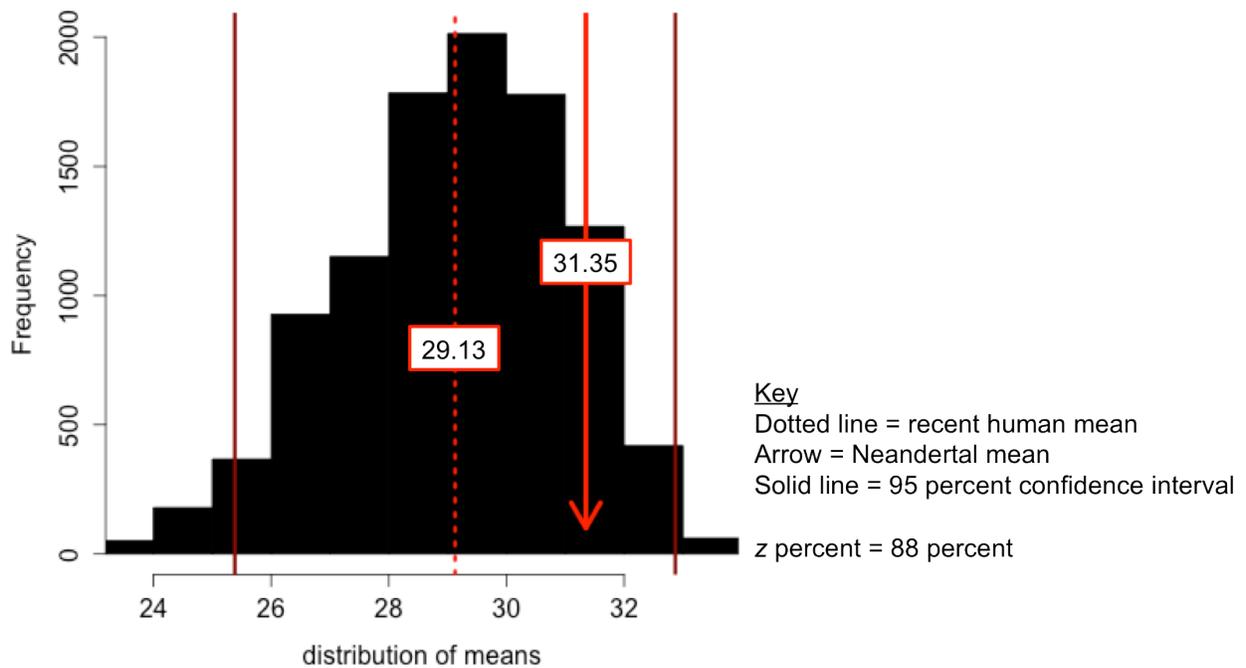
For the measurement superior acetabulum to arcuate superior acetabulum, the Neandertal female mean is based on two individuals, Krapina 208 and Krapina 209/212. The results are illustrated in Figure 6.17. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

Figure 6.17: Superior acetabulum to arcuate superior acetabulum results.
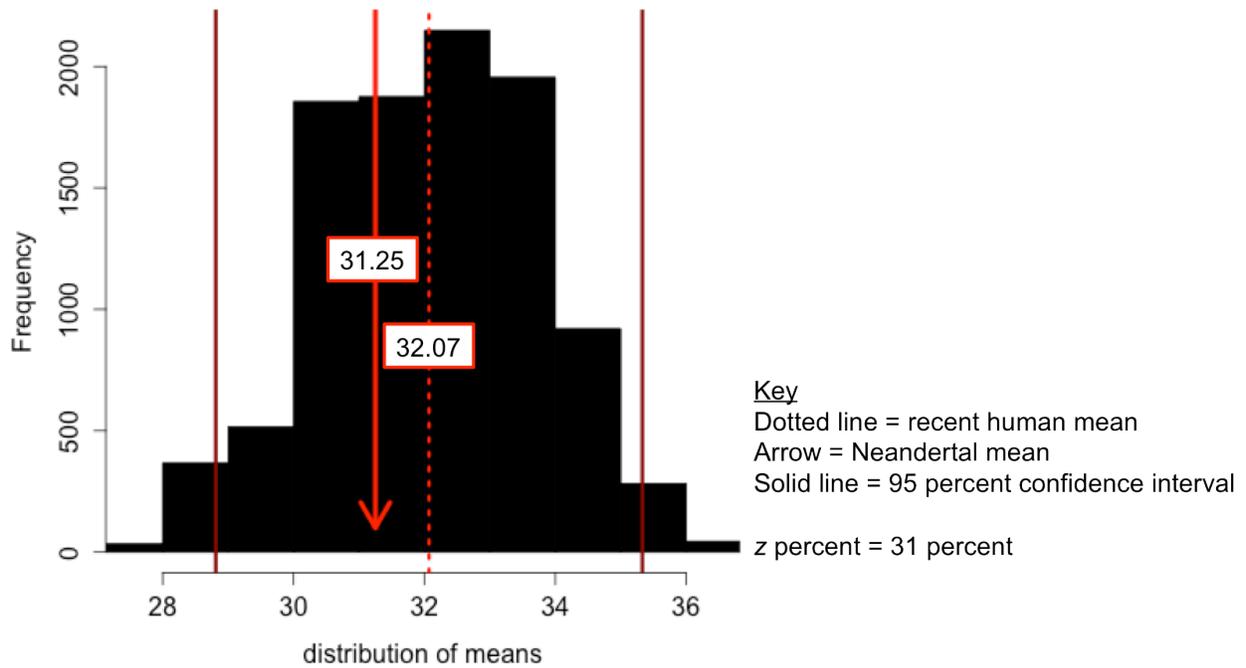
For the measurement maximum pubic breadth, the Neandertal female mean is based on three individuals, Krapina 208, Krapina 209/212, and Tabūn C1. The results are illustrated in Figure 6.18. There is a 95 percent probability that the Neandertal female mean is not quite significantly different than the recent human female resampled mean.

Figure 6.18: Maximum pubic breadth results.

For the measurement acetabular notch to iliopubic eminence, the Neandertal female mean is based on two individuals, Krapina 208 and Krapina 209/212. The results are illustrated in Figure 6.19. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

Figure 6.19: Acetabular notch to iliopubic eminence results.

Key
Dotted line = recent human mean
Arrow = Neandertal mean
Solid line = 95 percent confidence interval

z percent = 59 percent

For the measurement acetabular notch to arcuate superior acetabulum, the Neandertal female mean is based on two individuals, Krapina 208 and Krapina 209/212. The results are illustrated in Figure 6.20. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

Figure 6.20: Acetabular notch to arcuate superior acetabulum results.

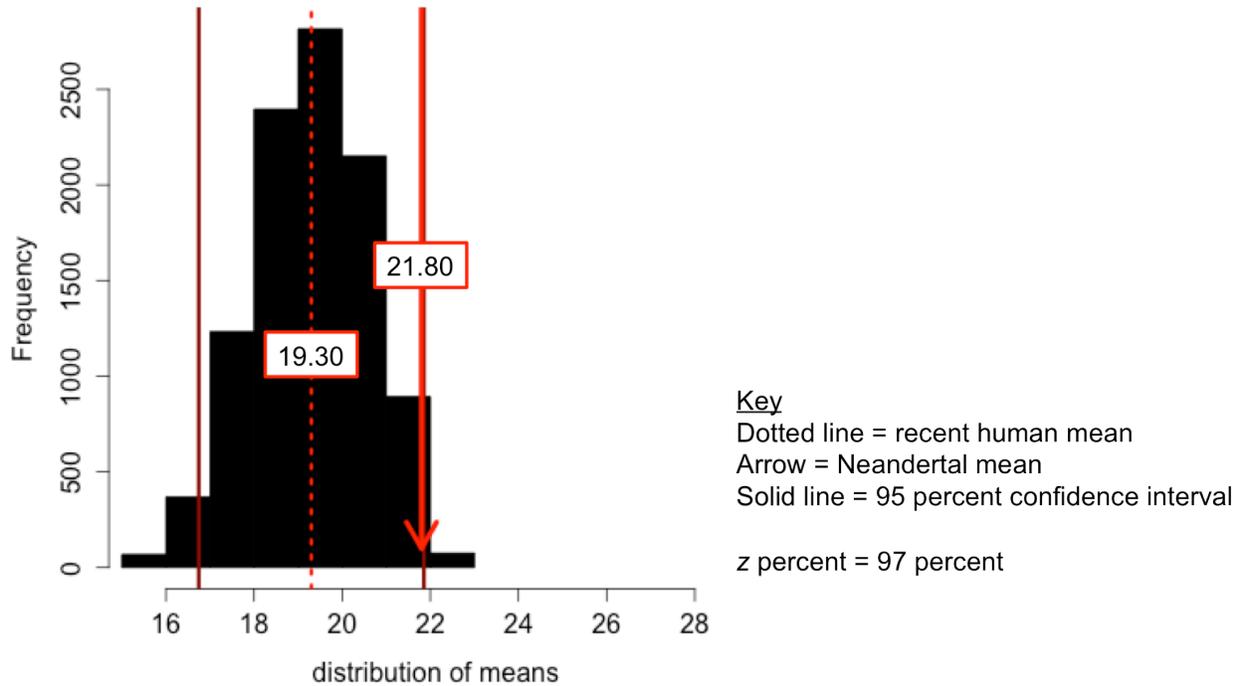*Figure 6.20: Acetabular notch to arcuate superior acetabulum results.*
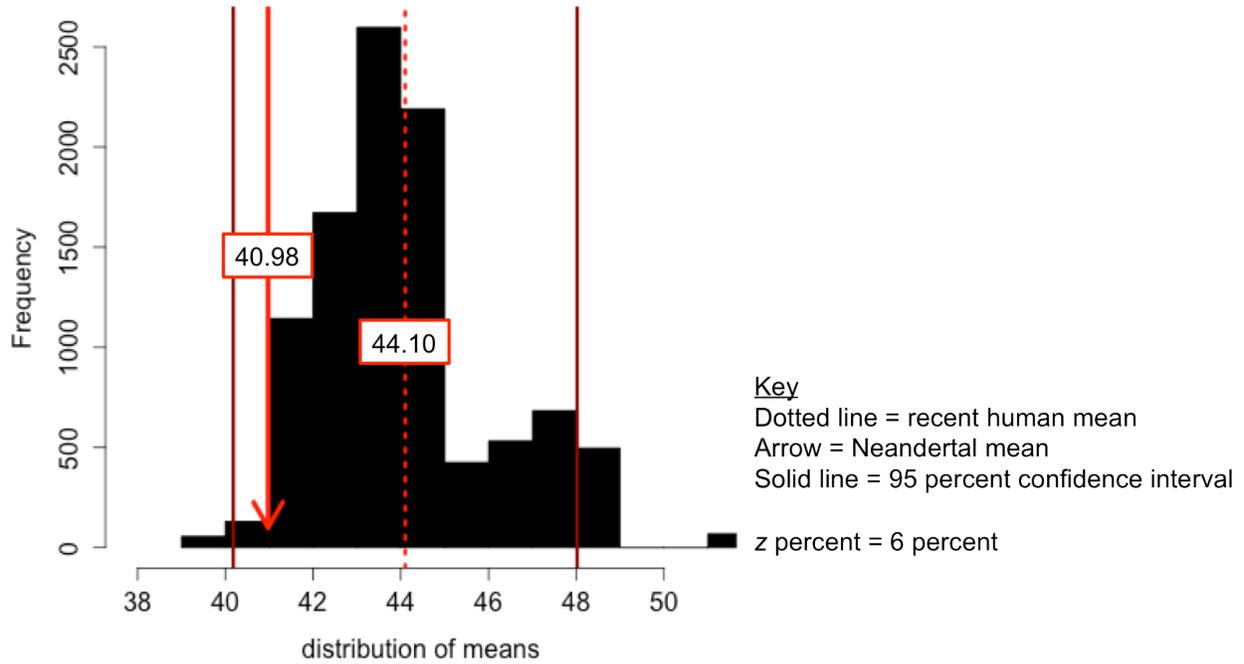
For the measurement pectineal eminence to arcuate superior acetabulum, the Neandertal female mean is based on two individuals, Krapina 208 and Krapina 209/212. The results are illustrated in Figure 6.21. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

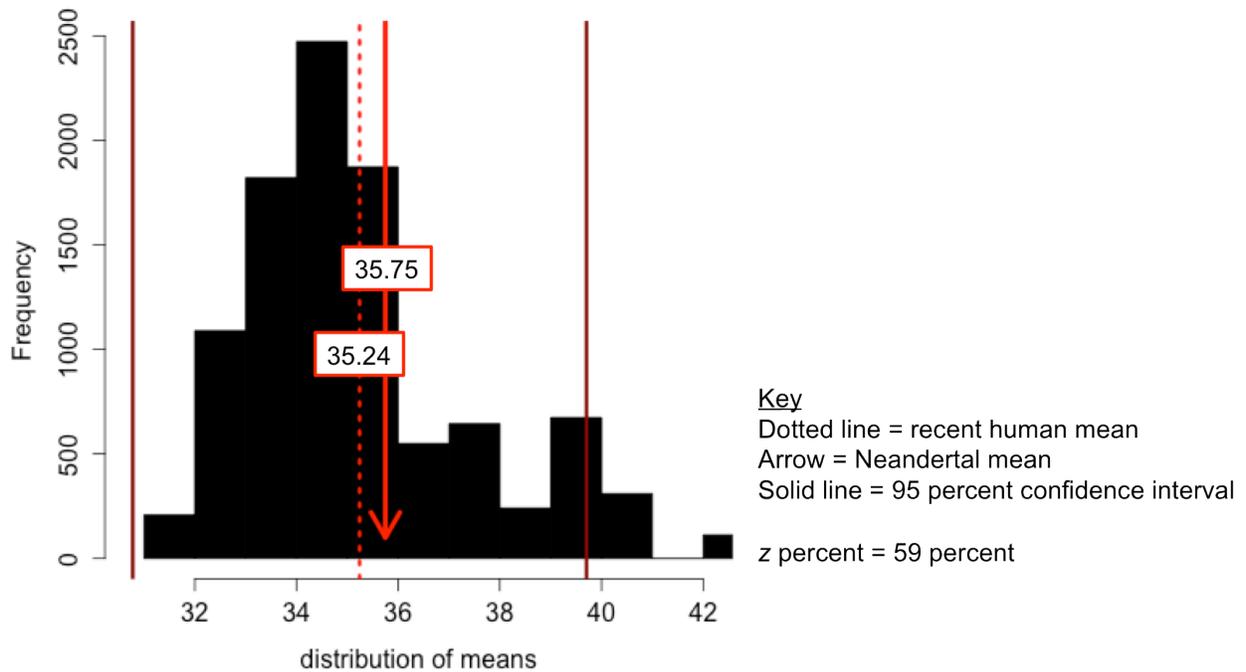*Figure 6.21: Pectineal eminence to arcuate superior acetabulum results.*

Key
Dotted line = recent human mean
Arrow = Neandertal mean
Solid line = 95 percent confidence interval

z percent = 31 percent
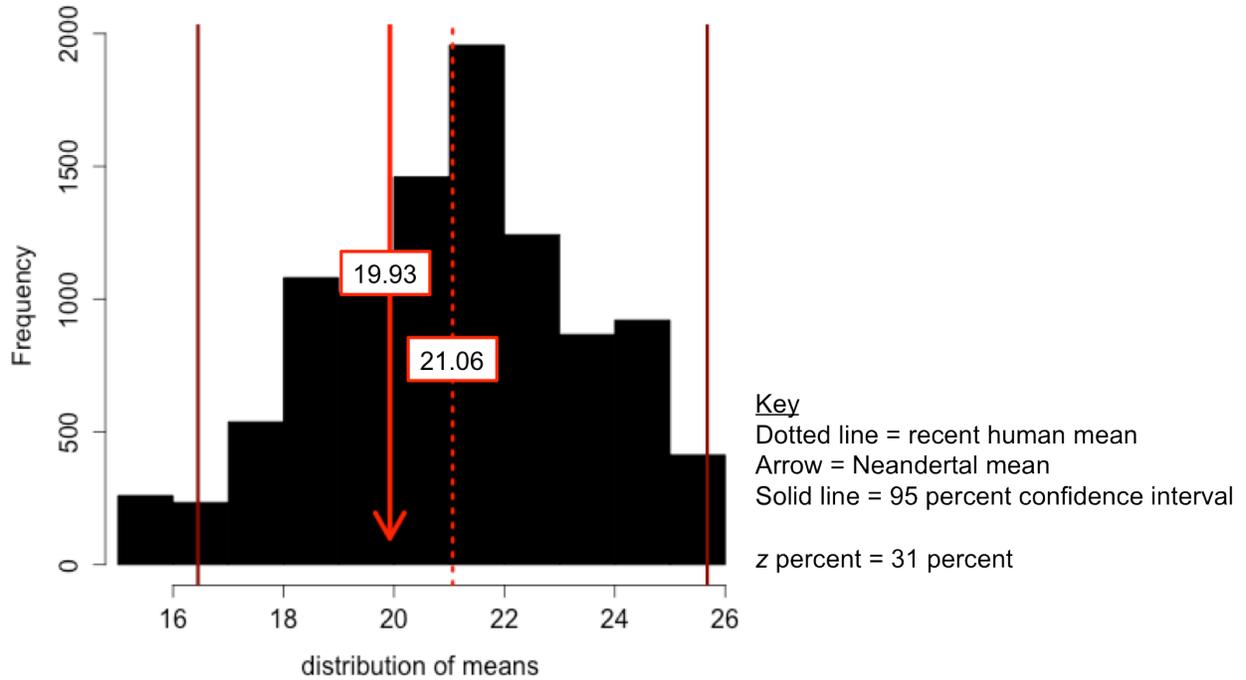
For the measurement arcuate superior acetabulum to arcuate greater sciatic notch, the Neandertal female mean is based on two individuals, Krapina 209/212 and Tabūn C1. The results are illustrated in Figure 6.22. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

Figure 6.22: Arcuate superior acetabulum to arcuate greater sciatic notch results.

Key
Dotted line = recent human mean
Arrow = Neandertal mean
Solid line = 95 percent confidence interval

z percent = 92 percent

For the measurement lateral acetabulum to greater sciatic notch apex, the Neandertal female mean is based on two individuals: Krapina 209/212 and Tabūn C1. The results are illustrated in Figure 6.23. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

Figure 6.23: Lateral acetabulum to greater sciatic notch apex results.

Key
Dotted line = recent human mean
Arrow = Neandertal mean
Solid line = 95 percent confidence interval

z percent = 76 percent

For the measurement anterior ischial tuberosity to posterior ischial tuberosity, the Neandertal female mean is based on two individuals, Krapina 208 and Tabūn C1. The results are illustrated in Figure 6.24. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

Figure 6.24: Anterior ischial tuberosity to posterior ischial tuberosity results.

Key
Dotted line = recent human mean
Arrow = Neandertal mean
Solid line = 95 percent confidence interval

z percent = 94 percent

For the measurement anterior inferior iliac spine to greater sciatic notch apex, the Neandertal female mean is based on three individuals: Krapina 209/212, Krapina 255.8, and Tabūn C1. The results are illustrated in Figure 6.25. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

Figure 6.25: Anterior inferior iliac spine to greater sciatic notch apex results.

Key
Dotted line = recent human mean
Arrow = Neandertal mean
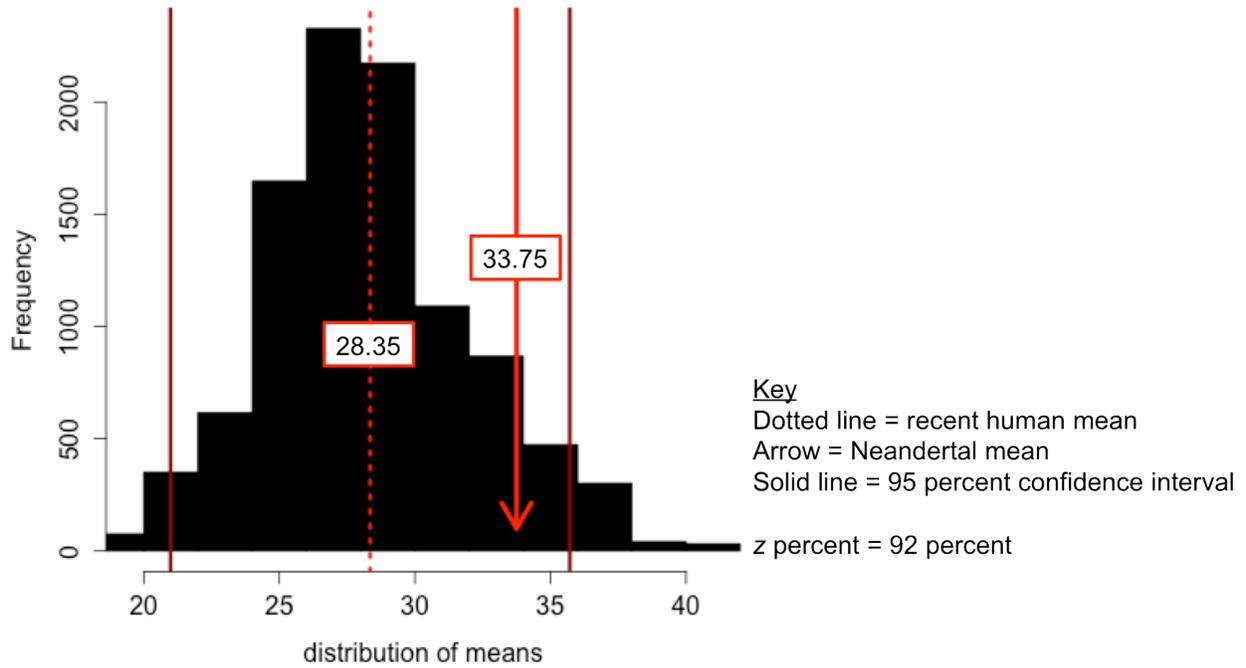Solid line = 95 percent confidence interval

z percent = 62 percent

For the measurement posterior ischial tuberosity to arcuate superior acetabulum, the Neandertal female mean is based on two individuals, Krapina 208 and Tabūn C1. The results are illustrated in Figure 6.26. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

Figure 6.26: Posterior ischial tuberosity to arcuate superior acetabulum results.
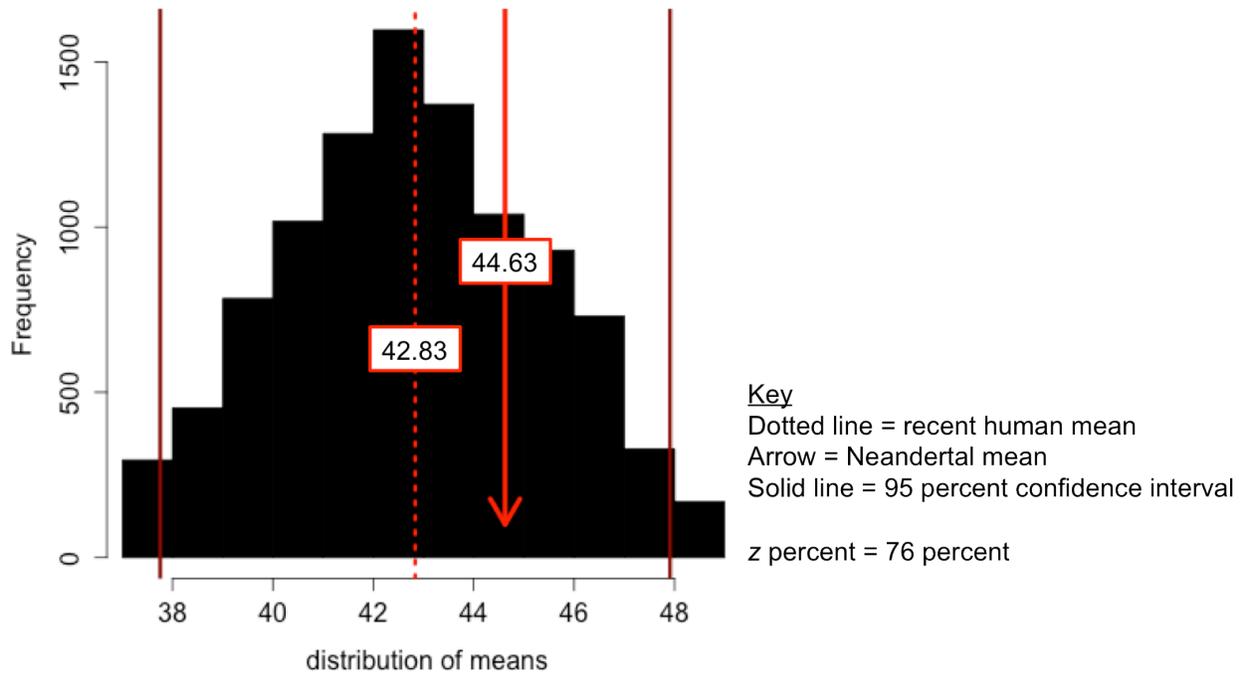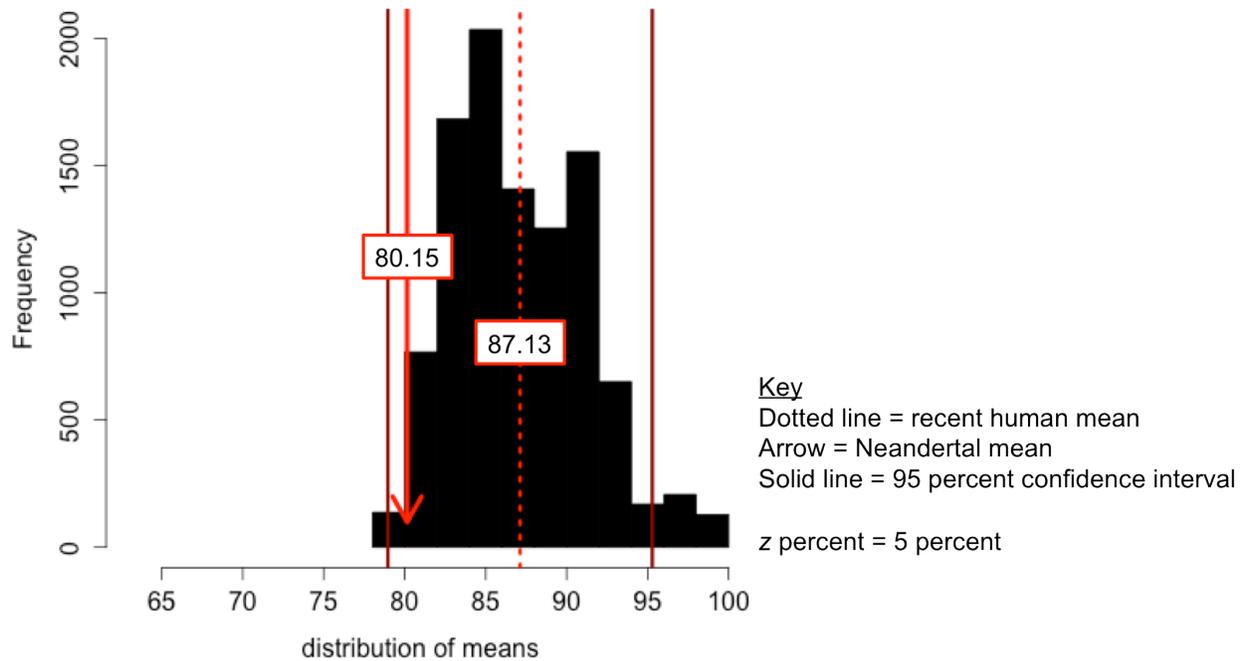
For the measurement anterior auricular to greater sciatic notch apex, the Neandertal female mean is based on two individuals: Krapina 209/212 and Krapina 211. The results are illustrated in Figure 6.27. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

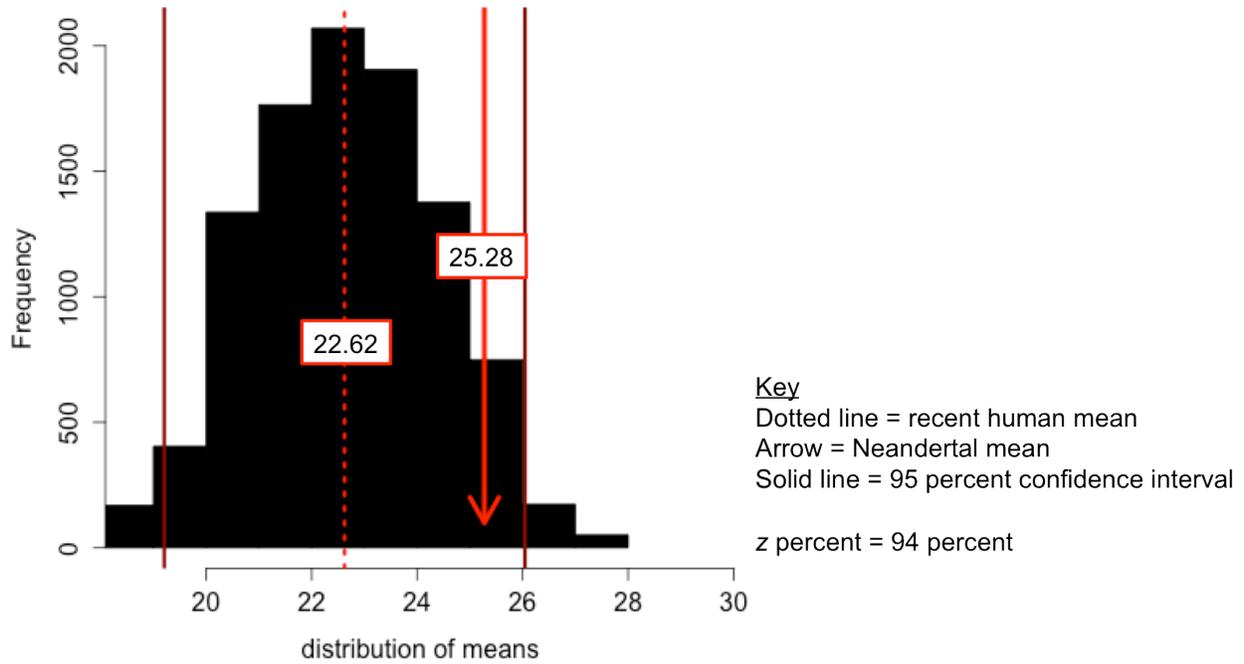Figure 6.27: Anterior auricular to greater sciatic notch apex results.
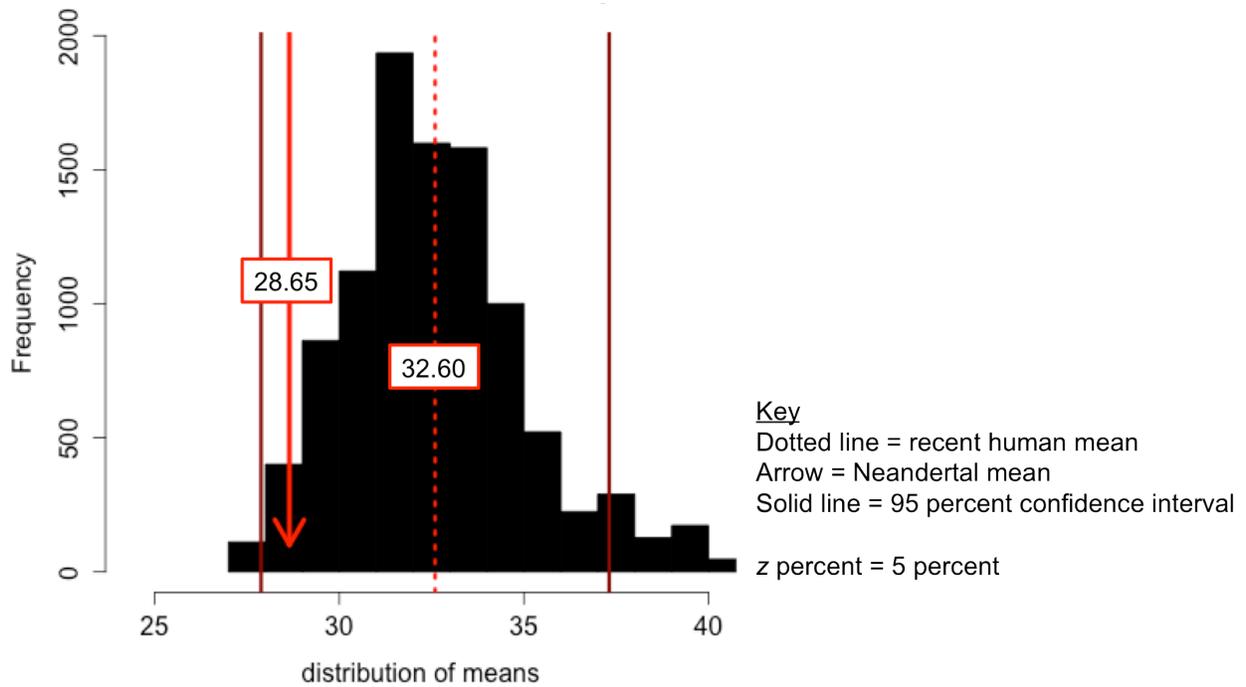
For the measurement anterior inferior iliac spine acetabulum notch to inferior acetabulum, the Neandertal female mean is based on two individuals: Krapina 209/212 and Tabūn C1. The results are illustrated in Figure 6.28. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

Figure 6.28: Anterior inferior iliac spine acetabulum notch to inferior acetabulum results.

Key
Dotted line = recent human mean
Arrow = Neandertal mean
Solid line = 95 percent confidence interval

z percent = 14 percent
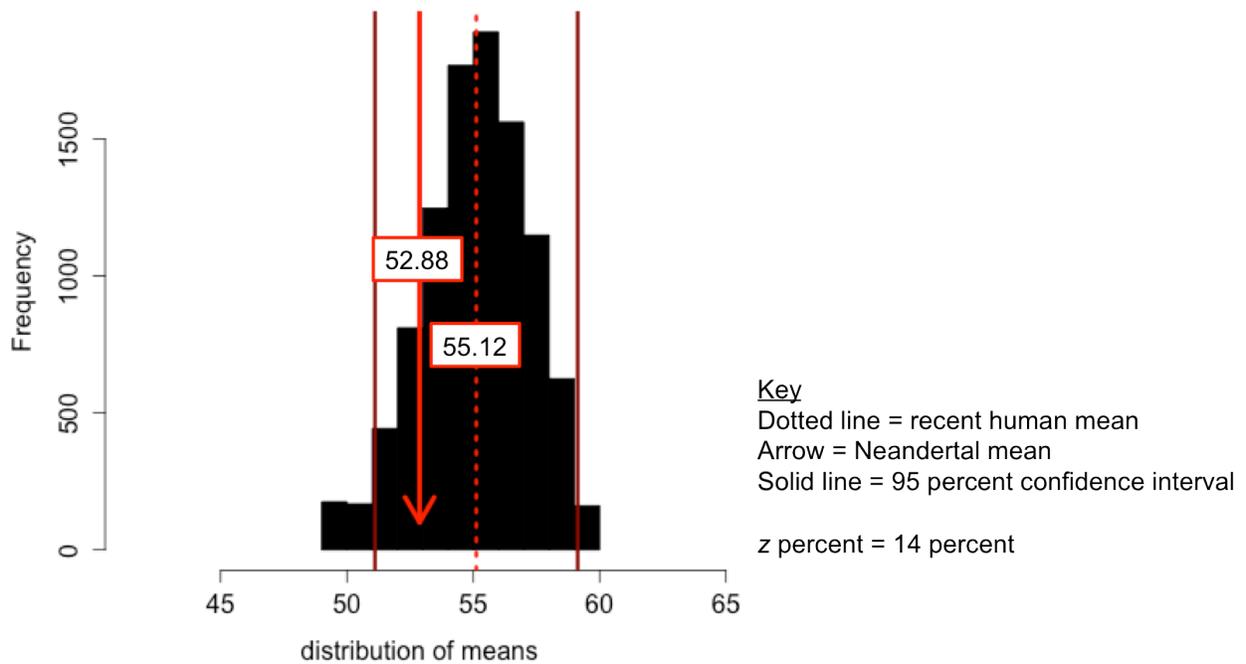
For the measurement superolateral acetabulum to inferior acetabulum, the Neandertal female mean is based on three individuals: Krapina 208, Krapina 209/212, and Tabūn C1. The results are illustrated in Figure 6.29. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

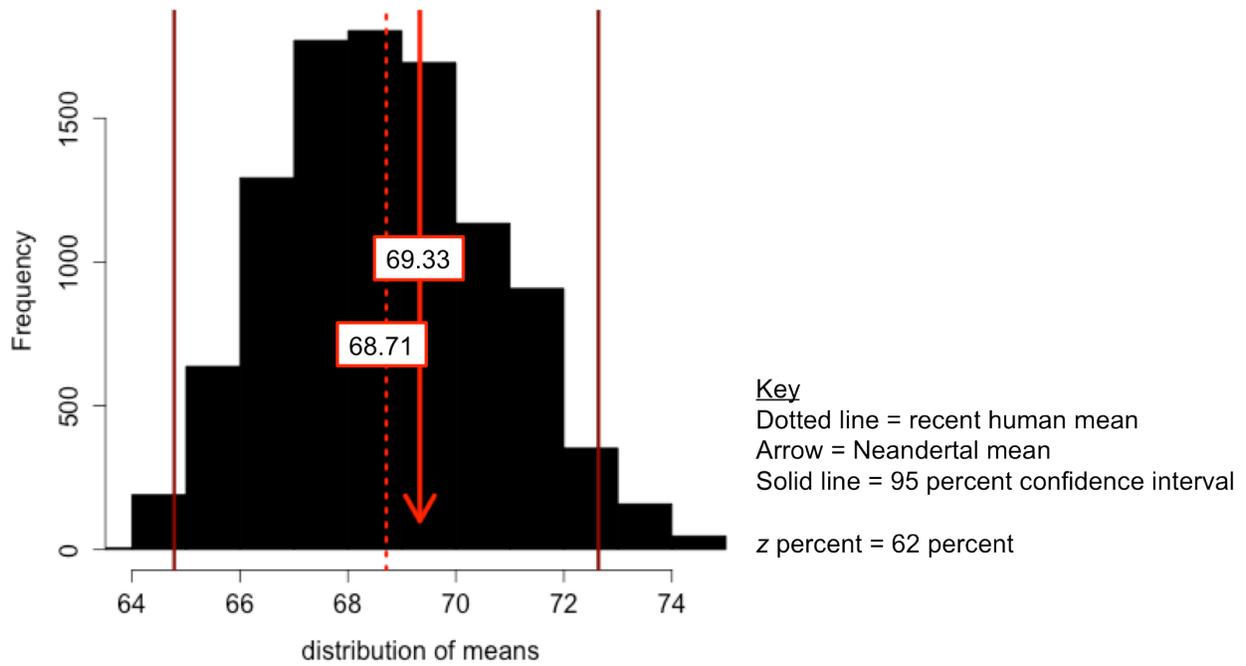*Figure 6.29: Superolateral acetabulum to inferior acetabulum results.*
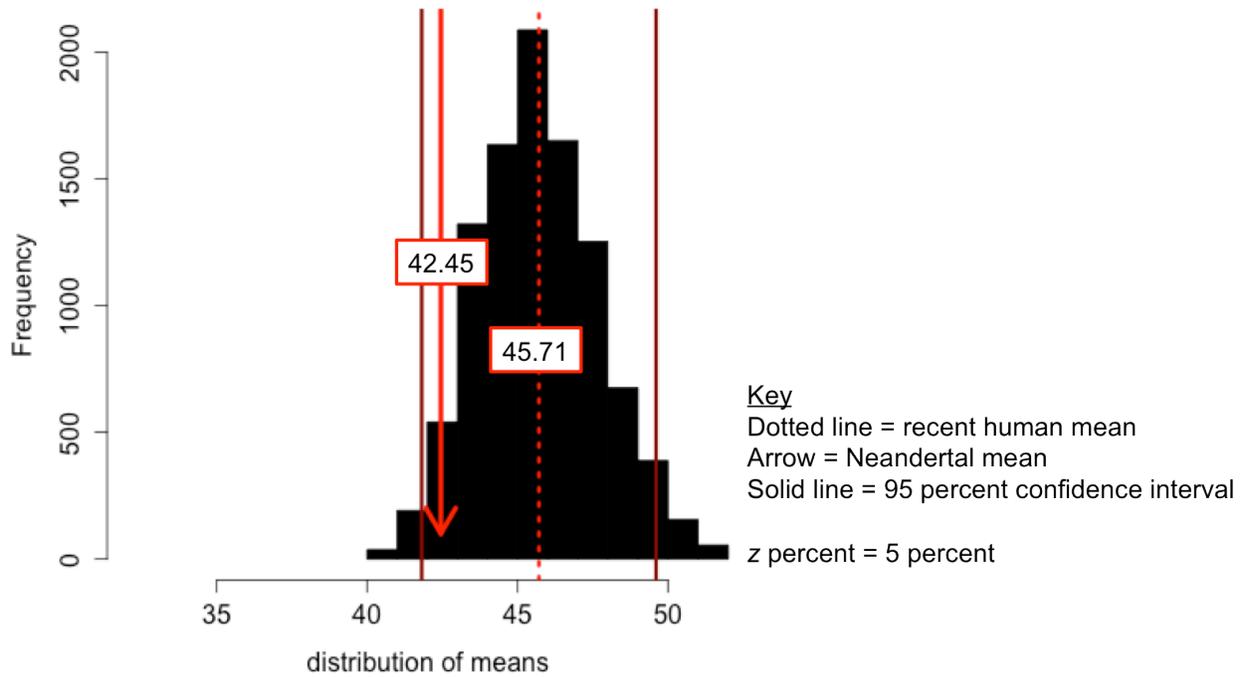
For the measurement lateral acetabulum to inferior acetabulum, the Neandertal female mean is based on three individuals: Krapina 208, Krapina 209/212, and Tabūn C1. The results are illustrated in Figure 6.30. There is a 95 percent probability that the Neandertal female mean is not significantly different than the recent human female resampled mean.

Figure 6.30: Lateral acetabulum to inferior acetabulum results.
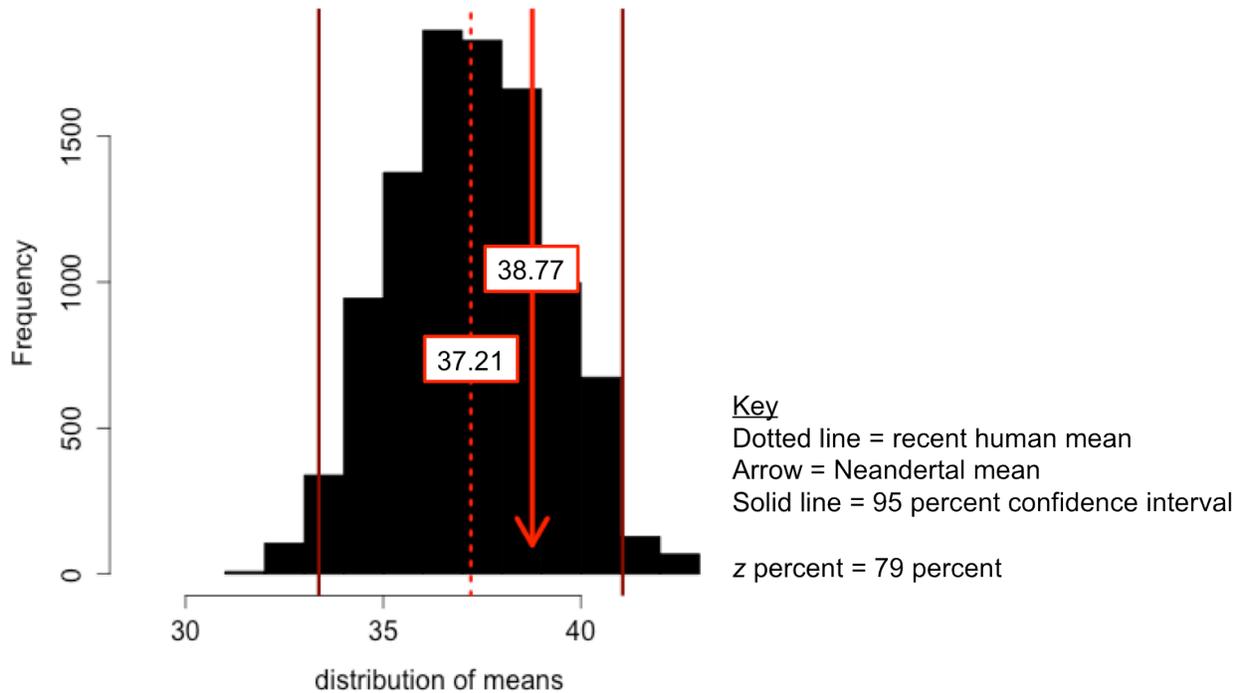
Conclusion

This study compares the Neandertal female mean for a measurement to a generated distribution of similarly sized subsamples drawn from a larger cold adapted recent human comparative sample. By comparing the pelvic measurements available in the female Neandertal sample that relate to the true pelvis, which frames the birth canal, the null hypothesis that there is no significant difference in female Neandertal pelvic dimensions compared to recent human females can be tested. The results given in this chapter demonstrate that generally, this hypothesis must be rejected: 15 of the 30 measurements tested were found to be significantly different in Neandertals. Of these, Neandertals were larger than recent humans for eight measurements and smaller for seven. The implications these results may have for understanding the evolution of childbirth will be discussed in the following chapter. However, the raw results

support the hypothesis that the pelvic morphology that may affect the birth process differs between Neandertals and recent humans, as signified by female pelvic morphology.

Chapter 7: Discussion

Introduction

In this chapter, I evaluate the results of my analysis and examine whether and how the measurements that differed in Neandertal females impact the birth process. In general, the null hypothesis of no difference is rejected, as differences in pelvic dimensions were observed between Neandertal females and cold adapted recent human females.

Here, I describe how these differences could have affected pelvic shape, particularly as it relates to the three planes of the bony birth canal (inlet, midplane, and outlet). I found that many of the differences observed could be explained using the Neandertal pelvic morphology model predicted for the male Kebara 2 pelvis (Rak 1990; Rak and Arensburg 1987). I also explain that my analysis did not correct for body size because Neandertal females were larger than the cold adapted recent human females for only half of the measurements that were found to be different. Based on this result, I determined that reducing the female Neandertal sample by correcting for body size was not warranted.

I then hypothesize how the differences in pelvic shape may be interpreted to affect birth, using the evolutionary models of birth described in Chapter 2. The obstetrical dilemma model could explain the observed pelvic differences as being the result of locomotor differences between Neandertals and cold adapted female recent humans. The ecological variation model could predict that an ecological factor, such as nutrition, affected pelvic shape in Neandertals. The energetics of gestation and growth model could indicate that differences in Neandertal birth canal shape are the result of differences in neonatal cranial size or shape. While the differences in pelvic morphology found between female Neandertal and cold adapted recent human females do not directly demonstrate differences in the birth process, they can be used to form hypotheses about Neandertal birth that are based on the dimensions of all female Neandertal pelvic remains available.

Testing the null hypothesis

This study was designed to test a null hypothesis concerning differences in pelvic shape and size between female Neandertals and cold adapted female recent humans, to add quantitative information to discussions of the Neandertal birth process. To address the issue of obstetrical differences, I compared relevant female pelvic morphology in Neandertals to an appropriate sample of cold adapted female recent humans. This comparison tested the null hypothesis that there is no significant difference in female pelvic morphology between Neandertals and recent humans. I argued that if this hypothesis could not be disproved, it would imply that differences in the birth process could not be established.

Based on the results (given in Chapter 6) of the bootstrap resampling analysis, the null hypothesis is rejected. For 15 of the 30 measurements analyzed, Neandertal females were significantly different than the recent human Ipiutak females. However, the linear measurements considered only represent two dimensions on the *os coxae,* which means that the direction the difference takes is still unknown. For example, in Neandertals the distance between the lateral acetabulum and the anterior inferior iliac spine is smaller than it is in the cold adapted female human sample; however, this single dimension only demonstrates that these two features are closer to each other, not whether the acetabulum is more anterior or lateral relative to the spine in Neandertals. This reflects a limitation of the female Neandertal fossil record, which does not preserve enough portions of the pelvis to allow for orientation to be tested directly. In the discussion below, I therefore use the differences demonstrated by the measurements analyzed to hypothesize how they might have affected female Neandertal pelvic size and shape.

How Neandertal female pelves were larger than Ipiutak

The measurements for which Neandertal females were significantly larger than the Ipiutak females are illustrated in Figure 7.1. These measurements demonstrate that Neandertal female pelves differed from the cold adapted female recent human sample in the orientation of the iliac blade, the dimensions of the acetabulum, and the orientation of the ischium.

Figure 7.1: Illustrations of all measurements that were significantly larger in the female Neandertal sample compared with the Ipiutak sample. Figures traced and modified from White et al. (2012). A. lateral view, B. medial view, and C. superior view.
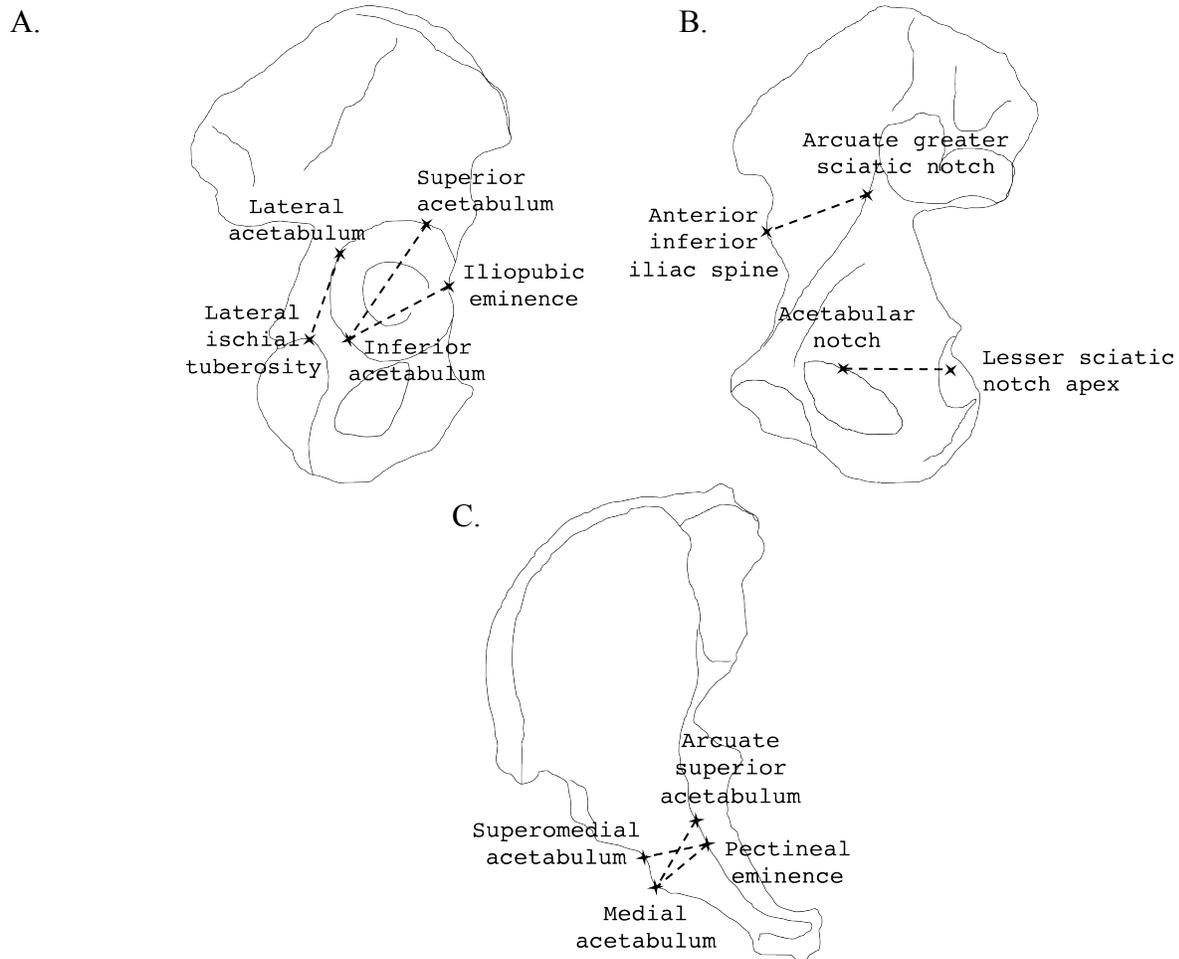
The measurement anterior inferior iliac spine to arcuate greater sciatic notch shows that in Neandertal females the anterior ilium was further away from the greater sciatic notch than in the Ipiutak females. This may reflect a longer iliac blade in Neandertals, or a more flared iliac blade. Increasing the angle of flaring for the iliac blade would move the anterior inferior iliac spine further away from the greater sciatic notch without increasing the anteroposterior depth of the ilium. Based on the Kebara 2 male pelvis, Rak and Arensburg (1987) and Rak (1990) describe Neandertals as having more flared iliac blades than recent humans, so this result is not unexpected.

Most of the measurements that were larger in Neandertals relate to the acetabulum. The following measurements reflect the increased height of the acetabulum: inferior acetabulum to

iliopubic eminence and superior acetabulum to inferior acetabulum. These measurements reflect the increased depth of the acetabulum: medial acetabulum to arcuate superior acetabulum, medial acetabulum to pectineal eminence, and superomedial acetabulum to pectineal eminence. The large size for these measurements indicates an increased surface area for the femoroacetabular joint, which has been related to body mass (Ruff 1994).

The following two measurements relate to how the ischium is oriented relative to the acetabulum: lateral acetabulum to lateral ischial tuberosity and acetabular notch to lesser sciatic notch apex. Increasing the distance between the lateral acetabulum and ischial tuberosity would change the orientation of these two features. If the ischial tuberosity orientation changes, this could reflect a change in the outlet, though the exact characterization of this change cannot be determined. The outlet may be moved further from the midplane, but keep the same shape. This might complicate how the shoulders pass through the midplane. This measurement may indicate that the outlet also could be larger (if the ischial tuberosity is located more laterally) or smaller (if the ischial tuberosity is located more medially). Conversely, this measurement may reflect a difference in the orientation of the acetabulum. In their description of the Kebara 2 pelvis, Rak and Arensburg (1987) predicted more laterally placed acetabula relating to the anterior placement of the pelvic aperture. According to these authors, this would have potential implications for Neandertal locomotion. The second measurement relating to the orientation of the ischium increases the distance between the lesser sciatic notch and the acetabular notch. The lesser sciatic notch apex can be used as a proxy for the ischial spine, which defines the midplane boundary but does not preserve in the Neandertal female fossil record. Increasing this distance cannot be explained by a more lateral orientation for the acetabulum; such an orientation would suggest that this dimension would be smaller in Neandertals. Instead, increasing this distance may indicate that the position of the ischial spine differed in Neandertals, which would certainly affect the pelvic midplane. However, without a more complete female Neandertal pelvis (or at least one preserving this dimension and a sacrum), how the ischial spine was positioned in Neandertal females cannot be determined. It is possible that it was moved more laterally, increasing the transverse diameter of the midplane in Neandertal females, similar to what was predicted in the Weaver and Hublin (2009) reconstruction of Tabūn C1. It also could be that the ischial spine was moved posteriorly, increasing the anterior space of the Neandertal midplane, but not the width. This might have implications for the birth process in that it would likely

further encourage occiput anterior presentations in Neandertal neonates, but this interpretation does not explain why the ischial spine position differs in cold adapted female recent humans.

In summary, the dimensions that are significantly larger in the Neandertal sample reflect differences in body size, acetabulum orientation, or the make-up of the midplane and outlet. Only two of the eight measurements can be potentially related to birth canal dimensions, and there is a chance that they instead influence locomotion without causing differences in the birth process. The minimum birth-related conclusion that can be drawn from the dimensions discussed here is that there was likely some difference in the shape or size of the Neandertal midplane.

How Neandertal female pelves were smaller than Ipiutak

The measurements for which Neandertal females were significantly smaller than the Ipiutak females are illustrated in Figure 7.2. These measurements demonstrate that Neandertal female pelves differed from the cold adapted female recent human sample in the flaring of the iliac blade, the orientation of the acetabulum, the orientation of the sacrum, and the dimensions of the iliopubic ramus relative to the cold adapted female recent human pelvis.

Figure 7.2: Illustrations of all measurements that were significantly smaller in the female Neandertal sample compared with the Ipiutak sample. Figures traced and modified from White et al. (2012). A. lateral view, B. medial view, and C. superior view.
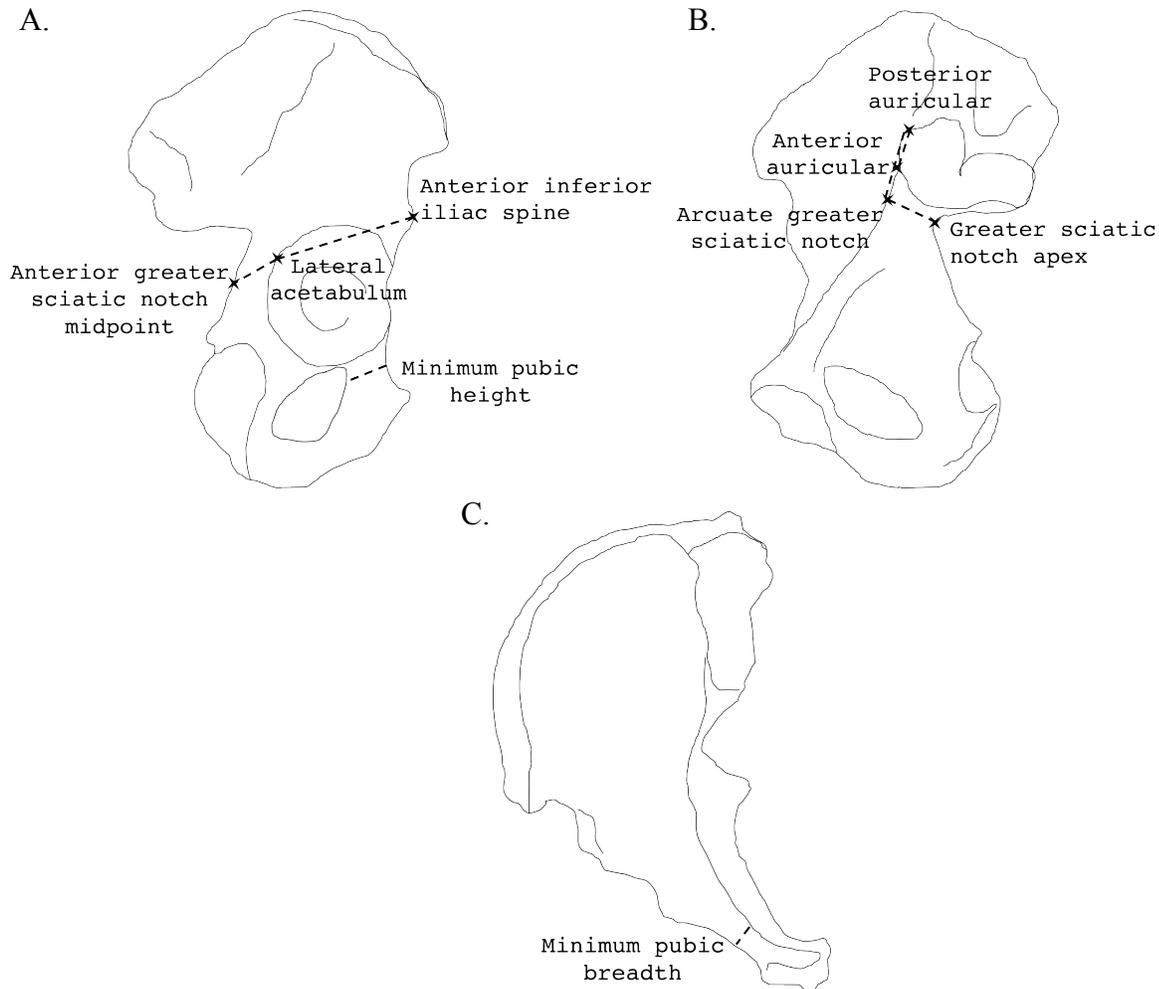
The measurement lateral acetabulum to anterior inferior iliac spine indicates that the female Neandertal ilium was more flared than that of the Ipiutak females. This supports one of the interpretations of the larger anterior inferior iliac spine to arcuate greater sciatic notch measurement discussed above, as well as the prediction of a more flared ilium made by Rak and Arensburg (1987) for Kebara 2. Increasing the flare of the iliac blade would move the anterior margin of the iliac blade, including the anterior inferior iliac spine, laterally and somewhat inferiorly relative to the acetabulum. This would lead to the anterior inferior iliac spine being closer to the lateral edge of the acetabulum than it is in cold adapted female recent humans. As discussed above, this also would move the anterior inferior iliac spine further away from the greater sciatic notch and the portion of the arcuate line closest to it. Based on these two measures

and the morphology of Kebara 2, it is very plausible that Neandertals, both male and female, had more flared ilia than female recent humans.

The measurement lateral acetabulum to anterior greater sciatic notch midpoint reflects a difference in the orientation of the Neandertal acetabulum. Decreasing this dimension suggests that Neandertal females had more laterally oriented acetabula than the cold adapted female recent human sample, which is what was predicted for male Neandertals based on Kebara 2 (Rak and Arensburg 1987). Alternatively, this measurement could potentially indicate a larger greater sciatic notch width for female Neandertals relative to the female Ipiutak, however it would be unexpected for Neandertal females to have extremely wide notches given that Neandertal males have very relatively narrow notches compared with recent human samples (personal observation). Based on my personal observations of notch shape across recent human populations, I can attest that while there is variation in this feature between populations, typically an increase (or decrease) in width in one sex is accompanied by a complementary increase (or decrease) in the other (see also Walker 2005). Therefore, for Neandertal females to have extremely wide greater sciatic notches compared to the recent human female sample, I also would expect a wider notch in male Neandertals, which does not occur. It is more likely that the reduction in this dimension reflects the acetabulum moving posterolaterally in Neandertals relative to the recent human form, and not a difference in greater sciatic notch width.

The decrease relative to the Ipiutak female pelves for the measurements anterior auricular to posterior auricular, arcuate greater sciatic notch to posterior auricular, and arcuate greater sciatic notch to greater sciatic notch apex indicate a difference in the position of the sacrum in Neandertal females. This, too, was predicted by Rak and Arensburg (1987) based on the morphology of Kebara 2, yet this is the first time it has been shown in female Neandertals, for which no sacrum is preserved. The decrease in the breadth of the auricular surface indicates that the sacroiliac joint was small; this is discussed further in the body size section below. The orientation of the arcuate greater sciatic notch to the posterior auricular surface and to the greater sciatic notch apex demonstrates a difference in the placement of the sacrum. The former indicates that the sacrum is placed anteriorly, closer to the greater sciatic notch apex. The latter indicates that in addition to being located more anteriorly in Neandertals, the sacrum rotates to push the greater sciatic notch apex closer to the arcuate line. An anteriorly placed sacrum, combined with longer iliopubic rami, suggests that the pelvic inlet is more anteriorly placed in

Neandertals (see also Rak and Arensburg 1987). This does not necessarily indicate a difference in the shape or size of birth canal planes. However, the rotated sacrum may decrease the anteroposterior dimensions of the midplane and outlet if sacrum morphology does not account for this difference.

The measurements minimum pubic height and minimum pubic breadth indicate that like Kebara 2, Neandertal females had an iliopubic ramus cross-section that was smaller than that of cold adapted female recent humans. In Kebara 2, this is associated with a longer pubis overall; though since a long pubis is seen in female recent humans without the cross-sectional area reducing so dramatically, it is uncertain whether these features are linked. If they are, this may indicate that total iliopubic length (which can not be adequately measured on any of the female Neandertals, though Tabūn C1 comes close to preserving enough of the pubic body for this measurement to be taken) was longer in Neandertal females compared to recent human females. This would suggest that like Kebara 2, the pelvic aperture (or birth canal) in female Neandertals is positioned more anteriorly than it is in female recent humans. If Neandertal females have longer iliopubic rami than Neandertal males (see Chapter 4 and Rosenberg 1988), this also may indicate that they had a larger pelvic inlet than humans.

To summarize, the pelvic measurements that are smaller in Neandertal females compared to the Ipiutak female sample mimic the differences predicted by the Kebara 2 pelvis. This demonstration that the morphology that distinguishes Kebara 2 from female recent humans also applies to Neandertal females may indicate that pelvic shape is not driven by obstetrical adaptations, though it does not preclude them from affecting the Neandertal birth process. The dimensions that seem most relevant to the birth canal dimensions (based on the three pelvic planes) do not clearly demonstrate birth differences between the samples. My results show that the female Neandertal inlet is likely anteriorly placed relative to its position in female recent humans, based on the sacrum position. The dimensions of the inlet may differ depending on how iliopubic ramus cross-section size relates to iliopubic ramus length: the iliopubic results from this study could indicate that the inlet was wider transversely, deeper anteroposteriorly, or identical in size compared to the cold adapted female recent human sample. The results presented above demonstrate that the Neandertal midplane differed in shape from humans, based on the positions of the ischial spine and sacrum. What particular form the Neandertal midplane took is less certain; it could have been wider mediolaterally, shaped similar to humans but with the widest

dimension being more posteriorly located, and/or shortened anteroposteriorly. The results suggest that the female Neandertal outlet also differed from female recent humans. Based on the ischium, the outlet may have been either mediolaterally wider or narrower; based on the combination of the sacrum position and the length and orientation of the pubis, the outlet may be anteroposteriorly similar, shorter, or longer to that of recent humans. Overall, the results demonstrate the existence of differences between recent human and Neandertal female pelves that could affect the shape of the obstetrically relevant pelvic planes. However, what shape those differences indicate for each plane in Neandertal females can only be hypothesized. In the rest of this chapter, I will consider what I found to be the most plausible hypothesis of female Neandertal pelvic shape based on these results, and describe what I envision to have been the Neandertal birth process.

Implications of body size

The analysis presented in this study does not correct for body size for three reasons. First, of the 15 measurements where Neandertal females were significantly different than the cold adapted female recent human sample, Neandertals were found to be significantly larger for half of them, and smaller for the other half. This indicates that the differences found in the female Neandertal pelvis cannot be explained by their being significantly larger or smaller in mass compared with recent human females. Second, Neandertal females had significantly larger femoroacetabular joints (based on the measurement superior acetabulum to inferior acetabulum), but significantly smaller sacroiliac joints (based on the measurement anterior auricular to posterior auricular). Of the areas of the pelvis that may relate to body size, in the absence of bi-iliac breadth (which is not available for any Neandertal female), these joint surfaces are the best proxy for body mass because the weight of the upper body is supported at these joints (Ruff 1994). The conflicting findings from these surfaces in the present study suggest that there may be variation in body size for female Neandertals, as each joint surface is measured on different female Neandertal individuals. In any case, they do not conclusively show that Neandertal females were larger (or smaller) than the cold adapted female recent human sample. Finally, correcting for body size would reduce the female Neandertal sample from six individuals to four. I determined that the results of the raw analysis (given in Chapter 6) do not support correcting for body size, and that given this fact, limiting the sample used in the analysis is unmerited.

Interpretations of birth

While direct knowledge about the shape and size of the Neandertal birth canal is unavailable from the current Neandertal sample, it is still possible to apply the differences in pelvic measurements found in this study to the evolutionary models about birth described in Chapter 2. This project was not designed to test these models, nor do I think that it is possible to test these models based on the current fossil record. What follows is a theoretical exercise that demonstrates possible implications of this study for future discussions of hominin birth evolution. If more complete female Neandertal fossils are discovered in the future (which may include the Palomas 96 pelvis once it is available for study), it may become possible to test the hypotheses developed here.

The obstetrical dilemma model predicts that changes in pelvic anatomy reflect selective pressures for changes in locomotion. Under this model, the differences found between the Neandertal and cold adapted female recent human samples would imply that there are locomotor differences between Neandertal and recent human females. This supports the hypothesis proposed by Rak and Arensburg (1987), who predict that the pelvic morphology of Kebara 2 reflects differences in locomotion and posture between Neandertals and recent humans. Therefore, it may be that the observed pelvic differences, regardless of how they actually affect childbirth, may be caused by differences in locomotion.

When it comes to Neandertal birth, if the female Neandertal pelvis included three transversely wide planes, as some of the results here may indicate, the pelvis may be characterized as platypelloid. This was how the pelvis of *Australopithecus afarensis* was characterized (Tague and Lovejoy 1986). If this is the form also found in Neandertal females, then this may be the primitive pelvic shape in hominins, with *Australopithecus africanus* and either *Homo erectus* or *Paranthropus* species (whichever the Gona pelvis ends up being) having derived pelvic forms. However, when it comes to birth, it is important to note that *Australopithecus afarensis* birthed a much smaller neonate than Neandertals. A platypelloid shaped pelvis in Neandertals, who were birthing a recent human sized neonate, would have complicated birth, as predicted by Weaver and Hublin (2009) based on their platypelloid shaped reconstruction of Tabūn C1. As for affecting locomotion, a wide inlet combined with flared ilia would increase the overall width of the pelvis. Increasing the width of the pelvis previously has been predicted to decrease locomotor efficiency (Lovejoy 1975; Lovejoy et al. 1973), though

studies on recent humans testing this prediction have found no difference in locomotor efficiency associated with different pelvic widths (Dunsworth et al. 2012; Lewton 2012; Warrener 2011). This may suggest that musculature elsewhere in the lower limb accommodates for the locomotor efficiency caused by different pelvic morphology.

The obstetrical dilemma model predicts that the increased size of the Neandertal neonate compared with earlier hominins and pelvic morphology adapted for walking bipedally both constrain the Neandertal birth process. However, as shown above, it is possible to argue that Neandertals had a birth canal that would have made birthing a large-brained neonate more difficult (Tague 1992), and that the overall pelvic morphology may have been less efficient for walking (Lovejoy 1975; Lovejoy et al. 1973). However, the results from this study fit the predictions Rak and Arensburg (1987) made based on the Kebara 2 pelvis. They suggest that the Neandertal pelvic morphology seen in Kebara 2 is best explained by posture or locomotor differences, though they do not elaborate further. Therefore, it could be that the pelvic differences between recent humans and Neandertals are due to differences in locomotion or posture. This would at least explain why these differences manifest similarly in both males and females; whereas an explanation driven by adaptations for birth would need a reason for why male pelves differ in these groups. I hypothesize that the obstetrical dilemma model is not mutually exclusive with the other evolutionary models for birth, and that while locomotor adaptations may affect some pelvic features, it is not necessarily the only explanation for Neandertal pelvic morphology.

The ecological variation model predicts that pelvis shape alters in response to ecological factors that may vary across populations, and that this alteration affects the birth process. Interpreted under this model, the results of the present study could suggest that the differences found are caused by some ecological factor affecting the Neandertal population relative to recent humans. Because I am comparing Neandertal females to a cold adapted female recent human sample, it is unlikely that the pelvic differences observed are the result of differing thermoregulatory adaptations. However, Weaver and Hublin (2009) suggested that Neandertals were not adapted to the cold, but that they had the ancestral form of the hominin pelvis. Instead, they suggested that the recent human pelvic form evolved in response to a hot environment, which narrowed it relative to the Neandertal form. This would imply that recent humans in general have narrow pelves, and that cold adapted female recent humans are not going to develop

the wide hips once seen in Neandertals. Thus, it may be possible for two hominins to have different reactions to a cold environment, which may explain how the differences found here could be caused by climate adaptations. I hypothesize that if an ecological factor explains the differences found in this study, it will not be climate since both samples were cold adapted. Wells et al. (2012) discussed the impact nutrition has on the pelvis. If the Neandertal pelvic morphology was indeed platypelloid shaped, that is a shape that in recent humans has been associated with rickets (see Chapter 2). Genetic studies have suggested that light skin color has evolved relatively recently (Mallick et al. 2013), after the end of the Pleistocene. Therefore, it is possible that Neandertals, as a group living in high latitudes and potentially without light skin, were more susceptible to rickets because they could not synthesize vitamin D from the sun. This would provide a very strong ecological pressure on pelvic shape that has been known to affect the birth process in recent humans who are similarly susceptible to rickets. However, this hypothetical scenario only would explain platypelloid shaped pelves in Neandertal females, not the less platypelloid shape associated with Kebara 2. Furthermore, the rest of the Neandertal skeleton does not show signs of rickets to support this model. While nutrition still may be part of the explanation for Neandertal female pelvic shape, thus supporting the ecological variation model, it is a topic that requires more research as the precise nature of how nutrition or other ecological factors affect Neandertal pelvic morphology is currently unclear.

The energetics of gestation and growth model predicts that obstetric dimensions of the pelvis have adapted to the typical size of the fetus when the pregnant female's body can no longer produce enough energy to sustain fetal growth. When this model is applied to the current study, it suggests that the only reason obstetrical dimensions would differ between Neandertals and recent humans would be if neonate size also differed. This would require either a longer gestation period (as predicted by Trinkaus 1984), faster growth (as predicted by Dean et al. 1986), or larger overall body size (as predicted by Rosenberg 1986, 1988). Ponce de León et al. (2008) predicted that Neandertal neonate size was similar to human neonate size, based on their reconstruction of the Mezmaiskaya infant cranium, which assumed a human-like growth rate. Future studies may show that this growth rate is incorrect, in which case a large Neandertal birth canal may predict a larger Neandertal neonate under the energetics of gestation and growth model. If the areas for the Neandertal birth canal planes are all similar to that of recent humans,

the energetics of gestation and growth model provides no explanation for the pelvic dimensions that differ between these groups.

Differences in the shape of the pelvic planes may be more relevant to the energetics of gestation and growth model than predictions about its size. Some of the measurements described at the beginning of this chapter suggest possible differences in the ratio of anterior to posterior space in each pelvic plane. The Neandertal inlet may be similar in shape to female recent humans (note that this is a different interpretation than the platypelloid pelvic shape interpretation used for the previous models), but may have a larger anterior space in the midplane. A larger anterior space may accommodate a differently shaped Neandertal fetal cranium. Adult Neandertal cranial shape differs from that of recent humans: instead of the largest cranial breadth being located superiorly and posteriorly on the parietal bones as it is in recent humans, it is located anteriorly and inferiorly on the parietal bones in Neandertals (Harvati 2007). This suggests that instead of the back of the head being wider, as it is in recent human fetuses, the Neandertal fetal head may have been wider toward the anteroposterior middle of the cranium (see Ponce de León et al. 2008). This means that a Neandertal fetus might rotate differently through a recent human birth canal. Instead of needing to rotate from transverse-facing to occiput anterior, to accommodate the larger posterior portion of the fetal cranium, the Neandertal fetus may have more flexibility and be able to rotate from transverse-facing to occiput posterior without the same negative consequences observed in recent humans. However, since the Neandertal female pelvis is not the same shape as a recent human female pelvis, the differences observed may be explained by the Neandertal fetal cranium shape. A larger anterior space in the midplane may accommodate a fetal cranium that is wider more anteriorly than what is seen in recent humans; this would still result in an occiput posterior presentation, even with the differently shaped cranium. The energetics of gestation and growth model supports this interpretation, though more research on the relationship between Neandertal fetal head shape and predicted maternal pelvic shape is needed.

I hypothesize that while it is possible for all three models to be affecting differences in the birth anatomy of Neandertal and recent human females, the pelvic differences identified by the current study are most likely related to the obstetrical dilemma and the energetics of gestation and growth models. The obstetrical dilemma model offers locomotion as an explanation for why pelvic morphology would change in both males and females. While this would affect both sexes,

it would have the potential to impact the birth process in females. The energetics of gestation and growth model suggests that neonatal size is determined by non-pelvic factors – in this case the metabolic requirements of the neonate compared to the energetic productivity of the mother – and that maternal pelvic morphology is only affected by birth in that it must be adapted to birth a full-term fetus. This sets up a scenario where major pelvic morphology differences between Neandertals and recent humans are explained by locomotion, but slight differences in the dimensions or shape of the bony birth canal can be explained as adaptations to birthing a Neandertal or recent human neonate.

Conclusion

The findings of this study show significant, quantifiable differences in female pelvic morphology between Neandertals and a cold adapted female recent human comparative sample. In this chapter, I described what these differences might mean for Neandertal pelvic shape. Many of the differences mimic those expected based on the shape of the male Kebara 2 pelvis (Rak and Arensburg 1986; Rak 1990). Some suggest differences to the makeup of the three birth canal planes. I hypothesize that the female Neandertal pelvis resembles the male Neandertal pelvis more than it does the recent human female pelvis. This hypothesis leads me to further suggest that Neandertal females had a differently shaped birth canal compared to recent human females. I hypothesize that that the birth process was identical to that of recent humans because the observed pelvic differences make it possible for a differently shaped neonate to be born via three rotations and in an occiput anterior presentation.

Of the three evolutionary models for childbirth considered, my hypothesis best fits a mixture of the obstetrical dilemma and the energetics of gestation and growth models. The obstetrical dilemma model predicts the pelvic morphology is shaped by different locomotor or posture adaptations, which is a hypothesis that still needs testing but could be true for Neandertal and recent humans. The ecological variation model requires an ecological factor to differ between the Neandertal and recent human samples that also affects pelvic morphology and therefore birth. Since both samples compared were cold adapted, it seems unlikely that this ecological factor would explain the differences observed. Nutrition may be a factor, but there is little evidence in the Neandertal sample to demonstrate that their pelvic form is directly influenced by diet. The energetics of gestation and growth model predicts that the maternal pelvis is shaped by the neonate in response to maternal energy constraints on the fetus. This

model allows for pelvic morphology in general to be shaped by posture differences, as was predicted for Kebara 2 by Rak and Arensburg (1986). It suggests that any birth differences are due to pelvic adaptations to birthing different shaped or sized fetuses. Under this model, the small differences between Neandertal and recent human neonates would cause slight differences in the birth canal of each group. Most of the differences in pelvic morphology may be driven by non-obstetric adaptations, per the obstetrical dilemma, but those that are birth-related stem from an adaptation to a particular type of neonate. Since this study shows that the female Neandertal pelvis mostly differs from recent human females in ways that are similar to how Kebara 2 differs from recent human males, I hypothesize that these differences are not driven by obstetrics. However, as discussed above, this does not preclude differences in the pelvis from reflecting differences in the birth process. The results of this study are most plausibly explained as pelvic adaptions to birthing a particular neonate combined with pelvic adaptions to a particular posture.

In conclusion, the pelvic differences observed in the female Neandertal sample can be characterized as changing the orientation of different pelvic features, as described at the beginning of this chapter. These linear measurements suggest differences in pelvic morphology, but do not demonstrate what the female Neandertal pelvic shape would have looked like. I hypothesize that the differences found are explained most plausibly by the female Neandertal pelvis resembling the male Kebara 2 pelvis as described by Rak and Arensburg (1987). They described Kebara 2 as having a pelvis that, relative to recent humans, has a pelvic aperture that is moved anteriorly relative to the iliac blades; this elongates the pubic bones, orients the acetabula more laterally, and moves the sacrum anteriorly. My findings may be used to support a similar pelvic shape for female Neandertals. Based on this predicted pelvic morphology, I further hypothesize what Neandertal birth would have been like. I suggest that Neandertals had the same birth process as recent humans, including three rotations and a neonatal head born in occiput anterior presentation. My reasoning is that the increased anterior space of the midplane indicated by my results and the Kebara 2 model would accommodate the differently shaped Neandertal neonatal cranium.

Chapter 8: Conclusion

The study presented here was designed to address Neandertal childbirth by systematically comparing female pelvic morphology between Neandertals and cold adapted recent humans. Based on the premise that Neandertal male pelves have a different morphology than recent human male pelves – which may be caused by locomotive or posture differences – I questioned whether the same was true for females, who in both groups were able to birth large brained bipedal neonates. I hypothesized that if female pelves also differed in morphology for these two groups, then it might be reasonable to expect differences in birth process. Future work will need to address the meaning of features that are similar in male and female Neandertals but differ in recent human females. Birth in recent humans is sometimes associated with high risks of maternal or infant mortality, and some have hypothesized that those risks are due to evolutionary compromises in pelvic morphology. Since Neandertals represent a relatively recent fossil hominin population, and since male Neandertals display differences in pelvic form, I was interested to know whether these same evolutionary compromises surrounding birth affected this group of ancient humans. Below I summarize the subject of each chapter in this study, to show how I approached this research question.

Chapter 1 provided a brief outline of this project. It set up the problem addressed in this study, the hypothesis to be the tested, the methodology to be used, the results found, and the interpretations made.

Chapter 2 focused on the recent human birth process. I described the cardinal movements and resulting fetal rotations associated with typical recent human birth. I discussed evidence supporting the view that recent human birth is a risky endeavor, and explained how variation in maternal pelvic morphology and neonate brain and body size could intensify or relieve these risks. I then presented three models that seek to explain the evolution of hominin birth. The obstetrical dilemma model predicts that selective pressures for bipedal locomotion drive hominin pelvic morphology, which leads to birth complications when neonates are large-brained or large-

bodied. This model has been used to explain why recent humans are born less cognitively developed than other primates, why birth attendants are nearly universal among humans today, and why most recent human births involve a rotating fetus that is born in an occiput anterior position. The ecological variation model predicts that bipedalism did not cause birth complications, instead ecological factors – such as a population's adaptations to a particular climate or their nutritional health – that arose after bipedalism affect pelvic morphology and birth. This model has been used to explain the potential increase in maternal and infant mortality associated with the emergence of agriculture. The energetics of gestation and growth model predicts that maternal energy production is the determining factor for when gestation ends, and therefore how large a fetus grows before it is born. This model suggests that obstetrically related pelvic morphology is an adaptation to average fetus size at the end of gestation.

Chapter 3 introduced Neandertals as an anatomically distinct population of ancient humans living in Europe and West Asia during the Late Pleistocene. I described the Neandertal sites relevant to this study, including Kebara (Israel), Tabūn (Israel), Krapina (Croatia), La Ferrassie (France), and Sima de las Palomas (Spain). I then presented the various hypotheses about Neandertal birth that have been proposed by previous researchers, There is a limit to how well these previous hypotheses can be tested given the Neandertal pelvic sample. Hypotheses were typically based on either limited evidence from the female Neandertal sample (e.g., long iliopubic ramus implies a larger birth canal), reconstructions of the most complete Neandertal female pelvis (i.e., Tabūn C1, which does not preserve the posterior pelvis), or inferences made based on the most complete Neandertal pelvis (i.e., Kebara 2, a male whose anatomy is therefore not adapted to obstetrics). Based on the problems with these types of hypotheses, I proposed a more systematic study that provides a basis for discussing Neandertal birth by first determining whether female pelvic anatomy differs between Neandertals and recent humans, a fact that had not previously been established. My project was designed to test the null hypothesis that there are no significant differences in female pelvic morphology between Neandertals and a cold adapted recent human sample.

Chapter 4 details how this null hypothesis was tested. First, I applied sex estimation techniques developed for recent humans to the Neandertal sample and found that the only reliably sexually dimorphic features were greater sciatic notch width and acetabulum height. Using these, I assessed the Neandertal pelvic fossils to identify eight females. Based on the

preservation of these eight, I developed 30 measurements that could each be taken on at least two Neandertal females and that related to the size and shape of the true pelvis. I then described how these measurements were taken on the female Neandertals and on a cold adapted recent human female sample, and these results compared using a bootstrap resampling approach. This approach compared the small female Neandertal sample size for each measurement to a generated distribution of recent human subsamples. The Neandertal sample and each of the recent human subsamples were identical in size, making the comparison more appropriate than if the groups were compared directly using more common statistical tests. I determined that if the mean of the Neandertal sample fell outside of 95 percent of the recent human subsample means, the null hypothesis would be rejected for that measurement.

Chapter 5 presented the Neandertal sample. For reference, I started by describing the most complete Neandertal pelvis that has been found, Kebara 2. Although this is a male, and therefore not appropriate for addressing questions of birth, Kebara 2's pelvic form is the best evidence available for what Neandertal pelves in general looked like. I then described each of the eight female Neandertal pelvic fossils, detailing their preservation and morphology. I described the Palomas 96 pelvis, though I explained that this individual was excluded from the statistical analysis because at the time of study it was still covered in too much breccia to make measuring it possible. I ended the chapter by describing the Ipiutak recent human sample. This sample was chosen because like the Neandertal sample it represented a cold adapted recent human population.

Chapter 6 presented the results of the statistical analysis comparing the female Neandertal and female Ipiutak samples for each of the 30 measurements. The results demonstrated that 15 of the 30 measurements had Neandertals falling outside of the 95 percent confidence interval for the recent human distribution of subsamples. Of these 15 measurements for which the null hypothesis was rejected, the Neandertal mean was significantly larger than the Ipiutak subsample means for eight of the measurements and smaller for seven measurements.

Chapter 7 discussed the implications of these findings. Overall, the null hypothesis was rejected, as the female Neandertal and female recent human samples differed for some pelvic measurements. However, although differences were identified, how those differences for individual metrics translated to differences in pelvic shape was less certain. I described the possible ways linear measurement differences could translate into shape or size differences in the

birth canal. Most of the differences fit the model predicted by Rak and Arensburg (1987) for the pelvic morphology of the male Kebara 2 pelvis, suggesting that Neandertal female pelves may differ from recent human pelves in the same ways that Kebara 2 differs from recent humans (i.e., Neandertals in general have a flared, posteriorly placed iliac blade and a longer iliopubic ramus relative to recent humans). While many of the measurements that were different could affect the dimensions of the three birth canal planes, this analysis could not confirm which differences (if any) were found in Neandertal females. Instead, I hypothesized what a Kebara 2-like Neandertal female pelvis that differed from recent human female pelves for the measurements tested in this study would look like. I hypothesize that the pelvic morphology of Neandertals, since it likely affected both male and female pelvic shapes, was not driven by selection for obstetric constraints. Instead, I speculated that if pelvic differences affecting both sexes had any impact on birth, it was likely a secondary response to adapt the internal true pelvis (or birth canal) to the size and shape of the neonatal cranium. This, I suggested, fits the predictions of the energetics of gestation and growth model, with some influence from the criteria of the obstetrical dilemma model. The former predicts that pelvic morphology does not determine the timing of birth, but instead that the size of the neonate shapes the bony birth canal. The latter predicts that pelvic morphology is shaped by locomotor or posture requirements, that constrain birth to varying degrees. Future studies should test whether locomotor differences explain the pelvic differences found in Neandertals; it certainly seems like a plausible hypothesis. If so, there would be some general pelvic constraints on birth that might explain any differences found in the bony birth canal due to the energetics model. I suggest that these two models together explain the different pelvic morphology found in Neandertal females compared with cold adapted recent human females.

In conclusion, this study confirmed differences in pelvic morphology for Neandertal and recent human females, similar to what had already been demonstrated for males. A future direction of this research will be to test the same hypothesis for male Neandertals compared to a cold adapted sample of male recent humans. This would be one way of confirming that Rak and Arensburg (1987) were correct about their explanation for Neandertal pelvic differences. Importantly, the present study shows that Neandertal females were more similar to Neandertal males than to females today, which indicates that these groups were not responding to selective pressures for a single obstetrically beneficial pelvic form that persists today. Some of the

morphological differences found have the potential to affect the shape or size of the birth canal, which may suggest that Neandertals had a different birth process than humans today. I hypothesize that these findings are best interpreted using a mixture of the obstetrical dilemma model and the energetics of gestation and growth model. In the future, should a more complete female Neandertal pelvis be discovered, it can be used to test the accuracy of this study's conclusions. In the meantime, I urge paleoanthropologists to approach the topic of Neandertal birth cautiously, as how Neandertal female pelvic features relate to each other to form the birth canal remains uncertain, even in light of the differences in pelvic morphology identified here.

Appendix 1: R program

Below is the R program used for this analysis. In R, the "#" symbol is used to denote comments on the code. For ease of reading, I have made the commented text green. This program was written in the integrative development environment (IDE) RStudio, which uses the computing package R (R Core Team 2013; RStudio 2014).

```
############################################################
# Written by: Caroline VanSickle
# Created on: 13 Jul 2014
# Packages installed:
#    Base: datasets, graphics, grDevices, methods, stats, utils.
#    Non-Base: dplyr.
#
# Description: This script includes all of the analyses
described in the dissertation thesis VanSickle (2014). Briefly,
the analyses are:
# 1.) Test whether the human sample size includes enough
variation to be informative.
# 2.) For each measurement, resample the recent humans using
group sizes identical to the Neandertal females. Then compare
the mean of those recent human resamples to the original
Neandertal sample mean by calculating the probability of the
Neandertal mean being larger than the recent human subsample
means.
############################################################

################ Define variables and functions ###############
```

```r
# Set the working directory.
  setwd("~/");
# Load the CSV data. In this file, each row is a different
individual. Column 2 = Recent Human or Neandertal; Columns 3+:
values for one of 30 measurements.
  data <- read.csv(".csv",header=TRUE);


# Load non-base packages.
  library(dplyr);


# Create new folder for saved results.
  setwd("~/Results/");
  dir.create(paste("~/Results/",Sys.time()));
  x<-list.dirs();
  setwd(x[length(x)]);


### Function used to structure data and define variables:
  # Input: .csv file, number representing the measurement being
isolated (1 = first measurement, 2 = second measurement, etc.),
label for group to be included (e.g., "Neandertal" or "Recent
Human").
  # Output: list of values for one measurement (i) for
individuals matching the label.
dataOrg <- function (csvFile,i,label) {
  x <- filter(csvFile,Hum.Nean==label);
  x <- x[,i+2];
  x <- na.omit(x);
  return(x);
  };


### Function used to resample a group:
```

```r
  # Input: large sample, small sample, number of repetitions.
  # Output: vector of the resampled means.
resample <- function (large,small,reps) {
  x <- numeric();
  for (iter in 1:reps) {
    x <- c(x,mean(sample(large,length(small),replace=FALSE)));
    iter+1;
    };
  return(x);
  };


### Function to calculate z:
  # Input: resample results, small sample to compare
  # Output: z value that can be turned into a percentage with z
table
calculate.z <- function (resampledlarge,small){
  z = (mean(small)-mean(resampledlarge))/sd(resampledlarge);
  return(z);
  };


### Function to create a histogram:
  # Input: resampled results from large sample, small sample, i
(# measurement), title for histogram.
  # Output: histogram.
hist.resample <- function (resampledlarge,small,title) {
    mSm <- mean(small);
    mLg <- mean(resampledlarge);
    allData <- c(small, resampledlarge, mSm, mLg,
mLg+2*sd(resampledlarge), mLg-2*sd(resampledlarge));
        resampledHistogram <-
hist(resampledlarge,breaks=10,freq=TRUE,col="black",main=paste(t
```

```r
itle),xlab="distribution of
means",xlim=c(min(allData),max(allData)));
        abline(v=mLg, col = "red",lwd=3, lty=3);
        abline(v=(mLg+1.96*sd(resampledlarge)),col="dark red",
lwd=3);
        abline(v=(mLg-1.96*sd(resampledlarge)),col="dark red",
lwd=3);
        arrows(x0=mSm, y0=100, x1=mSm,y1=10000,
code=1,lwd=4,col="red");
  return(resampledHistogram);
  };


# Set parameters:
  reps=10000;
  nMeas=ncol(data)-2; # Number of measurements


########## Test 1: Human Sample Size Appropriateness #########
# Define data frames that will save the results.
  resMean <- data.frame();
  resSD <- data.frame();
  resSE <- data.frame();
for (i in 1:nMeas) {


# Structure data:
  # Define vector that includes all recent human (Ipiutak)
measurements.
  ipiHum <- dataOrg(data,i,"Human");


  # Add measurement labels to results data frames.
  resMean[i+1,1] <- colnames(data)[i+2];
  resSD[i+1,1] <- colnames(data)[i+2];
  resSE[i+1,1] <- colnames(data)[i+2];
```

```r
for (iter in 0:length(ipiHum)) {

    # Name columns in results data frames.
    resMean[1,2+iter] <- paste("Mean for N=",length(ipiHum)-
iter);
    resSD[1,2+iter] <- paste("SD for N=",length(ipiHum)-iter);
    resSE[1,2+iter] <- paste("SE for N=",length(ipiHum)-iter);


    # Generate a resampled distribution from the sample given.
    if (length(ipiHum)>=23-iter){
      newSample <- sample(ipiHum,(length(ipiHum)-
iter),replace=FALSE);


    smSam <- c(1,2); #same number of individuals as Neandertal
sample, values do not matter.
      if (length(newSample) < length(smSam)) {
        smSam = newSample;
      } else {
        NA;
      };


      # Test sample.
      x <- resample(newSample,smSam,reps);
      resMean[i+1,2+iter] = mean(x); # Mean of resampled
distribution.
      resSD[i+1,2+iter] = sd(x); # Standard deviation of the
distribution.
      resSE[i+1,2+iter] = sd(x)/length(x); # Standard error of
the distribution.
    } else {
      NA;
    };
```

```r
  };


  # Export a plot the standard deviation results for all sample
sizes. These plots are available in Appendix 3.
    y <- as.numeric(rev(resSD[i+1,2:24]));
    png(paste('SampleSizeMeas',i,'.png'));
    plot(y, main=paste("Variation in SD
for",resSD[1+i,1]),xlab="Sample Size",ylab="Standard
Deviation",pch=20);
    dev.off();
  };


######### Test 2: Compare Neandertals and Recent Humans ########
# Define data frame that will save the results.
  resResampling <- data.frame();
  labels <- c("Measurement","Neandertal Mean","Human Mean","z-
score","probability","Test H0","# Reps");
  for(i in 1:length(labels)){
    resResampling[1,i] <- labels[i];
  };
  resResampling[2,7] = reps;
for (i in 1:nMeas) {

  # Structure data.
  resResampling[i+1,1] <- colnames(data)[i+2];
  ipiHum <- dataOrg(data,i,"Human");
  neand <- dataOrg(data,i,"Neandertal");

  # H0: No difference between Recent Human and Neandertal
samples.
  if(length(ipiHum)>length(neand)) {
```

```r
    # Resample humanSample for sets of neandertal-sized samples.
    HumNeandRes <- resample(ipiHum,neand,reps);


    # Record Neandertal and human resampled means.
    resResampling[i+1,2] = mean(neand);
    resResampling[i+1,3] = mean(HumNeandRes);


    # Calculate z score and transform it into a percent
(probability).
    zScore = calculate.z(HumNeandRes,neand);
    probability = pnorm(zScore);


    # Record z score and probability.
    resResampling[i+1,4] = zScore;
    resResampling[i+1,5] = probability;


    # Test H0.
    if (probability <= pnorm(-1.96) | probability >=
pnorm(1.96)) {
        resResampling[i+1,6] = "Reject H0";
    } else {resResampling[i+1,6] = "Support H0"};

# Create histogram showing how Neandertals compare to human
distribution. These are available in Chapter 6.
  hist.resample(HumNeandRes,neand,colnames(data)[i+2]);

# Export histogram as .png to Results folder.
  dev.copy(png,paste('HumNeandMeas',i,'.png'));
  dev.off();
  } else {NA};
};
```

```r
##################### Save All Results #####################
# Save results of Test 1.
write.csv(resMean,file="ResultsHumSampleSizeMean.csv",eol="\r\n"
);
write.csv(resSD,file="ResultsHumSampleSizeSD.csv", eol="\r\n");
write.csv(resMean,file="ResultsHumSampleSizeSE.csv",
eol="\r\n");

# Save results of Test 2.
write.csv(resResampling,file="ResultsMainResample.csv",
eol="\r\n");
###########################################################
```

Appendix 2: Raw data

The following tables include all of the raw data used in this study. The measurements and individuals are listed in alphabetical order. All units are in mm.

Table A2.1: Measurements for Neandertal female sample.

	Acetabular notch to arcuate superior acetabulum	Acetabular notch to iliopubic eminence	Acetabular notch to lesser sciatic notch apex	Anterior auricular to greater sciatic notch apex	Anterior auricular to posterior auricular
Krapina 208	44.2	37.7	51.2		
Krapina 209/212	37.8	33.8		33.0	8.2
Krapina 211				24.3	19.9
Krapina 255.5					
Krapina 255.8					
La Ferrassie 2			50.0		
Tabūn C1					

Table A2.1: Measurements for Neandertal female sample. (CONTINUED)

	Anterior inferior iliac spine to arcuate greater sciatic notch	Anterior inferior iliac spine to greater sciatic notch apex	Anterior inferior iliac spine acetabulum notch to arcuate superior acetabulum	Anterior inferior iliac spine acetabulum notch to inferior acetabulum	Anterior ischial tuberosity to posterior ischial tuberosity
Krapina 208					29.6
Krapina 209/212	58.9	66.1	33.6	64.4	
Krapina 211					
Krapina 255.5					
Krapina 255.8	63.8	70.1			
La Ferrassie 2					
Tabūn C1	66.1	71.9	29.2	41.4	21.0

	Arcuate greater sciatic notch to greater sciatic notch apex	Arcuate greater sciatic notch to posterior auricular	Arcuate superior acetabulum to arcuate greater sciatic notch	Inferior acetabulum to iliopubic eminence	Lateral acetabulum to anterior greater sciatic notch midpoint
Krapina 208				56.2	28.7
Krapina 209/212	19.2	36.7	30.6	56.5	
Krapina 211	9.8	29.5			
Krapina 255.5	13.8				
Krapina 255.8	21.5				
La Ferrassie 2	21.7				
Tabūn C1	10.9		36.9		30.0

Table A2.1: Measurements for Neandertal female sample. (CONTINUED)

	Lateral acetabulum to anterior inferior iliac spine	Lateral acetabulum to greater sciatic notch apex	Lateral acetabulum to inferior acetabulum	Lateral acetabulum to lateral ischial tuberosity	Maximum pubic breadth
Krapina 208			43.5	62.3	29.0
Krapina 209/212	54.8	42.8	44.2		20.8
Krapina 211					
Krapina 255.5					
Krapina 255.8					
La Ferrassie 2					
Tabūn C1	31.8	46.5	28.7	28.9	15.7

	Medial acetabulum to arcuate superior acetabulum	Medial acetabulum to pectineal eminence	Minimum pubic breadth	Minimum pubic height	Pectineal eminence to arcuate superior acetabulum
Krapina 208	43.1	32.9	10.7	9.0	19.4
Krapina 209/212	47.0	29.5	5.4	9.5	20.5
Krapina 211					
Krapina 255.5					
Krapina 255.8					
La Ferrassie 2					
Tabūn C1		36.0	6.2	5	

Table A2.1: Measurements for Neandertal female sample. (CONTINUED)

	Posterior ischial tuberosity to arcuate superior acetabulum	**Superior acetabulum to arcuate superior acetabulum**	**Superior acetabulum to inferior acetabulum**	**Superolateral acetabulum to inferior acetabulum**	**Superomedial acetabulum to pectineal eminence**
Krapina 208	97.3	30.3	55.8	49.8	28.0
Krapina 209/212		32.3	56.4	45.4	23.5
Krapina 211					
Krapina 255.5					
Krapina 255.8					
La Ferrassie 2					
Tabūn C1	63.0			32.2	45.3

Table A2.2: Measurements for Ipiutak female sample.

	Acetabular notch to arcuate superior acetabulum	Acetabular notch to iliopubic eminence	Acetabular notch to lesser sciatic notch apex	Anterior auricular to greater sciatic notch apex	Anterior auricular to posterior auricular
I99.1-84i				37.0	27.8
I99.1-84ii	41.3		46.5	26.5	34.9
I99.1-86A				31.3	26.2
I99.1-91	50.0	33.7	46.2	35.2	27.0
I99.1-99	42.9	32.9	42.2	32.1	22.5
I99.1-101				32.9	27.3
I99.1-102	45.8	34.2	44.7	30.0	28.7
I99.1-104	45.2	35.8	43.0	32.2	24.5
I99.1-107				30.2	26.9
I99.1-111	52.2	44.9	49.4	32.7	24.1
I99.1-160	42.7		44.6	27.6	28.1
I99.1-168	45.0	30.5	42.6	34.8	28.0
I99.1-169	43.0	34.4	49.0	34.9	25.6
I99.1-180	39.6		50.5	33.7	26.1
I99.1-182	44.1		49.8	35.3	28.0
I99.1-191	44.1	39.3	40.3	31.1	24.3
I99.1-197	44.3	34.1	40.5	34.9	30.2
I99.1-198	43.8	31.6	46.7	33.4	34.3
I99.1-199	45.0	35.8	48.6	31.1	28.7
I99.1-200	42.7	34.9	43.3	31.9	17.7
I99.1-203	44.0	36.0	46.6	43.3	25.5
I99.1-204	42.6		44.3	28.6	32.0
I99.1-210	40.0	34.9	43.4	28.8	39.1

	Anterior inferior iliac spine to arcuate greater sciatic notch	Anterior inferior iliac spine to greater sciatic notch apex	Anterior inferior iliac spine acetabulum notch to arcuate superior acetabulum	Anterior inferior iliac spine acetabulum notch to inferior acetabulum	Anterior ischial tuberosity to posterior ischial tuberosity
I99.1-84i	63.9	75.7	28.9	56.3	19.8
I99.1-84ii	55.4	66.8	25.0	54.7	23.9
I99.1-86A	51.7	64.7	23.4	47.5	21.7
I99.1-91	61.4	71.2	31.0	55.6	23.9
I99.1-99	54.6	66.2	28.3	53.5	18.7
I99.1-101			32.7	54.3	21.7
I99.1-102	51.9	65.8	31.3	58.2	27.2
I99.1-104	55.3	70.7	28.8	51.6	20.9
I99.1-107			30.0	52.3	
I99.1-111	56.6	72.1	30.1	59.0	22.3
I99.1-160	56.2	68.8	26.7	52.9	22.9
I99.1-168	56.7	66.8	31.3	53.2	18.3
I99.1-169	52.8	63.8	33.9	58.9	25.2
I99.1-180					19.3
I99.1-182	57.2	71.9	30.6	60.1	26.4
I99.1-191	55.0	65.6	28.3	52.1	24.8
I99.1-197	50.0	63.3	26.2	57.1	21.8
I99.1-198	56.4	68.2	27.9	56.2	22.7
I99.1-199	57.9	71.9	32.5	58.0	23.4
I99.1-200	56.2	69.4	28.7	51.6	26.9
I99.1-203	50.8	66.4	23.8	56.4	23.4
I99.1-204			29.8	56.7	19.0
I99.1-210	61.0	76.5	32.1	56.4	23.4

	Arcuate greater sciatic notch to greater sciatic notch apex	Arcuate greater sciatic notch to posterior auricular	Arcuate superior acetabulum to arcuate greater sciatic notch	Inferior acetabulum to iliopubic eminence	Lateral acetabulum to anterior greater sciatic notch midpoint
I99.1-84i	26.4	45.7	42.4	51.6	36.2
I99.1-84ii	18.0	49.4	26.5		31.0
I99.1-86A	21.9	43.1	25.5		28.2
I99.1-91	24.2	49.7	30.8	50.9	36.3
I99.1-99	19.8	44.3	16.6	48.8	28.0
I99.1-101	25.6	49.2	31.6		36.6
I99.1-102	23.4	46.1	27.7	53.9	34.9
I99.1-104	24.4	41.5	29.1	50.1	32.6
I99.1-107	21.7	36.2	34.8		37.0
I99.1-111	25.7	42.9	26.2	53.8	34.6
I99.1-160	23.6	43.1	22.4		37.5
I99.1-168	22.3	45.5	24.3	53.0	31.5
I99.1-169	26.7	45.3	23.6	53.0	37.6
I99.1-180	21.9	45.5	32.1		35.6
I99.1-182	25.0	55.8	29.6		35.8
I99.1-191	20.1	50.6	27.0	44.0	33.3
I99.1-197	22.8	45.1	24.2	48.9	33.2
I99.1-198	23.2	55.0	23.2	55.3	30.7
I99.1-199	25.8	38.6	31.2	55.6	37.5
I99.1-200	21.9	37.9	30.4	49.9	37.1
I99.1-203	24.1	56.5	40.0	53.3	34.6
I99.1-204	22.7	45.1	27.3		35.3
I99.1-210	22.8	56.8	26.1	53.8	39.5

Table A2.2: Measurements for Ipiutak female sample. (CONTINUED)

	Lateral acetabulum to anterior inferior iliac spine	Lateral acetabulum to greater sciatic notch apex	Lateral acetabulum to inferior acetabulum	Lateral acetabulum to lateral ischial tuberosity	Maximum pubic breadth
I99.1-84i	56.7	50.1	38.6	35.0	19.1
I99.1-84ii	50.8	41.6	36.8	32.3	
I99.1-86A	53.9	38.0	30.2	23.7	
I99.1-91	64.4	46.8	35.9	33.7	22.8
I99.1-99	54.2	36.6	32.4	30.0	16.5
I99.1-101		40.8	38.7	37.3	20.9
I99.1-102	59.8	38.5	34.7	30.8	17.8
I99.1-104	50.6	41.0	33.2	32.8	14.4
I99.1-107		47.9	42.1	34.0	
I99.1-111	58.7	47.5	37.4	35.1	19.3
I99.1-160	47.2	45.6	37.4	34.1	15.5
I99.1-168	57.7	40.0	32.4	36.1	21.5
I99.1-169	44.8	43.7	43.4	32.9	21.7
I99.1-180		43.7	34.9	31.9	
I99.1-182	51.5	43.9	43.0	41.5	
I99.1-191	47.8	38.1	41.8	36.8	21.4
I99.1-197	56.6	37.7	36.5	32.2	18.9
I99.1-198	52.7	39.3	37.6	27.9	18.6
I99.1-199	56.5	45.9	41.2	36.5	22.5
I99.1-200	52.7	43.7	36.1	37.5	16.0
I99.1-203	56.1	41.8	36.0	37.8	19.5
I99.1-204		45.4	33.7	31.9	20.4
I99.1-210	63.8	46.9	41.9	32.1	21.0

Table A2.2: Measurements for Ipiutak female sample. (CONTINUED)

	Medial acetabulum to arcuate superior acetabulum	Medial acetabulum to pectineal eminence	Minimum pubic breadth	Minimum pubic height	Pectineal eminence to arcuate superior acetabulum
I99.1-84i	37.9	25.1	8.6	11.9	22.0
I99.1-84ii					
I99.1-86A					
I99.1-91	43.2	28.6	10.5	12.6	24.6
I99.1-99	35.8	23.8	8.4	11.1	17.0
I99.1-101		30.8	10.0	10.3	
I99.1-102	36.2	23.3	12.2	12.7	17.5
I99.1-104	33.3	23.5	9.7	14.7	18.7
I99.1-107					
I99.1-111	45.0	28.9	13.9	10.8	21.8
I99.1-160			7.7	14.7	21.0
I99.1-168	39.3	24.5	9.1	12.9	23.8
I99.1-169	35.2	28.4	9.8	13.9	13.4
I99.1-180					
I99.1-182					
I99.1-191	36.0	24.6	7.9	15.6	19.1
I99.1-197	36.7	20.8	9.9	11.6	24.1
I99.1-198	37.3	22.3	7.6	12.3	24.6
I99.1-199	43.1	23.7	13.0	16.4	26.6
I99.1-200	38.3	21.0	7.4	10.0	24.3
I99.1-203	35.9	21.5	9.9	15.6	19.6
I99.1-204	35.5		8.9	10.7	
I99.1-210	38.8	24.5	10.7	12.3	18.2

	Posterior ischial tuberosity to arcuate superior acetabulum	Superior acetabulum to arcuate superior acetabulum	Superior acetabulum to inferior acetabulum	Superolateral acetabulum to inferior acetabulum	Superomedial acetabulum to pectineal eminence
I99.1-84i	98.9	32.8	50.4	45.7	24.0
I99.1-84ii	81.1	30.5	47.6	39.4	
I99.1-86A	83.2	27.5	43.3	39.5	
I99.1-91	97.5	32.6	51.7	47.0	22.8
I99.1-99	87.9	28.6	48.0	41.8	18.4
I99.1-101	84.7	32.7	47.0	45.8	
I99.1-102	80.6	32.7	49.7	47.8	24.1
I99.1-104	78.4	31.9	45.3	45.3	21.2
I99.1-107		34.5	48.2	48.2	
I99.1-111	95.6	27.5	50.5	46.7	20.1
I99.1-160	83.1	32.0	47.7	43.3	17.4
I99.1-168	87.2	33.3	49.7	42.8	25.1
I99.1-169	89.9	36.6	51.6	49.4	24.6
I99.1-180	80.4	33.6	44.9	42.6	
I99.1-182	99.0	33.7	54.1	55.2	
I99.1-191	84.2	28.6	45.4	45.3	19.8
I99.1-197	82.9	29.7	50.2	44.9	26.1
I99.1-198	84.1	33.7	51.3	49.8	21.6
I99.1-199	93.9	36.3	52.8	49.1	24.2
I99.1-200	84.1	29.9	47.3	45.0	18.3
I99.1-203	85.3	31.9	48.3	43.1	23.8
I99.1-204	88.0	33.5	47.2	43.1	
I99.1-210	87.7	33.1	49.7	50.7	22.3

Appendix 3: Ipiutak sample standard deviation

In Chapter 4, I described bootstrap resampling. This method requires that the large sample used is representative of the true population (Lee 2001). To test this for the sample of Ipiutak human females used in this study, I reduced the Ipiutak sample size by one, generated a distribution of subsamples based on bootstrap resampling, and then calculated the standard deviation of distribution. I did this for all possible sample sizes, and then plotted the results. Here, I provide those plotted results for each measurement. The *x*-axis shows sample size, typically from 0 to 23, though for some measurements the maximum sample size was smaller. The *y*-axis shows the standard deviation for the distribution based on that sample size. All show that as sample size increases, the change in standard deviation reduces and approaches a single value. Since this is the case for all samples, it is appropriate to use the maximum possible sample size for the Ipiutak females to represent population variation for these pelvimetrics.

Figure A3.1: Variation in standard deviation for acetabular notch to arcuate superior acetabulum.
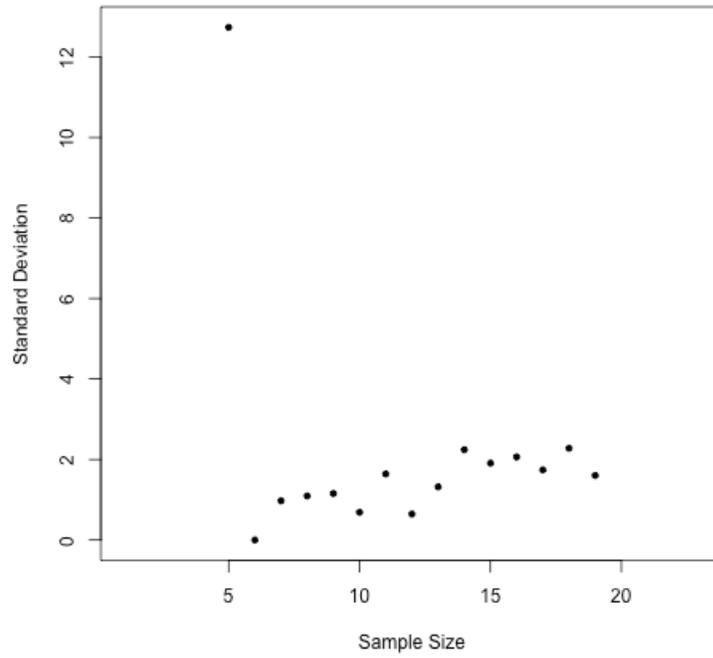
Figure A3.2: Variation in standard deviation for acetabular notch to iliopubic eminence.
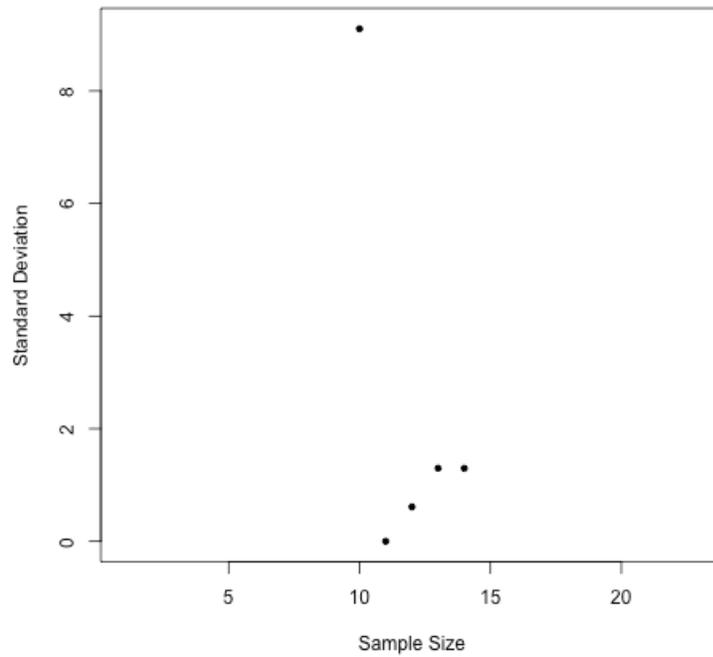
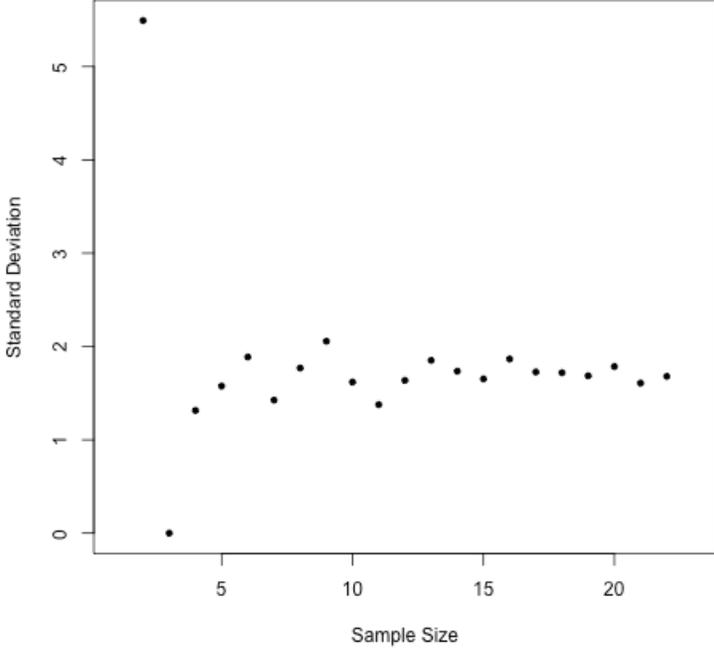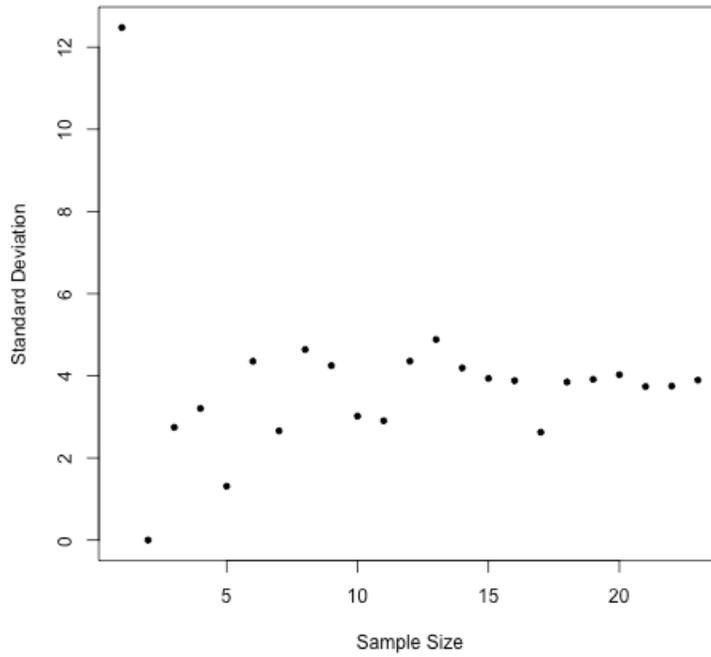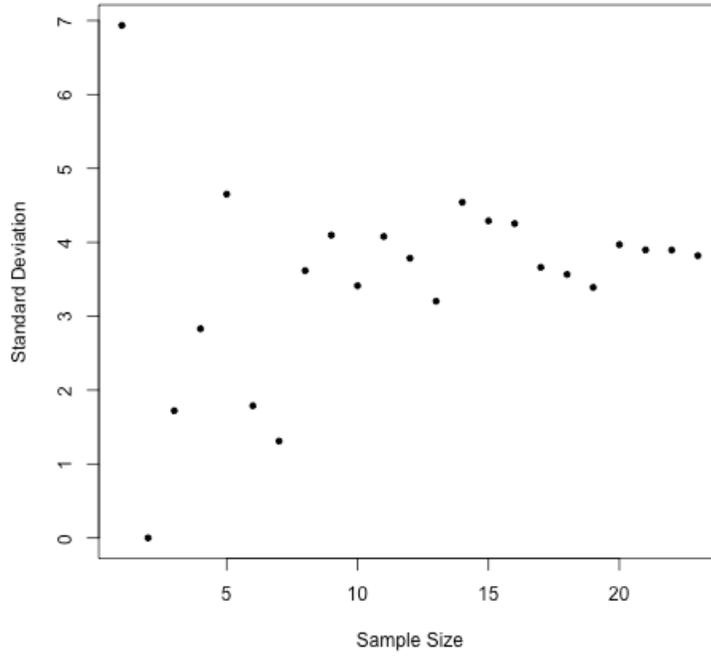*Figure A3.3: Variation in standard deviation for acetabular notch to lesser sciatic notch apex.*
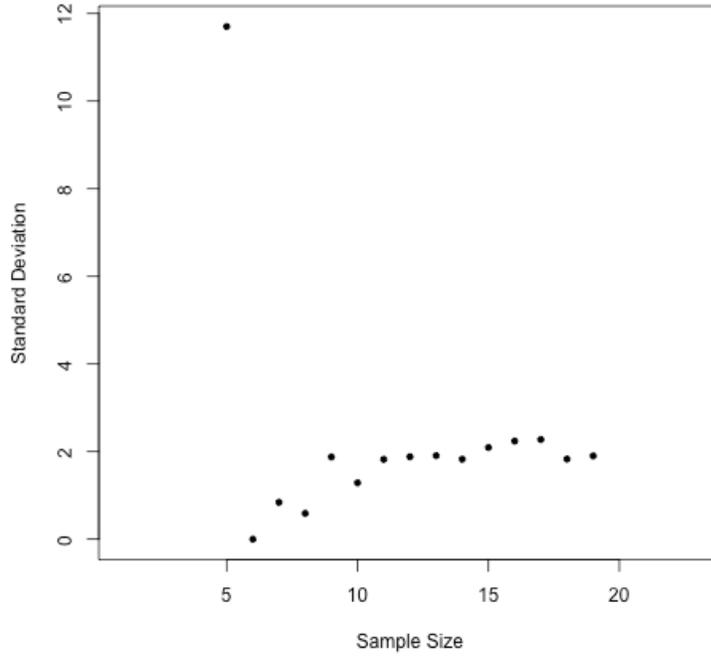
Figure A3.4: Variation in standard deviation for anterior inferior iliac spine to arcuate greater sciatic notch.
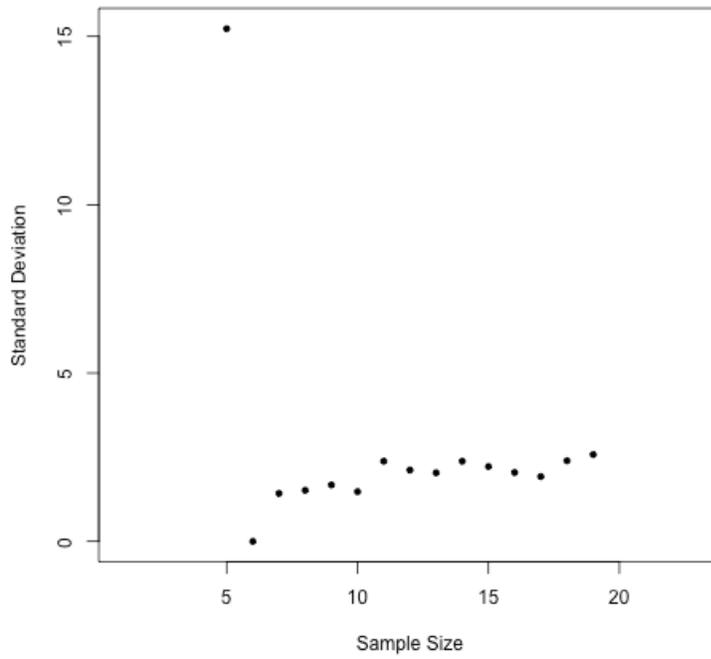
Figure A3.5: Variation in standard deviation for anterior inferior iliac spine to greater sciatic notch apex.
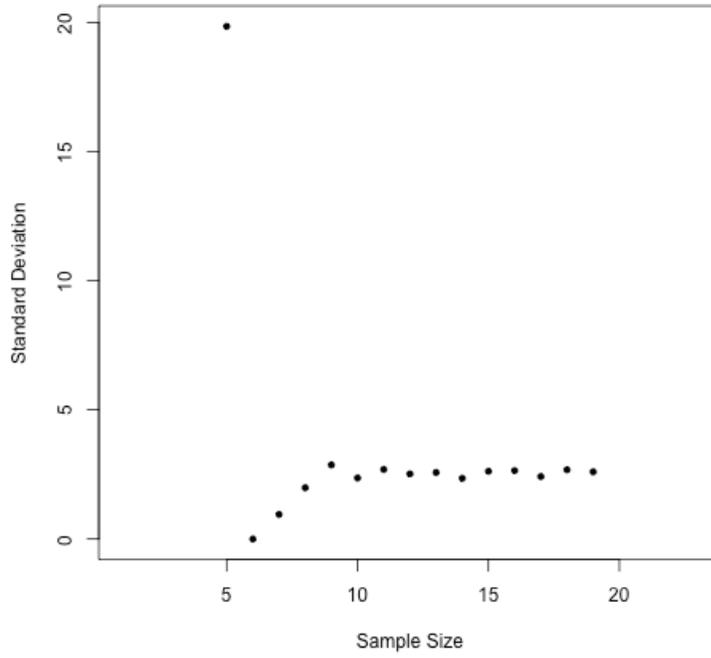
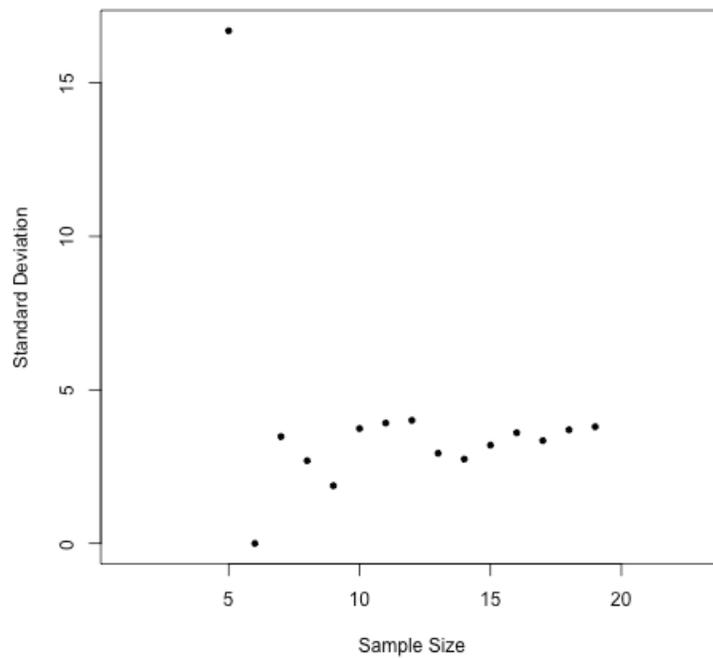*Figure A3.6: Variation in standard deviation for anterior auricular to greater sciatic notch apex.*
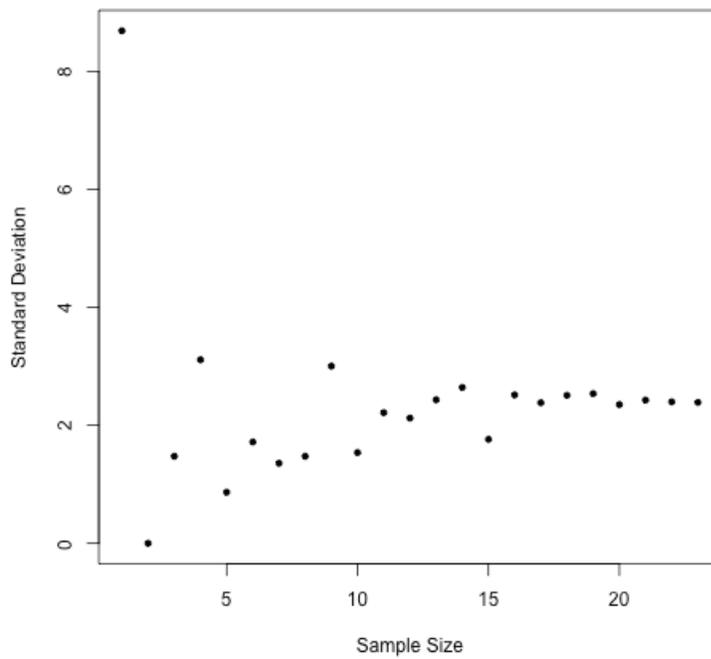
Figure A3.7: Variation in standard deviation for anterior auricular to posterior auricular.
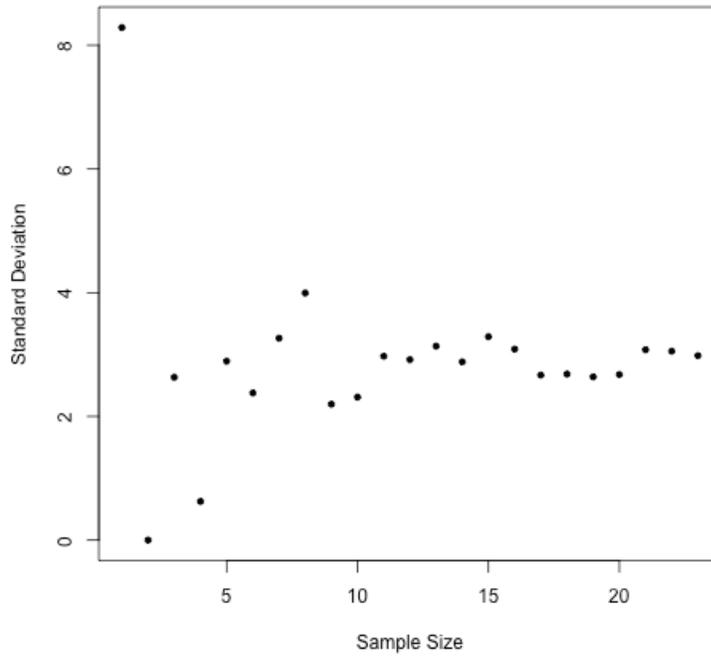
Figure A3.8: Variation in standard deviation for anterior inferior iliac spine acetabulum notch to arcuate superior acetabulum.
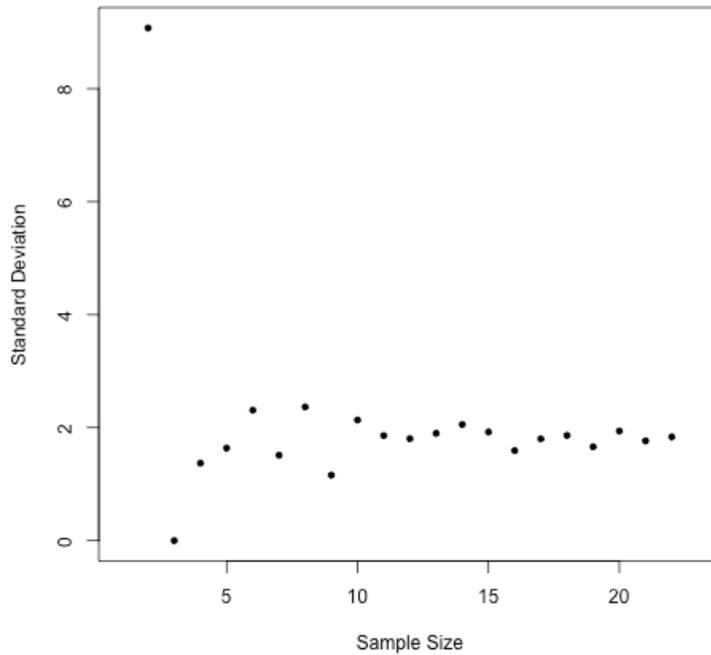
Figure A3.9: Variation in standard deviation for anterior inferior iliac spine acetabulum notch to inferior acetabulum.
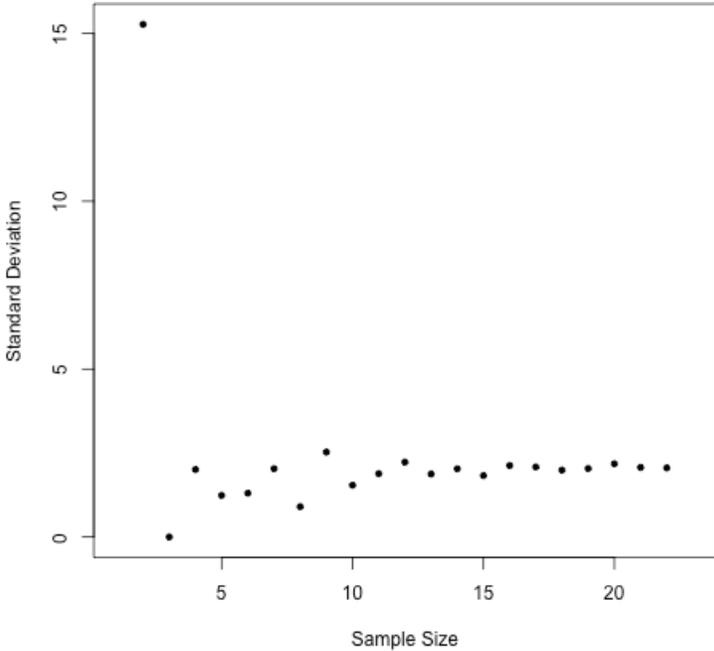
Figure A3.10: Variation in standard deviation for anterior ischial tuberosity to posterior ischial tuberosity.

Figure A3.11: Variation in standard deviation for arcuate greater sciatic notch to greater sciatic notch apex.
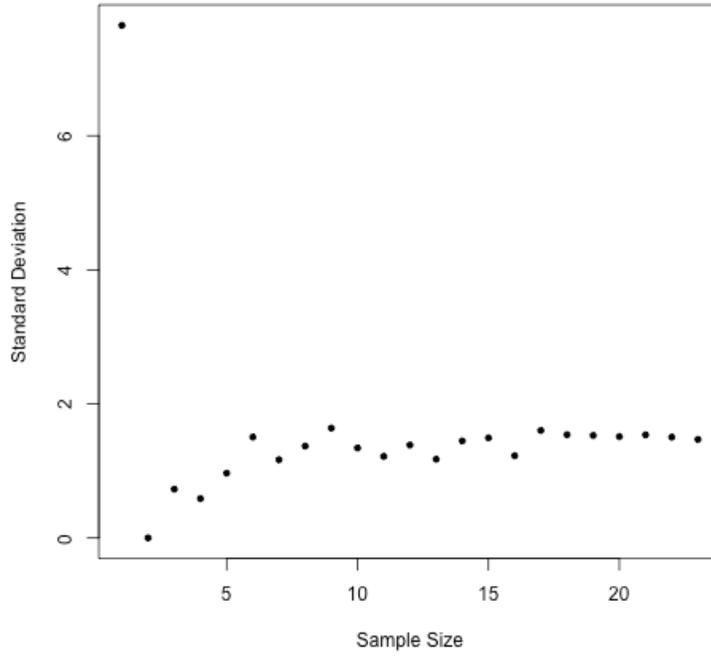
Figure A3.12: Variation in standard deviation for arcuate greater sciatic notch to posterior auricular.

Figure A3.13: Variation in standard deviation for arcuate superior acetabulum to arcuate greater sciatic notch.
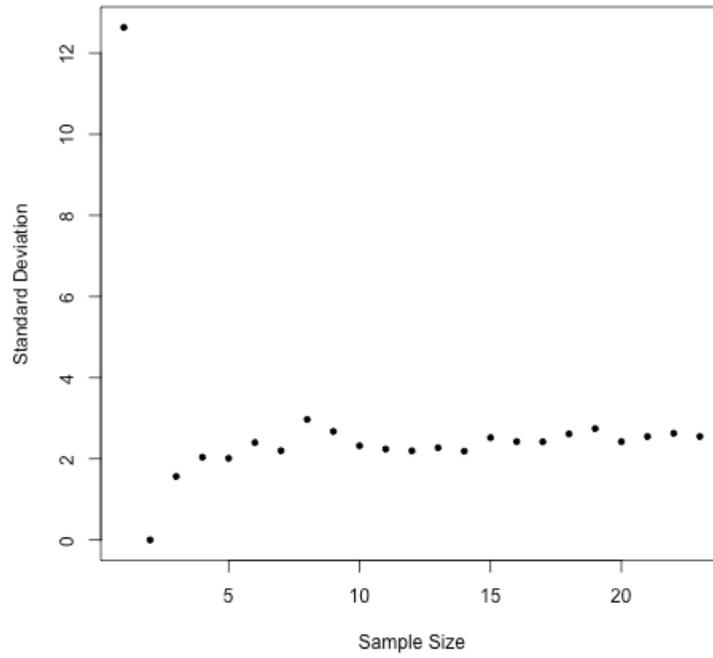

Figure A3.14: Variation in standard deviation for inferior acetabulum to iliopubic eminence.
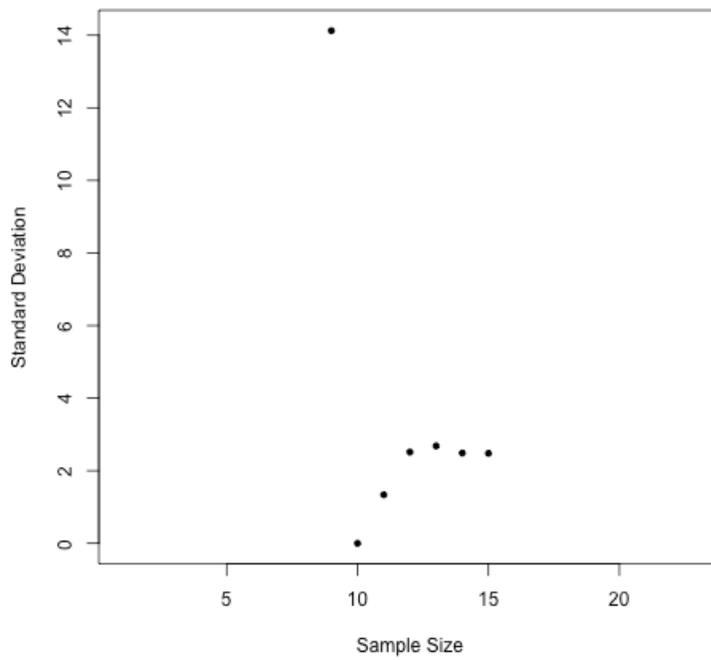
Figure A3.15: Variation in standard deviation for lateral acetabulum to anterior greater sciatic notch midpoint.
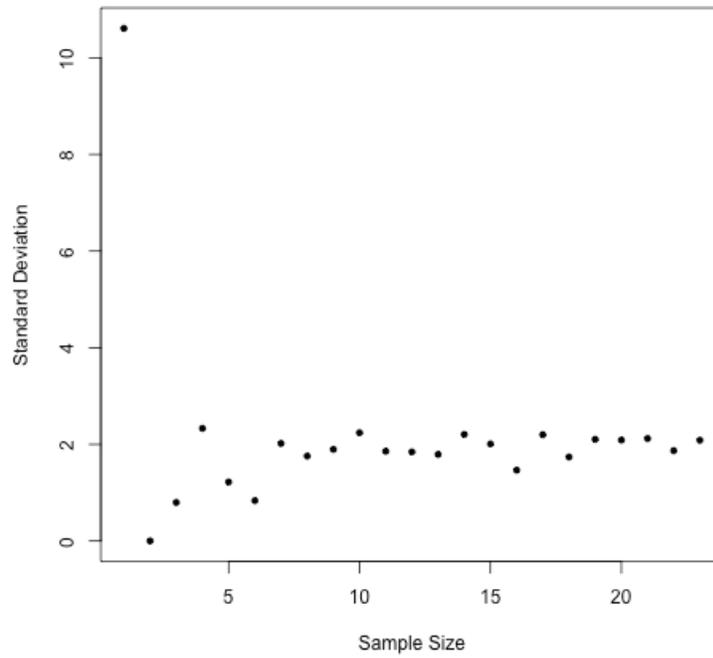
Figure A3.16: Variation in standard deviation for lateral acetabulum to anterior inferior iliac spine.

Figure A3.17: Variation in standard deviation for lateral acetabulum to greater sciatic notch apex.

Figure A3.18: Variation in standard deviation for lateral acetabulum to inferior acetabulum.
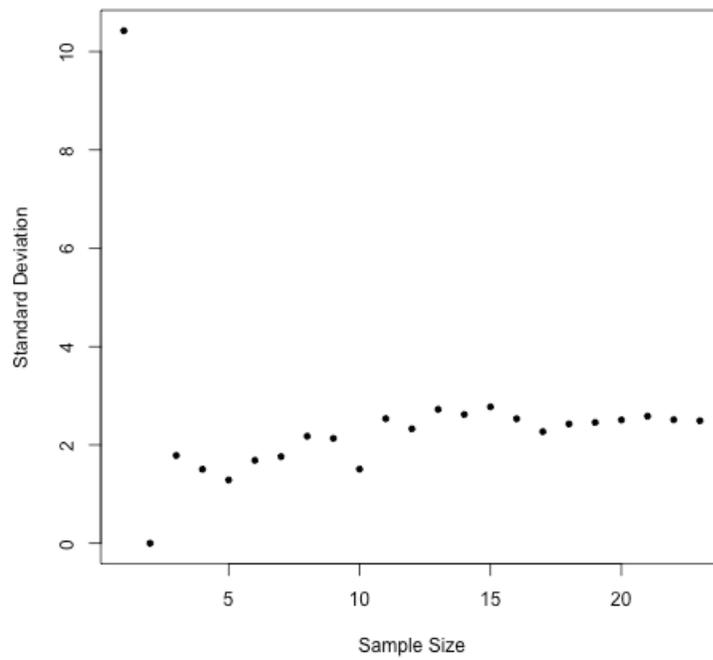
Figure A3.19: Variation in standard deviation for lateral acetabulum to lateral ischial tuberosity.
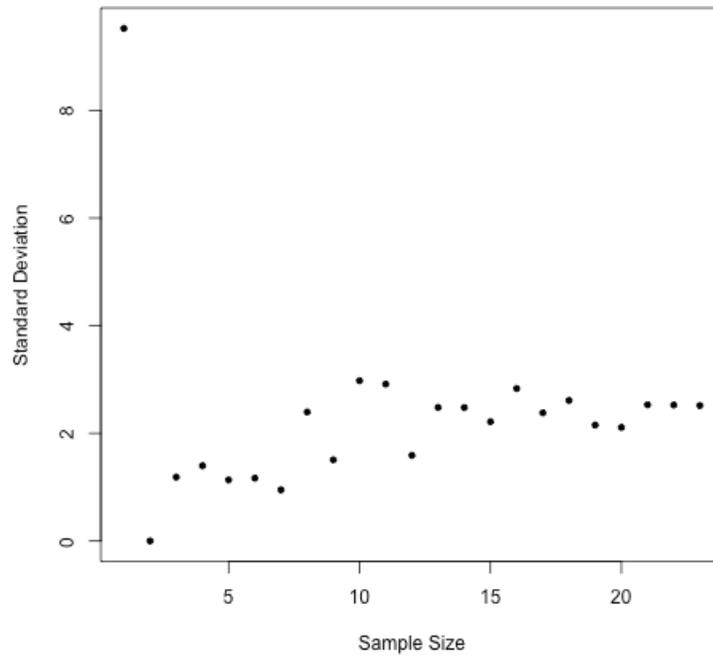

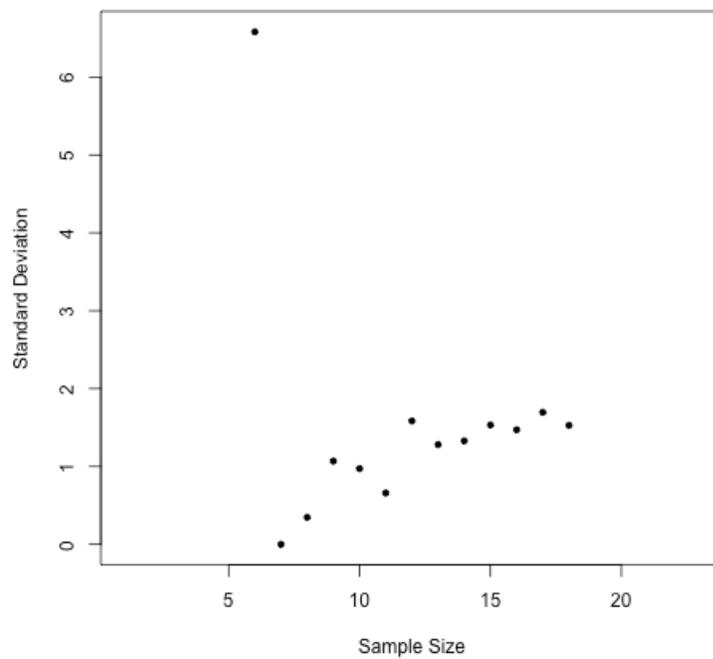*Figure A3.20: Variation in standard deviation for maximum pubic breadth.*

Figure A3.21: Variation in standard deviation for medial acetabulum to arcuate superior acetabulum.
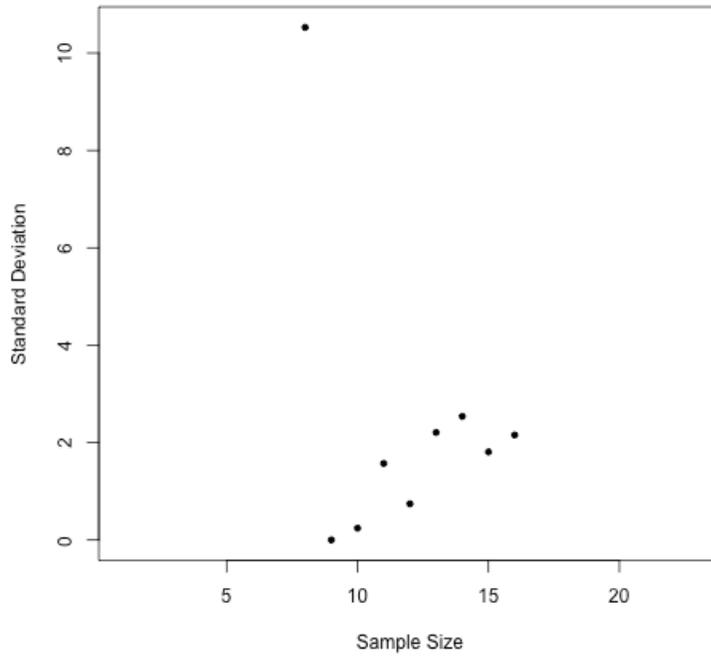

Figure A3.22: Variation in standard deviation for medial acetabulum to pectineal eminence.
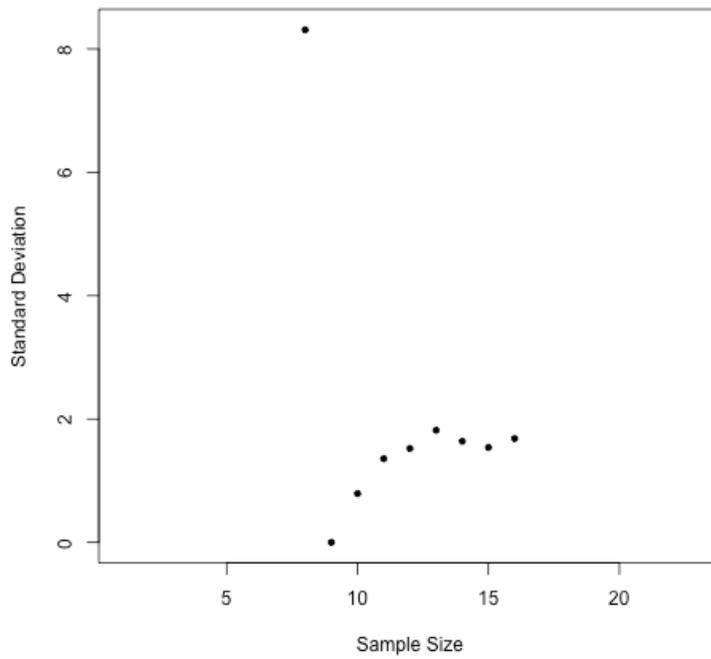
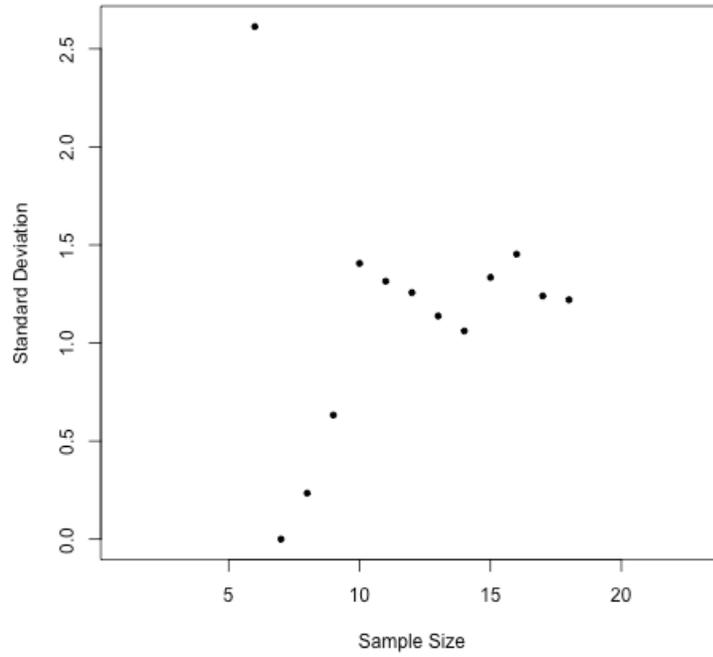*Figure A3.23: Variation in standard deviation for minimum pubic breadth.*

Figure A3.24: Variation in standard deviation for minimum pubic height.

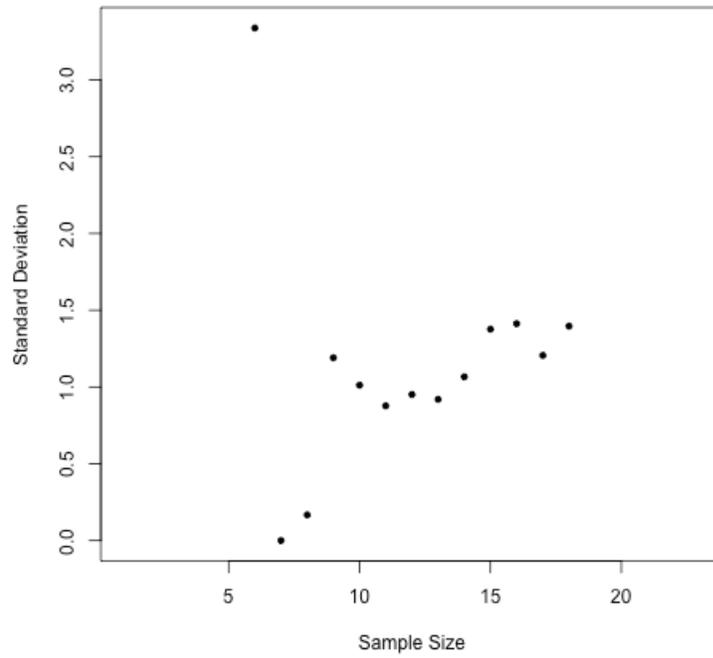*Figure A3.25: Variation in standard deviation for pectineal eminence to arcuate superior acetabulum.*

Figure A3.26: Variation in standard deviation for posterior ischial tuberosity to arcuate superior acetabulum.

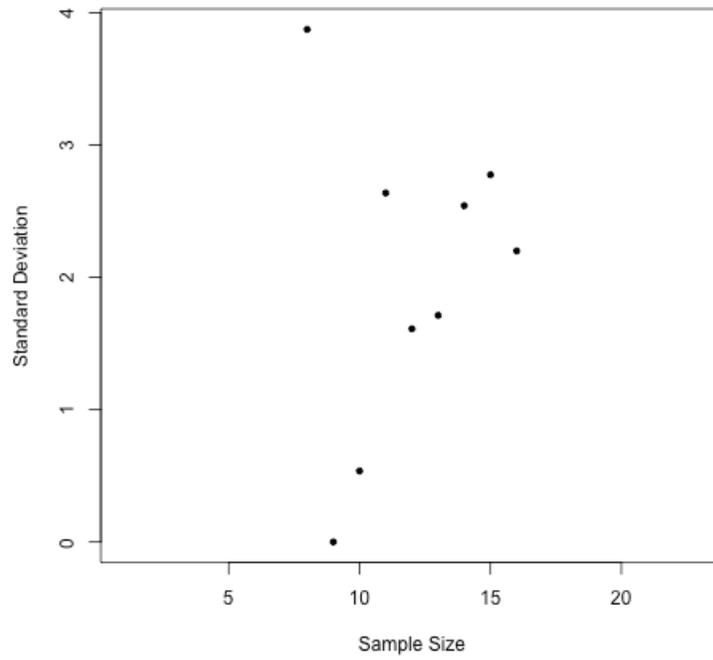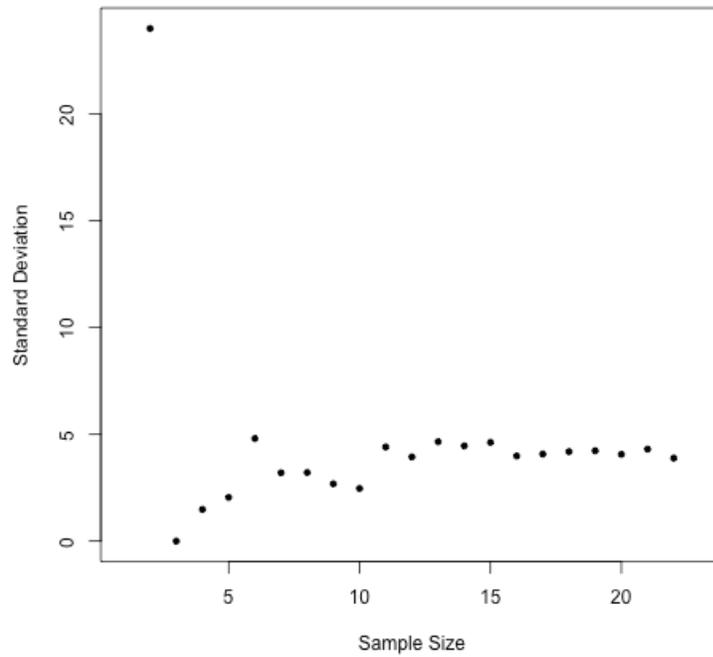*Figure A3.27: Variation in standard deviation for superior acetabulum to arcuate superior acetabulum.*
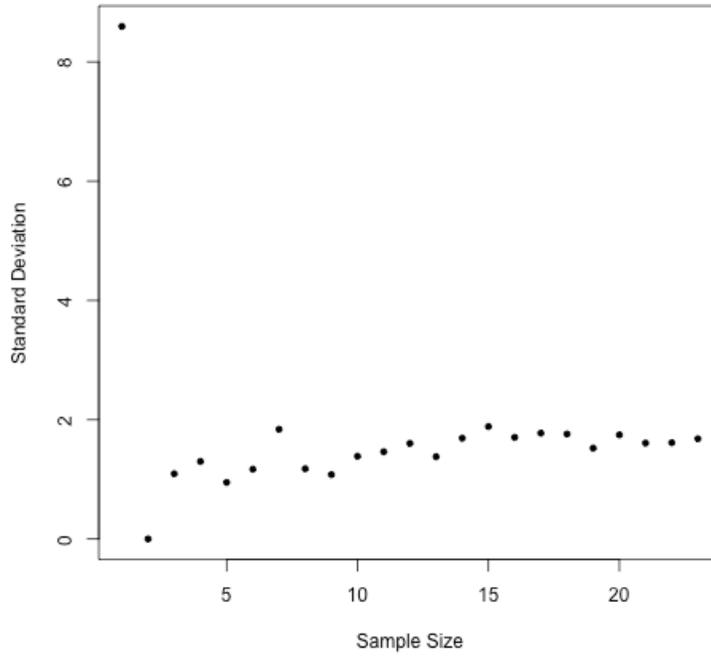

Figure A3.28: Variation in standard deviation for superior acetabulum to inferior acetabulum.
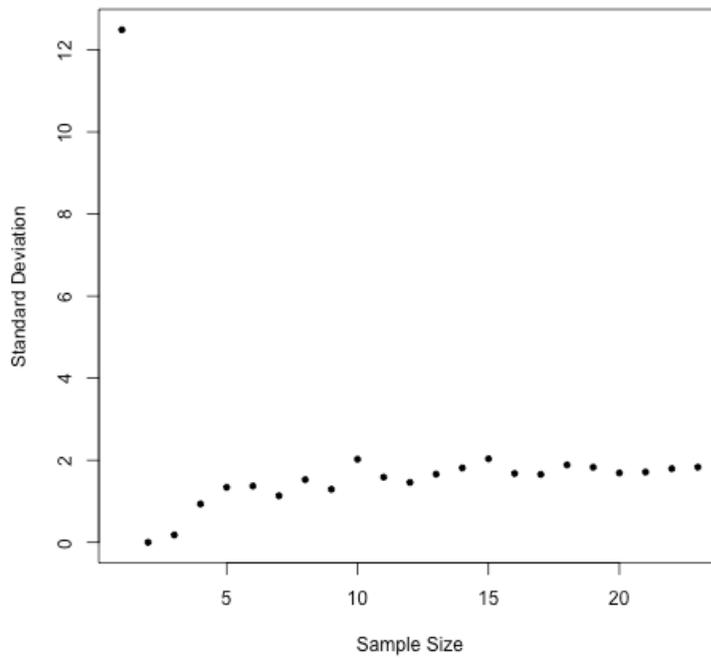
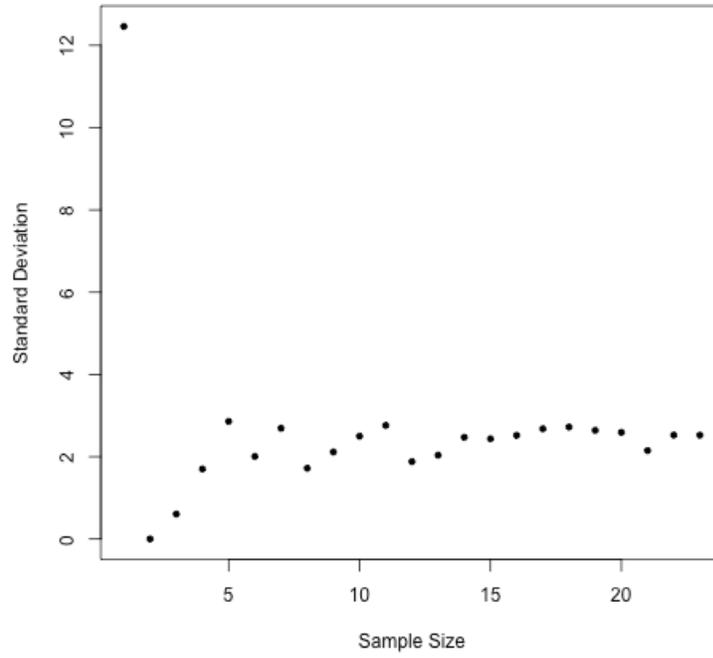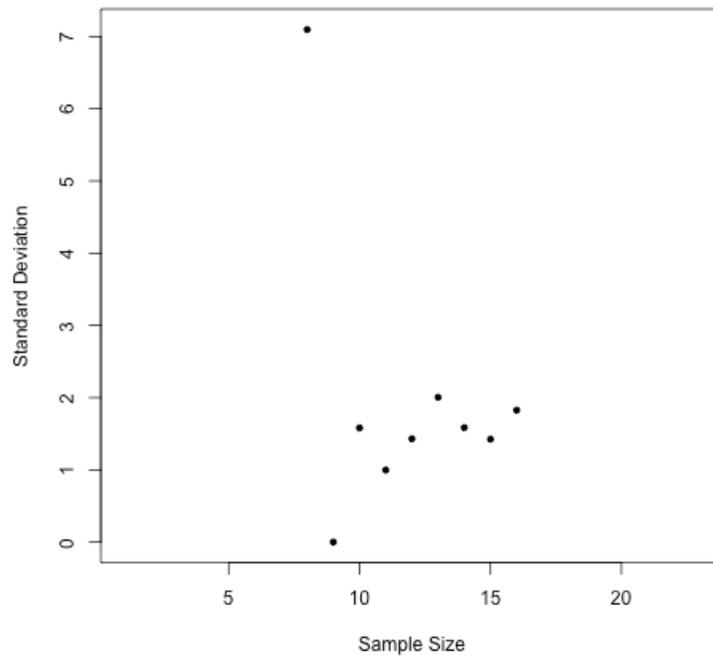*Figure A3.29: Variation in standard deviation for superolateral acetabulum to inferior acetabulum.*

Figure A3.30: Variation in standard deviation for superomedial acetabulum to pectineal eminence.

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