The Emergence of the ‘Obstetric Dilemma’ and the Evolutionary Origins of Prosocial Birthing Behaviour in Humans and Non-Human Primates

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Abstract

Kristian Boote – The Emergence of the ‘Obstetric Dilemma’ and the Evolutionary Origins of Prosocial Birthing Behaviour in Humans and Nonhuman Primates

Birth assistance has emerged as a typical feature of human behaviour, yet investigations into the evolutionary origins of these behaviours are sparse. The traditional anthropological argument under the ‘obstetric dilemma hypothesis’ reasons that cephalopelvic disproportion and increasing maternal mortality, drove the emergence of prosocial birthing behaviour, and is unique feature of human reproduction. Therefore, if increasing risk precedes prosocial birthing behaviour, then species experiencing higher mortality as a result of birth should present prosocial birthing behaviours. However, emerging behavioural evidence of prosocial birthing among primates contravenes this, including a capacity for intentional, directed birth assistance.

This thesis alternately proposes a ‘social birthing hypothesis’ model of birth assistance evolution, where highly prosocial birthing behaviours were already a feature of hominin and wider primate birth events, operating as a behavioural buffer which facilitated increasing maternal cephalopelvic disproportion and birthing risk in later hominins. Following a review and consistent quantification of primate birthing prosociality, alongside corresponding values for sociodemographic, morphological and life history variables, this thesis shall additionally use statistical modelling methods to determine potentially evolutionary signals and potential evolutionary trajectories of primate birthing behaviour. Additionally, by using available maternal and neonatal mortality records of captive primate species from UK Zoos will be compared with observations of birthing sociality in order to identify potential correlation between birthing risk to mother and infant, and any qualitative patterns of birthing behaviour. Ongoing research into primate morphological and socioecological evolution will provide further understanding of the development and significance of prosocial birthing behaviours in

humans and other primates. Conclusions on the role of birthing sociality will have crucial consequences for ensuring optimal captive breeding environments for primates, as well as affirming the need for prosocial environments in combating issues of global human maternal health.

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Chapter 1: Introduction

Typical modern human labour has been historically described as an evolutionary ‘scar’ – a product of selective pressures faced by our hominin ancestors (Krogman, 1951; Rosenburg, 1986; Rosenberg and Trevathan, 1996). The evolution of orthograde posture and habitual bipedalism which defines our lineage has traditionally been argued as the primary driver of much of the characteristically modern human pelvic morphology (Lovejoy et al, 1974; Aiello and Dean, 2002:443; Fleagle, 2013). Previous physical and palaeoanthropological literature argues that whilst this form of locomotion and posture conferred many selective benefits in our evolutionary history, the tailoring of hominin pelvic morphology has had adverse effects for obstetrical adequacy in birthing mothers (Ruff, 1995; Abitbol, 1996; Rosenberg and Trevathan, 1996; Walrath, 2003; Wittman and Wall, 2007; Weiner et al, 2008; Buck, 2011; Hirata et al, 2011; Wells et al, 2012).

From the archaeological evidence, increasing neonatal cranial dimensions placed greater selective pressure on females to increase obstetric dimensions in tandem (Abitbol, 1996; Walrath, 2003; Ponce de Leon et al, 2008; Wells et al, 2012). In this evolutionary scenario, a maternal pelvis adapted for bipedal locomotion becomes a limiting factor on neonatal brain size (Martin, 1983; Abitbol, 1996:5). As stated by Abitbol (1996:5), freedom from such restriction on neonatal brain size by the maternal pelvis coupled with progressive encephalisation may be the two key factors in future human evolution. These antagonistic pressures are predicted to have resulted in the emergence of a morphological ‘dilemma’, where females faced the evolutionary challenge of a hip that is both mechanically efficient for bipedal locomotion, and obstetrically spacious for passage of the infant (Ruff, 1995; Rosenberg and Trevathan, 1996; Walrath, 2003; Wittman and Wall, 2007; Weiner et al, 2008; Buck, 2011; Hirata et al, 2011; Wells et al, 2012). As this literature highlights, the evolutionary scenario presented by the ‘obstetric dilemma hypothesis’ is widely utilised to model the evolutionary emergence of species-typical difficulty in human births, and a resultant reliance on supportive interventions by social groups members or contemporary clinicians.

Indeed, obstructed labour as a product of cephalopelvic disproportion (CPD), where the neonatal cranium is too large for the birth canal, is reported by the World Health Organisation (2005:1) as one of the most common causes of maternal fatality during or after birth at ~12% of all incidents of neonatal death. A large body of evidence from multiple populations demonstrates that a large foetus and a narrow pelvic inlet are strongly associated with required intervention such as caesarean delivery (Magnin et al, 1975; Chassar Moir, 1949; Morgan et al, 1986; Thurnau, 1988; Morgan and Thurnau, 1988a, 1988b; 1992; Stahlberg et al, 2006; Selin et al, 2008; Fremondiere et al, 2017). Although there is some contention, with Fergusen et al (1998:1186)’s sample of 91 patients showing that fetal-pelvic index was a minimal predictor of fetal-pelvic disproportion. Overall, it is widely accepted that from approximate estimations of pelvic size, researchers can begin to predict whether extinct hominin populations would have required assistance during labour to mitigate any increased risk of maternal and infant mortality as a product of CPD and dystocia, where the neonate delivery is difficult or slow (Perkins, 1987). Reconstructing such specific mortality rates among past populations can be particularly for extinct species, whether utilising direct or indirect methods. The lack of significant evidence from fossil and archaeological collections reduces the reliability of conclusions, and the incompleteness of specimens available further reduce the accuracy of analyses. Whilst not wholly unreliable or inaccurate, a number of factors must be considered when drawing conclusions from such analyses and highlights the limitations of previous analyses which couch on anatomical reconstructions and neglect behavioural observations. The crucial question of why our species experiences such difficulty, is the first step in determining the vital adaptations present in ourselves which minimise risks to maternal and neonatal health, sister taxa and closely related taxa (both phylogenetically, and taxa which share similar morphological constraints). Identifying these features of our evolution will provide essential context for optimal medical and veterinary practice for females and infants today, alongside understanding group dynamics and demography in historical populations.

Despite the difficulties in reconstructing ancient birthing, an emerging and strong body of evidence in recent years challenges the previously widely accepted uniqueness of human birthing behaviour, and in fact nonhuman primates display a wide suite of behaviours traditionally thought exclusive amongst humans and human ancestors. Nakamichi et al (1992:418) report that not only did a parturitient free ranging *Macaca fuscata* maintain social contact and proximity, but also appeared to be "strongly motivated to remain within the group". This observation contradicts early work by Brandt and Mitchell (1973:520), who state that "primate births in the wild apparently happen at night away from the main troop". This is reiterated by Rosenburg and Trevathan, who state that "unlike nonhuman primates, which seek solitude at this time, human mothers actively seek assistance in childbirth" (Rosenburg and Trevathan, 2002:1201). Turner et al's (2010) report on free-ranging parturitient Japanese macaques observed that all three births witnessed exhibited significant social tolerance during labour and birth. Turner et al (2010) argue that this demonstrates social proximity during birth is more common in nonhuman primates than the consensus of previous literature. This focus on the proximity of primate group members to parturitient females, whether mediated by the mother actively remaining with the group, or group members actively moving to be with the mother, is of particular interest when contrasting the typical isolationist behaviour commonly asserted or implied by previous literature (Rosenburg and Trevathan, 2002; Pusey et al, 2008), reinforcing the status quo that nonhuman primates seek isolation during birth. This emerging body of evidence suggests that prosocial birthing behaviour is not a unique behavioural novelty that defines our hominin lineage, but could arguably be a significant feature of the wider primate birth event. As a central phrase posited within this thesis, prosocial birthing refers to behaviours which actively or passively promote interactive and positive social behaviours, such as touching, close proximity, inspection, and other behaviours which suggest a positive interaction during the birth event between the birthing female and other group members. The identification and exploration of prosocial behaviours during the birth event shall form the primary focus of this thesis.

1.1. Organisation of the thesis

With this background of research in mind, this central aim of this thesis will be to explore the previous consensus on the uniqueness of human birthing behaviour – whether we really are unique as a species in having social and assisted births, coupled with a high degree of mechanical difficulty. This shall be explored through an assessment of the current understanding of modern human obstetric morphology, the adaptive significance of these elements, and their emergence along the hominin evolutionary tree. By additionally comparing this with observations of extant primate examples, as well as other comparative mammalian taxa, Chapters 2 and 3 will provide a critical review of the 'obstetric dilemma hypothesis' and its accuracy in modelling the emergence of birth assistance behaviours in hominin evolution, on the basis of morphological and osteoarchaeological evidence.

This will be followed by a further review within Chapter 4, exploring the potential evolutionary benefits of prosocial birthing behaviour. Using examples of observations of prosocial behaviours, direct birth assistance in the delivery of the neonate, and a review of potential factors influencing the expression of such behaviours, this chapter will engage with previous primatological and anthropological work, framed within the context of prosocial birthing behavioural evolution. This chapter will additionally explore the relevance of understanding the benefits to prosocial support in issues faced in contemporary human birth. Furthermore, through evaluating and understanding the context underlying the expression of such behaviours, the capacity for highly assistive, human-like behaviours, we can begin to explore the likelihood of more deep-rooted birthing behaviours in hominin evolution.

By quantifying observed primate birthing behaviours using a simple but consistent methodology, Chapter 5 will investigate the potential relationships between relative levels of birthing sociality, alongside sociodemographic, morphological, and life history factors potentially driving or coevolving with birthing prosociality. This will also include a small-scale study of the use of neonatal body mass as a proxy for absent neonatal cranial dimension data, something severely lacking from previous research. The aim of this will be to support the use of other morphological metrics, for which data is available, as a proxy for obstetrically relevant variables. With this basis for understanding potential relationships between birthing behaviour and other factors in extant species, this chapter will further investigate potential phylogenetic signals within the datasets. Using multiple statistical methodologies, this chapter will aim to determine potential evolutionary trajectories for the emergence of prosocial birthing behaviours, and the possibility of a deep-rooted capacity for birth assistance or supportive behaviours.

Lastly, Chapter 6 will utilise data obtained from captive primates (Twycross Zoo, UK) to investigate the possible mechanisms by which evolutionary selection for birthing behaviours may operate. By analysing mortality data available, the expected relationship between high maternal and neonatal mortality risk, and prosocial birthing behaviours under the model of the ‘obstetric dilemma hypothesis’, will be examined within case studies of neonatal mortality incidents at Twycross. Additionally, a potential consistent methodological framework for application will be discussed as a significant future methodological application to primate behavioural research.

The ramifications for the findings of this thesis will not only be observed within the palaeoanthropological community, but additionally for primate conservationists and primate breeding centres. Perhaps most significantly, it is hoped that the evidence presented on the evolutionary basis of birthing sociality, will additionally highlight the importance of prosocial birthing behaviours for improving maternal and neonatal health.

Chapter 2: A review of obstetric evolution in humans and nonhuman primates.

2.1. Introduction

Following from the inference of the ‘obstetric dilemma hypothesis’ of difficult birth being a primary driver of the establishment of cooperative and prosocial birthing behaviours, termed ‘obligate midwifery’ by Rosenburg and Trevathan (Rosenburg, 1986; Trevathan, 1987; Trevathan and Rosenburg, 1996), findings on the reproductive costs and benefits are crucial in understanding the establishment of modern human birthing behaviours. Furthermore, an accurate conceptual model of the evolutionary scenario for the emergence of birth assistance, which encompasses the selective pressures enforced on mothers and neonates (e.g. birthing mortality), is vital in reconstructing hominin sociodemography and reproductive success.

Among nonhuman primates, Schultz (1949) states that the bony pelvic brim, for example, is not nearly as much of a restriction to normal labour. However, Stoller (1995) notes that no actual measures of constrictive diameters had been published to support Schultz (1949). This symbolises many of the assumptions previously made in anthropological literature in comparisons of obstetric morphology between humans and primates. Further to this, work by Abitbol (1996:3) follows the consensus that humans are unique in requiring assistance at birth as a necessity, where “rarely can a human female give birth without assistance at all.” This is not backed up by empirical data in terms of a genuine necessity for assistance, but seems more a consensus among physical anthropologists of an apparent ‘inability’ of modern humans to give birth without assistance.

Whilst the assignment of specimens to particular species can further complicate the debate (Groves et al, 2014), the term will be used in this thesis as a term defining individuals representing closely related populations, both in morphology and estimated genetic components. This is important as the overarching aim of this thesis is to investigate the evolutionary history of social birthing behaviour in hominins, using a wider reflection on data available and collected from extant primate species. In order to appropriately model the emergence of social birthing behaviours, both positive and antagonistic, among primate taxa, distinct species naming, and assignment will be crucial in understanding distinct morphological traits in hominin species, as well as in subsequent chapters for extant primate species. The correct classification of these species is also crucial in identifying whether the evolution of similar patterns of morphology are the result of convergent evolution, or ancestrally inherited. Furthermore, the assignment of archaeological specimens to distinct hominin taxa, will be essential to phylogenetic models testing the relative signal strength of prosocial birthing behaviours in conjunction with assessments of morphological variation.

In order to answer the question as to whether a connection exists between obstetric morphology and birthing behaviour in both humans and nonhuman primates, and by extension extinct hominins, this thesis must first explore the morphological variation in primate obstetric morphology. Primate studies often highlight obstetric morphology for which the function is well established in humans, but may not have any identifiable obstetric significance in other primates (Stewart, 1984). Given the shared ancestry of hominins and extant nonhuman primates, this necessitates the use of comparative morphological references in order to understand the alternate evolutionary trajectories between ourselves and other primates, and why the divergence (or convergence in some cases) may have occurred. To provide a basis for understanding, this chapter will first examine the obstetrical adaptations in our own species.

2.2. Birth in modern humans

Obstetric morphology

In order to understand the obstetric adequacy and relative difficulty of parturition in extinct hominins, it is necessary to first outline obstetrical adaptations in the modern human female pelvis which facilitate normal delivery of the neonate. This provides the researcher with a framework to model obstetrical adequacy in comparison with nonhuman primates and hominin remains, and thus predict the likely mechanism of birth and its relative difficulty in extinct species. In turn, a prediction of likely behavioural response and potential mortality risk can be further predicted, in relation to observed behaviours in humans and nonhuman primates. White and Folkens (2005:246) state that the sexual dimorphism present in the pelvis, or os coxae, represents a compromise between locomotor and birthing demands. Traditionally, this observed sexual dimorphism within the human pelvis has been interpreted under the framework of the ‘obstetric dilemma’ hypothesis (Huseynov et al, 2016), whereby successful delivery of a larger brained infant requires a wide pelvis, antagonistic to a narrower pelvis needed for efficient bipedal locomotion.

Washburn’s (1960) original development of the obstetric dilemma hypothesis posited that this conflict was ‘solved’ by delivery of the human neonate in a much earlier stage relative to closely related taxa, argued by Martin (2003) to be around a year ‘early’ compared with Chimpanzees. This traditional framework has recently been challenged by a body of work investigating the biomechanical, metabolic and biocultural adaptations of humans and nonhuman primates. In order to accommodate for the passage of the at term neonate, much of the characteristically female morphology forms part of a general adaptation to maximise the dimension of the birth canal and minimise risks to the mother and neonate during delivery, shown in **Figure 1.1**.

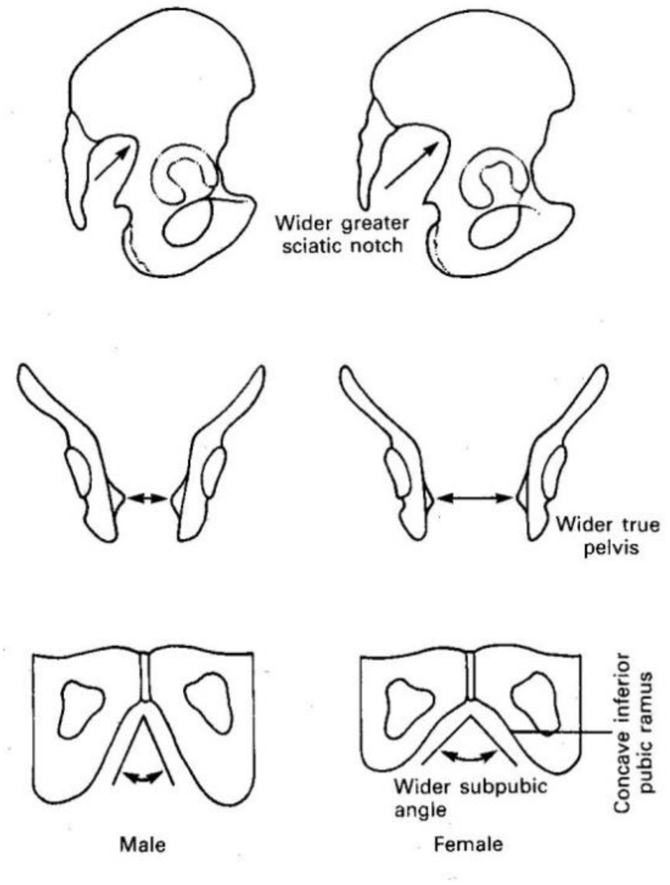


Figure 1.1. Sexually dimorphic traits of the modern human pelvis, adapted from Aiello and Dean (2002:444).

A wide greater sciatic notch typical in the human female pelvis results in an increase in the distance between the ischium and sacrum, coupled with a shorter, less curved and more posteriorly orientated sacrum than in males, reducing any dorsal protrusion into the birth canal (Aiello and Dean, 1994). The shortened female ilium also serves to lower the sacrum into the pelvic cavity, resulting in posterior enclosure of the midplane and outlet (Aiello and Dean, 2002:443). This intrusion of the sacrum also reduces the anterioposterior diameter in the midplane and outlet (Tague and Lovejoy, 1986).

In addition, greater eversion of the ischial bodies produces a parallel-walled birth canal, and increases the transverse diameters of each plane, unlike the narrow ‘funnelling’ of the male pelvis (Aiello and Dean, 2002:444) – a measure of the change in transverse diameter between pelvic inlet and outlet. The superior pubic ramus is elongated in females, which serves to further increase the anteriorposterior diameter (Aiello and Dean, 2002:444), minimising the effect of the intruding sacrum. Finally, the inferior pubic ramus is significantly more concave in females, producing a much broader subpubic angle which elongates the transverse diameter of the pelvic outlet and encourages an anterior final trajectory of the neonate, promoting typical rotation under the pubic symphysis (Aiello and Dean, 2002:446).

However, this sexually dimorphic obstetric morphology is not present at birth in humans, but develops in response to hormonal cues during puberty (Huseynov et al, 2016). The ontological trajectory of obstetric morphology in females is demonstrated by Huseneyov et al (2016). Utilising Computer Tomography (CT) scans and geometric morphometrics, Huseynov et al (2016) studied changes in pelvic morphology from late foetal to adult ages in humans. Their results demonstrated that only after puberty do human males and females develop and exhibit significant sexual dimorphism, with females showing rapid expansion of obstetric-relevant and obstetrically favourable pelvic morphology (Huseynov et al, 2016), shown in F**igures 1.2** and **1.3**.

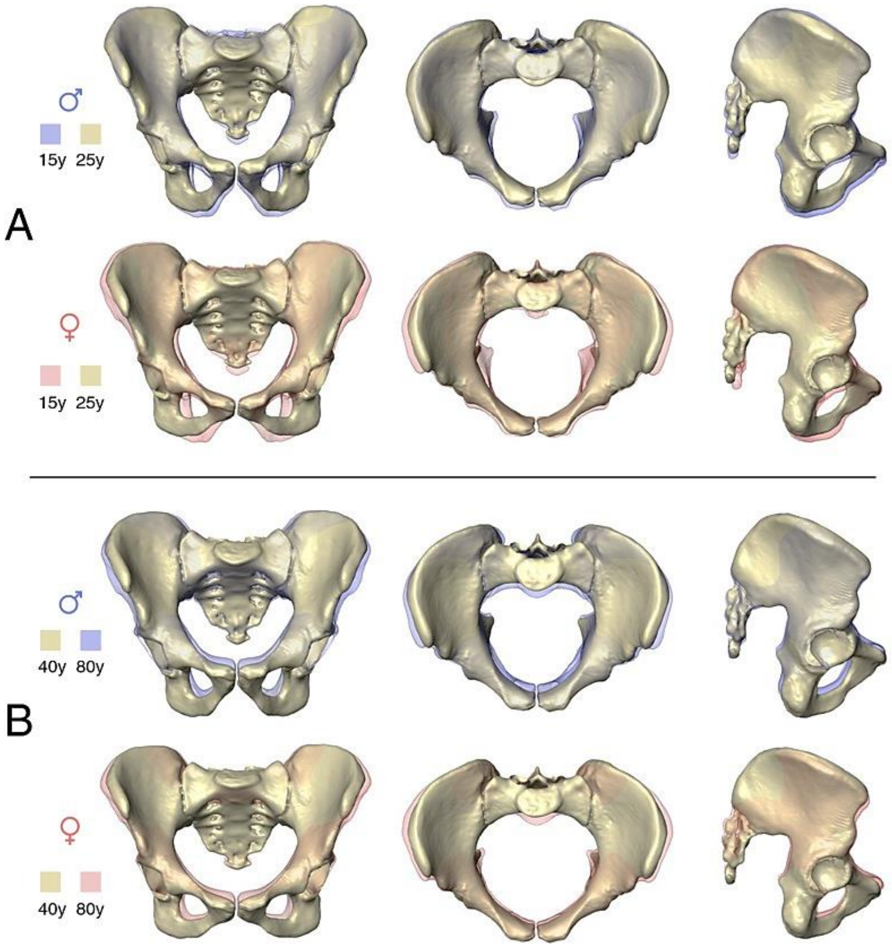


Figure 1.2. Anterior, superior and lateral views of male and female ontological changes in pelvic shape at A) ~15y (transparent) and ~25y (solid), and B) at ~40y (transparent) and ~80y (solid), taken from Huseynov et al (2016:5229).

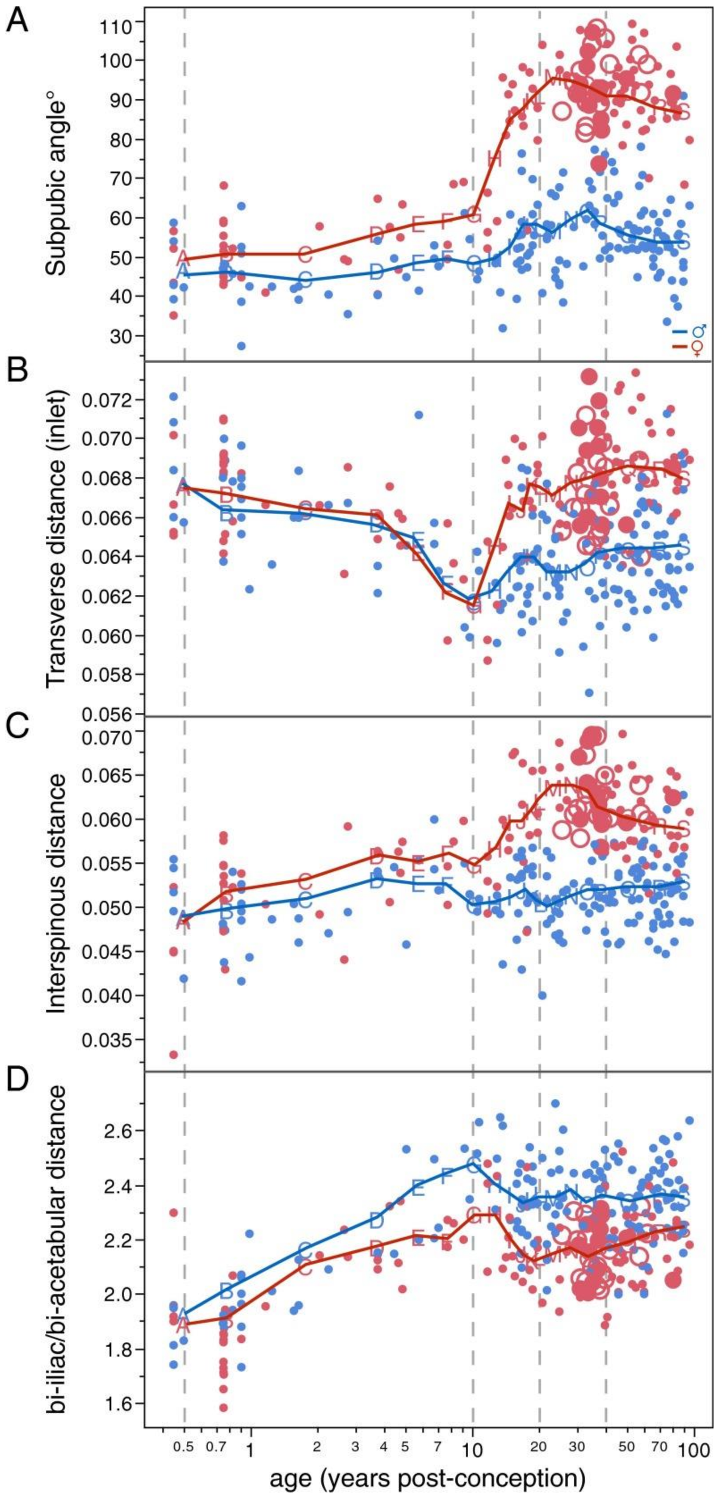


Figure 1.3. Graph depicting sexually dimorphic changes in: A) the subpubic angle; size-normalised linear B) transverse distance of the inlet and C) the interspinous distance; D) ratio of bi-iliac to bi-acetebular distance, taken from Huseynov et al (2016:5230). Colours are red for female, blue for male.

Between 15y and 25y, the female sacrum and ischiopubic region develop significantly greater eversion whilst the iliac blades invert, significantly increasing the transverse dimension of the inlet and anterioposterioir dimensions of the midplane and outlet (Huseynev et al, 2016). The subpubic angle and angle of the greater sciatic also become much wider compared to the male pelvis, additionally producing a wider biacetebular distance and reduction of bi-iliac width (Huseynev et al, 2016).

Interestingly after 40y, females revert to a similar trajectory of development to males and a reduction in obstetric dimensions (Huseynov et al, 2016). This is likely related to the early onset of reproductive senescence (or menopause) seen in human females, reflecting pubertal rise and premenopausal fall of estradiol levels and resultant timing of the most fertile period during the most obstetrically adequate (Huseynov et al, 2016). Together, Huseynov et al (2016) conclude that their results support a hormonal mediation of female pelvic ontogeny, and that solutions to the ‘obstetric dilemma’ depend on both hereditary selection and adaptation, as well as plastic responses to ecological and dietary factors.

What is important to note in reconstructing birth in our evolutionary history, is the importance of finding both male and female pelvises. As obstetrical features are likely to be most pronounced in female pelvises, male pelvises provide context in understanding the extent to which such features are conserved over other morphological functions, or as is more likely the case, adaptations in the female body overcome challenges in responding to the multiple functions of skeletal and soft tissue anatomy. This is perhaps where the phrase ‘obstetric dilemma’ feeds into previous misconceptions of the maternal pelvis as almost ‘maladaptive’ in locomotive mechanics. However, this evolutionary puzzle of competing selective pressures on multi-function morphology would have undergone multiple iterations of adaptations throughout human history. The results of these iterations can arguably be seen in the variation of maternal pelvic shape in modern humans, for which pelvic shape typology classification attempts to categorise these alternate morphological solutions. Whether this categorisation is adequately utilised in understanding and explaining the degree of variance, shall be further discussed.

Typical birthing mechanics

The basic principle governing the passage of the neonate through the birth canal is known as Joulin’s Law (1864), whereby the fetus passes through the birth canal by orientating the greatest diameter of each body segment with the corresponding greatest dimeter of the maternal pelvic plane. For example, the modern human foetal cranium will typically orientate itself obliquely within the anteriorposterior diameter of the pelvic inlet (Abitbol, 1996:90). The consequences for understanding the complexity of nonhuman primate and hominid births are that the simplest and least complex will be those where the two foetal planes (the cranium and shoulders) and three maternal planes (inlet, midplane, outlet) are all maximised in the same direction, i.e. anterior, posterior or transverse, and therefore not requiring rotation (Abitbol, 1996:90). Although variant mechanisms may occur in modern humans, depending on the orientation of the neonate and pelvic typology (Walrath, 2003), three events are common to all: the foetus will descend; the part of the foetus which is orientated most inferiorly and is resisted by pelvic floor muscles, will rotate forwards to lie anterior under the pubic symphysis; and the part that emerges first will hence pivot around the pubis (Ndala, 2005b). Typical, successful delivery of the neonate in modern humans follows a sequence of distinct phases in the second stage of labour (see Downe, 2003; Ndala, 2005).

In humans, the foetal head is strongly flexed against the chest, and orientated with the biparietal width crossing the sagittal diameter of the maternal inlet, or slightly oblique. Nuchal extension, typical amongst nonhuman primates, is rare in humans, occurring once in every 300-500 births

(Posner and Buch, 1943; White, 1954; Prevedourakis, 1966; Oxorn and Foote, 1980). The head then descends, rotating 45-90°, allowing the biparietal to pass through the bispinous diameter, with the head twisted relative to the shoulders. As the head passes between the ischial tuberosities, it curves under the subpubic arch and the head extends.

In modern humans the pelvic inlet is widest in the transverse diameter, whilst the outlet is widest in its sagittal diameter. In the case of all primates, the long axis of the neonate cranium is the sagittal diameter (Aiello and Dean, 2002:446). In order to understand the evolutionary trajectory of obstetric evolution in hominins, it is necessary to understand the differences in the mechanics of parturition in modern humans and nonhuman primates. This forms a basis for predictions of the transitional stages and evolution of complex rotational birth typical in humans, as opposed to typically non-rotational birth in nonhuman primates.

Pelvic typology

Within modern human populations, there exists a significant degree of variation in adult pelvic shape and dimensions. Early studies by Caldwell and colleges defined the *Caldwell-Moloy classification* (Caldwell and Moloy, 1933; 1934), used to categorise female pelvic morphology in both a clinical and research context, and predict obstetric adequacy and potential risks during pregnancy and labour. **Figure 1.4.** below demonstrates the effect of such alternate pelvic typologies on the orientation of the neonate cranium as it passes through the birth canal.

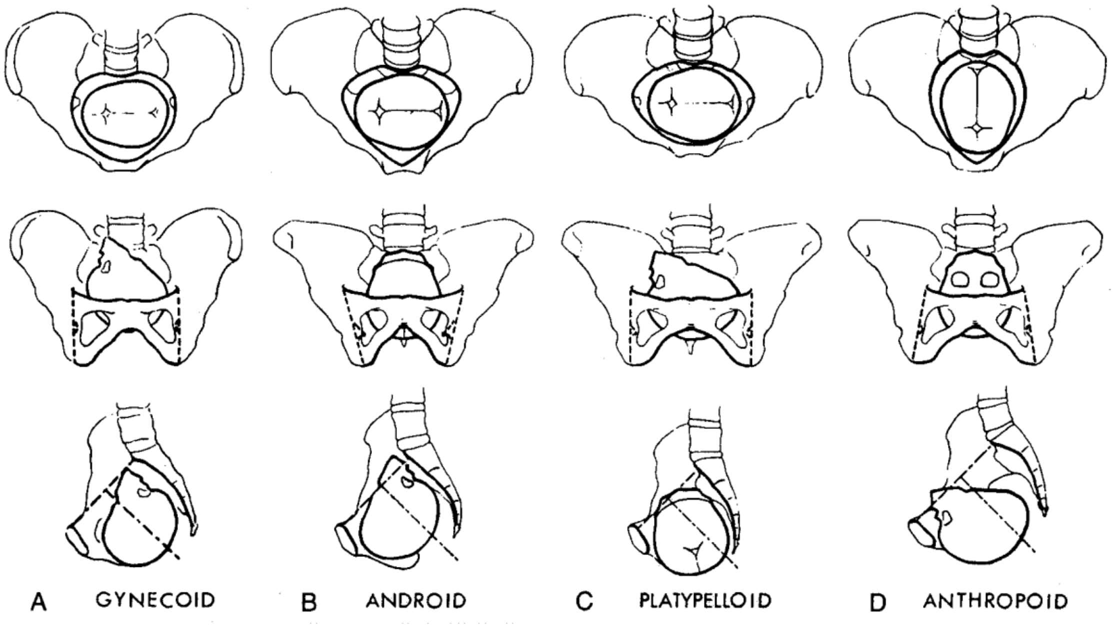


Figure 1.4. Schematic representation of alternate adult female Caldwell-Moloy pelvic typologies in humans, showing the passage of the neonate through the inlet, outlet and midplane. From Walrath (2003).

Walrath notes that the most common pelvic typology in modern human females, at ~50% (Walrath, 2003:11) is a gynaecoid shape typology that characteristically provides the greatest possible diameter through the inlet, midplane and outlet (Aiello and Dean, 2002:446; Walrath, 2003; Cunningham et al, 2005:34). This gynaecoid shape is an intermediate between a sagittally broad anthropoid typology typical of nonhuman primates, and a transversely broad platypelloid typology, and the morphological opposite of the male ‘heart-shaped’ android pelvis (Aiello and Dean, 2002:444).

Where this representation and categorisation of maternal pelvic variance falls short however, is the fact that the data used by Walrath (2003) of ~50% prevalence of gynaecoid shape comes from an early study of solely North American white females by Caldwell et al (1934). This was followed by a wider study (Caldwell and Meloy, 1938:8) of white (n=147) and non-white (n=121) participants which produced similar results for gynaecoid and platypelloid typologies (figures of which are displayed below in **Table 1.1)**.

	White	**African**
Anthropoid	23.5	40.5
Gynecoid	41.4	42.1
Platypelloid	2.6	1.7
Android	32.5	15.7
Sample size (n)	147	121

Table 1.1. Data from Caldwell et al (1938:8), depicting the percentage frequency of obstetric typologies according to the Caldwell-Moloy classification (Caldwell and Moloy, 1933; 1934).

Between the two sample groups, the prevalence of anthropoid and android typologies is notably different. Anthropoid typologies are observed to have an almost equal prevalence amongst the African sample, and android typologies among the white sample are more than double that of the African sample. The variation is notable between the two populations in this early and restricted analysis, but the encompassing of the sample for a white or African samples fails to acknowledge the significant degree of variation within both samples (see Ruff, 1995 and Kurki, 2013 for review). What this research fails to consider, is detriment to reliability in lumping white and African samples into binary categories, without accounting for the large scale of variation across the whole continent of Africa or those categorised as white.

Previous to Walrath (2003) however, Abitbol (1996:42) states that more recent research estimates gynaecoid prevalence at up to 70%, with populations in developing nations showing higher prevalence of android typology. Abitbol (1996:42) suggests this increased prevalence of android typology in developing nations is likely a product of increased exposure to strenuous work during childhood and puberty, which has been shown to result in abnormal pelvic development (Cunningham et al, 2010). This is arguably speculation, however, and has not been tested by larger scale analyses of trends between pelvic typology and activity during development across a large international sample, either in living or across historical populations.

What Abitbol (1996:49) does suggest in terms of human evolutionary trajectory, is that the shift in the hominid pelvis to platypelloid, where the anterioposterior diameter exceeds the transverse, is significantly related to erect posture and is evident from the anteriorposterior increase seen in more semi-erect pongids over quadrupedal monkeys. In humans, the pelvic inlet at birth appears anthropoid, but develops to greater platypelloidy with ontogeny of erect posture (Abitbol, 1987a) and the resulting lateral expansion of the sacrum under increasing vertical support (Abitbol, 1987b). In human infants who develop erect posture slowly due to orthopaedic issues or late development of erect posture, the pelvis continues developing as anthropoid (Abitbol, 1991). Abitbol (1993a) reasons that an ontological balance between anthropoid and platypelloid typology is significantly influenced by the timing of erect posture acquisition in childhood development.

In the midplane and outlet of the maternal pelvis, the force exerted by the trunk and abdominal viscera on the pelvic floor from orthograde posture increases the pressure exerted on the pelvic floor muscles and ligaments. In nonhuman primates with typically quadrupedal postures, the internal pressures are supported by the abdominal wall (Abitbol, 1996:51). However, in humans the pelvic diaphragm must take the full weight of abdominal and uterine pelvic organs directly, and so must be strengthened by a narrowing and secondary anthropoidy of the midpelvis (Abitbol, 1996:51). This in turn results in a narrowing of the bispinal and bi-ischial diameter (Abitbol, 1988a), and a strengthened pelvic diaphragm and perineal body. Support for the muscles of the pelvic floor is further increased in humans by prominence of the ischial spines (Abitbol, 1996:51), as well as medial intrusion into the midpelvis as a product of femoral head pressure exerted in the acetabulum (Rak, 1990). This serves to further reduce the transverse diameter in the midplane. It is arguable that these observations suggest bipedal locomotion has placed considerable evolutionary constraint on the maternal pelvis (through constriction of the biacetebular, transverse midplane diameter). However, significant limitations and transformation of the obstetrically relevant true pelvis are additionally conferred by downwards force exerted by abdominal and uterine organs on the pelvic floor, as a result of habitual orthograde posture. It would perhaps seem more appropriate for discussions and research to investigate the effect of posture and position of the central axis over the centre of gravity, rather than locomotive mechanics, to the evolution of modern human obstetric morphology.

In humans, maternal pelvic shape typology demonstrably results in varying orientation of the neonate during parturition, with non-gynaecoid typologies linked to numerous detrimental pathologies (Walrath, 2003). For example, women with a characteristically platypelloid typology commonly exhibit prolonged labour, with any excessive deformation of the transverse diameter of the neonate skull often resulting in neonatal death (Borell and Fernstrom, 1958). A recent study by Fremondiere et al (2017) investigated the reliability of using foetal-pelvic variables for predicting caesarean section and instrumental assistance in human females. The results suggested that the anterioposterior outlet diameter of the mother and biparietal length of the neonate were significantly effective variables in predicting need for intervention during labour (Fremondiere et al, 2017).   It is this observed relationship between pelvic typology and orientation of the neonate (inferred from estimates of neonatal cranial dimensions) which are employed by Rosenburg and Trevathan (e.g. Rosenburg, 1986; Rosenburg and Trevathan, 1996) to predict neonatal orientation and likely difficulty of birth in extinct hominins, providing an adequate reconstruction is possible.

It is worth noting that there is some degree of inaccuracy in medical and anthropological assessment of pelvic measurements. Due the poor preservation of ischial spines in the fossil record, reconstructions may not take these into account when reconstructing midplane values (Abitbol, 1996:44). Abitbol (1996:44) also notes that the anterioposterior diameter may be measured at the anterior limit from the inferior border of the pubic symphysis by anatomists, and the posteroinferior border by the obstetrician. Furthermore, the spines may not always be present on X-ray slides (Abitbol, 1996:44).

The ’pelvic floor hypothesis’

The influence of pressure on the pelvic floor has been previously suggested to have been a significant factor in driving the evolution of pelvic morphology in humans, and across mammalian taxa. It was Abitbol (1988) who proposed developed a ‘pelvic floor hypothesis’, whereby internal pelvic morphology is determined by the pressures on the pelvic floor exerted by locomotion, viscera and a potential foetus. Huseynov et al (2016) hypothesise that the evolutionary and ontological conflict observed in the female pelvis indicates a trade-off between obstetric adequacy and abdominopelvic stability. Huseynov et al (2016) note that whilst enlarged ischial spines and additional ligament and faciae of the human female pelvic floor do constrain the birth canal dimensions, they provide necessary support for the abdominal and pelvic organs, as well as sagittal stabilisation of the sacrum (Abitbol, 1988; 1996; Ashton-Miller and DeLancey, 2007; Tardieu et al, 2013). However, as high lumbar support created by greater intra-abdominal hydrostatic pressure is correlated with a wider pelvis (Grillner et al, 1978), this also results in greater strain on the pelvic floor. The relative strain on the female pelvic floor is therefore likely a limiting factor on birth canal dimensions, which is reflected in a higher incidence of pelvic floor disorders (Hander et al, 2003).

Recent work by Grustra et al (2019) supports this evolutionary explanation for obstetric pelvic evolution in mammals, for which a large-scale review of mammalian pelvic morphology. This review demonstrates pronounced sexual dimorphism in the pelvis of small bodied mammals with large neonates, notably amongst bats and guinea pigs, for which the typical closed male pelvis would not be able to facilitate the delivery of a neonate (Grunstra et al, 2019). Arguably, humans are not unique amongst mammals in having a small pelvic canal, where the mammalian context is often neglected in analysis by physical anthropologists (e.g. Abitbol, 1993; 1996; Trevathan and Rosenburg, 2002; 2016). Other mammals are able to significantly open the birth canal before and during parturition, demonstrated to the greatest degree among primates by *Saimiri* (Stoller, 1995). Among these species, the interpubic disc instead forms an interpubic ligament to provide greater flexibility for delivery, which is comparatively very limited in humans. However, these species are not bipedal, and so do not face the same pressures on the pelvis and internal pelvic floor. In contrast, Grunstra et al (2019) note that this flexibility in the female pubic symphysis is significantly constrained by functional demands on the pelvis, in regard to both body size and locomotion.

Amongst even-toed terrestrial ungulates, the female pelvis remains restricted despite birthing a relatively large bodied (though small brained) neonate, likely owing to strong biomechanical demands for effective fast-running locomotion (Grunstra et al, 2019). Grunstra et al (2019) suggest that amongst mammals, locomotion and posture are associated to varying degrees across species. Those species exhibiting large relative pelvic canals support their wide (and likely vulnerable) pelvic floors by engaging in postures effective in reducing pressures on the pelvic floor, or by living in water which counteracts the internal pressure exerted by viscera and the foetus (Grunstra et al, 2019). Together, this evidence across mammalian taxa supports Abitbol's alternate 'pelvic floor hypothesis' (1988). Further study of the attachment sites for pelvic floor muscles in fossil hominin specimens could shed more light on both the evolution of both orthograde posture and the obstetrical demands on the hominin pelvis.

Grunstra et al (2019) therefore hypothesise that bipedal locomotion in humans may not be the primary constraint on pelvic width, as proposed by Washburn's (1960) prevailing 'Obstetric Dilemma' hypothesis, but rather it is the degree of flexibility of the maternal pelvis. This flexibility is greatly reduced in hominids compared with smaller mammals with large neonates, but similar to the pelvis of large-bodied terrestrial mammals such as Kangaroos (Grunstra et al, 2019). This is supported by observations of a reduced level of sexual dimorphism in humans compared with other mammals, with smaller species with large bodied neonates displaying an open pelvic symphysis (Grunstra et al, 2019). It is therefore reasonable to suggest that the pressures exerted on the hominin pelvic floor, to varying degrees over the trajectory of hominin evolution, would have been a prominent driver of internal skeletal morphology in the pelvis. Any pressure to increase the maximum dimensions of the birth canal (as a result of pressure from selection favouring increasing neonatal brain size) would therefore be detrimental to pelvic floor stability, as well as bipedal mechanics.

Hormonal influences

As aforementioned, much of the specialisation of the maternal pelvis is orchestrated by elevated levels of maternal hormones (Downe, 2003). This not only occurs during maternal development, but also during gestation and labour. Becker et al (2010) demonstrated that raised levels of the hormone relaxin during pregnancy induce structural changes in the fibrocartilaginous disc between the pubic symphyses, which widens the symphyseal width and increases the anteroposterior. During labour, elevated levels of progesterone and relaxin also increase elasticity in the pelvic ligaments and allow minor posterior distention of the sacrum at the sacroiliac joint (Bjorklund et al, 1997; Bennet and Brown, 2003; Vleeming et al, 2012), increasing the sagittal diameter of the outlet by around 10-20% and the transverse diameter by around 5-7% (Russell, 1969; Bjorklund et al, 1997). This hormonal influence serves to increases obstetrically relevant dimensions of the maternal birth canal, and minimise risks associated with high CPD and promote successful delivery of the neonate and maternal survival. Although, these short-term changes only appear to affect soft tissues, which rarely survive in the archaeological and fossil record. Such activity may be genetically mediated, facilitating comparisons between modern and ancestral genes to provide insight into the evolutionary trajectory of hormonally mediated obstetric morphology. However, with ancestral genomic sequencing analysis of hominin ancient DNA currently limited to Neanderthals and Denisovans (see Liu et al, 2022), research on this subject is likely a distant reality. Researchers must alternatively rely on osteoarchological remains, or comparative extant species.

Hormonally mediated increase in sacral mobility also allows for extensive sacral nutation, which involves the anterior oscillation of the mother’s sacrum, encouraging complete engagement of the neonate cranium into the birth canal (Tourne, 1985), coupled with an increase in synovial and symphyseal fluid (Brooke, 1924). This is achieved through rotation of the sacrum, via action of the utero-sacral ligaments that form the true tendons of the contracting gravid uterus muscle (Tourne, 1985). Brooke’s extensive (1924) study utilising early radiographic analysis demonstrated a peak in sacroiliac joint (SIJ) mobility at ~25y. This increase in SIJ mobility is also achieved through a reduction in the curvature of the joint surface in women with the onset of puberty (Vleeming et al, 2012). Significant intra-pelvic movement during childbirth is argued to be responsible for SIJ lesions (Chamberlain, 1930), resulting in reported movement restriction and pain at the SIJ due to collisions of complimentary facets (Abramson et al, 1934; Gray, 1938).

Extensive nutation of the sacrum during labour may well be an adaptation that has evolved in hominins to open the pelvic outlet, reducing the obstructive effect of a lowered, larger sacrum in modern humans (Aiello and Dean, 2002:443). The prevalence of such SIJ lesions is perhaps something which may be identifiable from future study of archaeological remains to provide diagnoses of the evolution of modern human SIJ mobility. However, whilst maternal hormones may mediate change in the maternal pelvis, levels of stress hormones during pregnancy and crucially during parturition in both humans and nonhuman primates can have a significant effect of obstetric outcomes. Whilst this may not invariably affect heritable morphology, elevated levels of corticoid hormones have been shown to disrupt and even entirely prevent contractions during birth (Wadha et al, 2001). It is important to recognise the consequence of this physiological connection between both physical and psychological trauma, arresting typical delivery as a direct adaptation to risk (to either the mother or infant or both) or as a by-product of other biological mechanisms. The evolution of the interactions between stress and normal delivery are crucial not only to the understanding of normal birthing amongst our own species, but also of nonhuman primates, in order to ensure best practice in captive and conservation efforts globally. This will be further discussed in subsequent chapters, regarding the evolutionary adaptations to mitigate parturitional, maternal stress and mortality through adaptive, prosocial birthing behaviours.

Neonatal cranial moulding

It is also worth discussing the evolutionary mechanisms that have emerged in human neonate morphology to minimise risks from CPD and facilitate successful delivery in response to high levels of CPD (Wood and Quinney, 1996). One such adaptation is neonatal cranial deformation during labour (Hausler and Schmid, 1995; Abitbol, 1996:72), termed cranial moulding. Cranial moulding of the neonatal cranium during labour describes the mechanical changes in the neonatal cranium as a result of external compression by the maternal birth canal (Graham and Sanchez-Lara, 2015:243). Incomplete fusion between the sutures of the neonatal cranial vault allows some of the cranial bones to override one another (Bennet and Brown, 2003). In normal birth, anteroposterior compression forces the frontal and occipital to slide beneath the parietal bones, elongating the occipitofrontal diameter to its maximum and thus reduce the vertical diameter of the neonatal cranium (Ndala, 2005b; Graham and Sanchez-Lara, 2015:243).

This adaptation was demonstrated by Borell and Fernstrom (1958), who utilised radiographs which showed in-situ vertex moulding of the neonatal cranium through the birth canal, with an elevation of the vertex and an increase in the biparietal diameter through inward displacement of the occipital and frontal, reducing the presenting occipitofrontal diameter. Borell and Fernstrom (1958) observed that cranial moulding appeared to be the product of soft tissue contraction and pressure rather than pelvic size. The biparietal and suboccipitobregmatic diameters are reduced by up to 1.25cm (Bennet and Brown, 2003:161), whilst the occipitomental diameter is increased, as shown in **Figure 1.5.**

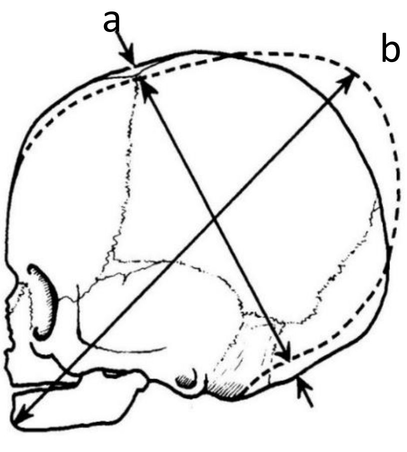


Figure 1.5. Typical moulding of the fully flexed modern human neonate cranium (left lateral view), adapted from Bennet and Brown (2003:161). (a) Represents the reduced suboccipitobregmatic diameter and (b) represents the increased occiptiomental diameter. The dotted line represents the moulded border of the cranial vault.

By measuring the change in neonatal cephalic diameters before and after delivery, Abitbol (1996:72) observed that 15.5% (n=123) of infants showed some change in cephalic dimensions after vaginal delivery, in which all cases were also categorised as prolonged and more painful. Here, the suboccipitobregmatic dimension shortened on average by 1.1 (±0.6)cm, and the occipitomental dimension increased by 1.9 (±1.1)cm (Abitbol, 1996:72). Abitbol (1996:92) also notes two further significant evolutionary features of the modern human foetus which allow for successful delivery – spheroidicity in vertex presentation, and foetal mobility. As a result of increased encephalisation of the human infant, the typical anterior flexion of the chin onto the chest, the occipital region is presented first, which results in a spheroid plane where the anterioposterior dimeter is close to the transverse (Abitbol, 1996:92). This is unique amongst the mammalian kingdom and is advantageous in facilitating the vertex portion of the infant to extend, flex, roll and rotate through the complex trajectory of the hominin maternal pelvis (Abitbol, 1996:92). Even minor deviation from spheroidicity, such as presentation of the brow or face, are strongly associated with highly pathological deliveries (Oxorn, 1980; Cunningham et al, 1993), where face presentations for instance produce dimensions too large to be accommodated by any maternal pelvic diameter (Abitbol, 1996:92). One can imagine that in the course of hominin evolution, changes in the degree of infant facial prognathism may have unintentionally resulted in a reduction of presenting diameters.

Further to this, Abitbol (1996:93) notes the adaptation of increased mobility of the human neonate head and body through delivery, enhanced by cranial spheroidicity. This is evident when facial presentation of the neonate results in reduced mobility of the cranium and body, and therefore prevents successful passage through the birth canal (Abitbol, 1996:93). Increased mobility of the foetal head also prevents prolonged, excessive pressure on any single region of the cranium during delivery, an area particularly vulnerable in comparison to nonhuman primates (Abitbol, 1996:93), which can lead to serious complications such as foetal skull hematoma (Borrell & Fernstom, 1958; Cunningham et al, 1993; Ndala, 2005b). Mitigating against excessive pressure exerted on the cranium during delivery, Holland (1922) observed that the dura matter which underlies the cranial bones, acts as a protective mechanism to minimise stress transmitted to the brain during delivery. This is perhaps a further adaptation which serves, in humans, to prevent excessive moulding resulting from stronger maternal uterine muscles and increasing infant encephalisation seen in humans.

Lastly, physiological changes as a result of CPD has also been observed. During prolonged abnormal labour, neonates have been documented to develop hypoxia as the body is starved of oxygen from interruption of placental blood flow by abnormal contractions and cranial and body compression by hypertonic uterine muscles (Hon and Quilligan, 1968; Beard et al, 1971 Stewart and Philpott, 1980). Research by Stewart and Philpott (1980) observed an adaptive response by the foetus during labour of early and prolonged foetal heart decelerations, restricting the flow of hypoxic blood as a result high CPD. This again may be a further example in humans of an adaptive physiological response in the neonate to increasing risk as a product of increasing CPD, and something which will likely have posed further risk in ancestral hominins facing increasing pressure on the neonate cranium within the transverse-sagittal dimension of the birth canal, and the proximal-distal pressure exerted by maternal soft tissue along the centre of gravity and uterine contractions. Distinguishing the strength of selective pressure exerted by these two factors is difficult, and is lacking from wider consideration in previous research. Whilst beyond the scope of this thesis, future study of the pressures determining the degree of cranial moulding should consider whether these are mutually exclusive, or both significantly contribute to the degree f neonatal cranial moulding.

This exploration of the morphological adaptations of the maternal human pelvis demonstrates a suite of features which have evolved in response to the mechanical pressures of birth, and the changing shape of the human pelvis and human neonate at-term. These adaptations to the changing mechanism of delivery appear in both soft tissue, physiology and the skeletal morphology of mother and infant, should theoretically be detectible in the ancestral fossil record. Whether this is the result of heritable phenotypes, Brownian motion and genetic drift, or an individual level plastic response to socioecological pressures, is a question which requires further investigation and will be explored through this thesis.

Morphological plasticity

One of the most significant factors affecting the estimation of hominin obstetric morphology is the prevalence of variation within and between populations of both modern and archaic humans. Whilst the morphological variation between and within nonhuman primates is relatively poorly understood, much research has been conducted which demonstrates a significant level of variation within the maternal pelvis of modern humans. It is therefore reasonable to assume that such variation has a deeper ancestry, and therefore may well have been a common feature of early hominin obstetric morphology. This section will briefly explore the concept of morphological plasticity (specifically phenotypic morphological plasticity), and the implications for understanding and reconstructing hominin obstetric morphology.

Genetic components of maternal stature do contribute significantly, as also demonstrated among nonhuman primates by Price et al (1999). Specifically in the context of obstetric morphological evolution, whilst neonatal head girth has relatively low morphological plasticity, neonatal body mass and maternal stature and pelvic morphology have relatively high plasticity (Wells et al, 2012). As previously discussed, cranial moulding and the plastic nature of the foetal cranium as a result of open cranial sutures is an adaptive feature minimising the presenting dimensions and pressures on the internal dimensions of the maternal pelvis. Given that neonatal head circumference is most strongly predicted by maternal head circumference (Leary et al, 2006), it is highly likely that a strong genetic component determines neonatal cranial dimensions across generations.

The plasticity and prevalence across global populations of modern humans results in a significant level of within and between group variations. The availability of modern medical care also has a predicted resultant effect of facilitating such variation – those with inherited pelvic structures typically deemed to be detrimental to birth, with the help of medical intervention, are able to pass on genetic components of such morphology. However, much of the variation seen in the maternal pelvis is a product of external ontogenetic and socioecological factors. Such factors include diet, life history, and life-time activity.

Early work by 20th Century obstetricians (Dick, 1922; Baird, 1949; Illsey, 1966) demonstrated clear links between maternal diet and poor-health, and perinatal mortality. An extensive study across a number of UK cities by Dick (1922) found that rates of maternal rickets were strongly associated with increasing rates of perinatal mortality and necessary caesarean interventions – those women with poor diets during early development were more likely to suffer rickets and therefore show reduced pelvic obstetric dimensions necessary for successful births. Illsey (1966) further confirmed these results in the UK, finding a clear North-South divide and a significant correlation between maternal stature and perinatal mortality. Additionally, pelvic obstetrical dimensions have been demonstrated to be affected by childhood nutritional stress (Sibley et al, 1992), and Vitamin D deficiency as a product of reduced UV exposure (Greulich and Thoms, 1938; Abitbol, 1996).

More recent work has continued to demonstrate clear and significant associations between maternal stature and incidence of complications necessitating caesarean delivery (Mahmood et al., 1988; Sokal et al., 1991; Kwawukume et al., 1993; Cnattingius et al., 1998; Khunpradit et al., 2005; Stulp et al., 2011). Further risks of maternal injury (Gudmundsson et al., 2005) and infant asphyxia are also strongly associated with developmentally reduced maternal stature (Lee et al, 2009). Furthermore, the increasing issue of maternal obesity during gestation has led to increased rates of neonatal macrosomatic growth and resultant increased levels of CPD (Gudmundsson et al., 2005; Monasta, 2011). However, it is of course important to separate incidence of short stature as a product of ontological development and dietary stress, with inherited contributions (although archaeologically, without adequate genetic samples and identified contributing genes, it is difficult to determine whether morphology is genetically or environmentally mediated).

The activities of individuals performed repeatedly throughout childhood development, have also been demonstrated to result in atypical obstetric morphology. Work by Ellison (2001:61) point to a body of evidence from morphological assessment of female athletes, whereby top runners, ballet dancers and gymnasts have pelvic breadths at the narrow end of normal range. Ellison (2001:61) suggested that this points to a locomotive cost of the broader typical female pelvis on locomotion, whereby women who are more ‘athletic’ have a narrower pelvis which has inherently ‘cheaper’ in locomotion. However, Ellison (2001:61) does note that this is different from muscular strength, where female swimmers typically do not have significantly narrow pelvises, likely being less constrained by orthograde, bipedal locomotion. Interestingly among historic American slave populations, Kelly and Angel (1987) found an association between resultant poor health and nutritional stress, and reductions of maternal stature and pelvic proportions. This demonstrates a clear role of socially enforced activity and poor socioeconomic condition on maternal health and birth risk, something which may well be visible in archaeological populations.

2.3. Birth in nonhuman primates

Stoller (1995) notes that despite a lack of comparative data, it is commonly assumed that humans are unique among primates in their birth mechanics, often emphasising pelvic measurements whose functional significance has little or no obstetric significance in nonhuman primates (Stewart, 1984). Stoller (1995) argues that the inconsistencies in anthropological estimations of CPD, are due to a lack of information on nonhuman primate foetal head attitude during birth, and the obstetric diameters of the maternal pelvis. Therefore, Stoller (1995) reasons that although skeletal material can provide some measure of CPD and birth mechanics, inferences on cranial moulding, the extent of ligament relaxation and typical neonatal attitude require direct investigation of extant nonhuman primates.

Since almost all nonhuman primates typically give birth at night (Jolly, 1972), detailed descriptions are scarce. Furthermore, whilst observations of primates in open habitats with clear visibility make observations of behaviour relatively straightforward, species occupying dense arboreal environments necessitate close proximity to the parturient female. This of course is problematic as the mother may not only attempt to avoid human disturbance, even among habituated groups (Dias, 2005), but is ethically challenging in minimising induced stress. This makes conclusions on the mechanism, complexity and difficulty of labour in wild nonhuman primates difficult to assess, and hence much of the comparison in obstetrics relies on captive observations. There are a small number of studies which utilised non-invasive techniques, such as radiography to examine birth among captive nonhuman primates that can provide some insight into birth mechanics in labouring nonhuman primates. Yet this small sample size does make inferences of species typical mechanism difficult to estimate.

Despite this difficulty, observations and greater exploration of the mechanism and nature of birth in nonhuman primates is essential to understanding the context of birth in other primates, and for understanding the response of other species to the delivery on the infant on an individual basis This individual response in terms of the explusion of the neonate, is in turn essential to theorising the likely individual and group responses to the birth of hominins in our evolutionary past – if nonhuman primates also demonstrate difficulty in delivery, coupled with increased behavioural stress, this would also likely have been observed in our own ancestral species.

Aiello and Dean (2002:442) note that in nonhuman primates, there is an allometric relationship between the size of the neonate cranium and maternal birth canal size. Interestingly, smaller primates, such as marmosets and tamarins, show a trend similar to humans in having infants with larger crania relative to maternal pelvic dimensions, and certainly larger than seen in apes (Leutenegger, 1982). Using data pooled from previous anatomical studies (see Schultz, 1949; Leutenegger, 1970a; 1970b), Leutenegger (1982) demonstrated that the neonates of smaller primate species have larger crania relative to the mother's pelvic inlet than larger primates, with the exception of human neonates with high CPD. Hausler and Schmid (1995) observed that in smaller species of New World monkey, the neonate cranium at full term is typically larger than the dimensions of the maternal pelvic inlet, necessitating greater temporary deformation of the skull during labour and dilation of maternal pelvic ligaments, similar to that seen in modern humans.

In terms of pelvic anatomy, species which show the greatest degree of sexual dimorphism are those which deliver the largest neonates in relation to maternal pelvic size (Straus, 1929; Schultz, 1949; Leutenegger, 1974; 1982; Mobb and Wood, 1977; Wood and Chamberlain, 1986; Aiello and Dean, 2002:445), and females in particular have relatively longer pubic rami, resulting in higher ischiopubic indices, although Aiello and Dean (2002:445) note that apes show greater overlap in ischiopubic indices than humans and monkeys due to a relatively smaller neonatal relationship to maternal pelvic size. Crucially in relation to obstetric morphology, Wood and Chamberlain (1986) demonstrated, contra to Streudel (1981), that the larger birth canal seen in nonhuman primate females, is true reflection of increased pelvic inlet size, rather than any allometric difference between males and females.

Given the alternate locomotive mechanics of nonhuman primates however, where humans tend toward platypelloidy with shorter iliac height, and habitually quadrupedal primates tend toward anthropoidy (Abitbol, 1996:43), comparisons of individual dimension without a complete assessment of the maternal pelvis, gives little indication of crucial CPD and the likely difficulty and risk of delivery. Therefore, any conclusions of obstetrical adequacy of fossil pelvic material would require assessment of multiple, obstetrically relevant dimensions.

Stoller (1995) notes that since the foetus passes the sacral promontory long before the pubic symphysis, measurements of the bony pelvic brim are not critical in understanding obstetrical characteristics in nonhuman primates. Therefore, Stoller (1995) measured the distance from the upper-posterior border of the symphysis to the nearest point on the anterior sacrum in the anteriorposterior diameter, and largest diameter across the superior margin of the acetabular for the inlet (these measurements are displayed in **Table 1.2.**). This measure was smaller than estimates used in previous research (Schultz, 1949; Leutenegger, 1970; Abitbol, 1991; Tague,1991; 1995), which Stoller (1995) argues more accurately represents the constraints of the maternal pelvis.

	Pelvic inlet (mm)		**Pelvic outlet (mm)**		
	Anterioposterior	Transverse	Transverse	Bi-ischial	Posterosaggital
***Papio* (n=7)**	27.1 ±0.6	22.4 ±0.5	23.2 ±0.2	18.3 ±0.9	7.8 ±0.9
***Saimiri* (n=4)**	80.6 ±7.5	63.2 ±3.9	61.4 ±4.5	49.7 ±5	44.9 ±0.6

Table 1.2. Figures obtained by Stoller (1995:65) of the obstetric dimensions in *Papio anubis* and *Saimiri sciureus*.

Stoller (1995) did not identify any significant characteristics of the midplane, where traditionally a measure of the distance between ischial spines represents this diameter whilst the ischial tuberosities provide a measure of the outlet. Stoller (1995) does note however that the ischial tuberosities do not appear obstetrically significant from the radiographs taken, and that the foetal head in both *Papio* and *Saimiri* passes in front of the tuberosities, fully exiting the maternal pelvis after the ischial spines. Furthermore, the ischial body forms a ventral boundary, but a significant gap between the foetal skull and this border is present in both *Papio* and *Saimiri*, meaning this is not significantly constrictive (Stoller, 1995). Stoller (1995) therefore reasons that a three-plane view of the maternal pelvis is not appropriate for studying nonhuman primates. The development of the midplane in hominin evolution is then perhaps and important defining feature of the constrictive morphology of the modern human pelvis, and its evolution is something which needs identifying from further research within the fossil record. However, Stoller (1995) was unable to reliably obtain an estimate of the widest transverse diameter of the posterior border between the ischial spines and sacral base from lateral radiographs, and so could only provide an anterioposterior diameter between the sacral border of the illum and the narrower ischial spines.

Abitbol (1996:49) notes that the nonhuman primate pelvis is far less distinct in its inlet, midplane and outlet, whereas the planes of the human pelvis differ to such a degree that it requires complex internal rotation to negate. Old World and New World monkeys have minimal differentiation, with pongids showing slightly more hominid-like separation between planes (Abitbol, 1996:49). This is perhaps an indicator of the more orthograde posture adopted by pongids (Aiello and Dean, 2002:286), and a reflection of the alternate, more human-like pressure exerted on the pelvic floor. Furthermore, among hominids, Abitbol (1996:52) reasons that the anterioposterior diameter of the pelvic outlet should not be given consideration in terms of any contractions on obstetric adequacy, given the open anterior-sagittal portion similar to the open posterior portion of the nonhuman primate pelvis. When passing through the outlet, the nonhuman primate infant is unimpeded posteriorly by the sacrum, given its higher position.

What is crucially lacking from a number of studies of cephalopelvic disproportion in nonhuman primates is consideration of ligament relaxation during parturition, as outlined recently by Grunstra et al (2019). Stoller (1995) interestingly observed a substantial degree of ligament relaxation and resulting increase in the transverse diameters of the maternal pelvis during labour in both *Papio* and *Saimiri*. The effect on the anteroposterior diameter however could not be determined from lateral radiographs taken (Stoller, 1995). Stoller (1995) however hypothesises that any effect from sacroiliac hypermobility would be minimal, but separation of the pubic symphysis would be significant, allowing the foetal skull to protrude into the anterior space created. The lack of significant increase in the anteroposterior diameter in both species observed suggests that dorsal displacement of the sacrum was also not significant (Stoller, 1995).

In both *Papio anubis* and *Saimiri sciureus*, Stoller (1995) found the submentobregmatic diameter to be significantly smaller than the occipitofrontal, allowing strong nuchal extension to minimise neonatal presentation (and in turn CPD) through cephalic presentation. Stoller (1995) crucially observes that, contra to previous assumption of an elliptical presentation (see Leutenegger, 1974; 1982; Tague and Lovejoy, 1986; Abitbol, 1991; Berge, 1993), the foetal cranium presenting in both *P.anubis* and *S.sciureus* approximates a circle. However, due to the irregular contours of the face in both species, the protruding muzzle leads descent of the neonate, with a long axis along the mandible and throat (Stoller, 1995). Stoller (1995) does observe however that the in both species, nuchal flexion would hypothetically also lower the presentation diameter to a similar degree as nuchal extension.

Interestingly, only in *P.anubis* did Stoller (1995:73) observe any cranial deformation, with a 1-2mm depression of the frontal bones in two of four births, but over a 72-hour period between measurements taken before and after labour, the dimensions were not significantly different. This contravenes Rosenburg (1992) and Hartwig (1995) who suggest that cranial moulding was a significant mechanism in birthing among nonhuman primates. Interestingly through dissection of a stillborn *P.anubis* neonate and from radiographs of successful births, no anterior fontanelle was observed in the skulls of either species (Stoller, 1995). This reinforces earlier observations by Schultz (1969) that in most monkey species, the fontanelles have nearly or entirely disappeared. This characteristic may indeed be a significant evolutionary feature in hominins allowing greater mobility of the foetal skull during labour and facilitating temporary reduction of neonatal cranial dimensions for delivery.

Stoller (1995) states that from observation of *P.anubis* and *S.sciureus*, the degree to which the cephalopelvic ratio reflects true obstetric dimensions is limited by maternal pelvic ligament relaxation, rather than foetal rotation. This is represented below in **Figure 1.6.** It is clear from these schematics that Saimiri experiences a significant level of CPD.

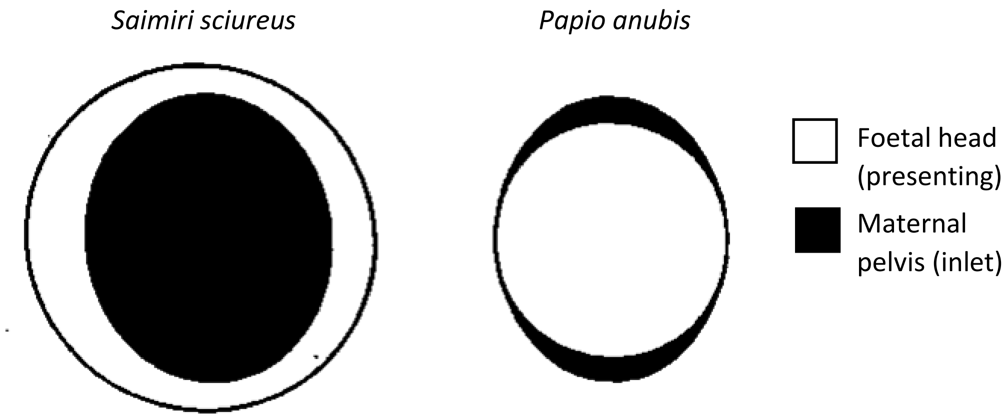


Figure 1.6. Schematic representation of the cephalopelvic ratio in *Saimiri sciureus* and *Papio anubis*, adapted from Stoller (1995:75).

Stoller (1995) notes that since the neonate cranium does rotate within the maternal pelvis, accurate estimates of the cephalopelvic ratio are difficult to calculate, as the diameters are not constant. However, since the cephalic presentation is relatively circular rather than elliptical, orientation is not considered as a significant issue by Stoller (1995). Although it is worth noting that the schematic represents the at-term undeformed profile of the presenting foetal head, and the level of cranial deformation afforded by the neonatal fontanelle, in conjunction with any maternal expansion of the birth canal (either normally mediated or morphologically afforded) may reduce this severe level of disproportion. This does not diminish however the scale of CPD observed, which appears relatively higher than that typically argued to be the mean for modern humans.

In conjunction with estimations of maternal pelvic metrics, Berge (1993) illustrated a flexed position of an ape foetal head, following on from previous work by Leutenegger (1970; 1974; 1984) who suggested that during birth, the foetal head would tilt into dorsiflexion so as to present cephalically, with the shortest sagittal dimension within the pelvic inlet. Leutenegger (1974) interestingly notes that strong dorsiflexion, similar to humans, must be important in callithricids and small cebids, along with most cercopithecoids, who show relatively high CPD among nonhuman primates. This relationship between CPD and neonatal flexion explored by Stoller (1995) during parturition is crucial to the optimal and typical trajectory of delivery in nonhuman primates and ancestral hominins, which will be further discussed in the following section.

Obstetric morphology

In conjunction with the curvature of the modern human female birth canal, the resultant CPD between the dimensions of the neonate cranial and maternal birth canal produces a unique pattern of typical rotational birth in modern humans (Ruff, 1995; Rosenberg and Trevathan, 1996; Walrath, 2003; Weaver and Hublin, 2009; Franclscus, 2009; Ding et al, 2013). The evolutionary significance of this mechanism of birth has been discussed to a limited degree in previous literature. Franclscus (2009) interestingly notes that having a neonate born occiput-posterior, as in most other living primates, makes it easier for the mother to prevent the umbilical cord from wrapping around the neonate’s neck, and remove any mucus obstructing the airways. With the modern human pattern of occiput-anterior birth, any attempt by the mother to re-orientate the foetus to correct these problems risks spinal damage (from pulling the head and neck backwards to vigorously). The risks to maternal and neonatal survival imposed by the difficult nature of modern human, and potentially reduced capacity for the mother to assist delivery, arguably necessitates either obligate midwifery behaviour, or alternatively a physio-morphological adaptation (such as increased birth canal dimensions or a reduction in neonatal dimensions) to increase the chance of survival for the neonate and mother (Weaver and Hublin, 2009; Franclscus, 2009). Although of course these adaptions may not be mutually exclusive, they may have varied and unequal degrees of influence on mortality risk. In either case, extant primate observations can provide insight into how birthing mechanics in morphologically similar species influence behavioural responses, both of the mother and potentially in social group members.

Though not the earliest attempt to investigate and document typical birthing mechanics in extant primates, work by Stoller (1995) provides the earliest thorough investigation, utilising radiographs of labouring *P.anubis* and *S.sciureus*. Stoller argued that an understanding of the mechanism of labour is critical in determining which foetal cranial and maternal pelvic dimensions accurately reflect the CPD relationship. Thus an understanding of the mechanics of birth is also essential in determining crucial features in fossil specimens which can be used to determine likely CPD and the potential increasing difficulty of birth in hominin evolution.

Earlier work by Danforth et al (1942) documented the anatomy of a labouring *Macaca mulatta* female by analysis of frozen sections post-mortem, for which a transverse presentation of the neonate was described. However, this did not provide an in vivo snapshot of typical birth mechanics, as the neonate may have changed position post-mortem and in fact the death of the mother and neonate during labour suggests an abnormal arrest in delivery. Therefore, the conclusions on typical delivery from this study are sceptical at best, other than demonstrating that rotation during the descent through the birth canal is possible in this species.

A reliable and accurate estimation or measurement of foetal head attitude during delivery is essential in determining CPD in nonhuman primates, and in predictions of CPD experienced among fossil species. Rydberg (1954) stated that the movement of the foetal head is widely accepted as not being determined solely by the maternal bony pelvis, but is also determined by the three-dimensional shape of presenting neonatal dimensions. Following Joulin's Law (1864), the neonate will occupy the smallest dimension and therefore the mobile foetal head will flex or extend to present the smallest diameter. Stoller (1995) observes that among all livestock, rodents and carnivores, the foetal head is flexed during gestation, and gradually extends to full extension at term resulting in cephalic presentation at the onset of labor. This is where the snout, not the occiput as in humans, dilates the cervix (Schuman, 1914; Rudolph and Ivy, 1933). Schuman (1914) predicted that in nonhuman primates, as in livestock, long-snouted species would present with head extension cephalically, whereas flat-faced species would present flexed. Both Schultz (1949) and Trevanthan (1987) assumed that the attitude was neutral, something which seems highly unlikely given the flexibility of the primate neck. Therefore, it should not be assumed that extinct hominin neonates would also show strong flexion of the head through delivery, but rather each species should be assessed for likely foetal head attitude through each plane of the pelvis.

Stoller (1995) reasoned that any attempts to model fossil hominin and nonhuman primate mechanics, must take into consideration observations of *in vivo* soft tissue and mechanics in nonhuman extant primates, alongside humans, rather than relying on linear pelvic measurements. Therefore, to provide greater insight into true birth mechanics, Stoller (1995:43) provided an extensive study of the mechanism of birth in two nonhuman primate species – *S.sciureus* (n=4) and *P.Anubis* (n=7) – by taking a series of radiographs of spontaneous and unrestrained, unsedated, labouring animals. *P.anubis* neonates are extremely prognathic, whilst *S.sciureus* are flat-faced (Stoller, 1995), enabling Stoller to test Schuman (1914) and Stewart's (1984) suggestion that foetal attitude is dictated by facial morphology. This is supported by Stoller's (1995) results, which demonstrated that in successful deliveries of both *P.anubis* and *S.sciureus*, foetal presentation was strongly extended and cephalic, for which Stoller (1995:55) notes that in three *P.anubis* and five *S.sciureus*, foetal head attitude did not vary by more than 10°. In the single case of flexion seen in *S.sciureus*, birth did not progress beyond engagement and necessitated caesarean delivery by veterinary assistance (Stoller, 1995). Together, Stoller's (1995) results supported the conclusion that foetal head extension throughout delivery is typical among nonhuman primates. Deviation from this (i.e. foetal head flexion) is detrimental to successful delivery (Stoller, 1995), and therefore a risk to maternal and neonatal mortality in these species regardless of craniofacial morphology.

In hominin evolution, the predicted increasing dystocia risk as a result of increasing neonatal size, coupled with constricted obstetrical dimensions, may have passively resulted in a shift to foetal head extension to flexion in typical labour. Interestingly, the *S.sciureus* birth that Stoller (1995) observed with foetal head extension and required veterinary assistance, was diagnosed as macrosomic with a malformed liver and brain. Here, the neonate was 37.9% larger – 158.6g vs 115g (Stoller, 1995:43) – than the next largest neonate and five standard deviations from the colony mean (Stoller, 1995:77), which is suggested to have also influenced the resultant dystocia. Furthermore, Stoller (1995), observed that in the breech-delivery of a *P.anubis* neonate, the neck of the foetus was extended before entering the birth canal. This suggests that in *Papio,* extension is not solely orchestrated by the bony maternal pelvis and in fact mediated by activity prior to engagement with the pelvis. Whilst this example within an individual of a single taxa does not provide a reliable basis for predicting exact hominin birthing mechanics, it can signal the presence of physiological and morphological factors influencing the presentation of the neonate, resultant CPD and dystocia risk, and in-turn the potential for adaptive responses to mitigate this risk. For hominins experiencing selective pressure for increasing neonatal cranial expansion, the degree of flexion or extension within the womb prior to delivery would have been the product of adaptive physiological or morphological response to mitigate risk associated with macrosomatic growth in-utero, restricting neonatal at-term dimensions and degree of CPD. Whilst this is of course difficult to identify from the fossil record, further investigation among extant primates of physiologically controlled somatic growth in utero and its relationship with birthing outcomes could provide clues into the evolution of our own species.

In terms of rotation, Stoller (1995) observed internal rotation of the neonate in both *Papio* and *Saimiri*, with mentum-anterior orientation in each successful delivery, with varied engagement of the head. Through the passage of the neonates in both *P.anubis* and *S.sciureus*, Stoller (1995) observed rotations of the foetus, with minor nuchal torsion – no more than 45° (Stoller, 1995:57) – as the trunk tended to align with cranial rotation. Stoller (1995) suggests that these rotations through delivery serve to manoeuvre the foetus through the restrictive portions of the bony maternal pelvis. Stoller (1995) demonstrated that after exiting the vagina at delivery, the neonate cranium in both *Papio* and *Saimiri* species flexed around the maternal pubic symphysis. Whilst this flexion of the cranium is also seen in humans, Stoller notes that in the majority of cases observed after vertex delivery, the mother grasped the neonate and manually assisted in delivery of the occiput, neck, shoulders and most of the body during a single contraction, with no significant delay between cranial and shoulder delivery. In four deliveries (n=11), no rotation of the shoulders or foetal head outside of the birth canal was observed (Stoller, 1995:64).

In passing the neonate shoulders, Abitbol (1996:15) notes that in general, the anterio-posterior diameter of the chest is easily compressible amongst all primates, due to the flexibility of the ribs and cartilaginous composition at term, but the shoulders are not always as easily compressed. Abitbol (1996:15) details that in Old World and New World monkeys, the pectoral girdle is located anteriorly and so easily compressed; in pongids and likely in australopithecines with more lateral shoulder joints, a narrowing of the upper chest allows for some compression; in *Homo*, the shoulders become relatively fixed laterally to an expanded upper chest (Jellema et al, 1993), resulting in negligible possible compression. Trevathan and Rosenberg (2000) argue that this is not the case, and that the neonatal shoulders should be factored into estimations of obstetrical adequacy. Comparatively, the shoulders are indeed more flexible and compressible, with shoulder dystocia contributing to much lower rates of arrested labour in modern humans (Abitbol, 1996:96). Whilst the greater degree of pectoral-girdle flexion in nonhuman primates (Aiello and Dean, 2002; Fleagle, 2013) is arguably unlikely to have been a significant risk factor in semi-arboreal early hominin births, the movement of this feature through changing hominin pelvises is of significant interest to determining the degree of difficulty in labour. This assessed level of difficulty is what lies at the heart of arguments for the emergent necessity of birth assistance behaviours in the absence of adequate morphological and physiological adaptations.

Trevathan and Rosenberg (2000) acknowledge that similar patterns of rotation between humans and nonhuman primates do occur in some taxa. Observations by Hirata et al (2011) demonstrate an occipital-anterior orientation of the neonate during delivery in three captive chimpanzees

(*Pan troglodytes*). In each case (shown in **Figure 1.7.**), the neonate was observed to emerge facing posteriorly, then proceed to rotate 15° in case 1 and 2 but only minimally in case 3 (Hirata et al, 2011:687). Whilst Hirata et al (2011) do correctly withdraw themselves from using the three cases to generalise birth in the species, they suggest the continuity between the cases is a result of species-specific regulating factors i.e. the orientation of the neonatal long axis through the widest dimensions of the chimpanzee birth canal.

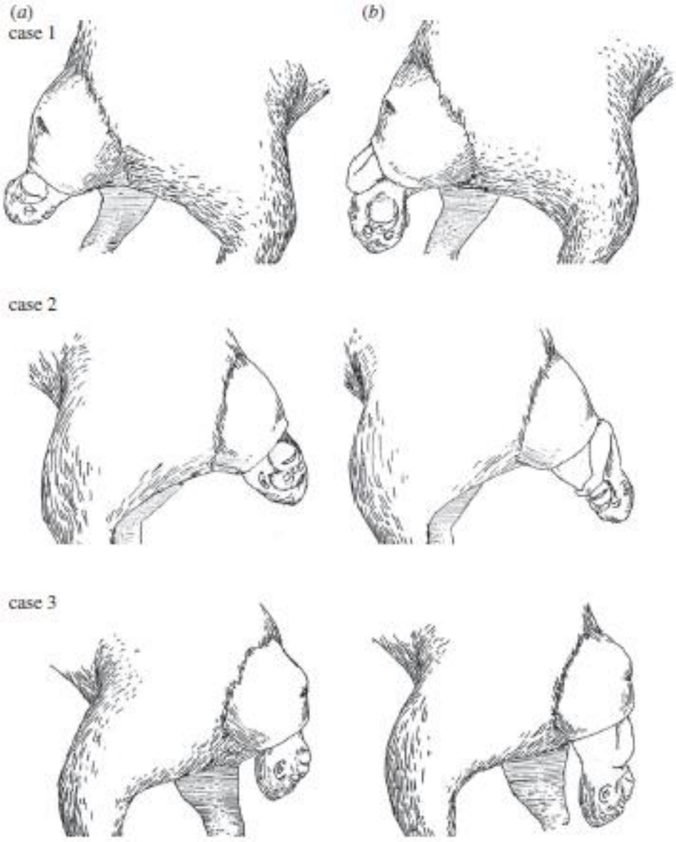


Figure 1.7. Schematic representation of the delivery of the *P.troglodytes* neonate in each observed case by Hirata et al (2011:687).

However, the typical mechanism and orientation of the neonate during parturition differs from typical occiput-posterior human delivery. Rotation does occur in some instances within the birth canal of nonhuman primates, but arguably does not appear common enough to be considered species-typical. In-fact, earlier work by Stoller (1995) suggests rotation appears both indicative of and leads to complications. Hirata et al's (2011:686) conclusion that their observations dispel the traditional association in hominin evolution of high CPD with the emergence of obligate midwifery needing "revision", is arguably misplaced since chimpanzees exhibit much lower CPD (Tague and Lovejoy, 1986; Rosenberg, 1986). Furthermore, there appears to be no direct sign that the neonate pivoted around the mother's pubis, as observed in humans.

Aiello and Dean (2002:445) note that the reduction of iliac height in relation to body size in hominins lowers the sacrum into the region of the true pelvis, forming an obstructive posterior wall to the maternal pelvic outlet. Among extant apes, this posterior feature of the true pelvis is formed by soft tissue (Aiello and Dean, 2002:443), providing greater flexibility of the maternal outlet dimensions. Much of the passage of the neonate also moves through the maternal sexual swelling of the individuals observed by Hirata et al (2011), comprising solely soft tissue. The neonate shoulders must have passed through the pelvic outlet in order for the head to be delivered through the sexual swelling. Therefore, Hirata et al's (2011) observed rotation is occurring within soft tissue and not the pelvis. This may indicate that in fact restrictions from the soft tissue necessitate internal rotation in this chimpanzee individual. Moreover, the posterior dimension of the nonhuman anthropoid midplane and outlet is not restricted by the sacrum but merely flexible soft tissue. Hence Hirata et al's (2011) conclusions that this observation in chimpanzees has implications for hominins are somewhat irrelevant, assuming hominins do not have sexual swellings. Though of course this is something which again is a question almost impossible to answer, given the lack of soft tissue survival in the archaeological record, or any associated genetic indicators. Sociocultural evolution may provide a clue as the conditions influencing the reduction of the sexual swelling in a potential common ancestor. However, it is not guaranteed that the last common ancestor between *Homo* and *Pan* did indeed have a sexual swelling – it may in fact be a derived characteristic along the *Pan* lineage. Future phylogenetic analysis could provide an evolutionary model for such morphology, and the resultant potential impact on birthing mechanics and behaviour.

Typical birthing mechanics

Parturition in modern humans is characterised as difficult relative to that of nonhuman primates, with complex rotation of the neonate cranium and shoulders in the birth canal, and with the infant typically delivered occiput-anterior - facing away from the mother (Rosenberg, 1992; Hirata et al, 2011; Trevathan, 2011; Pan et al, 2014). This has historically been deemed an evolutionary ‘scar’ (Krogman, 1951), a product of previous selection pressures and trade-offs in hominin evolution. Commonly, this ‘scar’ is referred to as the ‘obstetric dilemma’, where cephalopelvic disproportion between the increasing dimensions of the neonate cranium and shoulders and the maternal birth canal is linked to restrictions imposed by bipedal adaptation in the maternal pelvis (Ruff, 1995; Rosenberg and Trevathan, 1996; Walrath, 2003; Weaver and Hublin, 2009; Franclscus, 2009; Ding et al, 2013; Trevathan, 2015). In response, numerous anthropological and archaeological researchers suggest that highly prosocial birth assistance behaviours in humans have evolved to reduce the risk caused by CPD.

As highlighted within this chapter and further observed by Wells et al (2012), increased CPD is not unique to humans amongst extant primates, or even amongst other mammals. Although our species’ divergence in increasing levels of CPD appears to be the case amongst closely related apes (Trevathan and Rosenberg, 2000), evidence of a similarly high level of CPD has been highlighted in previous sections within this thesis among other non-ape primate taxa. Indeed, some mammalian species suffer much greater CPD, with an extreme case being that of the free-tailed bat, where to deliver the relatively large bodied neonate, the mother’s interpubic ligament stretches to around 15 times its original length (Crelin, 1969). Further to this, Grunstra et al (2019:1) suggest that in fact, humans could be considered “inverted bats”, which lack a true pubic symphysis and instead exhibit a significantly large interpubic gap, bridged by an interpubic ligament. This dramatically increased plasticity in birth canal dimensions in *Chiroptera* facilitates the delivery of neonates relatively larger than any other mammal order (Grunstra et al, 2019). Whilst this open pelvic floor would be detrimental to orthograde mammals, the head-down roosting behaviour of *Chiroptera* mitigates against weaker pelvic floor muscles (Grunstra et al, 2019). However, many of these species are not widely discussed as displaying human-like, prosocial birthing behaviours. Whether this is due to bias in research through an anthropocentric focus, a lack of prosocial capacity amongst other species, or a lack of direct observation of nonhuman taxa, warrants further exploration.

Whilst morphology has been demonstrated to play a role in driving the emergence of behavioural responses during birth, the adaptive significant of these responses by the mother and social group in both humans and nonhumans has been discussed within previous research. Franclscus (2009) suggests that having a neonate born occiput-posterior, as in nonhuman primates, makes it easier for the mother to intervene and prevent the umbilical cord from wrapping around the neonate’s neck (Cunningham et al, 2010), and to remove any airway obstructions. With the modern human pattern of occiput-anterior birth, any attempt by the mother to re-orientate or pull the neonate to correct from a breech complication risks spinal damage to the neonate (Trevathan, 1987; Dajini, 2014). Therefore, the risks to maternal and neonatal survival imposed by the modern human delivery mechanism arguably necessitates some form of parturition assistance or obligate midwifery to increase the chance of survival for both the neonate and the mother (Weaver and Hublin, 2009; Franclscus, 2009; Trevathan, 2015). However, this assumes that airway obstruction or umbilical cord strangulation among hominins was frequent enough to drive the selection of prosocial birthing behaviour. This reasoning also assumes such birthing mechanics are unique to humans. Furthermore, observations suggest that occiput-anterior birth also occurs amongst nonhuman primates, as will be discussed later in the chapter.

Whilst the relative cost and benefits of presentation orientation for intervention by the mother are difficult to empirically test, it is possible to quantify the rate of mortality from atypical fetal orientation and delivery. Bowden et al (1967:1) reported that, among captive monkeys, infant mortality from breech presentations without veterinary assistance was as high as 90%. Turner et al (2010) hypothesise that selection pressure on rapid birth for nonhuman primates is likely strong in order to minimise risk to neonatal and maternal survival from extended labour. In real world observation, two *M.fuscata* infants which were born quickly were of much better condition than those surviving protracted births (Turner et al, 2010:30). Conversely, a stillborn breech birth explains the longest birth stage observed, and marginal survival of an infant born after another relatively protracted birth supports their hypothesis (Turner et al, 2010). This is consistent with observations of a relatively lengthy birth of a wild mantled howler monkey, owing to a breeched but live-born infant (Moreno et al, 1991).

A common feature of pain management during birth in humans is the need for mobility during birth, with an observed typical position taken by humans cross-culturally (Trevathan, 2010:105). Early observations by primatologists (Kummer, 1968; Brandt and Mitchell, 1971; Abegglen and Abegglen, 1976) demonstrate a similar squatting birth position among nonhuman primates. More recent work by Yang et al (2016) suggests that birthing positions do appear to differ among primate species, with *Rhinopithecus roxellana* adopting a squatting posture during parturition, similar to that seen in Japanese macaques (*Macaca fuscata*; Turner et al, 2010), whilst the white headed langur (*Trachypithecus poliocephalus*) has been observed to birth quadrupedally (Yao et al, 2012), and the black and gold howler monkey (*Aloatta palliata*) is reported to give birth in a raised rump posture during contractions (Peker et al, 2009). It is important to note that these observations are of a relatively small number of individuals, however, and may not represent species-typical behaviours. Rather, they may in fact represent a primate pattern of high maternal mobility necessary to minimise discomfort and pain during parturition, as is observed in humans.

What is perhaps more significant in identifying divergence in typical human birthing behaviour, is the capacity lack of capacity as seen in nonhuman primates for neonatal self-assistance at birth – that is, the capacity for the neonate to pull itself from the birth canal. Several observations of this behaviour and active role of the neonate in nonhuman primates have been documented from a variety of taxa across the primate family (Hopf, 1967; Rothe, 1974; Richard, 1976; Kadam and Swayamprabha, 1980; Kemps and Timmerman, 1982; Nisbett and Glander, 1996; Turner et al, 2010; Yao et al, 2012). In an observation of birth in a captive, isolated Java-monkey (*Macaca fascicularis*), the neonate was observed to attempt to free itself during a breech delivery using its legs, but was ultimately unsuccessful as the neonate died during delivery (Kemps and Timmerman, 1982). The loss of this capacity in human neonates (assuming self-assistance is a conserved ancestral trait), likely as hominin offspring became increasingly altricial at birth (Trevathan, 2010), would have been a significant factor in necessitating increased manual assistance behaviours or increased strain of maternal effort. This observation in primates is rarely discussed in great detail within previous literature, in terms of exploring the evolution of self-assistance and the mechanism by which nonhuman primates are able to achieve this. The grasping Moro reflex observed at birth in both nonhuman primates and neonates is likely at play here, where human neonates with relatively underdeveloped motor skills at term, may grasp their hands but are unable to cling to the mother as seen in nonhuman primates (Trevathan, 2015). The loss of this self-assistance capacity in humans and hominins, would have added an additional pressure driving group assistance behaviours, where neither the mother or neonate can assist in delivery and therefore another group member is beneficial in delivering breech or otherwise challenging births. Specifically, this loss of self-assistance would have been a significant factor driving midwifery behaviours. If it can be reliably concluded at which point hominin neonates would have become similarly highly altricial at birth as in modern humans, this may additionally point to the species at which midwifery behaviour would have become similarly common.

It is important to note that nonhuman primates and other mammals are not excluded from the risk of birthing complications. Among pigs, mink and humans, extension of the labour phase of parturition is strongly associated with complications and neonatal death (Trevathan, 1987; Fraser et al, 1997; Hannah et al, 2000; Malmkvist et al, 2007). However, due to the limitations on the scope of this thesis, the focus will be on human and nonhuman primates – although further research into the sociality and evolution of obstetric mechanics in other mammals would provide a greater context to the conditions driving obstetric morphological and behavioural adaptations. In conjunction with the increase in maternal CPD and shift to complex internal rotation observed in the hominin fossil record, prosocial birthing behaviours and assistance in delivery of the neonate would have been a highly beneficial trait ensuring successful hominin reproduction. How this trait became an evolutionarily stable strategy over any alternative adaptational traits, and how these behaviours were passed between successive generations, remain unanswered questions.

2.4. Conclusion

Previous research into understanding of human and non-human primate obstetric morphology proposes that our species is unique in facing an evolutionary 'trade-off' between maternal morphology and the demands imposed by changing neonatal morphology. Critically, whilst the 'obstetric dilemma hypothesis' proposes that human obstetric morphology and difficulty in birth as a product of CPD is the result of this evolutionary trade-off, morphological evidence from a wide scope of primate and mammalian anatomy suggests that other, non-mutually exclusive factors would have significantly contributed to what we see today.

Granted, analysis of dry skeletal material demonstrates a high level of CPD in humans across populations (Betti and Manica, 2018), but the influence of physiological and soft-tissue mechanisms in mitigating CPD must be additionally accounted for – something which is difficult to determine for extinct species. Therefore, a lack of in-depth study and research into variation within nonhuman primate obstetric anatomy is something which hampers comparative morphological approaches to understanding the evolutionary trajectory of hominin birthing behaviour as a result of obstetric evolutionary trajectory.

Together, taxonomically wide-ranging evidence of birthing difficulty and delivery risk amongst nonhuman primates suggests that early hominins were likely to have experienced similar difficulty. However, the question remains as to the scale and occurrence of such difficulties, and the responses (both morphological and behavioural) to such difficulties. With this in mind, the following chapter will review previous attempts to determine the origins of human-like prosocial behaviour in hominin evolution, from osteoarchaeological evidence.

Chapter 3: A critical review of osteoarchaeological interpretations of hominin obstetric evolution.

3.1. Introduction

By examining interpretations of hominin obstetric evolution from osteoarchaeological studies, this chapter will review current understandings of the emergence of anatomically modern human birthing mechanics. Following presented context in the previous chapter of the obstetric adaptations in the modern human pelvis and neonate, this chapter will review research on hominin obstetric evolution. This chapter will aim to critically assess whether we can indeed track the emergence of high CPD and high-risk birth in hominin evolution from the archaeological record, and highlight the limitations of such research methodology. This will include comprehensive assessment of the most complete and reliable fossil specimens from individuals assigned to *Australopithecus afarensis, A. africanus, A. sediba, Homo erectus, H. heidelbergensis,* and *H. neanderthalensis*. The focus will be on the interpretation of the archaeological remains in comparison with that of contemporary human populations and nonhuman primates. This will be in conjunction with predictions of the relative risk and difficulty of birth in extinct hominins, with brief discussion of behavioural responses. This chapter will lastly discuss the implications of such findings for our understanding of the relative challenges of birth faced by ancestral hominins, and crucially, the accuracy of reconstructions in modelling mortality patterns central to hypotheses regarding the evolution of birth assistance behaviours, chiefly the ‘obstetric dilemma hypothesis.’

3.2. Obstetrics in Australopithecines

Obstetric morphology

For the *Australopithecus* genus, relatively few specimens have been identified for the same species. Therefore, this section will combine evidence across the genus. Indeed, Abitbol (1996:139) notes that with minimal direct evidence of australopithecine obstetrical mechanics, only indirect measures of obstetrical dimensions and reconstructed morphology can provide a (speculative) indication of the relative 'ease' of birth among members of the genus.

The most widely studied specimen is the pelvis of AL288-1, with numerous authors attempting to describe the fundamental obstetrical adequacy of the individual in comparison to modern human females and chimpanzees (see Leuteneger, 1972a; Lovejoy et al, 1973; Lovejoy 1979; Berge and Goulras, 1984; Tague and Lovejoy, 1986; Abitbol, 1995). Unearthed in the 3.2-3.4Ma deposits (Walter, 1994) at Hadar, Ethiopia and assigned to *Australopithecus afarensis* (Johanson and White, 1979; Hausler and Schmid, 1995; Tague and Lovejoy, 1998), the AL288-1 'Lucy' individual provides the most complete full adult early hominin skeleton to date.

Sts14 comprises a relatively complete proportion of an adult pelvis and vertebral column (Broom and Robinson, 1947), which was unearthed from 3-2Ma deposits at Sterkfontein, South Africa (Herries et al, 2013), and has been assigned to *Australopithecus africanus* (Weiner et al, 2008). The Sts14 remains yield the most complete australopithecine pelvis, and a more complete *A.africanus* pelvis than that of the more recent Stw431 remains also from Sterkfontein (Tobias, 1987; Haeusler, 2002; Toussaint et al, 2003).

The skeleton reconstructed from the AL288-1 remains includes a sacrum and near complete left innominate, if a little distorted (Johanson and Taieb, 1976). Initial descriptions describe the size as resembling early descriptions of the Sts14 pelvis, although the ilium appears higher and the anterior border appearing straighter, with a 'strongly developed' interior inferior spine, and characteristically female broad sciatic notch, obtuse subpubic angle and a pronounced ventral arc in the pubis (Johanson and Taieb, 1976). **Figure 3.1.** shows the AL288-1 pelvis in comparison with that of the Stw431 and Sts14 pelvis (from Haeusler, 2002:54).

Figure 3.1. Anterior and superior views of the Stw431, Sts14 and AL288-1 pelvises (from Haeuesler, 2002). Scale bar represents 5cm.

In assessing the sex of these specimens, the pelvic inlet of AL288-1 has a much lower posterior-sagittal-transverse index than both Sts14 and of modern human female ranges (Hausler and Schmid, 1995), which Tague and Lovejoy (1998) note is because the Sts14 pelvic inlet has a lower transverse diameter. Hausler and Schmid (1995) suggest that Sts14 shows greatest resemblance to modern human females' rounded gynaecoid pelvic inlet. Sts14 is also the only Australopith specimen to fall near the modern human female range of pelvic funnelling (Hausler and Schmid, 1995). However, if as Crompton (2016) argues AL-2881 represents a pygmy population, this has numerous implications for estimates of obstetric pelvic morphology. In modern humans, pygmy populations interestingly show a wider than predicted birth canal. This may suggest that the 'Lucy' specimen may in indeed reflect a wider hyper-platypelloid birth canal than was typical for larger Australopiths, supporting the conclusions of Abitbol (1996).

Initial reconstruction attempts of the Sts14 pelvis by Day (1973, 1978) used extensive amounts of glue, plaster, and a metal support rod through the pubis, all of which arguably compromise the integrity of the specimen for future study. Hausler and Schmid (1995) removed much of this plaster, and instead utilised mirror imaging for missing sections, producing two alternate reconstructions due to the ambiguous nature of the crushed and distorted SIJ and iliopubic angle. Following earlier use on the AL288-1 remains by Abitbol (1996:94), recent work by Berge and Goularas (2010) attempted to further correct this inaccuracy, utilising CT imaging to produce digital models of the Sts14 pelvis. Such methodology creates a more accurate reconstruction than previous work, with mirroring techniques and highly accurate digital interposition used to estimate morphology of missing elements, shown in **Figure 3.2.**

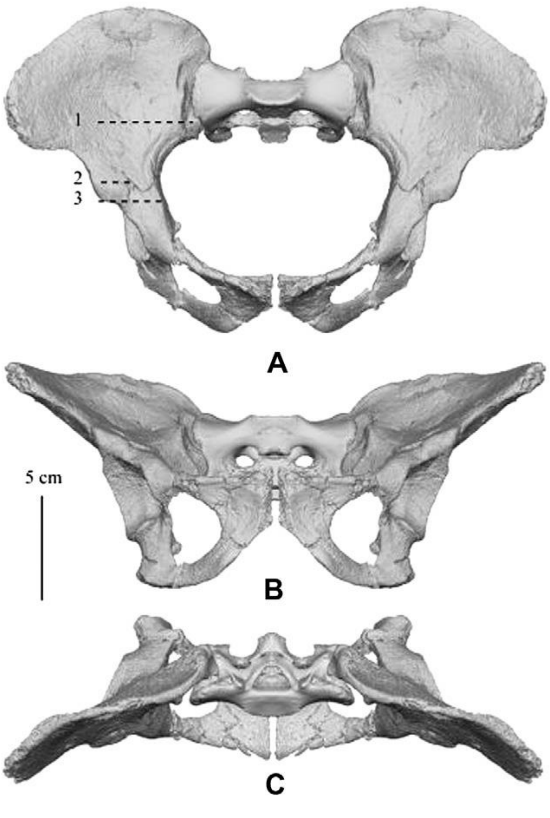


Figure 2.2. Berge and Goularas' (2010; 267) digital reconstruction of the Sts14 *A.africanus* pelvis from: (A) superior; (B) anterior; (C) posterior-inverted views. Scale bar represents 5cm.

Aside from the lower anterior flaring of the iliac crests, Berge and Goulras (2010) argued that the true pelvis of their Sts14 reconstruction closely resembles Hausler and Schmid's (1995) reconstruction of AL288-1. With a platypelloid, transversely broad pelvic inlet, the midplane of Sts14 shows a narrower transverse diameter than sagittal unlike that seen in modern human females (Berge and Goulras, 2010). Furthermore, the Sts14 pelvis did not show a heart-like shape of the inlet with a protruding sacral promontory, but rather resembled Hausler and Schmid's (1995) AL288-1 reconstruction without substantial protrusion (Berge and Goularas, 2010). Together, these assessments suggested that these specimens were indeed female, and thus sufficient in reconstructing likely obstetrical adequacy and evolution in early hominins.

However, Claxton et al (2016) note that this variance in individual reconstructions of the same fossils represent only morphological hypotheses, not certainties. Further to this, Claxton et al (2016) suggested that comparative 'checks' between additional fossil materials, of comparable anatomy, can yield more reliable conclusions on obstetric morphology. Whilst this is of course ideal, additional fossil material is rare. As stated by Abitbol (1996:139), in the absence of multiple comparative fossil specimens, it is more useful to compare morphology with extant nonhuman primate taxa, and perhaps deeper analysis with other mammals with comparative pelvic morphology.

Estimations of obstetrical adequacy

The areal index of obstetric capacity (AIOC) has been employed in previous research to estimate relative obstetrical adequacy, which measures the size of the largest cross-sectional area of the neonate cranium as a percentile of the cross-sectional area of each plane in the female true pelvis (Hausler and Schmid, 1995; Tague and Lovejoy, 1998). Hausler and Schmid's (1995) calculations of AIOC suggested that neither reconstructions of AL288-1 by themselves nor Tague and Lovejoy (1986) would facilitate delivery of a *Pan*-like 210g neonate brain, representing the mean anthropoid value. However, Tague and Lovejoy's (1998:86) subsequent calculations showed that even assuming a maximum neonate brain size of 210g, the AIOC for the pelvic inlet of AL288-1 is lower than six living anthropoid examples (out of 13 species measured), including that of modern humans. When Hausler and Schmid's (1995) estimates for *A.afarensis* are compared to that of extant Bornean Orangutan (*Pongo pygmaeus*), whose mean adult weight is heavier than calculated for AL288-1, the neonate brain mass of *P.pygmaeus* is lower than two of the three estimates for an *A.afarensis* neonate. Tague and Lovejoy (1998) suggest that this contradiction implies an error in Hausler and Schmid's (1995) estimates. Therefore Hausler and Schmid's (1995) estimates of AL288-1 brain weight are too high, and this suggests that the neonate cranium occupied a lower AIOC in *A.afarensis* compared with an average for modern anthropoids. It is worth commenting that Hausler and Schmidt (1995) reconstruct neonatal brain size by weight rather than relevant linear dimensions, which is arguably impractical in understanding the mechanical stress on birthing morphology in this case.

Although the same issue of underestimation is true for the midplane, Tague and Lovejoy (1998) argue the AL288-1 outlet AIOC appears larger than in humans but still lower than the midplane values for five nonhuman anthropoids. The outlet value is only critically comparable with that of modern humans since the nonhuman anthropoid outlet is not restricted by the sacrum and so has no skeletal dorsal confines. Alternately, Tague and Lovejoy (1998) suggested an estimate of internal pelvic area is a more accurate measure for understanding the obstetric qualities of AL288-1 and Sts14. Taking the assumption that the shape of the inlet, midplane and outlet is an ellipse, Tague and Lovejoy (1998) calculated the areas of each of these planes using Lovejoy (1986) and Hausler and Schmid's (1995) reconstructions of the AL288-1 and Sts14 specimens.

By area, the AL288-1 pelvic inlet was 765mm^2 larger than Sts14's (7825mm^2 vs 7060mm^2), the midplane was larger in AL288-1 (6349mm^2 vs 6011mm^2) and finally, the outlet was larger in Sts14 (at 7143mm^2) (Tague and Lovejoy, 1998:84). Compared to Tague and Lovejoy's (1986) earlier reconstruction of AL288-1, the area of the pelvic midplane is smaller than that reconstructed by Hausler and Schmid's (1995) and smaller than the Sts14 midplane reconstructed by Tague and Lovejoy (1998). What was particularly interesting was that AL288-1's value (5997mm^2) was almost identical to the midplane of Sts14 (6011mm^2) (Tague and Lovejoy, 1998:84).

Tague and Lovejoy's (1998) assessment of the diametral index of obstetric capacity (DIOC) in AL288-1 also similarly estimated a more spacious pelvis compared with modern humans and some anthropoid species, again in contrast to Hausler and Schmid's (1995) conclusions. The DIOC was calculated by using the flexed long axis, since Hausler and Schmid (1995) proposed that during labour, AL288-1's neonate would have fully flexed the head to the chest at engagement (as is typical in humans), producing a sagittal axis almost equal to that of the transverse.

Hausler and Schmid (1995) proposed that the AL288-1 individual would have been capable of delivering a maximum neonate cranial size of ~210g, but the increased dimensions of the Sts14 pelvis would have allowed the delivery of a larger 237g neonate cranium. But Tague and Lovejoy (1998) note a contradiction in Hausler and Schmid's (1995) reasoning. If a neonate with a 237g cranium could pass through Sts14's midplane, then surely it could also pass through AL288-1's outlet, assuming the same pattern of pelvic funnelling. Indeed, Tague and Lovejoy's (1998) data indicates that in fact AL288-1 is more obstetrically spacious than many living anthropoids. With all the clear contradictions of Hausler and Schmid (1995), and additional comparative data by Tague and Lovejoy (1998), one is more inclined to firmly agree with the conclusion of latter – that AL288-1 was certainly capable of giving birth to a neonate at with at least a 210g cranial size, likely with mechanisms similar to modern humans.

It is worth observing that subsequent physical anthropological study has not used AIOC or DIOC in assessment of other archaeological specimens, or indeed of primatological or anthropological samples. Both of these metrics are perhaps considerably less diagnostic of likely CPD, given the loss of specific maximum linear dimensions necessary for reconstructing birthing mechanics. A measurement of area does not indicate maximum dimensions, and further assumes a regular shape model of each pelvic plane, often with no consideration of possible asymmetry. This leads to a lowered reliability of such results when basic metric assessment of the anterioposterior and transverse diameters (or at least the widest diameter if oblique) can provide greater estimation of obstetrical adequacy, and likely risk of complications and mortality in hominin species and individuals. One thing that can safely be drawn from Hausler and Schmid (1995) is that that delivery in AL288-1 at least would have been more difficult than both Sts14 and in modern humans, crucially owing to the intrusion of the sacral promontory which would have increased the degree of CPD.

Implications for the mechanism of birth

Berge et al (1984) conclude from the morphology of both AL288-1 and Sts14 that the trajectory of the neonate in Australopithecines was ventral, so that the neonate was delivered anterior to the mother. Berge et al (1984) also interestingly conclude that the most likely orientation of the neonate skull at engagement with the pelvic inlet is oblique in both AL288-1 and Sts14 like that of modern humans, shown in **Figure 3.3.** Although in AL288-1, the neonate may have also orientated transversely (Berge et al, 1984).

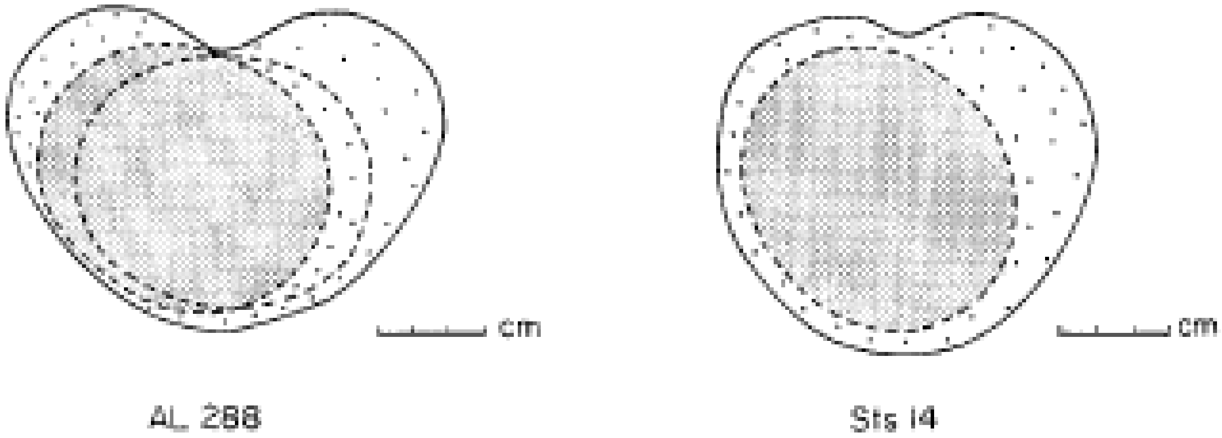


Figure 3.3. Berge et al's (1984:585) schematic representation of neonate cranial orientation in the AL288-1 and Sts14 pelvic inlet.

Tague and Lovejoy's (1986) study of Lovejoy's (1979) AL288-1 pelvic reconstruction proposed that dimensional restrictions in the midplane and outlet would have prevented rotation of the neonate during labour, remaining transversely orientated. Assessment of Schmid's (1983) AL 288-1 pelvic reconstruction by Berge et al (1984) argued that alternately, the dimensions of the pelvic inlet would have necessitated rotation in early hominin in the same way as AMH.

Hausler and Schmid (1995) argue that in Sts14, the most likely orientation of the neonate head during engagement into the pelvic inlet was in fact an oblique angle. In Sts14, noticeable restrictions in the midplane despite some mobility in the sacroiliac would have necessitated a larger degree of deformation of the neonatal cranium along sutures (Hausler and Schmid, 1995). Whereas in AL288-1, a less curved sacrum may suggest a less curved neonatal trajectory that would suggest the neonate did not pivot around the pubic symphysis.

Modern human females with a platypelloid pelvis exhibit prolonged labour, and any excessive deformation of the transverse diameter of the neonate cranium often leads to death (Borell and Fernstrom, 1958). From Tague and Lovejoy's reconstruction of AL288-1, the platypelloid shape and strong intrusion of the sacral promontory could have produced similar complications during labour (Hausler and Schmid, 1995).

Tague and Lovejoy (1986)'s reconstruction of AL288-1 shows a transversely flattened true pelvis which is argued to restrict the passage of the neonate to a nonrotational movement, with the occiput transversely orientated. Whilst Trevathan and Rosenberg (2000) agree with this conclusion that the foetal head did not rotate, they argue that the shoulders of the neonate must have rotated to pass through the birth canal. Indeed, Trevathan and Rosenberg (2000) believe the role of the postcranial skeleton in driving the evolution of the hominins is underestimated, stressing that neonatal rotation by definition includes both the movement of the head and shoulders through the birth canal. Hausler and Schmid (1995) devote only a brief paragraph to restrictions imposed by the postcranium of the neonate, but suggest that in order for broad shoulders to pass through the AL288-1 pelvic inlet, the head would have had to rotate sagittally in the birth canal. The alternate more challenging mechanism would be for the cranium to remain transversely orientated in the outlet, whilst the shoulders and trunk twist 90 degrees to pass through the birth canal. The latter would of course pose far greater risk of spinal damage to the neonate so would be less selectively beneficial.

Franclscus (2009) concurs with the assessments of the obstetric capabilities of Pliocene *A.afarensis* and *A.africanus* by Tague and Lovejoy (1998), where birth was likely occiput transverse and nonrotational. Franclscus (2009) reasons that the modern pattern of rotational birth and obligate midwifery must have hence emerged within *Homo* once a cephalopelvic threshold was reached. But this method of labour is unheard of within the mammalian kingdom (Hausler and Schmid, 1995), and arguably casts doubt upon the conclusions of nonrotational birth in any hominin species.

It is important to note that the lower part of the sacrum is not reconstructed by Berge and Goularas (2010), but is instead inferred from Abitbol (1995) to be relatively flat and less posteriorly shifted than modern humans. The sacrum in the reconstruction also shows a lower degree of posterior tilting than in Hausler and Schmid's (1995) reconstruction, and less than in modern humans (Berge and Goularas, 2010), all of which culminates in a less acute trajectory for the neonate during birth, represented by **Figure 3.4**.

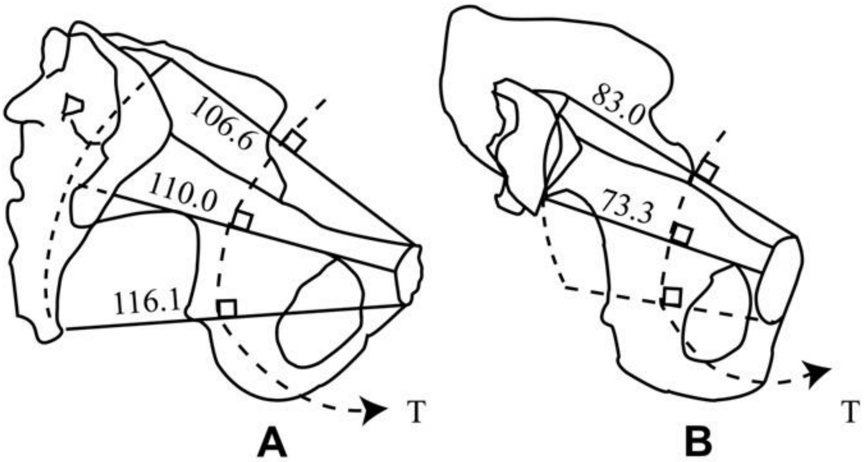


Figure 3.4. Berge and Goularas's (2010:268) Sts14 reconstruction (B) in comparison with that of modern human female (A) in a sagittal cross section. T represents a hypothetical neonate trajectory perpendicular to the inlet, mid and outlet planes.

Like modern human females, the Sts14 pelvis suggests rotation of the neonate around the pubic symphysis, and follows the curvature of the reconstructed sacrum very closely to that of modern humans. The lower part of the sacrum is not reconstructed by Berge and Goularas (2010), but is instead inferred from Abitbol (1995) to be relatively flat and less posteriorly shifted than modern humans. Berge and Goularas (2010) suggest this less curved sacrum in Sts14 would have hence reduced curvature of the neonate trajectory in australopithecines in comparison with that of modern humans.

Unlike in nonhuman primates where the pelvic outlet opens posteriorly, like humans the Sts14 pelvic outlet opens under the pubic symphysis (Berge and Goularas, 2010). The sub pubic angle of Sts14 [107.2° (Berge and Goularas, 2010: 267)] moreover is closer to the modern human female mean (90.7 °) rather than the male (69.0 °). As an adaptation, this would reduce the obstruction of the pubic ramus in the anterior margin of the birth canal, curving the trajectory more anteriorly and encouraging the neonate to passively pivot around the pubic symphysis under pressure from maternal contractions. Together, the birth canal shape and wide subpubic angle of Sts14 is reasoned to imply a human-like curved trajectory unlike other primates by Berge and Goularas (2010).

Berge and Goularas (2010) reasoned that compared with AL288-1, the less transversely flattened pelvis of Sts14 likely resulted in labour mechanics similar to those seen in modern humans – human-like rotation and flexion of the neonate during the second stage of labour. Each plane of the birth canal – inlet, midplane, outlet – appears platypelloid in shape and contra to Hausler and Schmid (1995), does not become more rounded in the midplane. In Berge and Goularas's (2010) reconstruction of Sts14, through each plane of the birth canal the sagittal diameters are reduced. Moreover, both species faced the issue of a significantly intruding sacral promontory into the birth canal.

However, what appears to have been only briefly discussed in much of the literature to date is an assessment of the problems incurred by passage of the postcranial skeleton, in particular the shoulders (Trevathan and Rosenburg, 2000). Indeed, Tague and Lovejoy (1986) fail to mention the restrictions of the postcrania at all. Trevathan (1987) was initially critical of early assessments of obstetrical adequacy, in proposing that platypelloid shape of the AL288-1 birth canal would have placed severe restrictions on the movement of the shoulders through the birth canal.

In attempting to estimate the difficulty of labour in fossil specimens, Stoller (1995) observes that Tague and Lovejoy (1986) and Leutenegger (1981; 1987) assumed foetal orientation within the AL288-1 *A.afarensis* pelvis was dictated solely by linear pelvic dimensions, without any rotation under Joulin's Law (1864) as seen in modern humans. Yet these assessments do assume a human typical level of flexion or neutrality of the foetal head attitude (Stoller, 1995), which again has consequences for resultant conclusions of birth difficulty and mechanics.

Given the limited platypelloid pelvic dimensions observed in AL288-1 (Abitbol, 1996:144), is it possible that (since a chimp neonate would hypothetically be unable to negotiate the AL288-1 pelvis) that such an australopithecine neonate in this case could have had smaller cranial dimensions – instead following a much more rapid post-natal brain growth trajectory closer to that seen in humans, in order to reach an adult chimp-like brain size. In this scenario, it could be that the typical life history traits characterising growth trajectories in *Homo*, may have evolved earlier in australopithecines in order to negotiate a dystoic, hyper-platypelloid pelvis. Abitbol (1996:144) also notes that in AL288-1, the lack of a *Homo*-like sacral curvature means the neonate would have been delivered posteriorly as is argued to be typical among nonhuman primates. The delivery of the neonate in this orientation, may have reduced the selective pressure to adopt prosocial birthing behaviours such as manual birth assistance by group members, as the mother would have a greater view of the delivery and reduced risk of manual delivery. In turn, the identification of evidence suggesting typically occiput-anterior delivery in Homo, may signify an evolutionary scenario whereby prosocial birthing behaviour conferred a much greater selective benefit to the mother and neonate, by significantly lowering mortality risk.

Abitbol (1996:144) concludes that since the anterioposterior dimension of the hypothesised neonate chest is larger than the transverse diameter, the neonate would not need to rotate out of an occiput transverse orientation, necessitated by the cranial dimensions. Further to this, any extension of the pubic symphysis through hormonal mediation, would only serve to widen the transverse diameter due to the hyper-platypelloidy in the AL288-1 individual (Abitbol, 1996:145). With this observation, Abitbol (1996:145-146) concludes that in this individual, delivery of a hypothetical chimpanzee-like neonate would have been "mechanically difficult if not impossible". It is potentially possible then that this individual may not have successful delivered an at-term neonate, assuming such a neonate would have been morphologically indistinct from a chimpanzee. However, without closely associated fossil neonate remains, both in time or geographically, any such assessment is speculative at best.

One can gather from the literature that in both Pliocene hominin species discussed, *Australopithecus afarensis* and *A.africanus*, birth would certainly have been more difficult than in ancestral Apes, and closer to that of modern humans. However, the degree of cephalopelvic proportion displayed by a few australopithecine individuals, was still relatively low. The shape of both the *A.afarensis* and *A.africanus* birth canal would not have definitively necessitated an occiput-transverse orientation of the neonate cranium, and certainly the modern human oblique orientation would have been equally likely.

3.3. Obstetrics in *Homo erectus*

Obstetric morphology

KNM-ER 3228 from Koobi Fora in Kenya was assigned to early *Homo* and dated to ~1.95Ma (Rose, 1984), and OH 28 from Olduvai in Tanzania was assigned to *H.erectus* and dated to 700Ka (Day, 1971). However, later reassessment by Simpson et al (2008; 2014) conclusively later classified OH28 as a male individual. Despite a large greater sciatic notch, the pelvis was too robust, as well as being simply too large; interestingly the largest known from Late Pleistocene Africa (Simpson et al, 2014). At the time of Ruff's (1995) assessment, there were no known examples of a complete early *Homo* pelvis, so no direct measurement of the sagittal dimension of the birth canal could be measured. But Ruff (1995) proposed that the preserved portion of the pelvic inlet of KNM-ER 3228 and OH 28 iliac elements could be used to produce estimates for the shape of the inlet.

Ruff (1995) distinguished the obstetric pelvis of early *Homo* from modern humans in having a transversely broad and sagittally narrow inlet and outlet, creating a platypelloid birth canal. Though to a lesser extent that in Australopithecines. By measuring an index of the iliac brim [depth/length (Ruff, 1995: 559)] and comparing with modern human samples, Ruff (1995) concluded that the inlet would have been platypelloid, akin to Hausler and Schmid's (1995) conclusions regarding AL288-1. Ruff (1995) also investigated at how the orientation of the ischium could be used to infer the shape of the pelvic outlet and proposes that the more lateral ischial tuberosity of KNM-ER 3228 suggests a degree of medial rotation of the ischiopubic ramus in the specimens, as opposed to the more anterior orientation modern human female. Since part of the pelvic outlet is formed by the ischiopubic ramus, the more medial orientation would theoretically reduce the size of the pelvic outlet in KNM-ER 3228 compared to modern humans. KNM-ER 3228 also exhibits a more anteriorly placed sacrum than in modern humans (Ruff, 1995), again compressing the sagittal dimension on the birth canal to for a platypelloid shape throughout.

This was then compared to a very late specimen of *H.erectus* (Ruff, 1995), dated to ~350Ka from Kebara 2, Israel (Stringer, 1981). Assessment of the iliac brim index in comparison with the earlier *H.erectus* specimens showed an intermediate value between that of early *Homo* and modern humans (Ruff, 1995), which suggests a shift in late *H.erectus* to a modern human like gynecoid pelvic typology. The intermediate brim index value of KNM-ER 3228 suggests a pelvic inlet shape divergent from the more platypelloid shape of Australopithecines and earlier *Homo* (Ruff, 1995). Hence implying that something was driving alteration in the shape of the hominin birth canal during this period – most obvious is rapidly increasing brain size in adults which would imply increasing neonate brain size (Ruff, 1995).

The discovery of a nearly complete adult female *H.erectus* pelvis from Gona in Ethiopia (BSN49/P27), was a major step forward in understanding the obstetric adequacy of early Pleistocene *Homo*, dated to between 1.4 and 0.9Ma (Simpson et al, 2008:1089). This specimen will form this focus of the following section, given the lack of complete early *Homo* pelvic remains. The Gona *H.erectus* pelvis included most of the sacrum, os coxae hemispheres and crucially, a complete pubis, with the functional articular regions and obstetrical dimensions requiring little or no reconstruction (Simpson et al, 2008), and is shown in **Figure 3.5.**. To produce a complete reconstruction, high resolution plaster casts and mirroring techniques were used where necessary, though some asymmetry remains (Simpson et al, 2008). The individual showed a long list of dimorphically female traits, including distinctly large greater sciatic notches, large subpubic angle, large sacral angle, and non-projecting sacral promontory, so could be unquestionably categorised as female (Simpson et al, 2008).

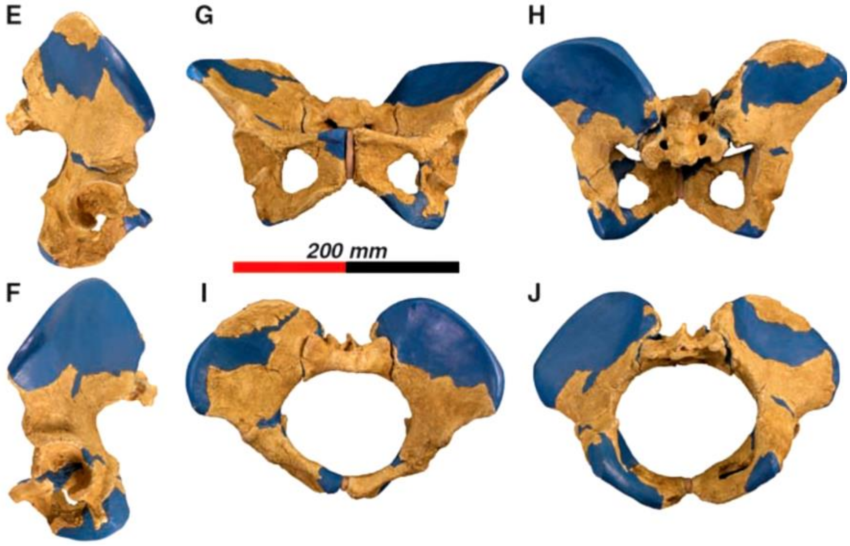


Figure 3.5. Simpson et al’s (2008: 1080) reconstruction of the female *H.erectus* pelvis from Gona. The blue portions are the reconstructed plaster elements: (E) right-lateral view of pelvic reconstruction; (F) left-lateral view; (G) anterior view (H) posterior view; (I) superior view of pelvic inlet; (J) inferior view of pelvic outlet.

Simpson et al (2008) argue that for such a short individual, the Gona female birth canal is particularly spacious and in fact the inlet circumference is within modern human female ranges. Although, the transverse diameters of the midplane and outlet are larger than modern human female values, the sagittal diameters do fall within the modern human female range sampled by Simpson et al (2008).

Estimations of obstetrical adequacy

Simpson et al (2008) conclude that unlike previously analysed specimens the Gona specimen showed an obstetrically spacious true pelvis and arguably demonstrates adaptations in response the pressures of neonate cranial expansion in the species.

The substantial risk of traumatic birth in humans is imposed by such narrow disparity between neonate cranial size and birth canal dimensions, which is unusually high amongst primates. Simpson et al (2008) reason that this minimal gap between the birth canal dimensions and neonatal head size can be used to estimate the size of the neonate cranium from the female *H.erectus* specimen. Simpson et al (2008) thereby estimated that the individual could have given birth to a neonate with a cranial volume up to 315cm^3 – 30% larger than estimated from the ‘Nariokotome Boy’ skeleton by Walker and Ruff (1993) and 50% larger than Tague and Lovejoy’s (1998) estimate (of a maximum neonatal size of 210g) for *A.afarensis* and *A.africanus*.

Simpson et al (2008) interestingly note that two alternate means (which are by no means mutually exclusive) could have produced the necessary larger birth canal necessary for successfully delivering the increasingly encephalised *Homo* neonate cranium (Aiello and Wheeler, 1995). The first being an overall increase in adult female body size, but the Gona individual is relatively small in stature and yet displays such a spacious birth canal (Simpson et al, 2008). Hence one can conclude that such changes in the individual's pelvis must have been the result of ontologically controlled (i.e. hormonally influenced) modelling of the pelvis, which resulted in high levels of sexual dimorphism in the pelvis of early Pleistocene *H.erectus*.

Simpson et al (2008) summarise that the Gona pelvis retained many Australopithecine traits, but selectively beneficial increases in brain size and resultant highly encephalised neonates drove much of the adaptation in morphology seen in the *H.erectus* obstetric pelvis. The increasing adverse CPD, which directly affects reproductive success (i.e. successful birth, non-fatal to neonate or mother), was a primary driving factor on obstetric pelvic morphology during this period.

Implications for the mechanisms of birth

The pelvic inlet of the Gona female is wide enough to allow the foetal head to engage transversely. Any increase in the transverse dimension of the midplane and outlet risks affecting the biacetebular distance or the distance between the gluteal lines which will adversely affect bipedal mechanics of the mother (Ruff, 1995; Franclscus, 2009).

By widening the sagittal dimension with a curved, non-protruding sacrum through the midplane and outlet, this provides an adaptive solution where the neonate head rotates during the second stage of labour, through the midplane – such as in modern humans. This adaption may have provided a selective advantage to *H.erectus* where individuals with a wider birth canal that could give birth to larger brained neonates, without affecting bipedal mechanics and avoiding raised chances of mortality from obstruction during birth.

Much of the previous study of *H.erectus* has concluded that delivery of the neonate was nonrotational. Ruff (1995) concludes that in *Homo erectus* and 'erectus-like' specimens, the dimensions of the transverse and sagittal true pelvis were more akin to those of the australopiths, being transversely broad and sagittally narrow. Hence suggesting, along with Hausler and Schmid (1995), that the second stage of labour in early *Homo* was also nonrotational, with the neonate cranium remaining occiput transverse throughout. Ruff (1995) proposes that the constrictions of locomotion on the transverse diameter of the true pelvis would have constrained more rapid cranial expansion in early *Homo*, until adaptations to rotational birth in, speculatively, the Middle to Late Pleistocene. Although at this point in hominin evolution, given the overall increase in maternal stature, cranial expansion was not relatively excessive from that of Australopithecines, so surely early *Homo* would have faced the similar restrictions of pelvic diameters on cranial size. Moreover, Trevathan and Rosenberg (2000) point out that a definitive nonrotational mechanism would not allow for delivery of the shoulders.

Franclscus (2009) interprets the findings of Simpson et al (2008) as further confirmation of a nonrotational mechanism in *H.erectus*. How Franclscus (2009) comes to this conclusion of however is curious, since Simpson et al (2008) do not mention rotation at any point during their assessment. Arguably, the morphology of the Gona pelvis would suggest a modern human-like rotational birth mechanism in *H.erectus*. The nonprojecting sacral body, unlike in Australopiths Tague and Lovejoy (1998), also effectively increases the sagittal dimensions of the birth canal. The large sacral angle in the Gona pelvis, as oppose to the straighter sacrum in AL288-1 and Sts14 noted by Tague and Lovejoy (1998), could also infer a much more curved trajectory in Mid-Pleistocene *H.erectus*, closer to that of modern human females. Since the long axis of the neonate cranium and the long axis of the shoulders orientate to occupy the widest dimension of each plane of the birth canal, a wider sagittal dimension would cause the neonate to rotate under the pressure of maternal contractions.

3.4. Obstetrics in Homo neanderthalensis

Obstetric morphology

Analysis of the first complete *Homo neadnerthalensis* pelvis from Kebara 2 (Bar-Yosef et al, 1986), though male, suggested that Neanderthals possessed an unusually long and slender pubis region compared to modern humans (Trinkaus, 1984), 20% longer in fact than the modern human male mean (Rak and Arensburg, 1987). If this was a sexually dimorphic trait, following modern human patterns of pubis length (Aiello and Dean, 2002:456), then one could expect an exceptionally large transverse diameter of the inlet and midplane of the birth canal. This lengthened pubic region serves to produce a much wider subpubic angle [at 110° (Aiello and Dean, 2002:456)], which in turn contributes to a more transversely broad pelvic outlet, and speculatively a greater area for the neonate to pivot around if orientated occiput-anterior. What is unusual however, is that contrary to normal hominin patterns of sexual dimorphism, the superior pubic ramus appears to be shorter in females than males (Rosenberg, 1986). Weaver and Hublin's (2009) hypothetical female based on the Kebara 2 male Neanderthal interestingly appears to show a longer pubic bone than their Tabun C1 reconstruction and a wider pubic body.

The reconstruction of the complete female Tabun C1 pelvis, excavated in Israel and dated between 100 and 60Ka (Garrod and Bate, 1937), by Ponce de Leon et al (2008) argued that the fragmented nature of the pelvis, particularly the ischium, and lack of sacrum meant that the midplane and hence mechanism of birth could only be assumed. Ponce de Leon et al (2008) reasoned that this mechanism was likely similar to that of modern humans owing to similar cephalopelvic values. Weaver and Hublin (2009) presented an alternate interpretation from their digital reconstruction from CT scans of the Tabun C1 pelvis, shown in **Figure 3.6**.

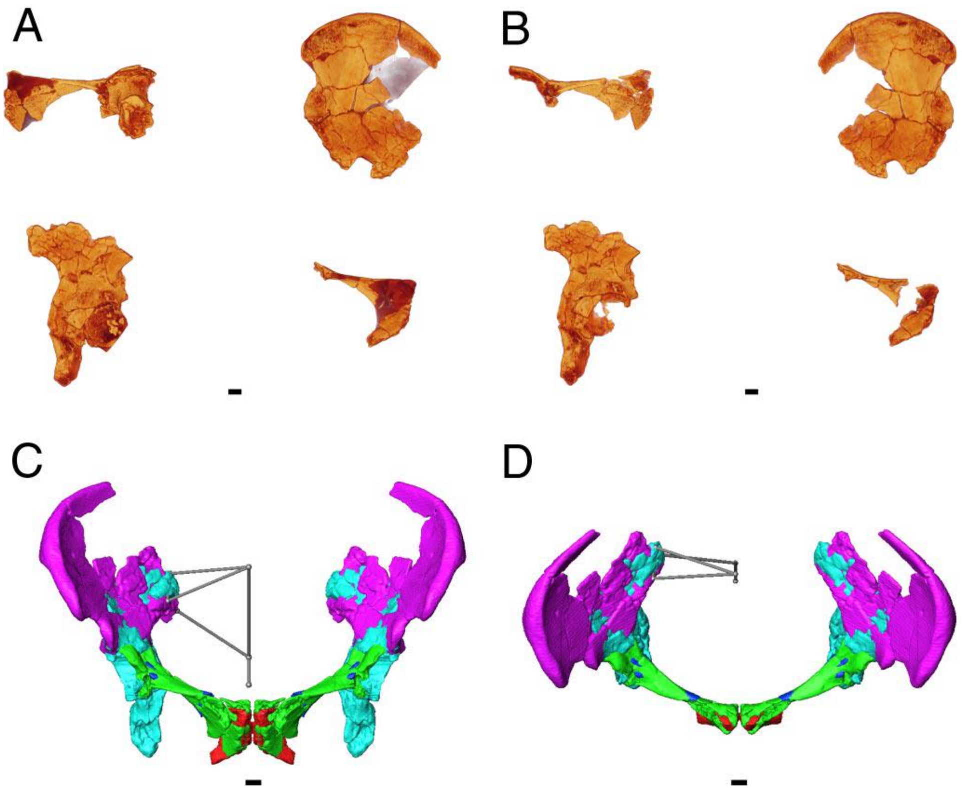


Figure 3.6. Weaver and Hublin’s (2009:8152) CT scan reconstruction of the Tabun C1 Neanderthal female pelvis. (A) and (B) are the left and right os coxae fragments (parts of the ilium, ischium and pubis) respectively used to mirror and reconstruct the pelvis shown anterior-superior oblique in (C) and superiorly in (D). Scale bar represents 1cm.

Weaver and Hublin (2009) explain that any attempt to reconstruct a sagittally broad birth canal like that of *H.sapiens* females resulted in disarticulation of the pubic part of the acetebular rim fragments. In order to create a more *H. sapiens* like round outlet, rotation of the ischial tuberosity is needed of around 2cm (Weaver and Hublin, 2009:8153) on each os coxae hemisphere, but only a few millimetres of alternation were possible. Hence a platypelloid shape was considered the most probable reconstruction.

Weaver and Hublin (2009) provide an interesting further assessment of Tabun C1's obstetric adequacy, by looking at how relaxation of the ligaments during labour may have affected these dimensions. Under the assumption that hormones released during labour would have had the same effect of relaxing the pelvic ligaments and expanding the dimensions of the birth canal (Russell, 1969; Bjorklund et al, 1997), the space in the transverse dimensions may have risen to between 139-141mm in Neanderthal, compared with 134-146 seen in modern humans (Weaver and Hublin, 2009:8154). In any case, the reconstructions of both Tabun C1 and Kebara 2 serve to support a conclusion that Neanderthal females would have had a transversely expanded pelvic inlet and outlet.

Estimations of obstetrical adequacy

As previously argued by Tague and Lovejoy (1998), the area of the maternal birth canal can give an indication of obstetric adequacy and the degree of CPD. From Weaver and Hublin's (2009) results we can see that the inlet and outlet areas - 21,485mm^2 and 19,176mm^2 respectively (Weaver and Hublin, 2009:8151) - fall within the range of modern human females, with the outlet being slightly below that of the mean. The retention of a large neonatal brain size at-birth from that of *H.erectus*, around 300cm^3 (Ponce de Leon et al, 2008:13766), and the subsequent increase, clearly suggests that the large brain conferred significant selective benefits to both juveniles and adults, despite the obstetric consequences of increasingly difficult and traumatic labour. Hence Ponce de Leon et al (2008) conclude that this rapid pattern of postnatal brain growth, likely evolved with the onset of the *Homo* genus and therefore predated the emergence of *H.neanderthalensis*. In the absence of evidence for alternative postnatal growth trajectories, it would be reasonable to assume Neanderthals faced a similar level of CPD to earlier *Homo*.

To test this assumption in the absence of multiple specimens of neonate across multiple life stages, extrapolation and comparison with extant species is necessary to estimate likely risk and selective pressure for birth assistance behaviours in Neanderthals. To estimate an initial rate of postnatal endocranial growth in Neanderthals, Ponce de Leon et al (2008:13765) used endocranial volumes of the Mezniaskaya 1-2week old Neanderthal neonate from Mezniaskaya Cave, Russia (Golovanova, 1999) and from two Neanderthal infants aged 19 and 24 months old from Dederiyeh Cave, Syria (Akazawa et al, 1995a, 1995b; 1999). Between birth and adulthood, the modern human brain increases in size by a factor of 3.3, in comparison with a factor of 2.5 in chimpanzees (Ponce de Leon et al, 2008:13764). Assuming a similar rate of perinatal growth to modern humans of 20cm^3 per week (Huppi et al, 1998), they estimated from the Mezniaskaya neonate (422-436cm^3) an endocranial volume for the Neanderthal neonate at birth of 382-416cm^3 (Ponce de Leon et al, 2008:13765). This corresponds closely to *in vivo* modern human values of 380-420cm^3 (Huppi et al, 1998) and contradicts calculations of a head size that was 15-20% larger than *H.sapiens*, which would have required a gestation period three (or more) months longer by Trinkhaus (1984) from the hypothetical Kebara 2 female. This value was then used in conjunction with the values from the older Dederiyeh Cave infants (1096cm^{3}and 1089cm^3), to calculate a rate of growth.

When compared with the rate seen in modern human neonates, the results suggest that Neanderthal brains grew much faster after birth than in modern humans to reach Neanderthal adult mean value, which is notably larger than the modern human [1500cm^3 as opposed to 1350cm^3 in modern humans (Ponce de Leon et al, 2008:13767)]. One could suggest that the rapid post-natal neocortex expansion in Neanderthal neonates seen in the results could be part of an obstetric adaptation to minimise the rate of cranial expansion seen in Pleistocene hominins. As opposed to further altering the mother's pelvic morphology, this would have the adaptive benefit of reducing the at-term size of the neonate cranium, whilst conversely increasing the rate of neocortex growth and adhering to the selective benefits of having a larger adult brain.

Since both Neanderthals and modern humans show such similar practically identical neonatal brain sizes, Ponce de Leon et al (2008:13766) conclude that their results point to a last common ancestor between *H. neanderthalensis* and *H. sapiens* which gave birth to neonates with a brain size of around 400cm^3, which was likely a *H. heidelbergensis* population (Stringer, 2012). Franclscus (2009) concludes that the morphology of the Tabun C1 female Neanderthal pelvis and of the Mezmaiskaya Cave Neanderthal neonate (from Golovanova, 1999) suggest a regression to a transversely expanded pelvis in Neanderthals in response to the pressure of increasing neonate cranial volumes. Future study could perhaps look at this neonate in greater detail in terms of comparisons with modern human patterns of cranial moulding, and perhaps what effect the distinct cranial morphology of Neanderthals may have had on the position of fontanel in the neonate – was the neonate cranium more vulnerable to compression and moulding?

Implications for the mechanism of birth

The ‘primitive’ morphology displayed by the Tabun C1 pelvis is argued to suggest that significant changes in the mechanism of birth occurred relatively late in hominin evolution (Weaver and Hublin, 2009). The variation demonstrated in comparison with *H. sapiens* shows that this evolution was discontinuous amongst populations of late Pleistocene hominins, with alternate species evolving different obstetric mechanisms and morphologies.

Ponce de Leon et al (2008)’s digital reconstructions have the useful benefit of being highly manipulative in their orientation. The *in-situ* reconstruction of the Mezmaiskaya neonate engaged within the Tabun C1 pelvic inlet (**Figure 3.7.**) is particularly useful in visualising the orientation of the neonate cranium (Ponce de Leon, 2008). In this case left occiput-transverse within Neanderthal female pelvis.

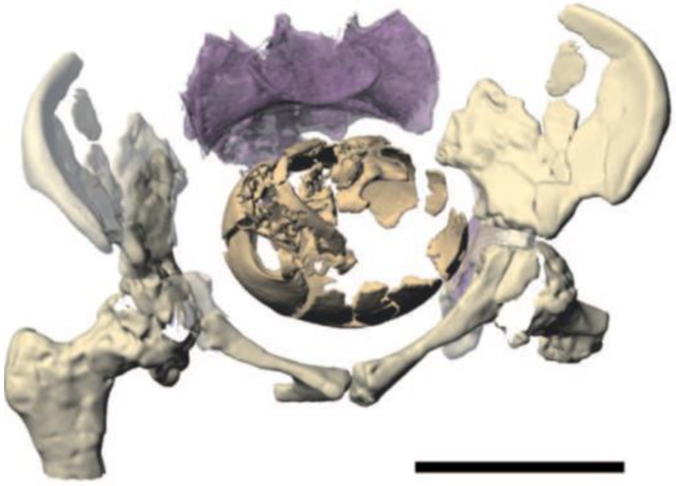


Figure 3.7. Ponce de Leon et al's (2008:13766) reconstruction for the Tabun C1 female Neanderthal pelvis and Mezniaskaya Cave Neanderthal neonate. The violet elements represent replaced with modern human specimens. Scale bar represents 10cm.

When the estimated Neanderthal neonate cranial dimensions are factored in, the transverse dimensions of the Tabun C1 outlet are further shown to be more spacious compared with modern human females – when occiput-transverse, a Neanderthal neonate would have 132mm of space in the Tabun C1 outlet, and 122mm in the human female mean outlet (Weaver and Hublin, 2009:8154). This suggest that unlike in humans, the Neanderthal neonate may have been delivered occiput-transverse. However, the restriction of the sagittal dimension compared with modern humans would conversely necessitate internal rotation of the shoulders in order to occupy the widest possible diameter, which would thereby induce external rotation of the head to either an occiput anterior or occiput posterior position.

Below, **Figure 3.8.** shows how the shape and areas of Weaver and Hublin's (2009) reconstruction of the Tabun C1 pelvis compares with a modern human female mean. This schematic clearly demonstrates the alternate transverse long-axis of the Neanderthal birth canal, which would necessitate typical orientation of the neonate of occiput-transverse when engaged with the pelvic inlet. However, whether this modern human mean used is an appropriate comparison (given the high level of variation) is questionable.

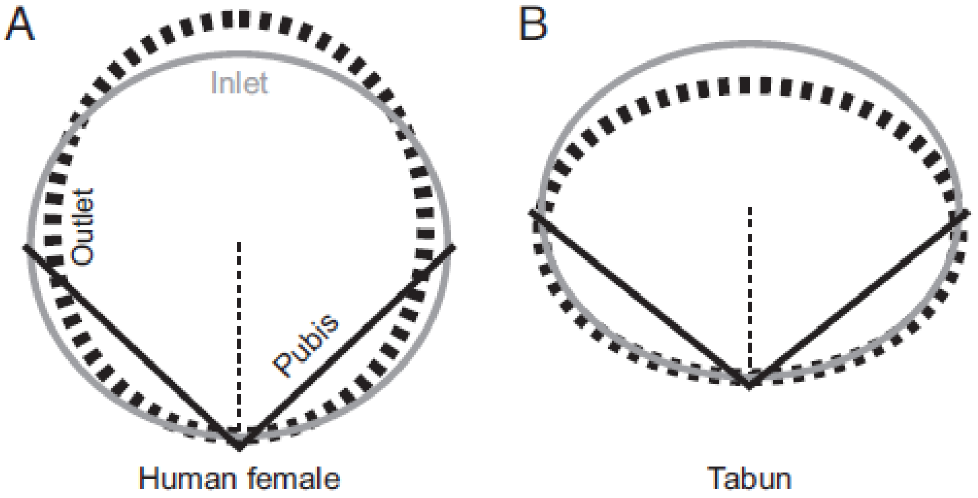


Figure 3.8. Weaver and Hublin's (2009: 8153) schematic of the inlet (continuous grey line) and outlet (dashed black line) areas of the Tabun female Neanderthal pelvis (B), in comparison with a modern human female mean (A).

Whilst the areas of the female pelvic inlet and outlet are close to the mean of Weaver and Hublin's (2009) modern human female sample, the inlet and outlet index values [0.79 and 0.70 respectively (Franclscus, 2009: 9126)] are very low compared to modern humans [the modern human female index values are typically just under 1.0 for the inlet and over 1.0 for the outlet (Weaver and Hublin, 2009:8151)]. The low index values in the Tabun C1 are a result of the lower sagittal (numerator) and higher transverse (denominator) dimensions of the pelvis. In modern human females, the long axis of the outlet is the sagittal dimension, but from these results, it appears the long axis of the Tabun C1 is the transverse dimension (Franclscus, 2009).The Kebara 2 hypothetical female demonstrates that the Tabun C1 shows an alternate pattern of sexual dimorphism in the pelvis to that of modern humans (Weaver and Hublin, 2009), which follow the observations of Rosenberg (1986). The implications for other reasoned patterns of sexual dimorphism in Neanderthals, and indeed other hominins, could arguably be to revaluate any assumed morphology based on gender assignment.

It would be useful to compare the adult female pelvis with juvenile specimens to see whether these traits were truly sexually dimorphic, developing from hormonal influence during adolescence. If not, one of two evolutionary scenarios may have produced such morphology: (1) the typical argument for locomotive selective benefits driving non sexually dimorphic morphology (Ruff, 1995; etc), where the resultant obstetric adequacy was just a by-product of this evolution or; (2) obstetric adaptions were a product of genes which are not affected by interaction with those on the sex chromosomes, and the resultant morphology conferred no selective disadvantage to males, so would appear characteristic to males as well as females, hence lowering sexual dimorphism in the pelvis. Again, this is an area which further study may provide interesting results, but for now, the lack of complete specimens means direct analysis is largely restricted.

The post-cranial skeleton of the neonate must also be factored into theoretical mechanisms of Neanderthal birth. The robust nature of the Neanderthal skeleton (Fleagle, 2013) means the neonate shoulders may have found it very difficult to negotiate the sagittally narrow birth canal, without a 90-degree rotation during delivery. Hence, one could argue that Neanderthal birth may have been similarly very complex, but the head may not have rotated from a transverse engagement. The shoulders may have needed to rotate in the midplane or outlet, after delivery of the head (Trevathan and Rosenberg, 2002). The internal rotation of the shoulders would cause the now exterior neonate head to turn either occiput anterior or occiput posterior. This would have conferred added selective benefits if reoriented occiput-posterior, typically seen in nonhuman primates, where occiput-posterior delivery allows mothers to remove any obstruction to the airways and assist delivery themselves, without risking spinal damage (Franclscus, 2009).

The adaptation of this more platypelloid trait in the Tabun C1 pelvis may indicate an evolutionary scenario where the increased transverse diameter of the birth canal, from lengthening of the pubis, facilitated increasing neonate encephalisation in later *Homo*. In turn, the selective benefits of adaptions to alternate locomotive mechanics and general robusticity in Neanderthals, resulted in a more transversely broad maternal pelvis. In conjunction with an arguable lack of selective pressure to develop a more sagittally spacious pelvis, this necessitated transverse cranial orientation of the neonate throughout birth under Joulin's Law (1864). Since the neonate cranial long-axis is orientated though the most spacious dimension, the outlet shape necessitates an occiput-transverse delivery of the neonate cranium in Neanderthals, and hence an alternate, occiput-anterior birth through the sagittal long-axis in modern human females (Franclscus, 2009; Weaver and Hublin, 2009). However, the incomplete nature of the ischial elements of Tabun C1 means that midplane dimensions cannot be accurately modelled (Franclscus, 2009), so the inlet and outlet values alone cannot conclusively rule out rotation of the foetal cranium during birth, but merely that the head was delivered through the outlet occiput-transverse. While a male Neanderthal pelvis from Sima de los Huesos, Spain (Arsuaga et al, 1999) is observed to have a sagittally broad midplane, which could suggest rotation of the neonate cranium into the long-axis of this midplane, Weaver and Hublin (2009) of course note that this is a male specimen, so an inference on the female midplane is rather dubious. Furthermore, modern human females have smaller midplane indices than males (Weaver and Hublin, 2009), as a result of the slightly larger transverse dimension in the female midplane.

As discussed earlier in this chapter, the sagittal expansion of the midplane and outlet in *H.sapiens* provides a selective advantage in providing a more spacious dimension of the birth canal for an increasingly large brained neonate (necessitating occiput anterior rotation), without affecting the bipedal mechanics (Ruff, 1995; Trevathan and Rosenberg, 2000). Ponce de Leon et al (2008) argued that their simulation of the Mezmaiskaya engaged in the reconstructed Tabun pelvis supports the theory of modern-human like rotational birth in Neanderthals, where the neonate cranium rotates into an occiput-anterior orientation in the pelvic midplane or outlet, and fits with the conclusions of Ruff (1995) that such a pattern emerged in *H.erectus* during the Mid-Pleistocene. They attribute this conclusion to their finds of a comparatively wide pelvic outlet and neonate cranium compared with modern humans which make human-like birth most probable. However, the fact that the Neanderthal maternal birth canal appears wider in conjunction with neonate cranium slightly larger, more likely points to alternate mechanism of birth in Neanderthals. In modern humans, the variation of maternal pelvic shape typology has been demonstrated to result in alternate orientation of the neonate during delivery (Walrath, 2003). Therefore it is reasonable to suggest that the Neanderthal platypelloid shape must have likely resulted in an occiput-transverse delivery, rather than the occiput-anterior delivery of the modern human female. It must be noted, however, that these findings are not necessarily representative of the entire Neanderthal species. The results are based on a very small sample of historical Eurasian populations of Neanderthal, who come from disparate geographical locations and populations.

Aside from mortality risk from the degree of CPD, numerous other external factors are known to contribute to pelvic shape and in turn obstetric morphology. Recent contention over the contribution of climatic adaptations to Neanderthal morphology, concerns the degree to which climatic factors have influenced obstetric morphology in the species. Work by Weaver and Hublin (2009; also see Franclscus, 2009) suggests that in the evolving female Neanderthal pelvis, the wide trunk produced by a transversely expanded pelvis, would have had thermoregulatory benefits to Neanderthals in colder Northern latitudes, reducing the mother's surface area to volume ratio and reducing heat loss. Conversely, the warmer African climates inhabited by early *H.sapiens* would selectively favour narrower body shapes with larger surface area to volume ratios and hence would have been a driving factor preventing further transverse expansion of the female birth canal (Franclscus, 2009). In this evolutionary scenario, there may have been stronger selective pressure to avoid effecting the bipedal adaptations in the female pelvis of *H.sapiens*.

Further to this, variance associated with climatic factors in human population is highlighted by Kurki (2013) and Betti et al (2014), with differences in average increases in anteroposterior and transverse diameters. Betti (2015) argue that a wide range of morphological variance within past human populations, would have enabled selection to operate and select for adaptive pelvic shifts in populations occupying alternate environments. Waxenbaum and Feiler (2020) note that in modern human populations adapted to higher cold stress, males have less energy available for musculoskeletal growth, whilst obstetric constraints on body form for females conforms to optimal cold climate body proportions. Interestingly, Beals et al (1983) and Katz et al (2016) work on cranial morphological relationships to climatic conditions demonstrate that extreme cold, winter temperatures place a higher environmental stress on morphological adaptation that any other season or climate. This may be the case as higher demands on homeostatic maintenance, alongside reduced food abundance and in-turn speculatively higher activity output to forage or hunt, compound stresses on the hominin body.

Whilst there is support for this conclusion of a climatic influence on Neanderthal obstetric morphology and CPD (and by extension behavioural responses), studies of modern human populations suggest that a causal link between ecogeography and morphology in the hominin pelvis is limited. Whether climatic factors directly drive the evolution obstetric constraints in the pelvis, remains contentious. Work by Betti (2015) demonstrated that the human pelvis is under lower constraints than other closely related primates, lowered covariance between morphological features, and a higher potential of adaptability. This high level of phenotypic plasticity and variance, or evolvability, allows selection to occur at a faster rate with more variance already present within the population. In applying this result from human samples however, this would require a significant number of samples of Neanderthals from multiple climatic zones, with both sexes well represented to factor sexual dimorphism into models of covariance. Additionally, comparison of Neanderthal male and female body plans, in conjunction with palaeoclimatic data would provide insight on the effect of climate on obstetric morphology. By observing variance in specific regions associated with obstetric mechanics, and the degree of this variance between male and female individuals, this would indicate which morphological features were under greater selective pressure from birth to be conserved, or conversely which features were under greatest pressure to adapt in response to climatic factors. Larger samples of reliably sexed remains of Neanderthals from known climatic contexts would be required to perform such an investigation, which would be limited from available specimens at present.

Given the lack of significant evidence that climatic factors have shaped the obstetric pelvis of Neanderthals, genetic drift other neutral evolutionary systems may alternatively have resulted in the morphology seen in Neanderthal female pelvises. Betti et al (2014) tested for the effect of climate on the size and shape of the os coxae on a large sample of modern humans, both male and females of which were relatively well represented. Their results found that neutral processes accounted for a substantial degree of the observed variance in both sexes, whilst temperature as indeed a significant predictor of both shape and size, with the size of the os coxae increasing with decreasing external temperature (Betti et al, 2014). If similar associations were seen in Neanderthal specimens, this could be argued to suggest the expanded transverse pelvis was the result of cold climate adaptions. Climate, however, had a minimal effect and this association was further reduced after factoring in population history (Betti et al, 2014) thereby concluded that both neutral and climatically driven adaption accounted or the modern human sample's variation. Further work by Grunstra et al (2021), Betti and Manica (2018), and Buck et al (2021) also supported the conclusion that neutral evolutionary processes were a significant factor in the divergence between Neanderthal and modern human pelvic typology. For Neanderthals, however, with much smaller populations prior to extended and substantial contact with modern human networks (Prufer et al, 2014; Kuhlwilm et al, 2017; Mafessoni et al, 2017), the variation is likely to have been very limited. Given the evidence towards the end of Neanderthal occupation in Europe of substantial inbreeding and a reduction in genetic variance (Vaesen et al, 2019), it is likely that the species would not have shared this potential for significant adaptive phenotypic plasticity of the pelvis to respond to varying climatic conditions.

3.5. Limitations of archaeological samples in maternal mortality reconstruction

In such an evolutionary scenario where maternal mortality was high enough without assistance as to drive the evolution of birthing behaviours, the demographic profile of hominin populations should reflect this. Higher representation of birthing females in the archaeological record (i.e. higher mortality of females at peak fertility) should be visible in this hypothetical scenario. However, Waldron (1994) notes that those specimens analysed may only be a small sample of the original living population, and are certainly not representative of typical risk experienced by an entire species. As shown in **Table 2.1.**, the number of complete pelvises for comparative palaeoanthrological analysis is limited. Whilst a number of fragmented specimens across a wide range of geological space and time are available, the proportion of those which could be considered suitable for meaningful reconstruction of obstetrical adequacy, are limited. Additionally, for each species assigned, only a small range of examples are available, again limiting species-wide conclusions on obstetrical adaptations, given the potential for significant local and global population level variation within the same species. Furthermore, Roberts (2009:136) notes numerous problems regarding the identification of age and sex of hominin remains, in particular with the datasets used to compile age and sex profiles used for cross comparisons. Whilst it is impossible to control all variables affecting ontogeny and the reliability of such datasets, it is also impossible to truly reconstruct exact physiology and profiles of past populations both modern and archaic from the fossil record.

Species	**Site/location**	**Date (years BP)**	**Specimen**	**Useful for obstetric analysis? (Completeness, age or sex?)**	**Reference**
Ardipithecus ramidus	Aramis, Ethiopia	4.4 mya	ARA-VP-6/500 left os coxae, partial right ilium, distal sacrum fragment	Too incomplete	Lovejoy et al, 2009
Australopithecus afarensis	Woranso-Mille, Ethiopia	3.6 mya	KSD-VP-1/1	Too incomplete	Lovejoy et al, 2016
Australopithecus afarensis	Hadar, Ethiopia	3.2 mya	A.L. 288-1 left os coxae and sacrum	Relatively complete, female	Hausler and Schmid, 1995
Australopithecus africanus	Sterkfontien, South Africa	2.0–2.6 mya	Sts 14 right os coxae, fragments of left os coxae and sacrum	Relatively complete, female	Berge and Goularis, 2010
Australopithecus africanus	Sterkfontien, South Africa	2.0–2.6 mya	Sts 65 ilium and pubis fragments	Relatively complete, female	Claxton et al, 2016
Australopithecus africanus	Sterkfontien, South Africa	2.0–2.6 mya	Stw 431 fragments of left and right ossa coxae, and sacrum	Too incomplete	Kibii and Clarke, 2003
Australopithecus africanus	Sterkfontien, South Africa	2.0–2.6 mya	Stw 441/442/465 fragments of an iliac crest	Too incomplete	Hausler and Berger, 2001
Australopithecus sediba	Malapa, South Africa	1.97 mya	MH1 juvenile partial left and right ossa coxae; MH2 partial right ilium, complete right and fragmentary left pubic bones, sacrum	MH1 - Relatively complete, juvenile; MH2 - Too incomplete	Kibii et al, 2011
Paranthropus robustus	Swartkrans, South Africa	1.8–1.0 mya	SK 50 partial right os coxae	Too incomplete	Robinson, 1972
Paranthropus robustus	Swartkrans, South Africa	1.8–1.0 mya	SK 3155 right ilium	Too incomplete	McHenry, 1975
Paranthropus robustus	Kromdraai	2.0–1.5 mya	TM 1605 left ilium (probable juvenile)	Too incomplete	Robinson, 1972
Homo erectus	Koobi Fora, Kenya	1.9 mya	KNM-ER 5881 partial left ilium	Too incomplete	Ward et al, 2015
Homo erectus	Bed IV, Olduvai Gorge, Tanzania	1.1 mya	OH 28 partial left os coxae	Too incomplete, adult male	Day, 1971
Homo erectus	Koobi Fora, Kenya	1.9 mya	KNM-ER 3228 partial right os coxae	Relatively complete, adult female	Rose, 1984
Homo erectus	Koobi Fora, Kenya	1.6 mya	KNM-ER 1808 fragments of right and left ilia	Too incomplete	Walker and Ruff, 1993
Homo erectus	Nariotokome, West Turkana, Kenya	1.6 mya	KNM-WT 15000 juvenile partial left and right ossa coxae missing pubic bones, and sacrum	Too incomplete, juvenile	Walker and Ruff, 1993
Homo erectus	Gona, Ethiopia	1.4–0.9 mya	BSN49/P27 partial left and right ossa coxae, and partial sacrum	Relatively complete, adult female	Ruff, 2010
Homo erectus	Danakil Depression, Eritrea	1.0 mya	UA-173/405 partial right os coxae (ilium-ischium); UA-466 partial pubis	Too incomplete	Bondioli et al, 2006
Homo heidelbergensis	Sima de los Huesos, Spain	430 kya	SH Pelvis 1, mostly complete left and right ossa coxae, and sacrum	Relatively complete, adult male	Bonmati et al, 2010
Homo heidelbergensis	Caune de l'Arago, France	450–350 kya	Arago XLIV partial left os coxae	Too incomplete	Day, 1982
Middle Pleistocene Homo; Taxon debated	Jinniushan, NE China	260 kya	Jinniushan left os coxae	Too incomplete	Rosenburg et al, 2006
Middle Pleistocene Homo; Taxon debated	Kabwe, Zambia	Age unknown	E 719 partial left os coxae	Too incomplete	Stringer, 1986

Homo naledi	Rising Star Cave, South Africa	335–236 kya	40+ pelvic fragments, best represented by ilia U.W. 101-477, 101-1100, 101-1370; ischia U.W. 101-791, 101-896, 101-1088, 101-1112, 101-1414, 101-1754, 101-1755; pubic bone U.W. 101-1700; and partial first sacral vertebra U.W., 101-723	Relatively complete, adult male and juvenile	VanSickle et al, 2018
Homo neanderthalensis	Kebara Cave, Israel	60 kya	Kebara 2 right os coxae, sacrum, and crushed left partial os coxae	Relatively complete, adult female	Rak and Arensberg, 1987
Homo neanderthalensis	Tabūn Cave, Israel	165–143 kya (Layer C) or 122 kya (Layer B)	Tabūn C1 fragments of left pubic bone and ishium, and right os coxae	Relatively complete, adult female	Weaver and Hublin, 2009
Homo neanderthalensis	La-Chapelle-aux-Saints, France	60 kya	La-Chapelle-aux-Saints 1 right ilium, partial sacrum, and left partial ischium	Too incomplete	Trinkaus, 2011
Homo neanderthalensis	Sima de las Palomas, Spain	50–60 kya	Palomas 96 left and right ossa coxae, and sacrum	Too incomplete	Van Sickle, 2014
Homo floresiensis	Liang Bua, Flores Island, Indonesia	100–60 kya	LB1 partial left os coxae, right ilium	Relatively complete, adult male	Jungers et al, 2009
Homo sapiens	Omo Kibish, Ethiopia	172–196 kya	Omo 1 partial left os coxae (KHS 1-60A) and iliac crest fragment (KHS 1-60B)	Too incomplete	Hammond et al, 2017
Homo sapiens	Qafzeh Cave, Israel	95 kya	Qafzeh 9 partial pelvis, poorly preserved and significantly distorted	Too incomplete	Rak, 1990
Homo sapiens	Skhūl, Israel	80–100 kya	Skhūl IV right and left ossa coxae, and lower sacrum; and Skhūl IX partial left os coxae	Too incomplete	McCown and Keith, 1939
Homo sapiens	Dolní Vestonice, Czech Republic	28–26 kya	Dolní Vestonice 13, 14, and 15 complete pelves	Too incomplete	Trinkaus, 2006

Table 2.1. List of available pelvic osteoarchaeological specimens (adapted from Wall-Scheffler et al, 2019:49). The second to last column indicates whether the specimens provide a viable specimen for obstetric analysis. Those for which the fragmentary nature of the remains prevent meaningful estimates of obstetrical adequacy are described as ‘Too incomplete’ for analysis, with ‘Relatively complete’ specimens further commented on whether they are (ideally) adult females, or males and/or juveniles.

Whilst locomotor mechanics may be relatively uniform across a species, in humans numerous studies suggest a high degree of variability in obstetric morphology. Studies on variability in primate and other mammalian species, however, are limited. Therefore, the degree to which a single hominin pelvis can represent population and species-wide morphology is tentative. However, a number of factors and process can result in preservation bias, hampering the collection of crucial archaeological and fossil specimens necessary for research on sexual dimorphism and species-typical morphology. Lieverse et al (2006) argues that due to an overall general robusticity of the male skeleton, one would expect females to be less commonly represented in the archaeology. Roberts (2009:59) notes that whilst this is not always the case, women are more susceptible to osteoporosis, particularly post-menopause, reducing bone density and increasing post-depositional fragility. Guy et al (1997) also note that sub-adult remains have lower mineral densities, making them softer and so more likely to suffer from destructive taphonomic processes, particularly crushing and decay in acidic soils. This further hampers the recovery of crucial neonatal remains necessary for palaeoanthropological reconstruction of CPD and the interplay between neonatal and maternal obstetric morphology.

Bayesian statistical analysis can provide more accurate and realistic estimates of palaeodemographic profiles (Roberts, 2009:136), such as mortality and developmental morphology (Gowland and Chamberlain, 2002). However, such analyses rely on direct data from archaeological, anthropological, and primatological study, for which maternal and infant mortality measurements are arguably sparse, particularly from the archaeological record, as well as primatological samples. In order to determine mortality estimates of past female populations as a result of maternal mortality (either before, during or after birth), an ability to accurately determine the sex of the individual is required. However, in determining the sex of early hominins, this can be difficult. The extent to which sexually diagnostic morphology is present in other hominin species is something which can affect the reliability of sex determination.

In determining the mortality risk in an evolutionary scenario of birth assistance, the likelihood of death is theoretically determined by the perceived risk of maternal and neonatal death from birth. This death can be during, such as extensive haemorrhaging by the mother, or delayed through infection. However, given that such pathologies can only be determined by soft tissue remains, this makes an attempt at assessing mortality risk difficult. ‘Coffin births’ where the mother dies with the infant remaining engaged within the birth canal are a likely example of a direct cause of death from birth. However, the only known examples are from more modern populations (Sjovold et al, 1974; Hawkes and Wells, 1975; Hogberg et al, 1987; Arriza et al, 1988; Malgosa et al, 2004; Cruz & Cohia, 2010), with no examples from prehistoric populations. Therefore, is it surely more parsimonious to argue that mortality as a result of CPD and dystocia was unlikely in archaic species – such births are not represented in the palaeoarchaeological record. It is worth noting also that all reconstructions of CPD use average values for neonatal cranial dimensions. However, younger mothers are shown to have smaller infants, with infant size increasing with maternal age as the mother is able to invest greater reproductive energy into infant growth, as opposed to maternal somatic growth (Marvin-Downle et al, 2018). Therefore, reconstructions of CPD must consider estimated age of the maternal individual(s) sampled, and the likely resultant size of the neonate at term for mothers of that age. In addition, it should be remembered that successful delivery pre-term could mitigate against predicted CPD.

Whilst extensive work by Abitbol (1996) is significant in highlighting relevant skeletal obstetric morphology and any differences between hominin species, Abitbol critically follows a limited view of human obstetric mechanics, shared by consecutive physical anthropological research. Scialli (1997:734) concluded that Abitbol’s (1996) description of primate skeletal anatomy was “unconvincing”, with Abitbol’s work further perpetuating the notion of relative ‘simplicity’ in nonhuman primate obstetric anatomy. Scialli (1997) highlights a neglect of deeper consideration by Abitbol (1996) and others of the potential overuse of medical intervention, and the possible compounding of obstetrical inadequacy not as a product of evolution but of systemic, detrimental medical practice. It is arguable that work by physical anthropologists reinforces the notion that modern human birth mechanics ‘necessitate’ assistance, which may perpetuate overuse of unnecessary intervention in contemporary medical practice.

One of the key assumptions of the ‘obstetric dilemma’ hypothesis is that maternal and (or) infant mortality was high enough among early hominins, who were in turn limited from increasing internal obstetric pelvic dimensions or reducing neonatal brain sizes. Therefore, ‘midwifery’ or manual intervention must have evolved to reduce significantly high mortality rates. However, not only does this scenario assume mortality rates as a product of dystocia and CPD were high, but it also implies that a ‘package’ of such behaviours emerged at this point only as a by-product of uniquely hominin forms of altruistic cooperation.

Furthermore, much of the literature focuses primarily on the external function of the pelvis, as a support of bipedal biomechanics, rather than the pelvis’ role in providing a stable pelvic floor minimising risk of pelvic prolapse. This in itself is a contributor to maternal mortality risk, as consecutive parity reduces the stability of the pelvic floor, essentially increasing the risk of pelvic organ prolapse with each birth and the risk of indirect mortality (Couri et al, 2012; Chene et al, 2017). Greater consideration of morphological limitations imposed by pelvic floor stability must be discussed in future research, with associated implications for palaeodemographic reconstruction.

Attempts have been made by previous authors to link pelvic morphometrics with mortality directly from archaeological samples. Tague (1994) tested the use of pelvic size at death amongst a prehistoric Native American sample as an indirect indictor of mortality rates, for which he identified a significant difference in the linea terminalis (which defines the pelvic inlet) between female young adult (18-24 years) and older (25+ years) groups. Tague (1994) argued that this observation could be due to differential survivorship from pelvic size (as CPD), or could alternately be a product of sustained pelvic growth after 24 years. However, Tague (1994) concluded that this was more likely the product of sustained late growth in females, which is further supported by Huseneyov et al's (2016) observations of significant sustained female pelvic growth post-adolescence, across varied contemporary populations.

However, Fuller's (1998) attempt to replicate Tague's (1994) results from contemporary African-American and European-American samples was unsuccessful, finding no significant differences between the two age groups. Fuller (1998) attributes this to differences in life-history characteristics between the populations, with age-at-menarche and the onset of adolescence determining the rate and extent of pelvic growth before age-at-death. Building on early work by Greulich and Thoms (1944), Clark (1971) observed that once adolescent growth and remodelling of the pelvis ceases, the pelvic inlet grows only minimally. Later work by Moerman (1982) demonstrated that internal pelvic dimensions were strongly correlated with the onset at menarche, with a significant extent of growth occurring during the first year post-menarche. However, this is extremely difficult to directly determine archaeologically. Rather, such life-history characteristics rely on indirect estimation from known or regressed growth trajectories such as early life weaning and dental eruption. This surely indicates the unreliability of archaeological samples in predicting palaeodemographic mortality rates, without accurate estimations of life-history variables influencing ontological growth of the maternal pelvis.

3.6. The influence of birthing intervention in hominin evolution

One form of contemporary (and historic) behavioural attempt to reduce maternal and neonatal mortality rates (both in humans and in captive primate practice) includes caesarean-section delivery, where the infant is surgically removed from the uterus at or near full-term. In contemporary populations, Molina et al's (2015) results demonstrated a significant relationship between population level caesarean delivery rates and maternal mortality ratios in humans.

However, an observed threshold of caesarean intervention is evident, with the highest caesarean delivery rates not correlating with maternal or neonatal mortality at a country level (Molina et al, 2015). Of 194 WHO member states assessed, those experiencing caesarean delivery rates of up to 19.1 per 100 live births significantly inversely correlated with maternal mortality ratios ($p=0.003$), and up to 19.4 per 100 live births correlated inversely with neonatal mortality ($p<0.001$) (Molina et al, 2015:2263). Caesarean delivery rates up to approximately 19 per 100 live births were associated with lower maternal or neonatal mortality among WHO member states - increasing caesarean section rates above this threshold was not associated with reductions in maternal or neonatal mortality (Molina et al, 2015). Further work by Betran et al (2016) supports this. Whilst the morphology is described in great detail, Abitbol's (1996) reinforcement of the relative 'necessity' of intervention and in turn justification of 'obligate midwifery' is typical of physical anthropological literature. This work fails to encompass valuable behavioural and cultural impact on the extent of birthing intervention, and importantly the scope of the effect of alternate behavioural and cultural practice on birthing outcomes, both contemporaneously on in prehistory.

Moreover, in the context of divergent hominin pelvic morphology, a rather troubling suggestion by Abitbol (1996:221) proposes that:

> *"for the human species to persist in spite of complete encephalization, a different species or a different racial stock has to emerge with encephalization directed frontally. In addition, a new cultural revolution is necessary where women may devote themselves to childcare and to less strenuous physical work, at least before adulthood in order for the pelvis not to be disturbed prior to full ossification."*

This is arguably both a misguided and insensitive approach to understanding both the evolutionary history of hominin obstetric morphology and the issues of modern human birthing, and should not form the basis of future changes of obstetric practice. This view does not consider the high variability in obstetric morphology observed globally (Betti and Monica, 2018), as well as suggesting a racially bias component in assessing obstetrical adequacy. Indeed, VanSickle et al (2022) rightly discuss the prevalence of racial bias in the use of classic Caldwell-Molloy pelvic shape typologies in medicine and physical anthropology. The authors argue that not only does the original basis for the classification system is inherently flawed in its methodology, but continued use in contemporary research reinforces long held stereotypes of optimal birthing morphology. This in turn hampers the validity of future research, for which VanSickle et al argue should focus on assessments which use recent, evidence-based practice which takes into account the high degree of observed variance in global populations. Simplifying this variance into outdated classification systems, themselves historically based in racial stereotypes, is of limited value with dietary, socioeconomic and environmental factors playing a significant role in health and pelvic development of women today.

3.7. Connecting the dots between obstetric morphology and birth assistance behaviours

Greater understanding of birth mechanics and likely CPD are crucial in evaluating associated theories in human evolution. Logically, behavioural adaptions such as midwifery, can be considered a behavioural adaption to a morphological phenomenon. Indeed, Pinkerton (1973) states that the maternal pelvis was an essential factor which resulted in the emergence of reflective human intelligence. In this evolutionary scenario, mortality risks presented by increasing CPD had a significant impact on the evolution of human intelligence, and its associated behaviours. However, the role of behavioural adaptions to CPD are arguably less well established or explored in previous literature.

At the most basic level, an essential requirement for successful evolution is the ability to successfully reproduce and specifically to the focus of this thesis, the successful delivery of neonates (Trevathan, 1988). The more successful the delivery (i.e. the survival of both mother and infant), the more evolutionarily successful the species (Abitbol, 1996:1). Much of our current understanding of the evolutionary mechanisms facilitating the emergence of typical human birthing behaviour and morphology, comes from exploration by Trevathan and Rosenburg, which is in-turn built on the predictions and assumptions of the ‘obstetric dilemma’ hypothesis first outlined by Washburn (1960). As aforementioned, physical anthropological and palaeoanthropological literature has often stated or implied that nonhuman primates typically seek seclusion during labour, that nonhuman primates are always unassisted during birth, and are mostly alone in care of the neonate (Abitbol, 1996:3). Abitbol (1996:3) goes perhaps the furthest in stating that nonhuman female primates have “all the necessary built-in biological mechanisms for successful reproduction and need no outside help”, and dismisses arguments to the contrary as “rudimentary, biologically determined and often part of the observer’s imagination”. These statements, however, are contradicted by the use of established veterinary practice of surgical intervention, coupled with an emerging body of observational data (Wolfensohn and Honess, 2005:138). This observational data and evidence for prosocial birthing behaviours will form the basis for the focus of this thesis, as an adaptive response to morphological evolution.

Some previous studies have attempted to hypothesise potential links between biomechanical adaptions and socioecological consequences. The exploration of human birth, and the impact on hominin demography and ecology by Lovejoy (1981; 1988), proposed that human bipedal morphology and mechanics were a consequence of adaptations to increase reproductive fertility. This consideration of the socioecological implications of adaptive obstetric morphology interestingly would also be applicable to other evolutionary adaptions to birthing difficulties.

Given the proposed association between morphological adaptations and behavioural responses, it is reasonable to suggest that alongside morphological adaptions, birthing behaviours also would have an impact on population socioecology. This suggested link between morphological evolution, behavioural adaptions, and socioecological strategies, builds on earlier work by Fischer (1982). Fischer hypothesised that a shift to habitual bipedalism would have educed the dimensions of the birth canal to an extent which necessitated premature birth of altricial neonate. In addition, Martin (1983) and Frost (1987) suggested that bipedal constraints necessitated significant and compensatory changes in postnatal brain growth trajectories, in order to minimise the risk of high CPD, hence resulting in highly altricial young in comparison to nonhuman primates. Fialkowski (1987) suggested that reduced fertility in humans was an adaptive response to the obstetric constraints imposed by bipedalism. Following on from this, Queiroz doAmarol (1989) interestingly suggested that further adaptations to bipedalism were hindered by obstetric constraints, coupled with increasing risk of maternal and neonatal mortality, and that pressures to adopt bipedalism were more extreme than contemporary theories could explain. With suggested links between, for example, obstetrics, altriciality (a behavioural response) and life history (with infants born earlier) provides an interesting example of factors which may be investigated for associations within extant primate taxa. These associations could in turn be used to propose an evolutionary model for the emergence of birthing behaviours in primates, and by extent among extinct taxa, such as early hominins. The identification of a direct or indirect impact of birthing outcomes on the relative success or failure of ancestral species, both on an individual level for local group reproductive ecology, and on a population level (if prosocial birthing behaviours can be determined to be species-typical), is crucial to understanding birth among extant highly social primates and our highly social hominin ancestors. Therefore, pinpointing the emergence of obstetrically relevant morphology is the first step in understanding the evolution of human behavioural responses to morphological challenges, and in turn the implications for reproductive ecology demography throughout human history.

Conversely, consideration of how behavioural adaptations to increasing CPD in humans may have impacted subsequent morphology, such as recent adoption of caesarean delivery practices, should also be factored into palaeoanthropological research and discourse. Mitteroecker et al (2016) used contemporary medical data to produce a model which suggests caesarean births have in fact removed the selective pressures and mortality risk imposed by incidences of CPD. Indeed, evidence for the procedure appears in written records as far back as the Roman and Egyptian periods (Mitteroecker et al, 2016; Rosenburg, 2018). Given that this practice alone has been established over a long enough period so as to affect global population-level patterns of morphology, this supports the line of reasoning that obstetric morphology reflects changes in obstetric and birth related behaviours. This research additionally highlights the interplay between obstetric morphology and sociocultural birthing behaviours. Chiefly, the potential role of prosocial birthing behaviour in mitigating risk associated with obstetrically challenging delivery of the neonate. Future investigation and exploration of this relationship will provide greater insight into the emergence of contemporary birthing behaviour among our hominin ancestors.

3.8. Conclusion

Much of the archaeological evidence points to a mosaic pattern of obstetric evolution in hominins (Wells et al, 2012). However, the ability to detail and track the evolution of the obstetric pelvis in hominins is greatly limited by the lack of complete specimens (Weaver and Hublin, 2009; Franclscus, 2009). Due to the fragmentary nature of many of the specimens, reconstructions are somewhat subjective to relevant technological limitation of time, limiting any conclusions on obstetrical anatomy or behaviour in represented species. Therefore, a principal prediction of the 'Obstetric Dilemma' hypothesis – that increasing maternal mortality drove the evolution of birth assistance behaviours – is difficult to observe and test from the archaeological record alone. Together, the material discussed presents a mixed rather than linear progression of obstetric evolution in primate and hominin evolution.

Between the specimens of Late Pliocene Australopiths and the specimens of *Homo erectus*, much of the evidence points to a conservation of much of the obstetric morphology, with the minimal increase in pelvic dimensions most likely responding to increased CPD. The lack of curvature of the neonate trajectory in Australopithecines could indicate that the emergence of delivery under the pubic symphysis is something which may well be a *Homo*-specific birth mechanism.

In terms of context, it is worth noting the significant lack of pelvic remains of early hominids from the fossil record, which could yield greater context in reconstructing the evolutionary trajectory taken by human obstetric morphology. Methodology and technology are often a major limiting factor on the understanding of archaeological remains. Future study may be able to utilise advances in digital three-dimensional modelling, in conjunction with soft tissue reconstruction techniques used to model locomotive mechanics, to produce an accurate musculoskeletal replica of the obstetric pelvis and neonate. This would facilitate further investigation into the mechanics and potential risk of birth in extinct hominins, where osteoarchaeological and fossil specimens are limited.

Further assessment of variation within contemporary primate specimens can provide a greater insight into pelvic variation, but this variation was likely under similar constraint from bipedal mechanics as well as pressures on the pelvic floor from an increasingly orthograde posture. It is perhaps likely that the platyeplloid shape observed in Australopithecines would exert a larger amount of pressure on transverse muscles and ligaments, so a reduction in the transverse dimension seen in *Homo* would reduce such pressures from an increasingly large neonate. It would appear that the ‘pelvic floor hypothesis’ would be a more appropriate framework for understanding constraints on the maternal pelvis.

Work by Simpson et al (2008) and Weaver and Hublin (2009) on the Gona *Homo erectus* pelvis demonstrates a divergence from a fully platypelloid pelvis to an intermediate between that of late Australopiths and modern humans. Although the degree of continuity in morphology between Early and Mid-Pleistocene *Homo* shown by Ruff (1995) could suggest that the pattern of birth in early *Homo*, whether rotational or not, was retained in later *Homo* and later *H.erectus* in Africa. Due to the coincidence with increasing neonatal encephalisation, the literature suggests that neonate cranial expansion was a primary driver in the evolution of the obstetric pelvis of ancestral *Homo*.

However, whether this preceded or was facilitated by prosocial birthing behaviour and assistance as proposed by the obstetric dilemma hypothesis remains arguably unanswered from the archaeology alone. Furthermore, it is important to note that there is a difference between morphologically necessary (or obligate) assistance at birth and preferred or culturally mediated assistance and support. The question of what our ancestor's response was to an obviously difficult birth experience necessitates the exploration of extant human and nonhuman primate behaviours in response to birthing mothers to provide a framework for understanding the evolution of the highly prosocial birthing exhibit by our species today.

An assessment of modern human obstetric morphology clearly demonstrates a significant level of variation between populations of the same species (Betti and Manica, 2018). Therefore, without a large-scale sample of hominin pelvises for direct comparison across similar locales in both time and space, any conclusions on species-level trends are speculative at best. In order to reconstruct levels of variation and trends in species-level pelvic morphology, future study must include large-scale assessment of intraspecies primate pelvic morphology. Furthermore, a lack of significant direct or indirect measures of maternal and infant mortality (for which our understanding of the evolutionary pressure on reproductive fitness relies) further weakens the argument that such demographic factors drove the evolution of such behaviours

In addition, the trend for comparing Australopithecine pelvises primarily with chimpanzee pelvises follows an assumption that the last common ancestor between the *Pan* and hominin lineage had a more chimp-like pelvis. Given recent evidence of a greater extent of derived morphology in *Pan* (Andrews, 2020), it is arguable that an ancestral form closer to a crown hominid could have been more platypelloid in morphology. Further pelvic finds could shed light on this; however, given the fragmentary nature of the less robust nonhuman primate pelvis, such finds are extremely rare and so future study of obstetric adequacy in pre-australopithecine species is drastically limited. Understanding the evolution of our own obstetrical capabilities should focus on comparisons with other extant populations from morphologically similar mammalian taxa.

Chapter 4: Why be social? Understanding sociality in human and primate birthing behaviour.

4.1. Introduction

‘Obligate midwifery’ has emerged as a near essential feature of human behaviour (Trevathan and McKenna, 2003; Weiner et al, 2008), yet little has been done to investigate and consider the origins of this behaviour as observed in nonhuman primates. In particular, there is as yet no real hypothesis encompassing the conditions necessary for ‘obligate midwifery’ (a necessity for birthing assistance) to emerge and become an typical feature of hominin birth. By tracing the socioecological, morphological and physiological factors in primate evolution, the emergence of highly prosocial birthing behaviours and typical birth assistance behaviours in humans can be better understood and explained.

A substantial body of work by Rosenburg and Trevathan (Trevathan, 1987; Rosenburg, 1992; Rosenburg and Trevathan, 2002; Trevathan, 2011) proposed that increasing CPD and a resulting increase in maternal mortality risk drove the emergence for (highly prosocial) birth assistance behaviours. In contrast to this typical pattern of behaviour in humans, nonhuman primates seek isolation during parturition (Rosenburg and Trevathan, 2002). Much of the latter work by authors have built upon this body of work, typically implying or stating that (what this thesis defines as) prosocial births, are a uniquely human occurrence. However, a review of the primatological literature shows a range of socio-spatial locations in wild and captive primates, with individuals giving birth in isolation (Chivers and Chivers, 1975; Rawlins, 1979; Goodall and Athumani, 1980; Ratnayeke and Dittus, 1989; Takahata et al, 2001), some within the range of their social group (Nash, 1974; Nigi, 1982; Stewart, 1984; Moreno et al, 1991; Nakamichi et al, 1992; Gorzitze, 1996; Takahata et al, 2001; Kumar et al, 2005; Peker et al, 2009), and others within relatively close proximity but still separate from their social group (Abblegen and Abblegen, 1976; Sekulic, 1982; Hammerschmidt and Ansorge, 1989; Kinnaird, 1990; Condit and Smith, 1994; Windfelder, 2000; Peker et al, 2009). Sekulic (1982) notes that of course these observations are not necessarily representative of optimal locations for each species for either mother or neonate, and any species-typical conclusions based on these observations are tentative. The influence of captivity on restricting the decisions of individuals in terms of movement activity during birth, must of course be considered when discussing the context of captive observations. Though limited, captive observations of course have a significant role to play in facilitating opportunity for observation by researchers, given the obvious challenges in obtaining observations in wild and semi-free ranging populations. Further to this, an observational bias emerges from the fact that, since most wild primate births occur at night (Jolly, 1972; Ding, 2013) and close intrusion may disturb the mother and group (Dias, 2005), detailed descriptions of individual and group behaviour are relatively rare. Whilst these difficulties in collection of crucial observational data are challenging to overcome, the value of successful analysis to furthering our understanding of both our own and primate birthing strategies are evident.

In contrast to the previous anthropological and archaeological consensus discussed so far, this thesis hypothesises that highly prosocial birthing behaviours were already a common feature of early hominin birth. In turn, this prosocial behavioural feature crucially served as a behavioural buffer, facilitating the archaeologically observed increase in CPD, and maternal and neonatal mortality risk birth in later hominins. This alternative hypothesis to the ‘obstetric dilemma hypothesis’ – the ‘social birthing hypothesis’ – would have two central predictions, and is outlined in **Figure 4.1**.

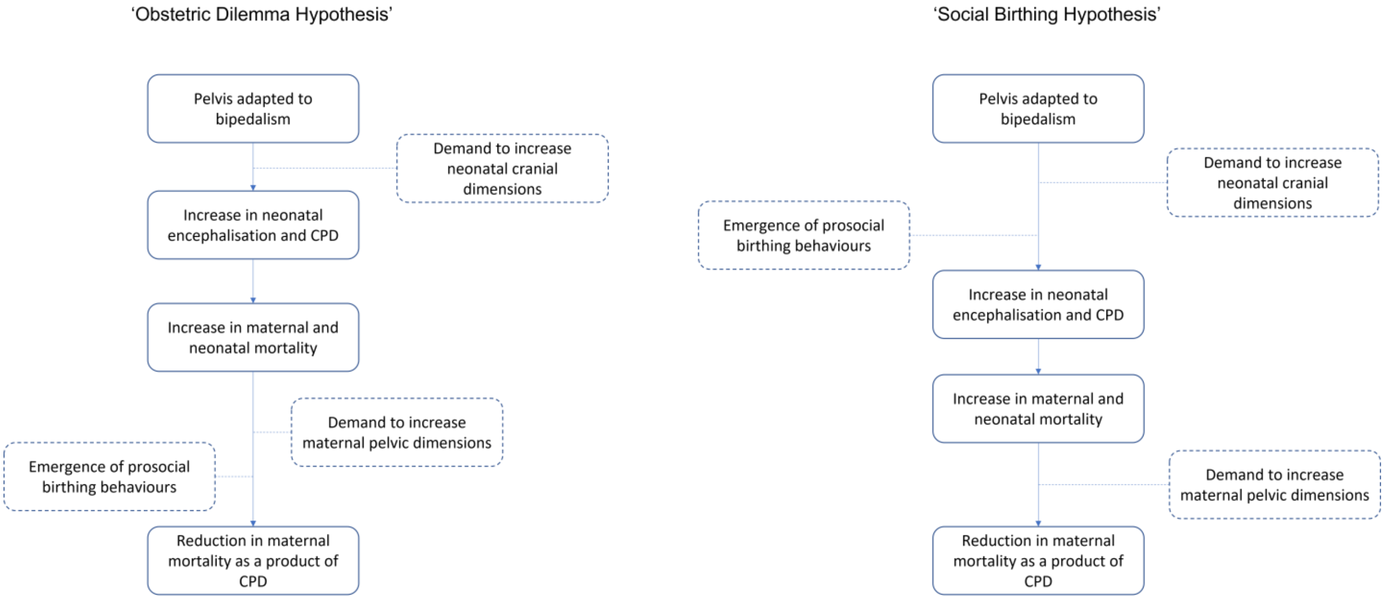


Figure 4.1. Flowchart outline of the 'obstetric dilemma hypothesis' and 'social birthing hypothesis'.

Whilst the 'obstetric dilemma hypothesis' centrally predicts that CPD drove the emergence of prosocial birthing behaviour exclusively in hominins (and indeed relatively late in hominin evolution), the 'social birthing hypothesis' predicts that (1) species which exhibit prosocial birthing behaviour would have relatively higher CPD compared with non-assisting taxa. This could be coupled with a potential correlation with higher encephalisation of the adult and/or neonate, where increasing neonatal cranial dimensions (and implied brain size) relative to postcranial dimensions could be facilitated by behavioural mitigation for increasing CPD. (2) typically highly prosocial taxa, accepted as being relatively more prosocial than closely related taxa, are more likely to display prosocial birthing behaviours.

With regard to prediction (1), this would build upon previous work on the associations observed between primate sociality and brain size. As Chapter 2 has highlighted, the medical and osteoarchaeological evidence which does demonstrate that CPD occurs in humans, alongside highly supporting prosocial birthing behaviours. However, whilst some species of nonhuman primate have been shown to experience high levels of CPD, these species do not appear to display prosocial birthing behaviours in response to this morphological ‘dilemma’. This therefore requires further investigation to explore the observations discussed. Following Dunbar’s (1998; 2003; 2009; 2012) ‘social brain hypothesis’, higher levels of encephalisation in adult primates show a significant correlation with social factors, in particular social group size. Dunbar argues that the selective benefits for management of extensive and complex social networks, drove the evolution of higher encephalisation amongst primate taxa, including the relatively higher encephalisation seen in hominin evolution. If the extent of prosociality of birth in primates can be demonstrated to correlate with social complexity (e.g. more prosocial birthing behaviour is seen in species with larger social groups), this could suggest birthing prosociality may have coevolved with encephalisation.

By extension, it could then be argued that relatively high encephalisation levels observed in hominins was facilitated by prosocial birthing behaviour. A correlation between social variables, such as social group size, would be expected to have a positive correlation with a quantitative measure of prosociality of birth. This in turn leads onto prediction (2). With the increasing evidence of prosocial birth assistance behaviours in nonhuman primates, this would initially appear to support the second part of this hypothesis, in terms of a capacity for nonhuman primates to exhibit intentional and directed prosocial birth assistance behaviours. This would seem highly likely, as a species showing a proclivity for a higher number of social interactions, or perhaps more specifically more high-quality prosocial interactions (i.e. social bonding opportunities), would be more likely to express prosocial interactions during the birth event.

To identify to the necessity, benefit and emergence of highly prosocial birthing, this chapter will first briefly explore fundamental themes previously argued to drive the emergence of prosocial birthing behaviours, such as obligate midwifery, in hominin and wider primate evolution. This chapter will review elements of typical human birthing behaviour which are observed in extant nonhuman primates, and could therefore be used to model the evolutionary origins of prosocial 'obligate midwifery' in humans. Building upon research into the relationship observed between sociality and cognitive evolution in humans and nonhuman primates, this chapter will also discuss the relevance of the 'grandmothering hypothesis' and the 'cooperative breeding hypothesis'. By linking in with these hypotheses, this will place the thesis within the network of overlapping theories regarding hominin social and morphological adaptations, as non-mutually exclusive aspects of our species evolution. Specifically, these well-established hypotheses will aid in understanding context for the emergence and selective benefit of prosocial birth assistance behaviours. Here, the cost and selective benefits which can be gained by the individual and individuals within social groups from prosocial birthing behaviours shall be considered. Additionally, to provide insight into the reliability of the predictions of a 'social birthing hypothesis' in explaining correlation between social behaviours and other variables, this chapter will also briefly discuss wider evidence of birth assistance behaviour in other social mammals.

4.2. Evidence of prosocial birthing behaviour in nonhuman primates

Whilst evidence of prosocial birthing behaviours has been evident within the literature, minimal focus has been granted to its significance. Trevathan (2015) does note that among nonhuman primates, social group members may be present at birth. However, Trevathan's review does not consider the importance of these behaviours and the facilitation of social inclusion in the birth event, other than for reasons of safety and infanticide avoidance by the mother. This possible driver for the expression of prosocial birthing behaviours is perhaps most evident amongst langurs who exhibit births in large social groups (van Schaik ad Kappeler, 1997; Kappeler and van Schaik, 2002) and high levels of infanticide (van Schaik and Janson, 2000; Hausfater and Hrdy, 2008). Here, the degree of interactions between langur mothers during labour and numerous social group members are of particular interest. Specifically, the social mechanisms which facilitate the birth event to occur within a social space (i.e. not in isolation), and could arguably characterise langur births as prosocial in terms of close social proximity. The implications of deciphering how prosociality during labour and infanticide risk may be linked, in the context of minimal evidence of morphological factors driving selection of behavioural adaptions, is of interest for investigation into social birthing behaviours.

The notion of psychosocial support during the birth event as commonly observed in human birth, whilst difficult to test, is likely similarly shared by other non-human primates. Observations by Kumar et al (2005) of a capped langur female grooming a parturitient female showing signs of stress arguably support a psychosocial element to birthing behaviour and prosocial assistance in nonhuman primates. In this case, the response of the grooming female to the high stress levels of the mother suggests a capacity for empathy and understanding during labour. This is something which could be crucial in driving the action and expression of prosocial birthing behaviours among primates, with no direct benefit identifiable to the reproductive fitness of the supporting individual. However, there is a potential for the supporting individual to increase their reproductive fitness through supporting the delivery of related offspring, and in the case of non-kin through an expectation of delayed return – that through helping an allied female the supporting individual may expect support in future interactions.

Earlier work by Trevathan (1987) alternatively posits that an evolutionary benefit to isolation during birth is reduced risk of infection, something which is perhaps an ultimate root of cultural memes of isolation during birth in non-industrialised human groups. For example, among peoples of the Nyob Nruab Hills, China, birthing women undergo confinement as their bodies are considered ‘polluted’, and are believed to present a significant risk factor for disease (Liamputton, 2009). Nepalese women are also confined for at least 11 days postpartum, in order to shy away from “masculine energy and the symbolic power of the male god”, and because it is believed to be “sinful to see them” (Acharya and Rimal, 2009:142). The exact risk of disease or infection as a result of invasive and intrusive interaction with the social group is unknown for nonhuman primates and among ancestral hominins, but further research would provide an understanding of the potential influence of disease in the evolution and expression of isolationist behaviours amongst birthing primates. One can assume as for humans, primate and hominin females would be highly vulnerable. Whilst no evidence exists to support the notion that nonhuman primates perceive any risk as the result of the supernatural, superstitious, or cultural taboo, patterns of birthing behaviour within the same group and between groups of the same species may hint at the presence of social birthing cultures. Such behaviour and cultural norms as observed across human populations today must have emerged at some point on our species cultural evolutionary trajectory, but precisely where is difficult to predict, given the lack of archaeological or genetic artefacts. By careful examination of observations among humans and nonhuman primates, it may be possible to theorise the emergence of the wide variety of social birthing behaviours reported.

The activity cycle of primates is also of interest in determining levels of birthing behaviours amongst humans and primates. A brief investigation of published medical literature demonstrates that humans have appear to have retained an ancestral primate pattern of nocturnal birth (Jolly, 1972; Bernis and Verea, 2012). However, the ability to see during birth is surely essential in facilitating the opportunity for interactions and awareness of birthing among group members, something which becomes increasingly difficult during nocturnal hours for diurnal species. The exact purpose of the retention of birth timing amongst primates is unclear, but evidence demonstrates that births occurring outside nocturnal hours are primarily those occurring with complications, or those influenced by anthropogenic factors such as medical or veterinary intervention – clinicians choosing to induce, or nominated caesareans for example (Bernis and Vernea, 2012). The factors driving nocturnal birth appear uncertain, and there is certainly merit in closer examination and investigation – i.e. is it a product of reduced nocturnal mobility, ancestral hominin predation risk, or avoidance of infanticide? Greater understanding of the retention of nocturnal birthing despite drawbacks for assistance and prosocial birthing behaviour, would aid in providing a better understanding of the evolution of birth assistance behaviours. One such avenue of research by archaeologists and palaeoanthropologists is perhaps the use of fire by hominins in lengthening of 'daylight' hours, facilitating the retention of nocturnal birthing whilst allowing for beneficial prosocial birthing behaviour and amongst humans, the development of unique cultural memes related to the birth event.

Further long-term study of the circumstances and behaviours displayed by birthing primate females, both between species and groups of the same species, will greatly expand the understanding of factors driving the expression and evolution of prosocial birthing behaviours. Such studies would also potentially be able to identify and quantify the extent to which behaviours are passed on between individuals, whether vertically through generations or through horizontal peer observations.

Observations of prosocial birthing behaviours

Turner et al (2010) note that whilst birth is an essential factor in mammalian reproductive success, detailed and quantitative descriptions of nonhuman primate parturition are rare. However, an increasing feature of such reports is the demonstration of highly prosocial birth assistant behaviour, both in captivity and in the wild (Price, 1990; Kumar et al, 2005). The exact reasons driving such expressions of prosocial behaviours are unclear. Assistance during labour may be a behavioural expression of kin selection, where those who assist may be reducing neonate or maternal kin mortality, raising their own direct or indirect fitness (Silk et al, 2003; Ding et al, 2013). Turner et al (2010), however, suggested that in primate evolution, non-isolated and assisted birth may have conferred selective benefits through increased social bonding. Within the context of hominin evolution, the emergence of more difficult labour that necessitated obligate midwifery may have conferred added benefits for prosociality in strengthening bonds between both kin and non-kin. This could explain why such high observed CPD remains prevalent in modern humans, with high mortality risk offset by direct or supportive assistance behaviour.

Ding et al (2013) observed an instance of direct assistance in a group of wild black-and-white snub-nosed monkeys (*Rhinopithecus bieti*), where a non-kin individual was seen to carefully (non-antagonistically) pull the emerging neonate from the mother, and then return it. Pan et al (2014) also observed a similar case of parturition assistance in the closely related white-headed langur (*Trachypithecus leucocephalus*), notably by another multiparous female (**Figure 4.2.**). This time, a more experienced older female was observed to assist in the delivery of a less experienced female – what is interesting here is that with known parity status of those involved, the multiparous ‘aunt’ was seen to assist the inexperienced nulliparous niece. Interestingly from the images provided by Pan et al (2014), the presence and close proximity of multiple female group members highlights the shared group experience of the birth event in this case, an opportunity to gain valuable insight and knowledge of birth for the females (no male was observed present).

Figure 4.2. Images (a-h) - stills taken from recordings of parturition assistance of twins in a wild white-headed langur by a multiparous female (adapted from Pan et al, 2014:485). Here the first infant is guided out by mother initially, then by the assisting female, who brings it to her chest and licks the neonate as is typical of parturient mothers, holding on to it for 10 minutes

and chasing away other adult females while the mother ingests the placenta. After 10 minutes, the infants are returned without resistance to their mother.

Yang et al (2016) report on observations of a multiparous golden snub-nosed monkey (*Rhinopithecus roxellana*) female receiving directed birth assistance from another multiparous female, within the same one-male unit. In this instance again the assisting female was non-kin, and therefore the high degree of sociality and direct assistance must have been driven by a factor other than direct reproductive fitness for the actor (in this case the assisting female). The parturitient female interestingly rejected an attempt to handle the neonate by a primiparous subadult female, but two other multiparous females were allowed to hold the infant for significant periods of time – 15 minutes in one case (Yang et al, 2016:159). This multiparous female will have had previous birthing experience, and this assistance behaviour may be an expression of empathic understanding with the nulliparous female. The lack of antagonistic behaviours by either party further supports the desire to both provide and receive assistance, a characteristic of highly prosocial birthing events. A desire to minimise discomfort previously experienced by the multiparous female may therefore have driven her assistance behaviour toward the nulliparous female.

Perhaps one of the most tantalising glimpses into the capacity for human-like, highly prosocial birth assistance was recently observed amongst captive bonobos. Demuru et al (2018) provided a detailed account of the proximity, protection, support and gestural behaviour amongst captive non-related female bonobos at a bonobo “social event” (Demru et al, 2018:502). In this case, the observers witnessed for the first time a unique gesture aimed at the parturitient female, and described the birth event as sharing elements typically defined as characterising human birth (close proximity, female birth attendants, control and protection, emotional engagement and practical support) (World Health Organisation, 1996; Demuru et al, 2018). Dumara et al (2018) also note that rather than give birth outdoors where mothers may more easily have hidden, each birth took place indoors with group members in close proximity. Multiple aspects of the birth events were discussed by Demuru et al (2018), including the increase in group members present in close proximity to the mother during labour, protective behaviours by female group members significantly more towards males and human observers, and most of the positive interactions by bystander females directed at the mother. Interestingly, aggressive displays towards human observers were significantly more frequent during the first stage of delivery (Demuru et al, 2018), which could suggest an awareness amongst the female bystanders of the events occurring and need for protection of the parturitient female. Furthermore, during two of the three births observed, adult females visually inspected the mother's anogenital region exclusively prior to the birth – again demonstrating an awareness of where pain may be occurring and potentially signalling an understanding of the imminent delivery of the neonate.

The unique gesture observed amongst the group and performed by bystander females (Demuru et al, 2018) is of great interest in documenting the capacity for understanding of the birth event by the group, as an awareness of the situation and expectancy of the delivery of a neonate would demonstrate a shared awareness and understanding of birth amongst bonobo females. The 'grab infant' gesture was described as resembling the movement of the mother's arm moments before the birth, and yet these actions by the bystanders (putting and keeping one or both hands under the genital region of the birthing female without touching her) were performed prior to the mother's action (Demuru et al, 2018). What is of particular interest in understanding the prevalence of direct manual assistance amongst nonhuman primates is the observation on multiple occasions where bystander females were observed manually guiding the neonate during expulsion. Here the neonate was held by the head and then arm guided out of the birth canal. The breadth and scope of the behaviours observed and the discussion by Demuru et al (2018) support the conclusion that nonhuman primates, and bonobos in particular, do share what is traditionally argued to be a uniquely human suite of birthing behaviours, and provides significant further evidence for the capacity of such behaviours among extant primate species. The behaviours appear to be driven by a desire to engage in protection of birthing female group members, psychosocial support, and maintenance of close affiliate bonds.

The evident sexual skew in terms of the higher commonality for female interest and inclusion across primate species seems logical, but the exact reasoning remains speculative. Work on social network analysis by Sueur and Pele (2015) shows that snub-nosed monkey females are more central to social interactions than males. Using eigenvector centrality coefficients to compare differences in social network maintenance in colobines and cercopithecines, Sueur and Pele (2015) found a significant phylogenetic difference in the key individuals maintaining social networks. Among taxonomically close female probiscus and snub-nosed monkeys were more central than males to social interaction, whereas males were more central than females in more closely related gelada monkeys and hamadryas baboons (Sueur and Pele, 2015). The stronger within-harem female bonding social system seen in the colobines may be a crucial aspect in determining strong female associations necessary for facilitating highly prosocial birthing. In attempting to understand the relative sociality of primate birthing behaviour, these observations suggest that direct assistance only occurs in groups where females are not highly competitive, and risk of offspring infanticide is low. This fits with the lack of direct evidence of female interest and prosocial interactions during birth amongst female-competitive species such has chimpanzees, when compared with closely related bonobos (Demuru et al, 2018). Therefore, it is possible that a relationship exists between quantified resource stress and birthing sociality, where those species for which females face higher competition for resources may demonstrate relatively low birthing sociality indexes and remain relatively isolationist (if mediated by the parturitient female) or exclusive (through a lack of interest by group peers).

In addition to female interactions, Fess (1975) provides an example of paternal assistance, where a cotton-top marmoset father and birthing mother manually assisted in the successful delivery of an infant by pulling until the shoulders emerged. This male assistance in callithricids – for which high levels of male allocare are common (Hrdy, 2009) – is also reported in common marmosets (Langford, 1963) and pygmy marmosets, *Cebuella pygmaea* (Caine and Mitchell, 1971), which may suggest that such behaviour is typical for cooperatively breeding callithricids. In contrast however, reviews of available data by Bo (1971) and Brandt and Mitchell (1971) both concluded that manual assistance by the mother in delivery is more common in Old World monkeys and apes than has been observed for New World monkeys. Although, this conclusion was of course based upon data only available at the time. This is a crucial feature in understanding the origins of social birthing behaviours, potentially as a derived feature evolving independently across Platyrrhine taxa, but ancestral to Catarrhine taxa and the evolutionary product of common decent. However, this observation may also suggest that birthing assistance behaviour and prosociality is driven by individual learned experience. Since males of course will not have given birth themselves, in the absence of complex communication, they would have limited understanding of the stress and pain experienced by the birthing female from direct observation alone. Whilst perhaps not directly testable, future study of male responses to vocalisations and behaviour by the mother during parturition, would be beneficial in providing further context to primate birth events.

Something which is absent from discussions of birthing behaviour in previous literature is the role of observed experience in influencing sociality of the primate birth event. Turner et al (2010) note that during the birth of a captive *Macaca fuscata*, adult females and juveniles were observed watching the births and taking great interest in the mother’s anogenital region. The findings of Timmermans and Vossen (1996) show that multiparous cynomologous macaque (*Macaca fascicularis*) mothers are more skilful and efficient in their birthing behaviours, supporting earlier suggestions that experienced nonhuman primates may be relatively more successful in dealing with potentially fatal birthing complications (Moreno et al, 1991). In this case, experience is assumed to be gained solely through direct experience of birth and labour by the individual (i.e. previous personal birth), with limited or no mention of the potential for understanding and knowledge gained from external observed experience. This is something which hints at a potential (but significant) evolutionary benefit of birth within a social context, in terms of the opportunity for learning by immature group members which may reduce stress during parturition (as a result of a lack of understanding and experience) as well as increasing the propensity for empathic responses by group members (i.e. increasing the chance of birth assistance and support by group members). This potential capacity for significant knowledge and experience exchange without the need for an extended period of mating, gestation and a risky process of birth for the female, is arguably a highly parsimonious factor driving the prevalence of prosocial birthing behaviours amongst prosocial primate species.

Infanticide risk as a factor influencing birthing sociality

Alternatively, female parturition assistance or sociality could have an adaptive benefit as protection or discouragement of infanticide (Trevathan, 2015), which is widespread among primates (van Schaik and Janson, 2000; Kappeler and van Schaik, 2002; Arnqvist and Rowe, 2005:53). Work by Abegglen and Abegglen's (1976) argued that their observations support the conclusion that self-isolation is an adaptive strategy to avoid inter or intra-group aggression, and any risk of infanticide. Within New World monkeys, in particular across *Alouatta* where births have primarily been observed to occur in isolation (*Alouatta belzebud* – Camargo and Ferrari, 2007; *A.caraya* – Peker et al, 2009; *A.palliate* – Moreno et al, 1991; Nisbett and Glader, 1996; *A.seniculus* – Sekulic, 1982), this may be a strategy by females to mitigate risk from male attacks. Martins et al (2015) reports on an incident in wild brown howler monkey (*A.guariba clamitans)* of suspected infanticide of a neonate, where at 35 days old the new-born received fatal wounds by aggressive males who chased the mother and injured the infant. For

A.seniculus where coalitions of closely related females are suggested to increase reproductive success through cooperative breeding strategies (Pope, 2000), birth in social isolation here may be an adaptive behaviour to minimise male infanticide risk, and would suggest prosocial birthing behaviour would not correlate with infanticide risk. However, among Old World monkeys such as in the golden snub-nosed monkey, a species in which highly prosocial birth assistance behaviour has been observed, Yao et al (2016) report on three observed instances of infanticide by new male leaders, in line with the 'sexual selection hypothesis' where removal of previous male offspring reduces female interbirth intervals. Whilst there are also strong affiliative bonds in this species between resident males and females (Yang et al, 2016), this collective evidence suggests that increased risk of male infanticide influences social birthing behaviours amongst colobines. Trevathan (2015) notes that this is the also case for closely related langurs, where both infanticide levels and proportion of births occurring in relatively close proximity to other group members are high. A deeper investigation into available observations of group responses and context of infanticide, with specific consideration of the birth event, would provide greater insight into the relationship between infanticide risk and birthing behaviour. Whether such behaviour is a derived response to infanticide risk in colobines and not the ancestral state in a shared cercopithcine ancestor, requires further investigation.

Among more closely related species to humans, chimpanzees are widely observed to live in greater isolation when pregnant or lactating (Furuichi, 2011; Fujisawa et al, 2016), where only direct reports of birth in the wild have been published (Goodhall and Athumani, 1980; Kiwede, 2000). For this species, male-led infanticide is hypothesised to be the primary driver of this isolation (Hamai et al, 1992; Watts et al, 2002; Gruber and Clay, 2016), but infanticide by female group members has also been documented amongst wild populations and hypothesized alternatively to be driven by resource competition (Pusey et al, 1997; Townsend et al, 2007).

Pusey et al (2008) suggest that isolation may be highly beneficial in minimising infanticide risk in chimpanzees, where parturitient females seclude themselves to minimise infanticide risk from unrelated females attempting to minimise future feeding competition. Demuru et al (2018) speculate that this difference between chimpanzees and bonobos in terms of the lack of any observed infanticide amongst bonobos (Gruber and clay, 2016) – although maternal cannibalism in the wild has been observed (see Tokuyama et al, 2017) – may be the product of stronger, affiliate bonds among female bonobos, more akin to human social structures.

Whilst it has been typically argued that bonobo promiscuity may be a strategy to increase paternity confusion and reduce levels of infanticide (Furuichi, 2011), more recent research suggests that the male bonobos may in fact have higher paternity assurance as a result of higher reproductive skew of male bonobos (Surbeck et al, 2017). Therefore, the distinct lack of observed prosocial birthing behaviour amongst female chimpanzees, compared with almost human-like prosociality observed amongst closely related bonobos could reasonably form part of a suite of behaviours in response to infanticide risk. Interestingly Demeur et al (2018) suggest that this shared level of female gregariousness between bonobos and humans may be evidence which supports the hypothesis that the common ancestor of *Homo* and *Pan* also shared this trait and associated behaviours, and the absence of the behaviours in chimpanzees is indeed derived. The factors influencing the conservation of this female gregariousness through common decent in hominin evolution is of particular interest in this scenario.

Alternatively to the risk of infanticide to neonatal mortality as a proximate cause for prosocial birthing behaviour expression, Trevathan (2015) suggests that close group members proximity during the birth provides a degree of protection to the vulnerable birthing mother from predation. However, no long-term study of parturitient female predation has attempted to investigate any correlation between predation risk and birth timing in primates. Only a single observation to support this has been observed in previous literature. A report on a daytime birth in a langur troop by Oppenheimer (1976:541) notes that the parturitient female came to the ground to give birth, accompanied 15 minutes later by two other adult females who appeared to "become aware of their exposure", increasing their vigilance. Whilst this observation does provide evidence of group responses to birth in response to what is reported to be predation risk avoidance, the authors do not actually observe a genuine predation threat during the event. If predation risk were a proximate cause for the expression of prosocial birthing behaviours, this would also imply that they would not occur in the absence of predation pressure. However, we know of course that humans and reports of captive primates demonstrate the expression of prosocial behaviours with no risk of predation. A long-term study of mortality rates of birthing fameless and neonates at the birth event, contrasted with social birthing behavioural expression, would provide insight into any possible link. Additionally, further investigation into a possible correlation between social birthing behaviours and predation risk would be able to provide greater understanding of the evolutionary adaptability in birth-timing to pressures such as predation.

Placentophagia as a prosocial feature of the birth event

One possible explanation for prosocial interest by observers and actors in the birthing event, is the desire to share in placentophagia – ingestion of the expelled placenta. Early work by Brandt and Mitchell (1971) states placentophagia to be a commonality among monkeys, but whether this is a species-typical phenomena or observed anomalies by individuals, remains inconclusive. Abegglen and Abegglen (1976) note that whilst an observed female hamadryas baboon did not ingest the placenta, it was likely she was primiparous but also equally likely that the placenta was consumed after dark. This observational bias is something which should be factored into any theoretical model of proximate and ultimate explanations for placentophagia amongst primates, and in turn as a possible factor in driving prosocial birthing behaviour. Turner et al (2010) report on a spectrum of behaviours of female *M.fuscata* mothers, ranging from little or no interest to avid consumption as a behaviour commonly observed among multiple species of macaque. Among a group of captive cotton-top tamarins (*Saguinus oedipus*), 14 births were observed between December 1986 and January 1989, of which there was one suspected and one verified breech delivery, with one infant dying during expulsion (Price, 1990:523). Price (1990) reports that fathers, and in some cases older offspring of both sexes, frequently shared in placentophagy, which is consistent with reports on tamarin paternal placentophagia (Willig and Wendt, 1970; Fess, 1975; Pryce et al, 1988). However, evidence from common marmosets suggests that paternal ingestion is less common, with older offspring and particularly young females far more likely to engage in sharing of the placenta (Rothe, 1974; 1977; Stevenson, 1976). What is missing from earlier reports of placentophagia among primates, is a deeper discussion of the possible adaptive significance and proximate causes of behavioural expression. In tamarins and marmosets, placentophagy is likely a reflection of the well-developed cooperative breeding systems seen in callitrichids, where the father, offspring and unrelated individuals contribute to infant care (Cleveland and Snowdon, 1984; Rylands, 1985; Goldizen, 1987; McGrew, 1987). This evidence among callitrichids also demonstrates that males may become involved in the birth event and express prosocial behaviours behaviours, and are not motivated to show maintaining close proximity solely for the purpose of hostile intention (e.g. infanticide).

However, what must be accounted for in understanding the prosocial nature of shared placentophagy is the extent to which this might be driven by group interference and interest, or mediation by the birthing female. As observed by Douglas (2014) in a bonobo group where the placenta and after-birth were shared between non-kin (**Figure 4.3.**), there is the potential for social inclusion in the birthing event, with food sharing behaviour being a central aspect post-delivery. This sharing of consumable birth related resources amongst bonobos similarly occurred in the form of cannibalising an infant by the mother and other group members (Tokuyama et al, 2017). Whilst no evidence suggested infanticide by the mother or group prior to consumption of the dead neonate, and indeed no antagonistic actions were recorded either, it suggests that resource sharing of the placenta or dead infant amongst bonobos forms part of the bonobo behavioural repertoire rather than aberrant behaviour.

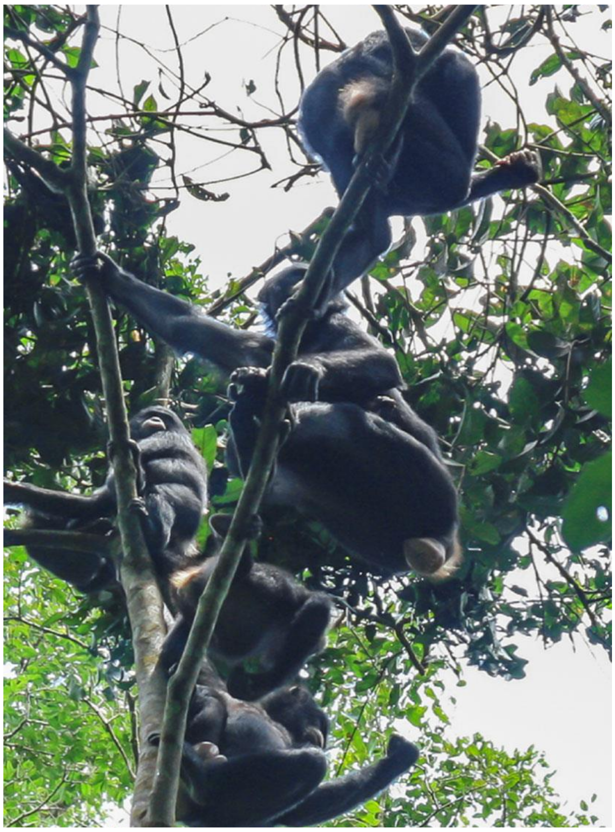


Figure 4.3. The new mother (top) shares pieces of placenta with two other adult individuals bottom and middle) (from Douglas, 2014:537).

Previous research demonstrates that placentophagia within a social context is determined by a number of socioecological factors (Hawkes and Bird, 2002; Stevens, 2004; Jaeggi and van Schaik, 2011; Jaeggi and Gurven, 2013a; 2013b), which can confer adaptive benefits to individuals within the group, and to the mother from sharing in placentophagia. Fujisawa et al

(2016) report on two daytime births in wild chimpanzees at Bossou, Guinea, where both were seen to build nests prior to parturition, and one of the individuals was observed sharing the placenta postnatally. Again in both instances, the parturient female gave birth socially, not in isolation (Fukisawa et al, 2016). Furthermore, earlier work by Kristal (1991) reports that placentophagia enhances opioid mediated analgesia, in addition to providing protection from predators by removing scent, and finally in providing nutrition to the lactating mother. This is something which may not only confer benefits to the mother, but may provide similar hormonally induced affect for social group members engaging in placentophagy. More recently, Kristal et al (2012) posit four possible proximate explanations for observed placentophagia in non-human mammalia: (1) increasing mother-offspring interaction; (2) inducing pregnancy mediated analgesia in the parturient mother; (3) stimulating maternal brain opioid networks facilitating onset of caretaking behaviour; (4) postpartum pseudopregnancy suppression. Kristal et al (2012) suggest that the suspension and cultural ‘taboo’ of placentophagy is perhaps more adaptive in humans than the practice itself, encouraging social minimisation of pain during childbirth, as opposed to physiological opioid suppression. In this scenario, a maximal threshold which necessitates social inclusion and minimisation would strengthen female within-group bonds and affiliation, whilst also providing opportunities for transmission of birthing experience and knowledge. These physiological proximate and ultimate explanations are of note, but focus solely on the expression of placentophagy, rather than the additional engagement in the behaviour by social group members. These explanations may hint at proximate mechanisms operating within group members, but further investigations into group member physiology after consumption would provide clarity on possible group benefits to placentophagy, in addition to a potential ultimate cause for this prosocial birthing behaviour.

However, it must be noted that these observations amongst nonhuman primates do not necessarily indicate species-typical reliance on assistance, but instead indicate a capacity in wild nonhuman primates for prosocial and directed behaviour. For placentophagy to provide Therefore, any evolutionary phylogenetic reconstructions of hominin birthing behaviour should factor in the presence or absence of such behaviours from observations of other primate species. The presence of such behaviours in the immediate context of birth suggest that a more complex suite of behaviours and response of primate social groups occurs across multiple species, relatively distant from one another. This may suggest that such prosocial placentophagia is mediated not by heritable innate drivers, but rather independently emerges at a population level (potentially cultural) as part of a repertoire of birthing behaviours passed via observation and social learning between generations and conspecifics.

4.3. Prosocial birthing behaviour as a cooperative breeding strategy

Prosocial birthing behaviour and ‘the grandmothering hypothesis’

A notable consequence of a slow life history in primates (Charnov and Berrigan, 1993) is increased generational overlap owing to greater on average longevity and reproductive span (Hooper et al, 2015). This work bult upon previous observations of an association between intergenerational group structure in humans, and female longevity past the point of menopause. Notably, Voland et al (1989) observed that within humans, the later women completed their genetic reproduction, the longer they lived, to which they regard beneficial post-reproductive intervention in offspring during the phase as the ultimate cause. The ‘grandmothering hypothesis’ posited by Hawkes et al (1998), proposed that human females contribute to the reproductive success of their daughters through parental care of grandchildren, where maternity is assured. Life history trade-offs in females such as post-reproductive longevity, could result in a population with mature females who can economically provision immature kin (Hawkes, 2006), or perhaps non-kin. If reproductive effort is alternatively devoted to grandchild provisioning, this could remove the mortality risk from continuing to bear offspring (Franculscus, 2009; Weaver and Hublin, 2009), whilst maximising the chances of grandchild survival. This would in-turn raise the reproductive fitness of the grandmother by increasing the reproductive success of her daughter, and selective fitness of her grandchild. Furthermore Hawkes et al (1998; Hawkes, 2006) suggest allocare assistance could decrease offspring mortality, as well as facilitating a reduction in the interbirth interval of reproductive females and raising reproductive output. Investment in parturition assistance and offspring care by grandparents thus arguably has benefits for increased protection from infanticide from grandparent intervention.

Furthermore, theoretical modelling of post-reproductive longevity suggests that an increase in post-reproductive lifespan does promote the evolution of cooperation which, relative to this argument, could include allocare (Ross et al, 2015) and prosocial birthing behaviour. This could be through parental manipulation and reproductive management, arguably imparting parental experience through social learning. In groups with an overlap of reproductive and post-reproductive females, there is the potential for facilitating prosocial assistance in birth as a product of sharing previous direct observation and experience of parturition. By disseminating experience of birth through prosocial grandmothering interactions, subsequent generations of females may raise opportunities for experience sharing, and in turn reduce levels of anxiety and stress during parturition. The previously discussed example of parturition assistance by a multiparous white-headed langur (Pan et al, 2014) is a potential analogous frame for such a scenario. Whilst any high-level communication seems unlikely for extant primates, it would have been communicated over the course of hominin evolution with the emergence of more complex communication and language. Furthermore, the evidence of observation by juveniles and opportunity for gaining birthing experience, suggests an avenue for selection for intergenerational overlap amongst female-affiliative groups which facilitate the expression of prosocial birthing behaviour.

Although, as a reproductive strategy, there is an antagonistic relationship between reproductive success and lifetime longevity, since they are dependant to a degree on the same limited resources (Voland and Engel, 1989). Whilst grandmothering could maximise reproductive success, the generational overlap produced by reduced mortality may result in greater rate of cumulative population increase, and thus require a stable strategy to increase and optimise the population carrying capacity. Whilst this may be the case for modern humans throughout recent history, how far this trend goes back into our evolutionary history is difficult to identify. The potential benefit from grandmothering is also difficult to quantify in relation to any demographic impact on the reduction of maternal and neonatal mortality and improvement in birthing outcomes in hominins. Yet this does not mean it would not have been an important feature of typical hominin behaviour and social dynamics as it is today in modern humans.

The ‘cooperative breeding hypothesis’

Kramer (2010) defines cooperative breeding as a parenting and social system where non-parental members help support offspring, but this definition has undergone much recent debate and reassessment (Cockburn, 1998; Russell, 2004; Clutton-Brock, 2006; Hrdy, 2009; Strassman and Kurapati, 2010). Explanations for cooperative behaviours focus on: direct and indirect benefits (Emlen, 1995); direct and indirect reciprocity (Trivers, 1971, 2006); or mutualism and coercion (Clutton-Brock, 2006). In humans, maternal mortality rises rapidly with age (Temmerman et al, 2004; Pavard et al, 2008), which van Schaik and Burkart (2010) suggest is due to the continued need for support after weaning in humans compared with other taxa (Williams, 1957), necessitating extended provisioning and care by the mother, or allomaternal care within a cooperative breeding system.

Turke's (1988) study of Micronesian islanders first recognised cooperative breeding behaviours in humans, demonstrating that cooperative daughters significantly increased completed maternal fertility. This expression of kin selection confers direct benefits to the mother in ensuring offspring survival, with cost to the sibling from provisioning. Since this study, numerous studies have provided evidence of cooperative breeding strategies amongst human foraging groups (Hrdy, 2005b, 2009; Mace and Sear, 2005; 2008), and the benefits to child survival from allomaternal care (see **Figure 4.4.**).

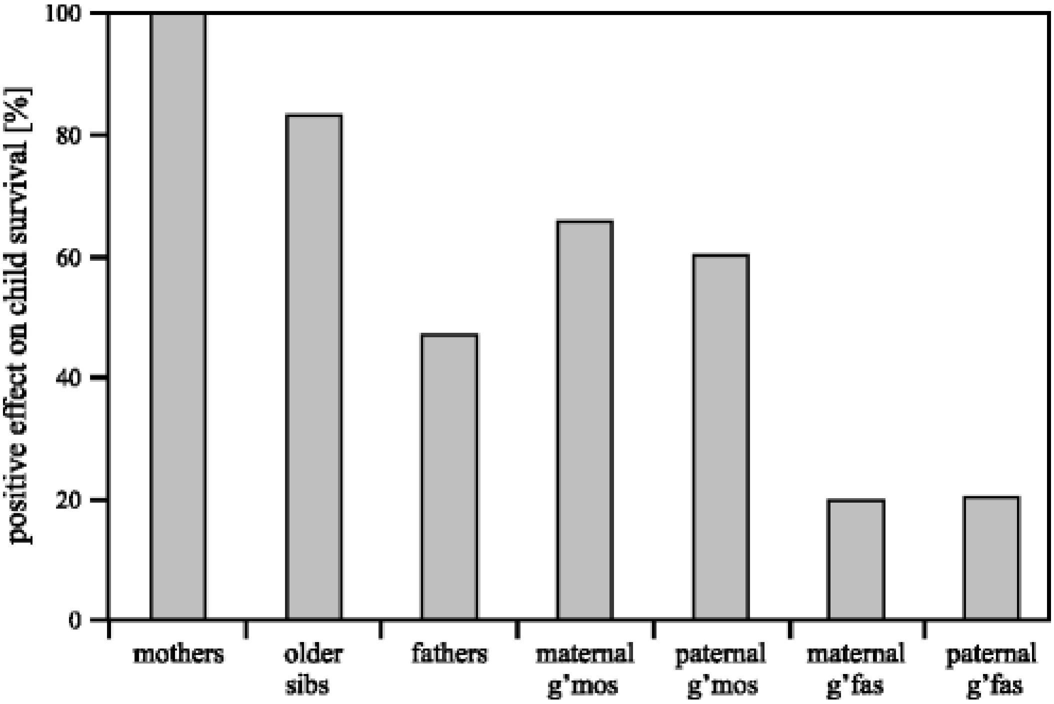


Figure 4.4. Graph summarising the positive effects of allomaternal care on child survival using data from Sear and Mace (2008: from van Schaik and Burkart, 2010:480).

Marlowe (2003) demonstrated that among the Hadza, men on average provide around two-thirds of the calories, both to the nuclear family and non-kin. Research by Hawkes et al (1989, 1998, 2009; also see Hawkes, 2003) has demonstrated that grandmothers also invest a significant amount into allocare in human societies. Work by Lahdenpera et al (2004) has also quantified the degree to which grandmother allocare benefit human societies, significantly improving infant survival rates and maternal reproductive rates among both settled and foraging societies. Lastly, older siblings have also been shown to significantly invest in cooperative breeding strategies, both provisioning and babysitting (Hawkes et al, 1995; Kramer, 2005). Kirkwood and Austad (2000) argued that cooperative breeding may have affected human longevity in reducing ‘unavoidable’ mortality through care of the sick and injured to a greater degree than among independent breeders, such as other great apes. In turn, this promoted the selection of the underlying physiology enabling greater longevity (Kirkwood and Austad, 2000). In ensuring both the survival of the neonate and the mother at parturition, birth assistance behaviours are therefore arguably a form of cooperative breeding. Whether this form of cooperation confers direct or indirect benefits, or is mediated via reciprocity, mutualism or coercion is unclear.

In order to understand how this behaviour emerges and is reinforced, the most important factor is to know who is helping, to understand why they help or cooperate in birthing infants. Hrdy (1999) first proposed that cooperative breeding strategies may explain the unique features of human prosocial cognition, as the product of derived cooperative breeding strategies in hominin evolution. Van Schaik and Burkart (2010) observe that among cooperatively breeding primates and canids, there is a prosocial, motivational predisposition in providing assistance to others spontaneously over a wide range of contexts. This cooperative breeding hypothesis has been further developed by Hrdy (2009), and van Shaik and Burkart (2010) further hypothesise that the evolution of uniquely human cognition, behaviour and life history are consequences of the adoption of cooperative breeding strategies in early *Homo*. Their hypothesis predicts that among early *Homo*, the input of increased allocare from cooperative breeders dramatically reduced maternal input, and crucially lifting constraints on encephalisation (van Shaik and Burkart, 2010). Van Schaik and Burkart (2010) identified three main consequences and side effects of cooperative breeding strategies on human life history, behaviour and cognition: (1) direct expression or consequences such as midlife menopause; (2) the evolutionary consequences in the social or cognitive domain (i.e. social systems or neural networks); (3) side effect of an increase in brain size. This builds on previous work by Hrdy (2009), which suggested that facultative paternal care and midlife menopause were a direct consequence of cooperative breeding strategies. Although cooperative breeding occurs amongst nonhuman primates, it is not a strategy recognised to be shared by other ape taxa (Silk, 2007; Kramer, 2010), and therefore suggests our cooperative breeding behaviour is an example of convergent evolution in ourselves and other nonhuman primates. With this in mind, the question remains as to what factors have driven the emergence of such behaviours in ourselves and other primates. To answer this, the next section will explore the associations between cooperative breeding and cognitive evolution, and their implications for the emergence of birth assistance behaviours in hominin evolution.

The role ‘cooperative breeding hypothesis’ in understanding human prosociality

Amongst most mammals species, the infant’s primary and sole caregiver is its mother (Burkart and van Shaik, 2010), but in some, care is shared amongst kin or other group members (Macdonald, 2001). Commonly in cooperatively breeding reproductive systems, non-parent individuals assist in provisioning offspring (Wilson, 1975; Ligon and Burt, 2004). Snowdon (2001) suggested that, amongst primates, cooperative breeding strategies are linked to higher level socio-cognitive strategies and communicative processes, which has subsequently been suggested to be a factor in the emergence of human cognition (see Hrdy, 1999, 2005a, 2005b, 2009; Burkart et al, 2009; van Shaik and Burkart, 2010; Burkart and van Shaik, 2010).

In cooperatively breeding callitrichids, which live in family units composed of a cooperatively breeding pair and their dependant offspring (Hrdy, 2009), helpers are usually the pair's offspring which, when mature, tend to be reproductively inactive (Digby et al, 2007). Moreover, the mother is not usually the primary caregiver, and in fact it is the father and older siblings, in particular older brothers (Garber et al, 1984; König, 1995; Kostan and Snowdon, 2002) who carry the infants and provision them with food (Ferrari, 1987; Feistner and Price, 1990, 1991, 2000; Brown et al, 2004). These groups are also characterised by high social tolerance levels, strong social bonds and minimal aggressive behaviour (Sutcliffe and Poole, 1984; Digby, 1994; Schaffner and Caine, 2000; Aureli and Schaffner, 2006). Burkart et al (2007) have also shown that the intensity of prosociality in callitrichids most closely resembles that of humans. Therefore, the intensity of prosociality may be a factor in the emergence of cooperative breeding strategies in humans.

The cooperative breeding model of human cognitive evolution proposed by Hrdy (1999, 2005a, b, 2009) predicts that differences between human and great ape cognition are a product of the extensive allomaternal care seen in humans. Several studies have suggested that cooperative breeding is linked with enhanced cognition, particularly those testing social cognition in adult callitrichids (Snowdon, 2001; Rapaport, 2006) and human juveniles (Chisholm, 2003; Hrdy, 2005a, 2009). The cooperative breeding model of human cognitive evolution proposed by Burkart et al (2009; Burkart and van Schaik, 2010), proposes that these cognitive changes were scaffolded onto an ape-level cognitive system capable of cooperation and understanding other's mental states. In conjunction with prosocial motivation, this could lead to cooperative behaviours and the sharing of mental states, allowing for the emergence of shared intentionality (Burkart et al, 2009). The idea of shared intentionality as the root of human level cognition emergence (Tomasello and and Rakoczy, 2003; Tomasello et al, 2005; Tomasello and

Carpenter, 2007) is argued by Burkart and van Shaik (2010) to be the cognitive and 'motivational' driving force behind extensive cooperative breeding in hominin evolution.

Alongside cognitive preconditions seen in great apes (Call, 2007; Deaner et al, 2006) and shared by humans through common descent, the 'motivational' factor is argued to be an example of convergent evolution (also seen in callitrichids), driven by selection for extensive allomaternal care (Burkart et al, 2009; Burkart and van Schaik, 2010). To demonstrate this, Burkart and van Shaik (2010) hypothesised that extensive allomaternal care displayed by cooperative breeders requires increased these motivational and cognitive faculties, and hence cooperative breeders would perform greater in cognitive tasks not directly linked to cooperative breeding. By comparing data on callitrichid socio-cognitive performance with that of their sister taxa, Burkart and van Shaik (2010) found that callitrichids systematically and significantly outperformed their sister taxa in socio-cognitive but not non-social tasks. Boddy et al's (2012) study of the association between brain mass, body mass and encephalisation quotient (EQ) in mammals, showed that both anthropoid primates and odontocete cetaceans have relatively much higher variance in EQ. This is argued to demonstrate convergent evolution of relaxation in correlation between brain and body mass, and that other factors such as neutral drift and selective factors have shaped anthropoid primate and odotcete brain-body allometry (Boddy et al, 2012). This uncoupling of predicted, strict brain-body allometry would fit with a model of a cooperative breeding system's influence on estimated increased hominin encephalisation and associated cognitive performance (Sherwood et al, 2008).

Cooperative breeding and prosocial birthing in social mammals

Alongside primates, many other social mammals also cooperatively breed (Macdonald and Sillero-Zubrini, 2004). In African wild dogs (*Lycanon pictus*), cooperative alloparental care includes babysitting and provisioning (Malcolm and Marten, 1982; Creel and Creel, 2002), and groups often adopt pups both related and unrelated (Estes and Goddard, 1967; McNutt, 1996). This non-kin allocare suggests regulation by intrinsic motivational factors (Burkart and van Shaik, 2010). Kunz et al (1994) observed a helper-assisted birth in the Rodrigues fruit bat, another highly social mammal. Here, a female was observed to attend another birthing female, grasping below the parturient mother, guiding her to a feet-down birthing posture, grooming the neonate, and physically manoeuvring the neonate into a suckling position on the mother (Kunz et al, 1994). Kunz et al (1994) argued that this example of non-kin assistance supports the hypothesis that among chiroptera, roost associations may be as important as relatedness in explaining the prevalence of altruistic acts. Given the evidence discussed in Chapter 2 for high CPD in bats, it's possible that the presence of prosocial birthing behaviours in social bats indicates a potential correlation with CPD in social mammals.

However, cetaceans have not been documented to show significant levels of CPD or restrictive obstetric pelvic morphology. Among highly social cetaceans, group members have been observed to display significant prosocial behaviour in aiding labouring mothers in guiding new-born infants to the surface to breathe (Stacey and Baird, 1998). Since cetacean births occur in water, infants must be capable of reaching the surface for their first breath, sometimes requiring maternal assistance (in the beluga whale, *Delphinapterus leucas*, Beland et al, 1990; in right whales, *Eubalaena glacialis*, Zani et al, 2008; in humpback whales, *Megaptera novaeangliae*, Ferreira et al, 2011; in common bottlenose dolphins, *Tursiops truncates*, Perrtree et al, 2015). It is worth noting that alongside demands in aquatic birthing mammals to reach the surface to take their first breath, highly encephalised cetaceans (see Jerison, 1973; Marino. 1998) also face demands on maternal morphology and physiology from increasing neonatal EQ. Cetaceans, however, only have a vestigial pelvis (Rommel, 1990), which means neonatal cranial dimensions (and by extension encephalisation demands) are not restricted by maternal pelvic dimensions as in humans (Rosenberg and Trevathan, 1992; Rosenberg, 2002). Therefore, levels of cetacean neonatal encephalisation are likely constrained by other factors such as demands on antenatal altriciality (i.e. to swim to the surface), which are arguably stricter than that seen in humans. Van Schaik and Burkart (2010) further note that cooperative breeding systems rely on social learning rather than individual exploration. As a cooperative breeding strategy, prosocial birth assistance behaviours are therefore reliant on social learning and require opportunities for such social learning (i.e. a social birth context). Therefore, one might predict that species which display significant evidence of social transmission and learning, would likely also display more prosocial birthing behaviours such as birth assistance, or significant interest and close proximity (non-antagonistic) during the birth event. Species which are categorised as typically cooperative breeders, would also be likely to display prosocial birthing behaviours.

It would be of significant scientific merit to further investigate whether external factors such as reduced levels of infanticide correlate with increased social inclusion during birth across the primate genera (and perhaps other mammals). However, this would require a larger scale study of behaviours of wild primates rather than captive primates. Given the difficulty of direct observation of births in the wild, coupled with the need for such a study to also observe birthing events alongside predation, such a study would be extremely difficult, and beyond the scope of this thesis. Further extensive study of patterns of social behaviour during birth in multiple social mammals, under the same objective methodology for assessment of the degree of prosociality, would provide an avenue for potential phylogenetic investigation of the evolutionary origin of birth assistance behaviours. If however no phylogenetic signal were present between a quantified measurement of prosociality, and genetic distance, it would suggest that the expression of prosocial behaviours evolves convergently across multiple taxa, in the presence of similar external stimuli.

4.4. The selective benefits of Doulas in humans

One of the primary areas of interest for this thesis is the role of supporters in childbirth, and from a palaeoanthropological, evolutionary perspective the role played by prosocial birthing behaviours in human reproductive fitness. Often termed doulas, non-clinical supporters to the birthing mother are increasingly shown to provide more than simply moral support. In actuality they convey a number of quantifiable psychological and physiological benefits. Whilst continuous social support throughout labour may vary across highly medicalised societies (Klaus et al, 1986), this is commonplace among other cultures. The earliest comprehensive study of social support benefits in humans by Klaus et al (1986), focusing on a sample of 456 Guatemalan women during labour, found that those who gave birth with a supportive female companion had significantly fewer perinatal complications. This included caesarean sections (7% compared with 17% for those without support) and oxytocin augmentation (2% compared with 13%), as well as a significant reduction in the number of neonates admitted to intensive care units (Klaus et al, 1986:585). Further to this, women with a companion also were reported to have significantly shorter durations of labour (7 hours compared with an average of 15.5 hours). This work laid the foundation for subsequent investigations into the quantifiable effects of prosocial birthing behaviours on birthing outcomes, and by extension the possibility of theoretical hypotheses on the evolutionary significance on birthing support.

Investigation into the specific benefits of doula support during birth in humans, does appear to demonstrate that this prosocial birthing behaviour does confer multiple benefits to the mother. Klaus and Kennell (1997) report on their randomised trial where the presence of doulas or professional midwives were compared in relation to outcomes on labour duration, pain relief medication use, surgical intervention, and postnatal depression, breastfeeding, and wellbeing. Their results showed that the support of the doulas rather than profession midwives, resulted in significant reductions in labour duration, complications, caesarean interventions, pain medication use, postnatal depression, and higher regard for their infants and confidence in their ability to care for them. Interestingly, the authors noted that the presence of infant's fathers did not result in the same outcomes, where fathers were in fact observed to stand further away from the birthing mother and communicated and touched mothers less than doulas (Klaus and Kennell, 1997). In addition, paternal behaviour was observed to improve when a doula was present alongside the father. The potential benefits of doula support during birth were further explored by Langer et al (1998), who attempted to investigate the specific effectiveness of a female relative in providing birthing support amongst a sample of women admitted to hospital in Botswana. Their results supported those reported in earlier work by Klaus et al (1986), with the additional observation that women from lower-socioeconomic backgrounds cared for in overcrowded hospital environments, with limited privacy and restrictions on visitors and companions through labour, had far worse birthing outcomes.

The choice by the mother to include a doula within the birth event, is of course an interesting focus for investigation, as to individual level selection for prosocial birth assistance behaviours. A study of supported birth by Gorden et al (1999) found that interestingly when mothers were given the option of an additional supporter of their choosing alongside the doula, only those births with a doula correlated with a reduction in epidural use to minimise pain experienced. An extensive review by Scott et al (1999b) of the significant positive effects on birthing outcomes by supportive doulas, further supports the adaptive significance of prosocial birthing behaviours in humans. Scott et al (1999b) reviewed evidence across 12 randomised clinical trials found that emotional and physical support significantly shorted the duration of labour and decreased the need for surgical interventions (including caesareans), as well as reducing the requested use of pain-relief medications. Post-partum, mothers supported by a doula reported much more positive experiences of birth compared with those unsupported or supported by the infant fathers, and also experienced lowered anxiety, rates of post-natal depression, and increased uptake of breastfeeding initiation and positive feelings towards their new-born (Scott et al, 1999b). The authors concluded that every woman (or for contemporary application, those who identify as cis-female) should have access to continuous emotional and physical support through labour, as an essential component of childbirth in humans. The first national survey of childbirth experience reported that mother's rank fathers of the child below doulas, midwives, and other family members in terms of their ability to provide adequate support through birth (Declercq et al, 2002). The exact reasoning for this observation is unknown, but what would be interesting to explore is the extent to which the decision to have a non-doula member present is culturally mediated – or whether another influencing factor at play.

Collectively, the evidence presented of the benefit to maternal and neonatal outcomes, would suggest prosocial birthing behaviours would have conferred significant evolutionary benefits for minimal cost in hominin evolution. However, the extent of potential costs to social group members in providing support is rarely considered. In particular, support for extended periods may have detrimental costs to group members through lost feeding times, increased predation risk, or other unexplored factors. Yet the benefits to the individual mother of this incurred cost, may override these costs to the group. Previous work by Scott et al (1999a) found that it was specifically continuous support not intermittent support that correlates with increased positive outcomes from prosocial birthing. This in turn suggests the proximate mechanisms by which support affects maternal wellbeing is something that requires a complex and extensive series of inputs in order to produce positive outcomes.

Social support here is not something influence by mere presence or absence, but rather is based on perceived socio-dynamic connection with the supporter. Work by Rosen (2004) found that of the trials investigated in previously published material, support by untrained lay women (rather than trained lay women, student midwives, midwives, and nurses) who consistently demonstrated a significant beneficial impact on birthing outcomes. The two trials reviewed involved untrained laywomen (Sosa et al, 1980; and Klaus et al, 1986) who simply provided emotional support (in the form of conversation, explanation and encouragement) and physical support (in the form back back-rubbing and hand-holding). Chalmers and Wolman (1993) note that among studies of women during the mid to late 20th century, women were often forced to give birth in crowded and unfamiliar environments, where hospital policy prohibited family members, friends and non-clinical staff from taking part, significantly raising maternal anxiety. Therefore, the reported effects of supportive caregivers may have been exaggerated from this context (Rosen, 2004). However, after the findings by Klaus et al (1986), work by Kennell et al (1991) attempted to replicate the findings in a sample of women entering US hospitals. Their findings further supported the conclusions of earlier work, reporting that among younger women from lower socioeconomic backgrounds birthing in overcrowded units with limited privacy and opportunity for support experienced much greater benefit when provided with a doula. Their study (as noted by Richards, 1992) relied on questionable practice, as women were confined to a hospital bed immediately after admission, on relatively crowded wards, with no visitors allowed and were instead surrounded by unfamiliar staff (and in many cases no staff were available who spoke the patient’s language). Rosen (2004) proposes multiple possible explanations for the results reported, the first of which is that lay women are not seen as part of a hospital hierarchy, and so are perceived to be an ‘ally without interest’. Moreover, the lay women were from the same community as the mothers, and were likely more capable of communicating, engaging and relating to the cultural norms and experiences of the birthing women (Rosen, 2004). Lastly, the lay women were instructed to focus on comfort, reassurance and praise, presenting an attentive one-to-one supporter who sees the mother as an individual rather than simply ‘another patient’.

It must be noted however the inherent challenges to studying birth in humans. Shockingly in this trial, women were essentially subjected to chemical restraint if clinical staff were unable to deal with their pain (Rosa, 2004). It is therefore no surprise that, as critiqued by Richards (1992:41), a doula would be highly favoured as a buffer for women under these conditions against “the worst excesses of institutionalised obstetrics”. Their methodology highlights perhaps some of the limitations to conducting substantial and often invasive trials which attempt to investigate birthing outcomes in humans. The risk to maternal and neonatal health, both physical and mental, must take precedence over the potential benefits of these studies. Additionally, the repeated testability of such studies across human populations is an inherent difficulty in obtaining reliable and broad-ranging conclusions on factors influencing maternal birthing outcomes. In terms of determining and controlling the various factors and context influencing the application of obstetric and gynaecological care, variations in medical policy and recommendations will have significant bearing on population samples. Studies among Finnish (Hemminki et al, 1990), South African (Hofmeyr et al, 1991), and Belgian and Greek (Breart et al, 1992), women did not find a significant correlation between reduction in caesarean interventions and doula support. This is something which Scott et al (1999b) suggest is the result of other non-controlled variables, and the variance in the stage at which support was introduced to the mother in the studies.

Further investigation carefully controlled and across a demographically and socio-economically diverse sample will provide greater insight into factors driving positive outcomes during and after birth, but of course these factors are likely non-mutually exclusive. Many of the studies into the effect of social support on birthing outcomes in the late 20th century highlight the issue of overcrowding of maternity wards and a lack of capacity for optimal birthing support. Scott et al (1999b) note that when cultural focus across the US shifted to birthing in hospitals during the early 20th century, childbirth became an emotionally isolating event for women (see Wertz and Wertz, 1977) where the focus now relied on drugs for pain relief. By identifying the positive benefits of social support on reductions in pain medication use and other outcomes, it is hoped that the role played by social support as a viable and crucial physiological factor can be used to support conclusions on the adaptive benefit of social support in human evolution. What can be concluded from previous studies, is that a strong connection with a social supporter is necessary to effect birthing outcomes for the better, and if such sociality is indeed present in other species, necessitates a capacity for dynamic and intimate social structures – something certainly not exclusive to humans.

Together, the medical literature discussed suggests that family members and non-kin are all capable of providing highly beneficial emotional and physical support through childbirth in humans. Therefore, it is reasonable to suggest that the presence of supportive individuals in hominin birthing events, where social groups contained multiple women and overlapping generations, alongside strong affiliative social networks, would have conferred strong selective benefits to both the mother and her offspring. Reduction in the perceptions of pain would have made the event less traumatic (particularly in species where increasing levels of cephalopelvic disproportion would increase mechanical difficulties) and improved the perception of the event for the mother, and reducing the likelihood of postnatal depression and feelings on animosity or rejection of the infant, reflected in increased allocare and bonding. It is likely the shared experience between parturient hominin mother and the supporter would also strength existing affiliative bonds, and by extension maintain close-knit social groups. Among hominins and other nonhuman species, it is further reasonable to hypothesise that similar positive outcomes would be observed in both female-kin based social groups and female non-kin groups. Further investigations into these factors will provide further insight, but due to the limitations of this thesis, will not form the focus of investigation. Furthermore, the validity of the research would require a deep consideration of the variation and factors influencing birthing outcomes across different international, cultural contexts.

Issues in contemporary evidence-based medical practice

Of course any conclusions or hypotheses on hominin evolution based on medical evidence relies on an assumption of the quality of the evidence. What is perhaps particularly telling about the state of medicalised birth in humans is the degree to which common practice uses peer-reviewed evidence. A report published by Wright et al (2011), which surveyed the quality of evidence used to support recommendations by the American College of Obstetricians and Gynaecologists, found that less than a third (30%, Wright et al, 2011:505) were based on 'level A evidence' (good and consistent). The remaining 70% used limited, inconsistent, consensus and opinion-based evidence to support recommendations. The authors state that this reliance on lower quality grade B and C evidence 'expert opinion' as open to implicit and subconscious bias, which is often inflexible to context of the individual patient's needs. (Wright et al, 2011). Furthermore, the authors note that adherence to these recommendations is often in itself used as a 'benchmark of quality', without critically engaging with the source material (if any). The demographic make-up of the population affected by these recommendations is of course huge in terms of the morphological variation and context of the individual patient across the US.

This observed lack of flexibility in recommendations which are themselves based on relatively low-quality evidence, is arguably large cause for concern. Furthermore, perhaps a result of the aforementioned variation in morphological and patient circumstances across the world, the Royal College of Obstetricians and Gynaecologists (RCOG) in the UK only reached the same consensus on 28% of those supported by their US counterparts, with a further 56% of recommendations incomparable (Chauhan et al, 2010:763). However, a more recent study by Prusova et al (2014:1) which reviewed the evidence standards of recommendations and guidelines by the RCOG, and found that only 9-12% of the guidelines and individual recommendations were based on the highest quality, grade A evidence. Again the authors note that strict guidelines may not provide appropriate responses in the context of individual patient’s needs, and evidence suggest that in some cases high quality evidence-based recommendations may be detrimental (for example, overly early interventions as a result of overly strict guidelines for slow labour progressions reported by Zhang et al (2002), which progression varies markedly depending on the parity status of the mother). In addition, Prusova et al (2014) note that grade A evidence is not of course infallible, as shown by the follow-up trial to recommendations implemented by the Term Breen Trial (Hannah, 2000), which recommended that caesareans be performed in all cases of breech delivery in the UK, US and Canada – for which subsequent inquiry found significant inconsistencies and cause for concern in the data collection and analysis (Kotaska, 2011). Greenhalgh et al (2014) further argue that whilst wide variation in implementing evidence-based practice is a significant hurdle for medical best-practice, in some instances evidence based-practice is severely limited in terms of actioning recommendations. An example given by Greenhalgh et al (2014:2) comes from a 2005 audit of a 24 acute hospital intake, where 18 patients had 44 diagnoses with an accompanying 3679 pages of national guidelines (112 hours of reading) relevant to immediate (not even secondary) care. This example gives perspective on the limitations of evidence-based care in giving specific solutions for individual patients with countless possible combinations of other conditions which may supersede prior obstetric or gynaecological guidelines. This is perhaps best summarised by Greenhalgh et al (2014), who conclude that is by studying other forms of knowing (‘mindlines’ or hospital culture, clinicians, and illness communities) that we can determine how best to produce expert clinicians and expert patients, in order to avoid overdiagnoses, overtreatment and overscreening. In the end, it is primarily down to the mother (with the support of the clinician) who determines the appropriate care, and the recognition of the importance of shared ‘expert’ understanding of birth which is needed to minimise risks to maternal and infant health.

This significant recognition of the relatively low quality of evidence-based practice in gynaecological and obstetric medicines (in the UK and US), suggests further work is needed to translate available scientific data and research into actionable targets and real-world results for women and neonatal health around the world. Whilst the demographic sample of the research discussed is somewhat limited, the lack of impacting peer-reviewed research of ‘medicalised’ practice implies that research and high-quality evidence intended to improve the lives of women at the supposed ‘frontiers’ of medical care, is somewhat lacking and still relies on what can be described as cultural memes, open to bias and interpretation (for better or worse). However, as noted by Hodnett (1997), despite the variation in specific conditions, patient risks, qualifications of supporters and practices across the globe, there is considerable consistency and similarities in results produced by having trained (non-clinical) supportive assistance during birth. Despite the high levels of variation in these practices, the common factor of the presence of a supporter does reduce risk factors for maternal mortality, maternal physical and mental health, and other obstetric and gynaecological outcomes. From an evolutionary standpoint, this commonality shared across the human species would therefore suggest a deep-rooted adaptive function for prosocial birthing, something shared by a common ancestral population to all *Homo sapiens*.

Contemporary relevance of understanding the benefits of prosocial birthing behaviour

For the past two years since the outbreak of the Covid-19 pandemic in early 2020, humans across the globe have been encouraged and actively prevented from expressing our typical social norms. More specifically to this thesis, maternal care has across the globe seen the introduction of national and international guidelines preventing family and friends from attending birth, and in many cases resulting in women giving birth in social isolation, with only clinical staff and relative strangers present. The importance of the findings and topics of discussion in this thesis run in stark contrast to well-meaning and arguably appropriate responses to the coronavirus pandemic, in order to minimise the spread of a potentially deadly virus.

Where evidence from primate and human research indicates an evolutionary, deep-rooted need for a prosocial birthing context for the mother (and in some respects the infant), which in many cases is not permitted in hospitalised treatments and births where at best only a single known family member or friend may stay with the mother (The Guardian, 2021). Furthermore, social-distancing norms have been reported to provoke anxiety in mothers from fear of transmission and in some anxiety around vaccine effects on in-utero infants (The Guardian, 2022). Evidence for the detrimental effect of intermittent support as a result of increasing patient numbers and stretched clinical services (Scott et al, 1999b) demonstrates the need to ensure maternal units are fully staffed and capable of providing continuous support to birthing patients. This is alongside ensuring non-hospital maternal services are able to function effectively to provide in-person, socially supporting care whilst also minimising risks of COVID-19 transmission. A perhaps further topic of future research would be to investigate the response of humans to widespread disease in terms of birthing practice, and how these actions may have affected cultural norms and taboos surrounding birth. Whilst archaeological evidence may be scarce, ancient artefacts, literature and images may provide insight into how humans responded to such widespread risks to maternal and neonatal health.

As discussed in this chapter, the role of males in birth shows evidence of significant lack of correlation with positive birthing outcomes (Scott et al, 1999a; 1999b). The cause of this is not alluded to, however what it clear is that in observations across western medicalised societies, the male behaviour observed does not confer the same benefits of the doula. However, it is the distinct lack of effective support given, rather than any lack of reception of care, that is clear. Whether this is a product of innate male lack of supportive behaviour, or far more likely a lack of cultural development of behaviours which determines male responses and support. Interestingly, Klaus and Kennell’s (1997) observations of increased supportive behaviour in the presence of a doula suggest a present capacity for care, but which is facilitated in its expression by the presence of other external support. In terms of the effect of the pandemic on social birthing contexts, the choice presented to many birthing mothers to either have the father or doula present, is a choice which (whilst self-determined) may incur a detrimental effect on maternal health and outcomes. Whilst adhering to social distancing and clinical safety protocols, provisions should be made a highest priority to ensure doula support is provided alongside a choice of birth-partner in all cases, which builds upon similar conclusions by multiple researchers (Hodnett; 1994; Scott et al, 1999b; Sauls, 2004; Hodnett et al, 2013). This aspect of maintaining patient choice in maternal care has been observed to have been hard-hit by the pandemic, for example with 59% of NHS services reporting the cessation of home-birth support (Relph et al, 2020). It is strongly recommended, as we enter the third year of the pandemic, that birthing support services across the globe prioritise efforts to offer patient-led choices for birthing environments, to mitigate the effects of sub-optimal environments during the pandemic.

Furthermore, as the NHS faces spirally costs across all departments, the provision of adequate support and doula support may in fact reduce costs associated with birth. The reductions in medicalised treatment through pain-relief medication and surgical intervention, would dramatically reduce costs and offset costs incurred by provisioning doula support. As concluded by Bolbol-Haghighi et al (2016), supportive behaviours in practice remain the simplest, cheapest and most accessible method to assist women in labour and relieve pain, in order to produce positive birthing outcomes. A study by the Chicago Health Connection Doula Project (CHCDP) (Pitts et al, 1999) in fact managed to quantify and estimate of such cost reduction, with an estimated saving of $66,000 - $67,920 as a result of reduced epidural use among 192 patients. By today’s estimates accounting for inflation (using current exchange rates of 0.76 dollars to the pound and 2.8% inflation at the time of writing), this could be as much as £88,419 - £90,991 by 2020 standards across only a relative handful of patients. Although given rising wages and costs of medications, this figure could be even higher for the NHS, and indeed for all international healthcare providers. Another solution suggested by Paterno et al (2012) is for midwifery, nursing and other clinical students to fill a supporting role during training. This would serve to provide valuable clinical and holistic experience of birth for students, whilst also filling an important and beneficial role for birthing patients, at a very low financial cost to medical services.

Moreover, the accessibility to doula supportive care is crucial to mothers from young, ethnic minority and lower socio-economic backgrounds where access to relatively (arguably) higher levels of maternal care is restricted. Again another report by the CHCDP found that among teenage mothers in the US and provided doula support by the CHCDP, the caesarean intervention rate was significantly below the national average for women of the same age group, as well as lowered epidural use and a higher-than-average continuation of exclusive breastfeeding at six weeks post-partum (Glink, 1998; Pitts et al, 1999). Further research by Sauls (2004) found that across a sample of 16 US teenage mothers, the adolescent’s needs from birthing support focused on pain relief and emotional support, alongside non-judgemental nursing care. It is therefore essential for those already hardest hit by the pandemic and already systemic issues of equality in healthcare (NMPA Project Team, 2021) that maternal care is bolstered, in order to minimise further risks for maternal and neonatal health. It is hoped that the evidence for the deep-rooted link between the social birthing environment and maternal health outcomes in humans and primates, will have beneficial ramifications for evidence based best-practice in healthcare, alongside care for our closest living relatives and indeed all captive animals.

4.5. Towards a quantitative measure of birthing sociality

Little is definitively understood about the origins of obligate midwifery in hominin evolution, but observations of extant nonhuman primates can begin to provide a picture of the necessary behavioural components and conditions. The adaptive significance of parturition assistance behaviour can be theorised with potential benefits from reduced infant and maternal mortality through kin and non-kin assistance and protection, as well as cooperative social benefits from sharing in the event itself. Further emphasis and investigation into the associations between observed levels of sociality during birth, and socioecological factors, can provide a possible explanation for the presence or absence of prosocial traits among primates and, by extension, possible evolutionary origins of birth assistance behaviour in humans.

As yet, no quantitative methodology for assessment of the degree of prosociality of behaviours by individuals during birth event have been devised. This lack of methodology thereby significantly hinders comparative and consistent assessment of behaviour of both the mother and social group during birth in humans and nonhuman primates. In order to determine the proximate and ultimate causes of such variable behavioural expression, devising such a method is the first step in modelling the evolutionary trajectory from isolated behaviour of the birthing female, to the complex and dynamic, highly social birth event we see in humans across the globe today. However, this variation in social behavioural expression is the primary hurdle to developing a consistent framework and methodology for quantifying just how prosocial birth is between different species, or indeed between different groups of the same species. What must be identifiable, is a tangible social factor consistent in each possible birth event. To address this issue, this thesis will provide the first attempt at quantifying prosociality in humans and nonhuman primates, using a consistent scoring system to facilitate comparative analysis of variation in social birthing behaviour. This methodology, outlined in the following chapter, will build upon previous qualitative discussion based upon observations of extant primates, and gain insight into potential correlation with other socioecological, morphological or life history factors in primate evolution.

4.6. Conclusion

A significant body of evidence presented in this chapter, supports the conclusion that primates do not universally seek isolation in birth, and alternatively demonstrate a propensity for social inclusion. This can be either through potential predation deterrence, provision of learning opportunity for immature females, or through both psychological or physical assistance and support. The fact that nonhuman primates display elements of commonly considered ‘human’ birthing behaviours, suggests that birth assistance may in fact have emerged much deeper in our primate ancestry. This contravenes previous consensus among archaeologists and anthropologists, that we are unique in having highly prosocial births. Indeed, birth assistance certainly would have played a more common role in the hominin ‘birth event’ than previously accounted for, buffering against increased risk and demands of risky and complex parturition.

Whilst osteoarchaeological analysis can provide some context the understanding the relative difficulty of birth in primates and extinct hominins, this relies on a relatively small sample of reconstructed pelvises, neonatal skeletons and assumptions of relevant soft tissue morphology. This reliance limits the reliability of conclusions drawn on obstetrical difficulty, and the behavioural response of the mother to delivery. Moreover, given the previously discussed plasticity of obstetric morphology during development in humans, it is likely that the hominin fossil record also is limited by assumptions on the level of heritability in the maternal pelvis. If it is assumed that obstetrical pelvic characteristics are passed through generations, then logically they would produce a phylogenetic signal. If birth assistance behaviours do evolve in response to obstetrical difficulties as a product of CPD for example, then one would expect a correlation to exist between birthing sociality and relevant morphological factors, increasing in correlation between closely related species. Phylogenetic modelling may be able to test theses hypotheses but would require an initial quantification of relative birthing sociality for primate taxa.

Studies of extant primate and mammalian behavioural responses to birth however can arguably provide a much more reliable estimation of what birth, both for the mother and the group level response, may have looked like in our hominin ancestors. Through direct observation of the interaction between birthing mothers and group members, patterns of behaviour can be identified. In-turn, hypotheses can then be drawn on the potential drivers of, for example, midwifery behaviour in humans, and evidently highly prosocial behaviours in nonhuman primates. The second prediction of the ‘social birthing hypothesis’ proposed in this thesis, proposes that more complex social primates are more likely to display prosocial birthing behaviours. Therefore, the degree of sociality of a species is a more likely and accurate predictor of how prosocial birth may be for a species. Evidence of this relationship could in turn be extrapolated to understandings of hominin sociality – e.g. reconstruction of social group size in extant hominins could identify likely emergence of more prosocial behaviours through their evolutionary trajectory.

It would also be of significant interest to assess whether prosocial behaviour is facilitated by group inquisitiveness (by the prosocial actor), or encouraged by the mother (the recipient of prosocial support) as a strategy to counter infanticide both between and within social groups, or as a response to increased predation risk. However, the exact methodology to quantify predation risk for example would require a larger scale estimation and standardisation of risk across multiple primate species in the wild. Instead, the focus of the current thesis will centre on social behaviours and responses to birth in primates. The thesis will utilise qualitative descriptive information provided on social group responses to birth, in relation to known sociodemographic, morphological, and life history factors which may influence the expression of behaviours during the birth event. In particular, the application of a quantitative assessment of the degree of prosociality of birthing behaviour will be applied to observations of individual and group behaviours in nonhuman primates. This will provide an original and beneficial contribution to our understanding of primate behaviour, as well as understanding the evolutionary origins of our own birth.

Chapter 5: An investigation of potential factors influencing birthing prosociality in extant nonhuman primates.

5.1. Introduction

In order to understand and evaluate the current consensus on human and nonhuman behaviour, this chapter will utilise previously published data and sources on primate birthing behaviour, morphology, life history and socioecology. By examining the available data on observations of behaviour, alongside available data on factors influencing and potentially influenced by such parturition behaviour, potential signals of direct and indirect drivers of (human-like) prosocial birthing behaviour can be identified. The 'obstetric dilemma hypothesis' predicts that an increase in CPD of the maternal pelvis and neonate (either as a result of increasing neonatal brain and body size relative to a reduced, or stable maternal birth canal dimensions), would in turn drive selection for morphology and/or behaviour to reduce any increase in maternal and/or neonatal mortality. This could simply be stated as an increase in CPD would result in behaviours which would reduce mortality e.g. prosocial birthing behaviours such as birth assistance. If a significant relationship were found to exist between obstetrically relevant morphology and the expression of prosocial birthing behaviours, this would support this prediction. Conversely, the second prediction of an alternative 'social birthing hypothesis' as stated in chapter 3, would be supported if a significant relationship was found between social factors and the expression of prosocial birthing behaviours. In sum, we would expect species which typically have large and closely affiliative social networks to express higher levels of birthing prosociality.

This chapter will investigate and explore the potential factors influencing the expression of prosocial birthing behaviour in extant nonhuman primates, focusing on observed and published data sources, alongside a small-scale study of primate neonatal morphology. The primary aim will be to test the ‘obstetric dilemma hypothesis’, where maternal and neonatal mortality as a result of CPD is argued to have driven the evolution of birthing assistance, exclusively in hominins. In order to find a wider ranging scope of influence, a number of sociodemographic, morphological and life history factors will be investigated in correlation with assessed levels of birthing prosociality. A novel methodology will be employed to assess the level of prosociality relative to highly prosocial human-like birthing. This comparison with modern human behaviour will serve to provide a primate-level context for the emergence of prosocial birthing behaviours in human and nonhuman primate evolution. The use of a quantitative scoring method, using qualitative observations, will facilitate a quantitative investigation of relationships between variables predicted to influence the expression of prosocial birthing behaviours. An initial correlation analysis will seek to identify which factors reliable correlate with prosociality, which will lead into an application of phylogenetic analysis methodology to model a potential evolutionary trajectory for the emergence of prosocial birth assistance behaviours.

The question of whether birthing behaviours (both on the part of the primate mother and group members) are inherited innate (or genetically mediated) responses to parturition and the vulnerable neonate, or whether they are culturally inherited learned behaviours is a difficult question to both test and answer. As of yet, there has been no attempt to reconstruct the evolution of prosocial birthing behaviours using phylogenetic analysis to predict ancestral behavioural states. Fundamentally, conclusions on the role of genetically mediated factors in the proximate expression of prosocial birthing behaviours are vital to understanding the ultimate drivers of birthing behaviour evolution. This doctoral research will be the first to utilise such reconstructions in understanding the reliability of morphological predictions on the origins of birth assistance, and in particular the accuracy of the ‘obstetric dilemma hypothesis’.

Centrally, the prediction that heritable morphological features are related to birthing prosociality.

This chapter will explore this question of ancestral origins among primates for prosocial birthing behaviour by utilising phylogenetic modelling, in order to test for a potential phylogenetic signal in BSS for the sample. In order to achieve this, this chapter will first utilise phylogenetically controlled methods for regression to in identify any correlation between birthing prosociality sociodemographic, morphological and life history variables. By utilising methods for Phylogenetic Independent Contrasts (PICs), Ordinary Least Squares (OLS), Phylogenetic Least Squares (PGLS), and phylogenetic Reduced Major Axis (RMA) a series of regression linear models of birthing behaviour evolution will aim to detect any phylogenetic signals of birthing behavioural evolution.

In order to first determine whether any phylogenetic signal is present amongst extant primate species (which would suggest an inherited, genetically mediated factor is influencing the expression of prosocial birthing behaviour), the use of phylogenetic statistical methods can attempt to answer this question (Pagel et al, 2004; Mace and Holden, 2005; Pagel and Meade, 2016). By evaluating which variables show the greatest likelihood of evolving in tandem with known phylogenetic distances between living primates, further insight can be provided to determine whether such behaviours are genetically conserved, derived, or learned. If the behaviours are inherited, then factors such as obstetric adequacy will likely drive the conservation of prosocial behaviours amongst extant species. However, if no phylogenetic signal exists, then this suggests that such behaviours are not driven by phylogenetic inertia, and instead could be the product of social learning, passed on between generations and peers among a population.

After performing PICS, OLS, PGLS and phylogenetic RMA regression on these variables, this chapter shall then attempt to statistically evaluate the likely evolutionary emergence of prosocial birthing behaviour amongst extant primates. This investigation will utilise Maximum Likelihood (ML) and Markov Chain Monte Carlo (MCMC) Bayesian Statistical modelling to identify any possible signal of phylogenetic signal within the BSS data sets, and whether species typical birthing sociality coevolves in primate taxa independent of phylogeny. By additionally theorising the observed level of prosociality as non-continuous, discrete traits, this chapter will attempt to further investigate the presence or absence of highly prosocial behaviours amongst extinct primate clades.

The aim of this chapter will be to provide a clearer understanding of factors driving the emergence of highly prosocial birthing behaviour and their adaptive significance, as well as in identifying the potential deep origins of the behaviour in primates. Furthermore, the evidence reported whether supporting a genetically inherited or non-heritable route for the transmission of social birthing behaviours, this will have significant implications for our understanding of hominin behaviour, the transmission of birthing knowledge in humans today, and the transmission of knowledge within the scope of nonhuman primate cultural repertoires.

5.2. Background

Factors influencing the expression of prosocial birthing behaviour

As defined by Williams (1996), direct reproductive fitness encompasses the total number of offspring who survive to adulthood for the consecutive generation of a population. In essence, birth is the very first step in ensuring this survival at what is potentially the most vulnerable point for both the mother – the primary caregiver – and the offspring. Birth is indeed perhaps the main period of time where risk is highest for both individuals. Therefore, it is in the best interest of the mother and indirectly to the benefit of the species, for birth to be optimised in terms of risk mitigation. As discussed in the previous chapters, this risk may be in the form of obstetrical mechanics and morphology, from infanticide by group members, or predation risk.

The ‘obstetric dilemma hypothesis’ and the anthropological consensus posits that the necessity of birth assistance and midwifery behaviour in humans confers a significant increase in direct reproductive fitness. However, previous research has yet to identify how the degree of birthing sociality ties in with this evolutionary boon, and to what extent the suite of assistance behaviours and prosocial birthing confer evolutionary benefits. In order to explore this question, it is first necessary to understand the possible factors which correlate with the degree of birthing sociality. Furthermore, in an attempt to theorise an evolutionary scenario for the emergence of birthing assistance behaviours, the ‘obstetric dilemma hypothesis’ infers that a relationship should exist between obstetric morphology and birthing behaviour. Specifically, that more highly prosocial birthing behaviour should be expressed by species experiencing increased mortality risk as a direct or indirect result of obstetric morphology. If a relationship does appear to exist from previously published data, this would support this prediction from the ‘obstetric dilemma hypothesis’.

However, based on the initial review of the primatological literature in Chapter 3, outlining the degree of prosociality among nonhuman primates, this thesis argues that the observations and capacity for highly prosocial birth assistance behaviours among nonhuman primates supports an alternative hypothesis. This ‘social birthing hypothesis’ proposes that a significant relationship instead exists between birthing behaviours and sociodemographic factors, such as social group size – hence a social birthing hypothesis. If such a relationship is identified from the previously published data and supported by statistical analysis, this would support an alternative hypothesis to the morphological basis and predications of the ‘obstetric dilemma hypothesis’.

Investigating the evolution of primate behaviour using phylogenetic analysis

The ‘obstetric dilemma hypothesis’ predicts that morphological demands of large-brained neonates were the primary drivers of increasingly high-risk birth amongst hominins and in response, prosocial birthing behaviours only emerged amongst increasingly socially complex hominins. Alternatively, the ‘social birth hypothesis’ proposed within this thesis proposes that the ancestral state amongst multiple primate species included a disposition for highly prosocial birthing behaviour. This ancestral capacity for prosociality, and likely common display of such behaviour, facilitated an increase in CPD as a result of favourably larger brained infants. Whilst no research has yet attempted to map the emergence of highly prosocial birthing behaviours using phylogenetic analysis, the evidence present in the previous chapter suggests that potentially heritable morphological traits do not significantly correlate with levels of birthing prosociality. This may be due to the fact that morphological traits may not reflect phylogeny, but rather be the product of ontogenetic development and plastic, somatic growth responses. However, in order to determine likely ancestral states from phylogenetic markers, statistical modelling must be employed to estimate the most likely behavioural traits observable in extinct species.

Nunn (2011:58) provides three primary methods for phylogenetic reconstruction and inferring ancestral states from discrete behavioural variables: parsimony, maximum likelihood, and Bayesian statistics. Nunn notes that the inference of characteristic traits (morphological or behavioural) often requires existing knowledge of how such traits co-vary amongst living species (Nunn, 2011:52). For palaeontological reconstruction, any predications are only possible for traits which leave a trace within the fossil or archaeological record, and where such evidence in unavailable, researchers must base their reconstruction on observation of variation amongst extant species. This involves mapping such variation onto established nodes of a phylogeny (i.e., pairing morphological and behavioural variation with genetically estimated evolutionary trees, in order to establish evolutionary trajectories of variation). The value of using estimated phylogenetic relationships in identifying trajectories of adaption in evolution is highly constructive in supporting models of how life has changed for primates throughout their (and our) evolutionary history. As stated by Nunn (2011:65), adaptations are derived traits which differs from an ancestral form, necessitating initial identification of derivative traits in order to access both phylogeny and a method for reconstructing ancestral states.

Maximum parsimony

Maximum parsimony refers to procedures for minimising the number of changes on a phylogenetic tree (i.e., the most likely evolutionary trajectory is the ones that requires the smallest number of trait changes across the tree). Parsimony does however assume that all branch lengths are equal (among extant species), and that evolutionary transitions are equally probable. Parsimony analyses may also produce ambiguous character states (a combination or two binary states), resulting in multiple equally parsimonious reconstructions; equivocal values are indicated with a node having multiple states. In order to mitigate this, Nunn (2011:59) suggests that including an outgroup known to possess an ancestral character can help resolve ambiguous reconstructions. Nunn (1999a) did this for a study of primate sexual swellings among Old Word Monkeys by including a New World Monkey outgroup, which lack the exaggerated character (the sexual swellings). The use of this outgroup further allows for wider factors to be accounted for in producing variation around regressed values through partial regression analysis. However, given the difficulty in consistently quantifying birthing sociality in primates, the application to an outgroup was not possible. Therefore, this recommendation to improve relative ambiguity would not have been practical, contributing to the case against using maximum parsimony to model the evolutionary history of social birthing behaviours.

Parsimony is also the most widely used approach aimed at reconstructing ancestral states (Nunn, 2011:58), used to study primate sociality and mating systems (Sillen-Tullberg and Moller, 1993; Mitani et al, 1996), reconstruct genetic and amino acid sequences (Krishnan et al, 2004), cultural traits and family organisation (Borgerhoff Mulder et al, 2001), sleeping patterns in primates (Kappeler, 1998), and analysis of homoplasy in primate and hominin evolution (Lockwood and Fleagle, 1999). In the context of human evolution, Gray and Jordan (2000) utilised maximum parsimony to map a geographic series onto a linguistic phylogeny in order to assess whether humans colonised Southeast Asia and the Pacific Islands within a single or multiple migration events. Their results supported the conclusion that their ‘express train’ hypothesis (Diamond, 1988), and the colonisation of the pacific by Austronesian-speaking peoples. Perhaps most interestingly to the emergence of female centred birthing behaviours, Di Fiore and Rendall (1994) used parsimony to track the emergence of social organisation characters in primate evolution in Old World Monkeys. Their results suggested that many of these traits hinged on female philopatry (where females remain in their natal groups) and found evidence that social organisation is characterised by female grouping within kin and the exhibition of coalitionary behaviour, displaying high levels of grooming, and providing for other female’s offspring. However, given the lack of prior evidence supporting a consensus that birthing behaviour or other social behaviours are directly inherited traits (Robinson, 2008; O’Connell and Hofmann, 2011), maximum parsimony would be highly unreliable in providing an insight into the origins of birth assistance behaviours. For this reason, Maximum Likelihood and Bayesian Statistical methods, aimed at determining the relative strength of phylogenetic signal in the data, are more appropriate methodologies. The detection of homoplastic traits is arguably more easily accomplished through these methods, rather than through maximum parsimony where homoplasy is absorbed within tree estimates (Sober, 1983; Ree and Donoghue, 1998; Omland, 1999; Wiens, 2001). Given the likelihood that birthing sociality has a significant homoplastic component, an initial study using maximum parsimony would be unreliable, determining the shared traits between non-sister taxa to be a false signal of close genetic ancestry (Cunningham et al, 1998; Maddison and Maddison, 2000). Hence this methodology would not be appropriate within the bounds of this thesis. However, alternate methodologies may provide an interesting insight into the likelihood of ancestral states in past primate and hominin populations.

Maximum likelihood

Maximum likelihood (ML) methods use a more explicit evolutionary model to reconstruct ancestral states in a way that makes the observed character states in extant species statistically most likely (Schluter et al, 1997; Link et al, 2002; Nunn, 2011:63; Bykova et al, 2013; Pagel 1999b). This methodology follows the basis of a Markov model, whereby the probability of change on a branch is independent of changes on other branches. This depends solely on the state and the beginning of a branch (i.e., other evolutionary changes do not affect the change of a transition between defined characteristics, rather the likelihood of transition depends solely on the starting trait). Mace and Pagel (1994) proposed phylogenetic analysis as a methodology which, when applied to examples of cross-cultural variation, could help to explain the factors influencing this variation whilst mitigating for the influence of shared ancestry. The methodology, used in phylogenetically controlled-for PGLS and phylogenetic RMA, works by testing for the association of a phenotypic trait with a second phenotypic or environmental trait, against an underlying model of known historical relationships between the sampled groups (Felsenstein, 1985; Harvey and Pagel, 1991; Fortunato and Mace, 2009). In particular for this thesis, this can be used to test observed relative BSS for a primate group with sociodemographic, morphological or life history variables, against a model of know genetic distances.

As outlined by Nunn (2011:63), the key parameters in this model involve estimates of the rates of change in character traits. The parameters can then be estimated from phylogenetic tree and species data, which are then used to calculate the likelihood of ancestral states on internal nodes (the branching species between the LCA and extant species sampled). In addition, an advantage of ML over parsimony (Nunn, 2011:64) is that ML utilises information on branch length, where longer branches provide increased chance for changes to occur than shorter branches (i.e. greater chance of mutation and speciation events). ML relies on the creation of a background matrix for the rate at which transitions between states occur, which is generated from a dated tree and current species values. ML also assumes a constant rate of change throughout a phylogenetic tree, but rates of change are independent across branches.

Furthermore, ML provides statistical advantage over parsimony, where ML models can assess the statistical support for one reconstructed ancestral state over another, moving away from viewing nodal states as fixed data and explicitly demonstrating their theoretical nature as outputs from statistical models (Pagel, 1994). However, the reliability of the genetic distance data on which the analysis relies for tree construction is still debated. Many of these models of tree construction assume a constant rate of mutation between speciation events and for all species involved (see Lynch et al, 2016 for review). Given the fact that this variation in mutation rate may operate on relatively short evolutionary timescales within the primate phylogeny, the differences could be argued to be negligible, and not result in significant unreliability of models utilising estimated phylogenies form genetic distance.

What is of course of significant interest to palaeoanthropologists is the capacity for ML methodologies to estimate the statistical likelihood of traits both physical and behavioural at the same node common to sampled taxa from observed values. With larger samples for individual taxa, this can additionally be used to estimate the relative proportions of traits within a historic population, assuming a population can exist as a single species whilst displaying multiple variants of a trait (Nunn, 2011:65). In palaeodemographic and evolutionary modelling terms, this could in turn be used to theoretically model the likelihood of founder effects, genetic bottlenecks and unequal distribution of trait means among divergent populations. If prosocial birthing behaviour were found to have a phylogenetic component determining its expression, the variation observed in founder populations could account for the distinct variation observed in genetically and behaviourally diverse human populations today.

However, the use of ML models for reconstructing ancestral states works on the assumption that changes between nodes are relatively difficult and do not occur frequently. With the observations presented on primate behaviour demonstrating a degree of variability between expression of prosocial behaviours and lack of expression in populations of the same species, ML methodology may therefore not provide an accurate estimation of ancestral states. As an alternative to parsimony methods, the capability for ML to ignore the basis of estimated states based on the minimum number of steps, (Nunn, 2011: 71) does support its advantage in producing more realistic models of punctuated evolution rather than a gradualist assumption of the evolutionary trajectory. Although, in estimating based on multiple possible trait states, models become more unlikely where the calculations rely on a higher number of assumptions (Schluter et al, 1997), and fall prey to chance for accumulated error. This is where Bayesian reconstruction methods can overcome this chance of uncertainty in the transition rate between states.

Bayesian statistics and MCMC

Ronquist (2004) highlights how Bayesian phylogenetic analysis can estimate the state of ancestral nodal species, calculating the probability of a nodal population having a particular character (or behavioural) state based on observed data and the genetic relatedness between observed sample populations, whilst additionally accounting for ‘mapping uncertainty’ in the estimation of transition rates between each possible state. Additionally, Bayesian methods can also account for errors in calculating relatedness between sampled species (Huelsenbeck and Bollback, 2001), or phylogenetic uncertainty (Ronquist, 2004), which is accounted for in the Bayesian methods by utilising multiple sets of trees or a consensus tree based on multiple estimated phylogenies (Arnold et al, 2010). Given the uncertainty in the relative ease or difficulty in transitioning between typically highly social or antisocial behaviour, and the potential uncertainty in phylogenetic models produced by variation in mutation rates (Chintalapati and Moorjani, 2020), this makes Bayesian statistical methods much more appealing relative to parsimony and ML methods.

In humans, work by Pagel and Meade (2005) utilised Bayesian statistical analysis, specifically the use of MCMC methods, to investigate whether marriage resource transference covaries with mating systems, whilst controlling for the phylogeny of the sampled cultures. For nonhuman primates Pagel and Meade (2006) also utilised similar methods for investigating the covariation between sexual swellings and mating systems, finding that the overwhelming majority of MCMC models predicted a dependent model of trait evolution. Here the covariation between sexual swelling presence and multi-male social systems were dependant on shared ancestry. This of course is highly likely given the heritability of sexual swellings, where a phylogenetic component would contribute towards the variation in the exaggeration of sexual swellings with multi-male mating system classification. The reliability in detecting phylogenetic signal and contribution to covariation between behavioural variables and other factors, is of course dependant on the assumptions used in the methodology. However, the flexibility of Bayesian MCMC methods in applications investigating evolutionary scenarios in palaeoanthropology is highly beneficial in assessing the likely model of birthing behavioural evolution in humans and nonhuman primates.

5.3. Methodology

Quantifying birthing sociality

To interpret the qualitative descriptions of primate birth events, the relative degree of sociality must be quantified on an ordinal scale. To achieve this, birthing sociality will be scored 0-3 as shown in **Table 5.1.**, which will serve to quantify the increasing degree of prosociality of primate birthing behaviour. Whilst this could be considered an arbitrary, the consistency in application of scoring will serve to provide a necessary comparative quantitative methodology across primate taxa. Using qualitative descriptions of observed birth events and individual and group responses, the aim is to provide a methodical and uniform score for individual events, relative to other primate birth events.

Score	Qualitative description (Proximity; Behaviour)
0	No individuals within 5m; no attention paid by group members or wholly antagonistic actions
1	Group members within 5-2m; obvious visual attention paid by group members, minimal antagonism
2	Closer proximity, observing 2-1m; some group member visual and/or olfactory inspection during delivery
3	Group member in continuous close proximity of <1m; continuous group member inspection and/or manual assistance by group members

Table 5.1. BSS scoring scale for relative birthing prosociality scale.

These values are applied based upon opposing scales of social interaction facilitated by proximity, with a score of 0 representing absent relative prosociality during birth, and 3 representing a comparably high level of relative prosociality as seen typically amongst humans. With distance maintained between the birthing mother and potential group members as a basis, scores additionally will factor in observations of interactive behaviours, such as visual attention, olfactory inspection, or manual assistance in delivery. Antagonistic behaviours, such as infanticide attempts or aggressive interactions, will be considered as a factor reducing the BSS value. Whilst this approach in scoring with human behaviour as the top level of score may appear relatively anthropocentric, for the purposes of comparative analysis amongst nonhuman primates, it will serve to provide a consistent quantitative scale for review as a scale between relative pro or anti-social birthing behaviour. Where alternate values are determined for samples of the same species, a mean value will be calculated for the species, in order to provide a single data value for comparison.

In order to account for the sourcing of material from both wild and captive primates, and the limiting space enforced in captivity, an upper proximity threshold of 5m was used to describe relative proximity. Here, individuals were classed as being in close proximity when they were less than 1m from the mother for the majority of the interaction, 1-2m where group members are out of arms reach but still close, and 2-5m where the mother would have more time to react to group member interactions. Following on from Nunn (2009) with regard the use of discrete numerical coding for behavioural traits within this thesis (i.e. for birthing sociality scores), values will represent an ordinal, scaled quantitative description and assessment of observed behaviours. The method utilised in this analysis also follows work by Sleutel (2002) who developed a Labour Support Scale (LSS) to indicate greater labour support behaviours in humans (nurses in particular, see also Barrett and Stark, 2010; Stark and Miller, 2010). However, this method utilises a 28-item questionnaire to assess the LSS based on answers to the questionnaire. As the use of a questionnaire is not possible to apply to secondary data on nonhuman species, this methodology is adapted here to apply more generally across 13 nonhuman primate species. Whilst BSS could be scaled according to the context (in terms of group size variation and captivity limitations), a standardised framework for scaling is not readily available. It is worth noting that since data was not available for Lorises, Lemurs or tarsiers, the results presented represent Simiiformes containing samples from both Catarrhines (Old World monkeys and Apes) and Platyrrhines (New World monkeys).

Comparative data source

The primary source for life history and sociodemographic data comes from the PanTHERIA (Jones et al, 2009) database. This database provides a relatively comprehensive compilation of data across extant species of primates (and other taxa). This data comprises a multitude of variables, with data sourced from multiple first-hand observations or studies. Whilst this thesis has discussed multiple potential factors driving the expression of prosocial birthing pressures (e.g. predation pressure and mortality risk), these factors were not determined to have substantial data sets within published literature to provide a comparative sample for species with available birthing sociality observations. Therefore, the variables presented in this chapter constitute those for which comparative analysis was possible within the scope of the research. The variables utilised in this analysis comprised the most complete set of sociological, morphological and life history variables from the PanTHERIA (Jones et al, 2009) database, which provided the least absent data set (<25% absent data) for comparison with available birthing sociality observations. To provide further life history variables for comparison, additional data was sourced from available published datasets (see **Table 5.4.**). Further primary data collection across multiple genera on relevant primate obstetric morphology may provide greater indication of any relationship between birthing sociality and morphology. However, the challenges of data collection (particularly during the COVID-19 pandemic) have limited the scope for data comparison as part of this thesis (see Appendix for a further discussion of this impact on primary research).

Using neonatal body mass as a proxy for obstetric morphology (and estimating neonatal brain volume)

Given the relationship between body size and obstetrically relevant morphology observed across primate species (discussed in Chapter 2), for example a strong correlation between adult brain mass and neonatal body mass demonstrated by data obtained from the PanTHERIA database (r=0.981, R^2=0.963, plotted below in **Figure 5.1.**), a number of proxy variables were used in place of fairly sparse datasets for neonatal brain metrics and obstetric morphology. These variables were adult body mass, neonatal body mass, adult female weight, adult male weight, and adult brain weight. The aim of utilising proxy values in the absence of primary obstetrically relevant data was to determine whether any significant relationship was identified between birthing sociality and obstetric morphology. Furthermore, without comparative neonatal brain volume or mass for the majority of species for which birthing sociality data was available, the relationship between BSS and neonatal body mass may also indicate any further relationship between sociality and neonatal brain weight at birth.

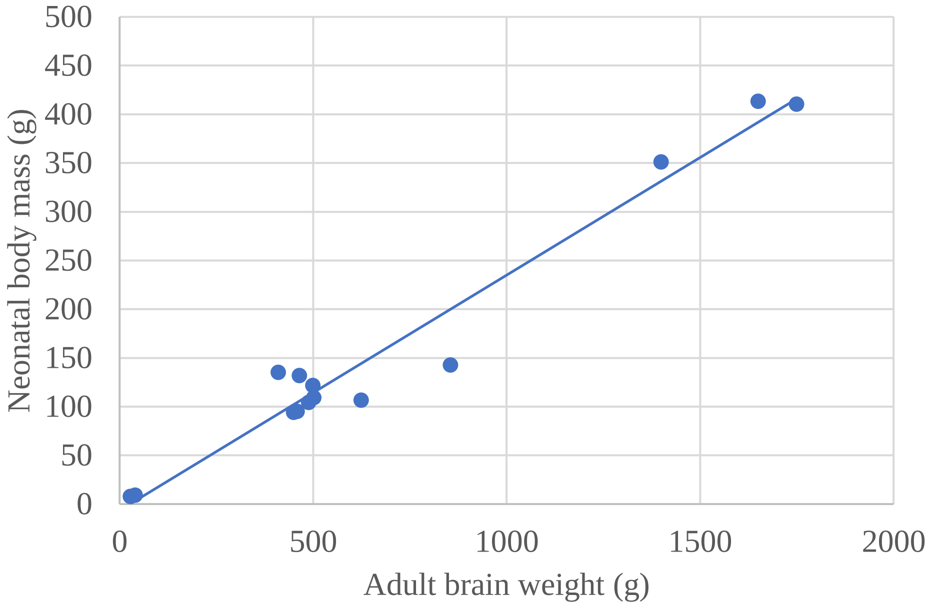


Figure 5.1. Graph plotting the relationship between adult brain weight and neonatal body mass in primates.

With the aim of strengthening the reliability of the use of neonatal body mass as a proxy for obstetrically relevant dimensions, a small-scale study of the relationship between neonatal cranial dimensions and neonatal body mass was conducted at Twycross Zoo, Warwickshire (UK). In total during the study period, data was collected from six primate neonates. Three of these were live samples and three were measured post-mortem, with the sample representing four different taxa (see **Table SI.1.1.** for raw data). However, the neonatal body mass was not recorded for one of these samples, bringing the sample size down to five.

To obtain neonatal cranial metric data and estimates for neonatal brain size, methods were employed following similar techniques used in human neonates, as such methodology does not appear to exist for primate neonates. Fergusen et al (2005) report a highly accurate estimation of intracranial volume (ICV) from intracranial area (ICA), assuming the ICA as a circle and in turn the volume as a sphere, finding a high correlation between predicted and actual ICV. This is further supported by Piper et al (2014) who found a similar strong correlation between ICA and ICV, and suggest that the assumption of the brain as a sphere to estimate ICV is relatively accurate. Martini et al (2018)'s study of human neonatal cranial volume in relation to maximum head circumference demonstrated a strong association between predicted and observed cranial volume. Martini et al (2018) further observed that a correction for measured ear-to-ear distance increased the accuracy of estimates of cranial volume from maximum circumference, which is why this measurement was also taken in this study.

All measurements were taken by Twycross veterinary staff as opportunities to take measurements were ad-hoc, and so necessitated on-hand teams to obtain measurements. Measurements were taken on live subjects following work by Kavangh et al (2018), infants were measured on day 4-10 of birth, or sooner in post-mortem cases. Given that the total head circumference measured by Twycross veterinary staff occupied the largest sagittal dimension around the cranial vault, it is reasonable to use this as the circumference of the sagittal ICA. Where the circumference (c) of a circle is typically given as;

$$c = 2\pi r,\ r = \frac{c}{2\pi}$$

the volume (v) can be expressed as;

$$v = \frac{4}{3}\pi(\frac{\mathrm{c}}{2\pi})^3, \text{ or } v = \frac{\pi c^3}{6}$$

Of course in the application to primates, the shape of the cranial vault is dramatically different. However, given the strength of this relationship in humans, it is likely that such an allometric relationship is a morphological trait not purely unique to humans, and instead follows a deeper primate origin. With such an absence of substantial published primate neonatal mass data (de Silva and Lesnik, 2008), the necessity for viable ways of obtaining neonatal cranial mass requires alternate and less direct methods. Whilst de Silva (2008) conducted a mass analysis of neonatal morphological data, this was focused primarily on anthropoid species, birthing observations were not available for most of these species. Therefore, a further collection of data was needed as part of this thesis to obtain reliable estimates of neonatal cranial dimensions. As this estimate would of course represent a species typical mean value, previous wider data collection also obtained relatively small samples of neonatal individuals (Sacher and Staffeldt, 1974; Martin, 1983; Martin, 1990).

Following the metrics utilised in humans by Bennet and Brown (2003) and Martini et al (2018), the variables measured here to calculate neonatal brain size were: true and/or reduced true and/or reduced subocciptobregmatic diameter, true and/or increased occiptomental diameter, true and /or reduced occipitofrontal diameter, total body weight, total head circumference, ear-to-ear measurement, glabella-to-opisocranion measurement, and cranial weight (see **Figure 5.2.** and **Figure 5.3.**). As cranial vault weight was only obtained for one individual (7689, a dusky-leaf langur), this variable will not form part of the analysis. To ensure consistency in the collection of data, staff were provided with the images below to reference the dimensions required for collection. Where the evidence supports the relationship between body mass and obstetrically relevant primate neonate ICA, the results of this study will be used to confirm the reliability of using neonatal body mass as a proxy for nonhuman primate neonatal cranial dimensions, in the absence of available published data.

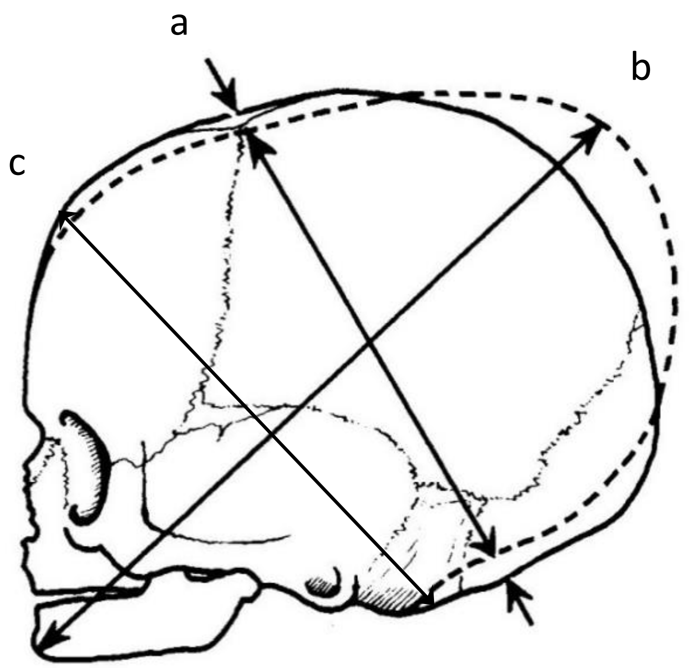


Figure 5.2. Schematic representation of typical moulding of the fully flexed human neonate cranium (left lateral view), adapted from Bennet and Brown (2003:161). The dotted line represents the moulded border of the cranial vault.

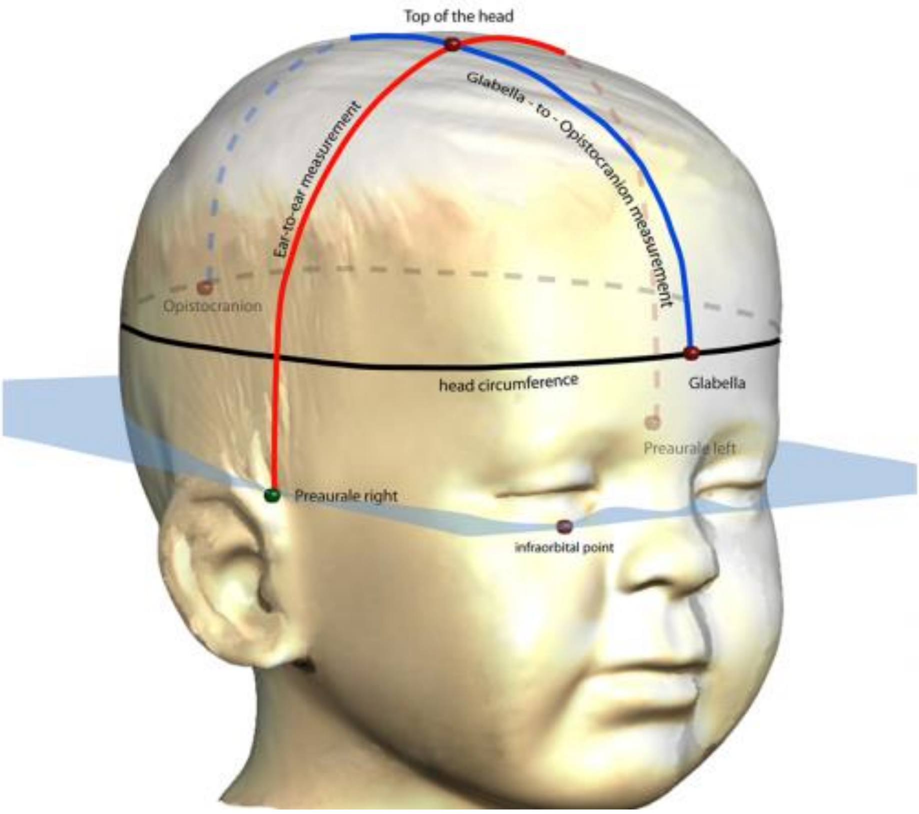


Figure 5.3. Schematic representation of the metrics taken in this thesis: head circumference (black line), ear-to-ear measurement (red line) and glabella-to-opistocranion measurement (blue line) in humans (adapted from Martini *et a*l, 2018:2) The intracranial area (ICA) is highlighted by the blue polyhedral section.

Phylogenetic analysis

In order to test a model of phylogenetic signal in birthing sociality, several statistical modelling methods were utilised. PIC analysis was performed to first identify potential variables utilised in the basic correlation analysis, for which a phylogenetic signal contribution towards variance in the correlation with BSS may be detected. Regression analyses were performed using R version 4.1.1, utilising the Ape (Paradis and Schliep, 2019), Caper (Orme et al, 2013), and Phytools (Revell, 2012) packages, using the Bristol CRANS mirror as well as genetic distance data sourced from 10kTrees (Arnold et al, 2010). Whilst the use of chronograms can provide a more accurate estimate of taxonomic lineages, this is based on the reliability of accurate and complete fossil records, with reliable date estimates for nodal fossil species. These dates are mapped onto known genetic distances of extant species, and in turn provide a more robust framework to model trait evolution. However, without a firm knowledge and sound interpretation of the fossil record, alongside detailed knowledge of shared morphological and physiological traits between extant and fossil species (which can provide unique markers for heritable rather than ontological or epigenetic trait evolution), chronogram trees lose their reliability. Therefore, for this analysis, phylogram consensus trees were utilised to provide a heritable, genetic model of obstetric and birthing behavioural evolution.

As noted by de Silva and Lesnik (2008), any potential estimates from the regression will be influenced by the technique used to calculate the regression equation or line, as well as the population sources (Smith 1994; Konigsberg et al, 1998; Hens et al, 2000). Following on from this concern, this thesis shall employ similar regression methods after de Silva and Lesnik (2008, also see Harper, 2016), calculating transformation regressions using phylogenetic independent contrasts (PIC), followed by the use of ordinary least squares (OLS), phylogenetic least squares (PGLS), and phylogenetic Reduced Major Axis (RMA), in order to control for any effect of phylogeny. Nunn (2011:57) notes that the first step in reconstructing ancestral states involves a decision on whether variables are coded discretely or continuously. When coded discretely into distinct states (e.g. blue or green), they can be considered as integer values. However, for phylogenetic comparison, such traits are often binary (e.g. present or absent), and so coded as a 1 or 0. Where more than two traits are possible, intermediate values can be added. In order to effectively be input within mathematical estimates, discrete values must be coded as integer values (e.g. 0, 1, 2, etc). This use of ordinal values will allow for the BSS scores to be utilised within phylogenetic models. However, given the possibility for variation in behaviour expression between these states 0 to 3, the data will be treated as continuous (for a review of treating ordinal data as continuous, see Liu and Agresti, 2005; De Leeuw and Mair, 2009). Additionally, future development of this methodology could utilise a scaling approach with phylogeny for ordinal BSS values (De Leeuw and Mair, 2009). Without understanding the relationship between birthing sociality and phylogeny, it is not possible to predict whether sociality would scale with phylogeny without first determining the level phylogenetic signal in quantified sociality. However, due to the limitations of the scope of this thesis, this assessment was not applied here.

Nunn (2011:57) also notes that when deciding which phylogeny to use in reconstructions, there is some debate over the use of trees which are generated by ‘traits of interest’ to the study (Coddington, 1988; Brooks and McLennan, 1991). Therefore, Nunn (2011:57) suggests that trait data used for phylogeny should be independent from the study goals. By utilising genetic distances and consensus phylogeny externally sourced from 10kTrees GenBank data, this analysis aimed to avoid any potential bias in identifying phylogenetic markers. The species for which birthing sociality data were available are presented in the below tree, which was created using the data from 10kTrees within FigTree **(Figure 5.4.)**. This was possible for all for the 18 species as analysed in the previous chapter in the case of social group size, population density, adult body mass, weaning age and gestation length. This was only possible for 17 species for adult female weight, adult male weight and adult brain weight, and for 16 species for neonatal body mass. Where appropriate, species for which data was missing for each regression run were omitted from reconstructions and analysis.

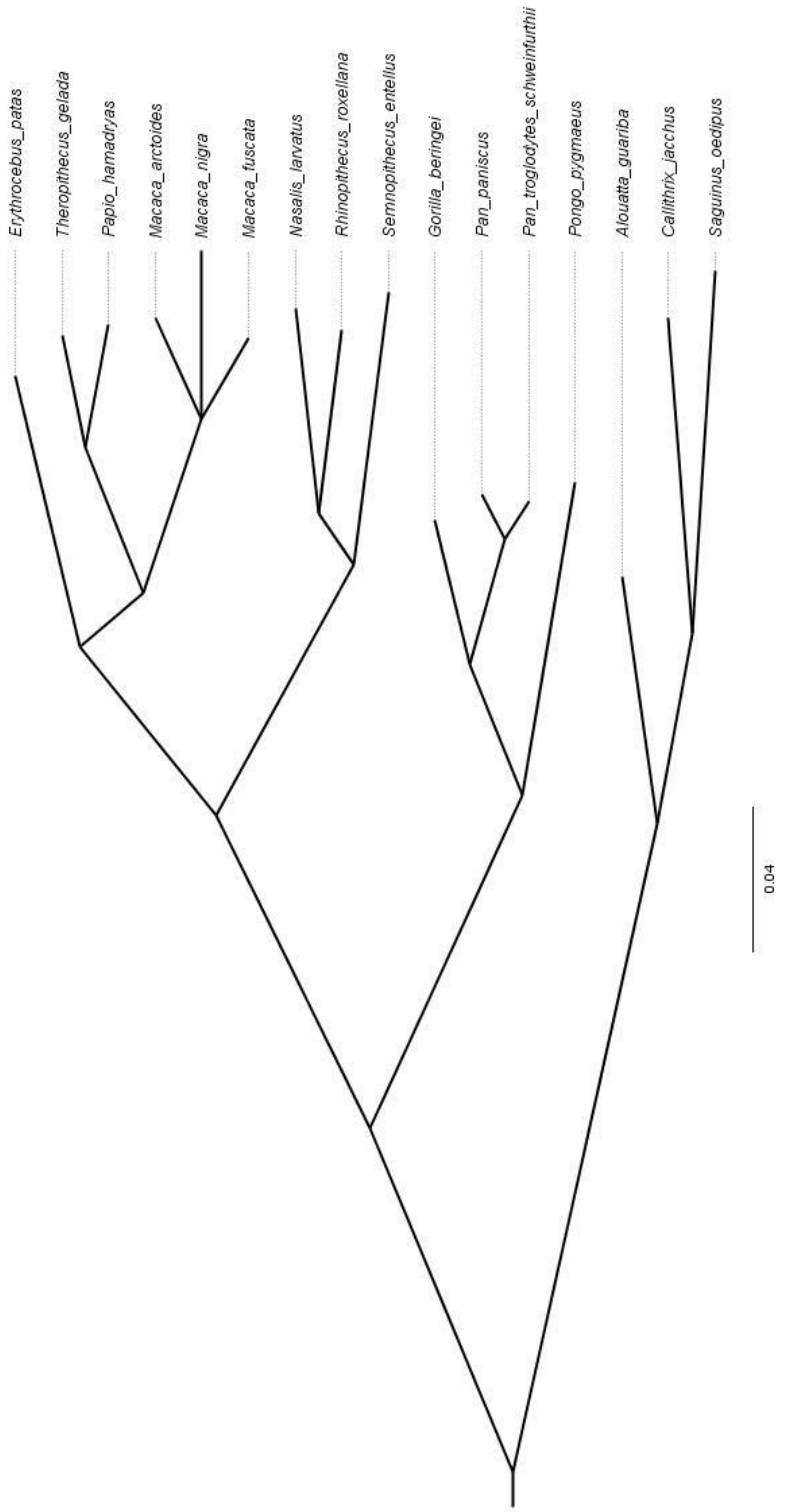


Figure 5.4. Phylogenetic tree constructed on FigTree using genetic distance data sourced from 10kTrees. Scale bar represents the genetic distance as a proportion of nucleotide base

substitutions per site. Tree represents known values for nonhuman primate species sampled in this analysis.

To further test the reliability of the correlation found between birthing sociality and social group size, BayesTraits (Version 3) was used to determine maximum likelihood values using Markov Chain Monte Carlo (MCMC) to derive posterior distributions (as a combination of the prior and maximum likelihood). The log-maximum likelihood values of these two methods are then compared using MCMC to determine the relative strength of the correlation between birthing sociality and social group size. Following from Pagel (1999), the number of 'stones' were set to 100, and iterations at 1000. Here, the number of 'stones' refers to the steps in the model which link the posterior estimate with the prior, and allows the model to estimate likelihood values used to calculate Bayesian factor values.

To test the likelihood of phylogenetic signal in the birthing sociality data for primates, these two methods of Bayesian statistical analysis will be further employed here to determine a most likely birthing sociality score value for a common primate ancestor. Here, birthing sociality score was treated as continuous data in order to utilise the Bayesian Statistics software. Iterations which produced node values outside of the 0 – 3 scale were omitted, though relatively few of the 1000 iterations in each run produced node values outside of this range. As a scoring system which theoretically could contain any value within the range, all values are excepted as relative indications of birthing sociality.

Predictions

In each case in the analyses, the null hypothesis will be tested against a 5% ($\alpha > 0.05$) confidence critical significance level (after Hawkins, 2014:187), and all linear regression was calculated within Microsoft Excel, using a residual sum of least squares. In order to test the underlying predictions of the ‘obstetric dilemma hypothesis’, that changes in morphology drove the evolution of prosocial birthing behaviour, the null hypothesis states that no significant relationship exists between non-morphological sociodemographic variables in primates. If a significant relationship between morphological variables and BSS was identified, this would support the central prediction of the ‘obstetric dilemma hypothesis’. With regard to sociodemographic variables, it is not expected that BSS will not significantly correlate to sociodemographic factors, as prosociality is only expected to occur in species with human (or estimated hominin) sociodemographic characteristics, and will be non-existent at lower values. Life history factors would also be predicted under the ‘obstetric dilemma hypothesis’ to correlate with BSS, as slower life history strategies, such as late weaning age and longer gestation length, are expected to increase with BSS (as BSS is hypothesised to have evolved to facilitate slower life histories seen in later hominins relative to other nonhuman primates).

If significant relationships between birthing behaviour and sociodemographic and life history variables, this would support an alternate hypothesis. Whilst there are potential confounds between life-history variables with morphological variables such as brain size, this will be considered within the wider discussion in terms of which hypothetical model of birthing prosociality evolution is best supported by the data. The null hypothesis tested for the ‘social birthing hypothesis’ – that no significant relationship exists between BSS and sociodemographic variables – will be the primary focus of this analysis, as this hypothesis predicts that a significant relationship exists between the relative degree of birthing behaviour prosociality, and sociodemographic factors such as social group size and population density. It is expected that the size of the affiliative social group should show a positive correlation with BSS, as more closely affiliative species would show greater interest in birth. Additionally, it is expected that BSS should also correlate positively with population density, as the frequency of interactions (the chance of which should increase with more individuals in close proximity) should increase the chance of interactions and therefore the chance of prosocial interactions. Although this could also theoretically also increase the number of antagonistic, antisocial interactions. With regard to life history variables, the ‘social birthing hypothesis’ predicts that morphological and life history variables would not significantly correlate with BSS. Given the evidence for highly prosocial behaviours in nonhuman primates, in the absence of significant evidence for similarly challenging obstetrical mechanics, this thesis does not expect a significant correlation between morphological and BSS values. Furthermore, with evidence for prosocial behaviour in species with varying life histories and the ‘social birthing hypothesis’ hypothesis theorising a shift to highly prosocial behaviour prior to the onset of characteristically hominin-like slow life histories, this thesis does not predict a significant correlation between BSS and life history variables.

Together, this thesis can summaries the predictions necessary to test the most appropriate hypothesis for the emergence of prosocial birthing behaviour in primates as:

1) BSS is predicted to significantly correlate with sociodemographic factors.
2) BSS is not predicted to significantly correlate with morphological factors.
3) BSS is not predicted to significantly correlate with life history factors.

Further to this, the ‘social birthing hypothesis’ predicts that BSS would not show a phylogenetic signal in the correlation with sociodemographic factors. A phylogenetic signal would be expected in both morphological and life history correlations, given the evidence for heritable components of obstetric morphology, as well as life history variables such as weaning age and gestation length as a result of physiological components.

5.4. Results

Using neonatal body mass as a proxy for neonatal cranial dimensions

Of the sample individuals for which both neonatal body mass and cranial metrics were measured, the relationship between estimated endocranial volume and neonatal body mass was highly significant (r=0.886, R^2=0.785, p=0.045 – plotted in **Figure 5.5.**, for descriptive statistics see **Table SI.1.2.**). This correlation is therefore reasoned to be significant enough to serve as a proxy for obstetrically relevant, neonatal cranial dimensions.

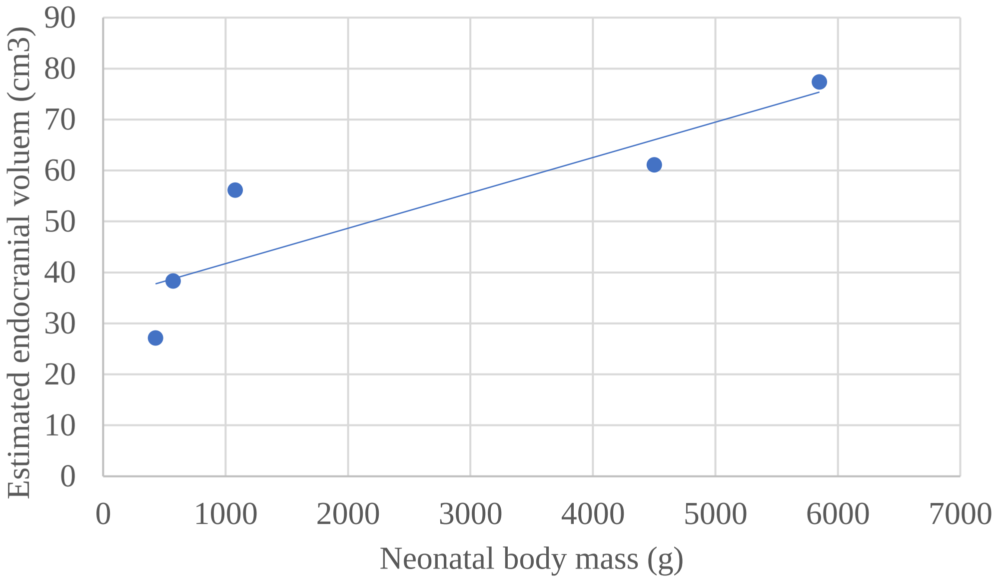


Figure 5.5. Graph of linear regression of neonatal body weight against estimated neonatal cranial volume (n=5).

From a further investigation of the relationship between these metrics used to calculate neonatal cranial volume and neonatal body weight (see **Table 5.2.**), all variables show a significant level of correlation, with true and/or increased occipitomental diameter showing the most significant correlation at r=0.972, highest account for the variation in the data at R^2=0.946, and the most confident value in rejecting the null hypothesis at p=0.001 (the null hypothesis being that no relationship exists between the metric and neonatal body mass).

	Neonatal metric					
	a	**b**	**c**	**e**	**f**	**g**
r	0.724	0.972	0.885	0.863	0.825	0.592
R^2	0.525	0.946	0.783	0.746	0.680	0.350
n	6	6	6	6	6	6
t	2.102	8.349	3.802	3.424	2.916	1.468
df	4.000	4.000	4.000	4.000	4.000	4.000
p	0.103	0.001	0.019	0.027	0.043	0.216

Table 5.2. Table of statistics for a test of correlation between neonatal cranial metrics and neonatal body weight: (**a**) true and/or reduced true and/or reduced subocciptobregmatic diameter (cm), (**b**) true and/or increased occiptomental diameter (cm), (**c**) true and /or reduced occipitofrontal diameter (cm), (**e**) total head circumference (cm), (**f**) ear-to-ear measurement (cm), (**g**) glabella-to-opisocranion measurement.

Conversely, both the suboccipitobregmatic and glabella-to-opistocranion measurements show the lowest r and R^2 values (r=0.724, R^2=0.525 and r=0.592, R^2=0.350 respectively). However, whilst these values still suggest a significant correlation in the data set, the high p values above the critical significance level do not support a rejection of the null hypothesis, suggesting that the small sample size may account for the significant level of correlation.

Assessment of nonhuman primate birthing sociality

The information collated on birthing behaviour in primates and used to estimate birthing sociality scores is presented below in **Table 5.3.**, for which statistical data is summarised in **Table 5.4**, highlighting the relationships identified between each variable. In terms of quantifying birthing sociality, the standardised approach applied in this thesis provided an interesting series of results for discussion.

Source	Species	Summary of published sample	Group 5-2m proximity	2-1m proximity	<1m proximity	Manual birth assistance?	Key behaviours	BSS score
Martins et al, 2015	*Alouatta guariba clamitans*	Observation of birth by a multiparous females.	0	Adult female feeding, though showed no interest.	0	No	Social group was within 2m of the birthing female, but they showed no interest and on later days infant attacked.	1
Stevenson, 1976	*Callithrix jacchus jacchus*	Study of captive family groups in cages ranging from 1-4m^3 (small enclosures).	0	In all births, small enclosure size limits proximity to ensure all group members within 3m.	Adult males in all cases showing most interest, with males often within arm's reach, grooming and observing.	No	Multiple births in captivity in family groups, with females in all cases not attempting to isolate herself. In all cases, adult males appeared most interested and remained in closest proximity.	2
Chism et al, 1983	*Erythrocebus patas*	Seven diurnal births in wild. Two observed. Took place on the ground.	Adult females in all cases	0	0	No	Both females were approached or watched from within 3m by one or more adult females before and during birth.	1
Stewart, 1977	*Gorilla gorilla beringei*	Older adult multiparous female (Marchessa) observed birthing in wild.	Silverback male, Marchessa's adult daughter (Pantsy), another adult, three juveniles.	Sub adult male (Puck) at ~1.5m initially	At point of birth, Puck moved next to mother.	No	Mother stayed within close proximity of group, and mother's offspring showed great interest, with adult son remaining in closest proximity, clearly inspecting at the moment of delivery. Adult offspring shadowed mother and possibly prevented unwanted interactions.	2
Stewart, 1984	*Gorilla gorilla beringei*	Two wild adult females birthing, UM and PD.	0	0	UM briefly inspected by two multiparous adult females. For PD's birth, two parous adult females and three juveniles (including son) four minutes prior to PD's birth. Adult parous female and female juvenile at delivery.	No	UM birthing within 10m of whole group, with two adult parous females inspecting in response to grunting vocalisations. PD birthing highly social with two adult females and juveniles remaining in close proximity during labour, and adult female and female juvenile gathered around during delivery.	2
Gouzoules, 1974	*Macaca arctoides*	Birth of an infant to highest ranking female in captive social group of stump-tail macaques.	0	0	Attempted mounting during labour by juvenile son and alpha male, to which female retreated to 15 feet.	No	Female labouring within 15 feet of group	1
Kemps and Timmermans, 1982	*Macaca fascicularis*	Five multiparous feral Java-monkeys observed in captivity	N/A	N/A	N/A	N/A	Four of the five females gave birth on the branch	N/A
Thomsen and Soltis, 2000	*Macaca fuscata*	Eight births to wild females, where females observed having fewer social interactions with males and other adults.	Adult females (indiscriminate number)	0	0	No	Births in all cases characterised as being in proximity of <3m with adult females a higher proportion of the time than with adult males.	1
Thomsen, 1997	*Macaca fuscata yakui*	Birth of a wild female Japanese macaque delivering in the early hours.	0	0	0	No	Birth observations obscured, but female noted to be self-isolated after not keeping up with group.	0

Source	Species	Summary of published sample	Group 5-2m proximity	2-1m proximity	<1m proximity	Manual birth assistance?	Key behaviours	BSS score
Turner et al, 2010	*Macaca fuscatta*	Free ranging group at a research centre in Japan. Three daytime births observed to multiparous females.	Numerous juveniles and adult females in all three cases.	In all births, juveniles remained within close proximity, as well as adult females	Inspection by adult females, juveniles, and observing.	No	Three births observed to multipara, with significant tolerance of close juvenile proximity and inspection, as well as some adult female inspection. Authors conclude that social proximity at parturition is more common in primates than previously highlighted in animal behavioural and anthropological literature, with potential evolutionary advantages.	3
Duboscq et al, 2008	*Macaca nigra*	Daytime birth of a wild baby crested black macaque.	0	Birthing female remained within 2m of group 15 minutes prior to delivery	Male juvenile inspected perineal area and touched hand then left several minutes before.	No	Female labouring in close proximity to social group but remained behind the group as they continued to move, being only briefly accompanied by a juvenile male.	1
Gorzite, 1996	*Nasalis larvatus*	Two wild births, one at night one mid-morning.	Male ~3m away, another juvenile male slightly further.	F2 ~1.5m away from F1 birth.	0	No	One observed birth during the day, where female gave birth in close proximity to female and two males, one adult and one juvenile.	1
Coppola et al, 2011	*Pan paniscus*	Birth in a captive group of bonobos by a primiparous female.	0	0	Two adult females and their respective daughters (one each)	No	Birthing mother followed around the enclosure by multiparous females and their daughters, who proceeded to inspect birth fluids visually and manually and anogenital region during delivery.	2
Demuru et al, 2018	*Pan paniscus*	Three births to captive bonobos in large enclosures (230m^2 indoor 5000m^2 outdoor at APP; 900m^2 indoor and 10000m^2 outdoor at LVDS). At APP group consisted of two adult males, six adult females, two juveniles. At LVDS, four adult males, five adult females, one juvenile at first birth, and five adult males, seven adult females, and five immatures during second birth. At APP, medium ranking primiparous female gave birth. At LVDS high ranking multipara Ukela and medium ranking female Lucy were observed birthing.	0	0	Adult female bystanders manually guiding infant and performing 'grab infant' gestures.	Yes. On two of three occasions, bystander females held infant during delivery	Three highly social births, with two deliveries involved extensive handling of the neonate while expelled, as well as performing grab infant gestures during labour, with manual and visual inspection also.	3
Goodall and Athumani, 1980	*Pan troglodytes schweinfurthii*	Birth by a wild multiparous chimpanzee, aged 18-20 years.	Multiparous adult female	Offspring of multiparous female, male and female (retreated to 4m when infant crowned but then returned)	Birthing mother's son Winkle remained in close proximity and licked the birthing infant as well as inspecting during delivery.	No	Female labouring accompanied by sub-adult son, as well as another multiparous female with two offspring in close proximity.	2

Source	Species	Summary of published sample	Group 5-2m proximity	2-1m proximity	<1m proximity	Manual birth assistance?	Key behaviours	BSS score
Fujisawa et al, 2016	*Pan troglodytes verus*	Wild adult female Fl (one previous birth), who had remained in her natal community. Second birth by a multiparous adult female Jr. The group consisted of four adult males, six adult females, and two juveniles including Fl's son FE.	0	0	0	No	Birthing female Fl climbed an adjacent tree to two adult females, who observed from a distance of 15-10m and made vocalisations argued to be specific to birth timing.	0
Ableggen and Ableggen, 1976	*Papio hamadryas*	Wild single male unit with birthing of a sub-adult female on the sleeping cliff.	0	Resident male primarily remains 2m away guarding female.	The same adult resident male briefly mounts and attempts to assist and catch the expelled infant. Juvenile female also sniffs and inspects birthing female's anogenital region.	Yes, as the adult male attempted to catch and prevent the neonate dropping over cliff.	Birthing accompanied by the resident male, who remains within 2m, briefly mounting in response to another troop's proximity and also attempts to catch the falling infant. A juvenile female also inspected (sniffed) the labouring mother's anogenital region.	3
Galdikas, 1982	*Pongo pygmaeus*	Two births (Fern, nulliparous female; Fran, Fern's mother) but only one observed, which took place in a wild reserve.	0	0	0	No	The authors note that no other group members were seen around the female during birth, and the female seemed to actively avoid interactions in the days prior to birth.	0
Oppenheimer, 1976	*Presbytis entellus* (documented in the source as *Semnopithecus entellus*)	One of seven observed births in wild langurs. Each troop had a single resident male.	0	0	Two adult females remained at birth mother's feet throughout.	No	The birthing mother was followed and accompanied while birthing terrestrially by two adult females in close proximity.	2
McKenna, 1974	*Presbytis entellus* (documented in the source as *Semnopithecus entellus*)	Adult captive female birth, kept in a multi-group enclosure.	0	0	Two adult females accompanied the birthing mother to ground.	No	Birthing female accompanied to ground to birth by two adult females.	2
Yang et al, 2016	*Rhinopithecus roxellana*	Observation of a wild, multiparous female (BD) birthing. Group contained one adult male, three multiparous females (BD, HH, BX), one primiparous female (XH), five juveniles, and one infant (no data on kin relationships among females).	0	The same juvenile daughter (J1) inspected the mother prepartum and observed during delivery.	Manual inspection of anogenital region by juvenile daughter J1 and also manual assistance by adult multipara HH	Yes, as the multiparous adult female (HH) pulled and guided the neonate out.	Inspection by juvenile daughter J1, and manual 'assistance' by adult multipara female HH.	3
Price, 1990	*Saguinus oedipus*	Captive breeding colony with 14 births to seven females recorded.	Family members often remain within indoor enclosure with max dimensions of 2.91m x 3.45m x 3.45m (not moving to outdoor area).	0	0	No	Birthing females remaining within 5m proximity of family groups. Considering the limited size of the enclosure and opportunity for interactions, these were still fairly limited.	1
Nguyen et al, 2017	*Theropithecus gelada*	15 births observed in a wild troop.	Four of the 15 birthing mothers remained less than 5m to conspecifics.	0	0	No	Of those births were relatively prosocial with group members in close proximity, these were all nulliparous females, whilst multiparous females did not remain in close proximity to other group members.	1

Source	Species	Summary of published sample	Group 5-2m proximity	2-1m proximity	<1m proximity	Manual birth assistance?	Key behaviours	BSS score
Dunbar and Dunbar, 1974	*Theropithecus gelada*	Wild population with three births observed, but only one directly (female 1, nulliparous).	0	0	0	No	Prior to birth, the mother was socialising through grooming, but at the onset of birth and expression of fear, other group members scattered. Juvenile was the first to interact after delivery.	0

Table 5.3. Table of details sourced to determine a relative Birthing Sociality Score, with 0 indicating an isolationist birth, and 3 representing a highly prosocial, interactive birth event.

Species	**BSS**	**SGS**	**PD**	**ABM**	**NBM**	**AFW**	**AMW**	**ABW**	**WA**	**GL**
Alouatta guariba	1.0	7.40	89.09	5188.33	-	-	-	-	365.00[h]	-
Callithrix jacchus	2.0	8.55	512.00	291.00	27.70	290	310	7.90[n]	60.04	148
Erythrocebus patas	1.0	28.00	0.26	8010.00	624.00	5600	10000	106.60[n]	210.41	163
Gorilla beringei	2.0	14.00	0.19[a]	149325.19	-	100000[d]	200000[d]	500.00[m]	1278.00[h]	255[i]
Macaca arctoides	1.0	68.00	1.09[b]	9400.00	489.00	8000	9200	104.10[n]	376.43	175
Macaca fuscata	1.5	40.65	30.20	10100.00	502.00	5900	9100	109.10[n]	263.32	173
Macaca nigra	1.0	24.75	66.70	7380.00	459.00	6600	10400	94.90[n]	365.00	176
Nasalis larvatus	1.0	11.25	9.00	12300.00	450.00	9900	20300	94.20[n]	210.37	166
Pan paniscus	2.5	85.00	2.00	35119.95	1399.53	33000[e]	45000[e]	351.00[g]	1081.31	230[j]
Pan troglodytes schweinfurthii	1.0	50.00	1.64	45100.00	1750.00	31100	41600	410.30[n]	1670.46	228
Papio hamadryas	3.0	43.50	3.90	16900.00	855.00	9400	21500	142.50[n]	450.71	172
Pongo pygmaeus	0.0	1.00	2.00	52100.00	1650.00	37000	69000	413.30[n]	1081.72	260
Rhinopithecus roxellana	3.0	65.00	17.30	12600.00	499.00	8900[f]	17000[f]	127.10[n]	400.79	200[k]
Saguinus oedipus	1.0	7.05	4.60	13456.80	40.00[c]	539[c]	539[c]	9.00[n]	50.00[h]	184[l]
Semnopithecus entellus	2.0	19.00	46.20	464.00	41.00	11300	15300	135.20[n]	49.69	145
Theropithecus gelada	0.5	10.00	51.40	16000.00	465.00	13600	20500	131.90[n]	493.34	170

Table 5.4. Table of variables obtained for comparison with Birthing Sociality Scores. Data sourced from PanTHERIA (Jones et al, 2009) unless otherwise indicated.

BSS – Birthing Sociality Score, **SGS** – Social Group Size, **PD** – Population Density (n/km^2), **ABM** – Adult Body Mass (g), **NBM** – Neonatal Body Mass (g), **AFW** – Adult Female Weight (g), **AMW** – Adult Male Weight (g), **ABW** – Adult Brain Weight (g), **WA** – Weaning Age (days), **GL** – Gestation Length (days).

[a] Plumptre et al, 2016, [b] Haus et al , 2008, [c] Caperos et al, 2012, [d] Watts, 1998, [e] Kingdon, 2013, [f] Zhu et al, 2015, [g] de Sousa, 2010, [h] Young and Shapiro, 2018, [i] Wright, 2014, [j] Reichert et al, 2002, [k] Jan et al, 2003, [l] Ziegler and Snowdon, 2000 , [m] Stephen et al, 1981, [n] Harvey et al, 1987.

The data presented shows that the highest frequency of BSS is for a score of 1, which at initial glace supports the conclusion that nonhuman primate births are not typically characterised by isolated births. Instead, primate mothers have a higher frequency of births within closer proximity of their social group. Moreover, a number of births are scored at a highly prosocial value. These births were considered to show the hallmarks of highly prosocial behaviour which have previously been considered uniquely human behavioural traits. Additionally, these births occurred in instances where females were in proximity of social group members and in the case of instances scored at 3, group members interacted directly and even manually assisted in the delivery of the neonate.

Correlation and collinearity in sociodemographic, morphological and life history variables

Statistical analysis of the variables utilised in this study initially suggest that the strongest signal of correlation with BSS exists between social group size at R=0.522 (see **Table 5.5.**). Additionally, this result should be considered statistically significant at p=0.019 and the null hypothesis should be rejected, and this is certainly worth investigating. Critically, the results of this analysis suggest that the null hypothesis can be rejected – that a relationship does exist between social birthing behaviours and an external sociodemographic factor.

		Variables									
		BSS	SGS	PD	ABM	NBM	AFW	AMW	ABW	WA	GL
Pearson correlation	BSS	-	0.522	0.122	0.047	-0.158	0.052	0.066	-0.069	-0.067	-0.097
	SGS	0.522	-	-0.294	-0.075	0.343	-0.061	-0.136	0.155	0.264	0.133
	PD	0.122	-0.294	-	-0.256	-0.391	-0.252	-0.228	-0.394	-0.326	-0.386
	ABM	0.047	-0.075	-0.256	-	0.937	0.984	0.988	0.847	0.716	0.785
	NBM	-0.158	0.343	-0.391	0.937	-	0.91	0.892	0.957	0.947	0.872
	AFW	0.052	-0.061	-0.252	0.984	0.91	-	0.99	0.848	0.737	0.78
	AMW	0.066	-0.136	-0.228	0.988	0.892	0.99	-	0.796	0.658	0.737
	ABW	-0.069	0.155	-0.394	0.847	0.957	0.848	0.796	-	0.939	0.975
	WA	-0.067	0.264	-0.326	0.716	0.947	0.737	0.658	0.939	-	0.869
	GL	-0.097	0.133	-0.386	0.785	0.872	0.78	0.737	0.975	0.869	-
Sig. (1-tailed)	BSS	-	0.019	0.327	0.432	0.295	0.427	0.408	0.408	0.402	0.366
	SGS	0.019	-	0.135	0.391	0.115	0.414	0.314	0.298	0.162	0.318
	PD	0.327	0.135	-	0.169	0.084	0.182	0.207	0.082	0.109	0.078
	ABM	0.432	0.391	0.169	-	<0.000	<0.000	<0.000	<0.000	0.001	<0.000
	NBM	0.295	0.115	0.084	<0.000	-	<0.000	<0.000	<0.000	<0.000	<0.000
	AFW	0.427	0.414	0.182	<0.000	<0.000	-	<0.000	<0.000	0.001	<0.000
	AMW	0.408	0.314	0.207	<0.000	<0.000	<0.000	-	<0.000	0.004	<0.000
	ABW	0.408	0.298	0.082	<0.000	<0.000	<0.000	<0.000	-	<0.000	<0.000
	WA	0.402	0.162	0.109	0.001	<0.000	0.001	<0.000	<0.000	-	<0.000
	GL	0.366	0.318	0.078	<0.000	<0.000	<0.000	0.001	<0.000	<0.000	-
n	BSS	-	16	16	16	14	15	15	14	<0.000	15
	SGS	16	-	16	16	14	15	15	14	16	15
	PD	16	16	-	16	14	15	15	14	16	15
	ABM	16	16	16	-	14	15	15	14	16	15
	NBM	14	14	14	14	-	14	14	13	14	14
	AFW	15	15	15	15	14	-	15	14	15	15
	AMW	15	15	15	15	14	15	-	14	15	15
	ABW	14	14	14	14	13	14	14	-	14	14
	WA	16	16	16	16	14	15	15	14	-	15
	GL	15	15	15	15	14	15	15	14	15	-

Table 5.5. Correlations matrix for sociodemographic, morphological and life history variables utilised for this analysis.

Model		Unstandardized Coefficients		Standardized Coefficients			95.0% Confidence Interval for B		Correlations			Collinearity Statistics	
		B	Std. Error	Beta	t	Sig.	Lower Bound	Upper Bound	Zero-order	Partial	Part	Tolerance	VIF
1	(Constant)	1.172	2.363	-	0.496	0.64	-4.902	7.246	-	-	-	-	-
	SGS	0.034	0.011	1.018	3.107	0.03	0.006	0.063	0.522	0.812	0.788	0.6	1.666
	PD	0.002	0.002	0.321	1.117	0.32	-0.003	0.007	0.122	0.447	0.283	0.78	1.282
	ABM	-4.38E-05	<0.000	-1.845	-0.85	0.44	<0.000	<0.000	0.047	-0.354	-0.22	0.014	73.719
	AFW	<0.000	<0.000	-3.594	-1.04	0.35	<0.000	<0.000	0.052	-0.42	-0.26	0.005	187.24
	AMW	9.90E-05	<0.000	5.694	1.314	0.25	<0.000	<0.000	0.066	0.507	0.333	0.003	291.76
	WA	<0.000	0.001	0.157	0.191	0.86	-0.003	0.004	-0.067	0.085	0.048	0.095	10.478
	GL	-0.004	0.014	-0.189	-0.31	0.77	-0.041	0.032	-0.097	-0.137	-0.08	0.174	5.760

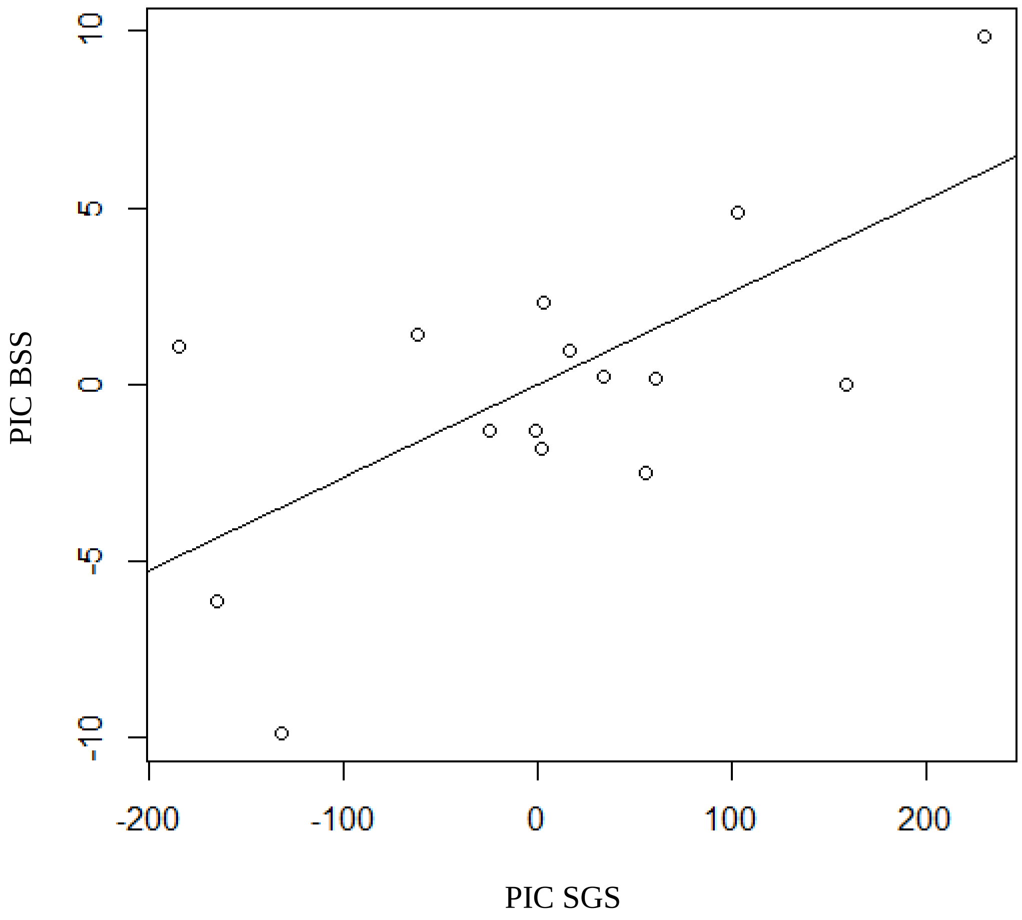
Table 5.6. Correlation coefficients values table, where BSS is the dependant variable.

Between BSS and the other independent variables, the results do not show a significant correlation, and instead supports the null hypothesis for no significant relationship between BSS and morphological or life history variables. These factors do not appear to explain the variance seen in primate birthing prosociality. After investigating a model of correlation between BSS and the independent variables, further analysis of the correlation coefficients and collinearity further supports the statistical significance of the relationship between BSS and social group size, even after accounting for the influence of other independent variables (see **Table 5.6.**). The low VIF value (after Midi et al, 2010). for social group size and population density within the regression models, supports the reliability of the observed correlations for these two factors. However, the high values for the other factors suggest significant interactions between other predictor variables within the model, and that the coefficient estimates an p-values are likely unreliable.

Together, these results demonstrate that a notable relationship exists solely between social group size and the degree of birthing prosociality displayed by non-human primates. The significance of this relationship is further strengthened after correcting for other assessed values. This merits further investigation of potential phylogenetic contributions to the variance seen in BSS, the results of which are demonstrated in the following section.

Phylogenetic signals

PICs analysis performed for BSS against sociodemographic, morphological and life history variables suggest only a significant correlation after correcting for phylogeny in only a single variable – social group size (for the results of other variables, see **Figures SI.2.1-8.** and **Tables SI.2.1-8.**). Social group size identified a significant positive correlation between species exhibiting highly prosocial birthing behaviours, and those species with typically large social



group sizes (multiple R-squared at 0.4455 adjusted R-squared at 0.4059 and a p-value of 0.004726), plotted below in **Figure 5.5** and **5.6.**

Figure 5.5. Plot of PIC BSS against social group size.

Residuals	**Min**	**1 Q**	**Median**	**3 Q**	**Max**
	-6.3804	-1.8365	-0.6942	2.2025	5.9245
Coefficients	**Estimate**	**Std Error**	**t value**	**Pr(>|t|)**	
PICsgs	0.026254	0.007827	3.354	0.00473	

Residual Std Error	3.316 on 14 degrees of freedom
Multiple R-squared	0.4455
Adjusted R-squared	0.4059
F-statistic	11.25 on 1 and 14 degrees of freedom
p-value	0.004726

Table 5.7. Statistical output for PIC of BSS against social group size.

The relatively high R^2 values (see **Table 5.7.**) suggest that a relatively high proportion of the variation in BSS (around 41% from the adjusted R^2) is explained by variation in group size. Here the observed data fits relatively closely to the regression value, and therefore suggests a reliably significant correlation where the variance of the dependant variable, BSS, can be explained by the independent variable, social group size. The fact that this relationship still exists after controlling for phylogeny suggests that the scale of birthing sociality is influenced in situ by external sociodemographic factors – in this case significantly by the typical group size for the individuals and species involved. Furthermore, the relatively low residual standard error suggests that the regression model predicts the birthing sociality of primates with a low average error, which combined with the low p-value suggests a highly reliable regression model.

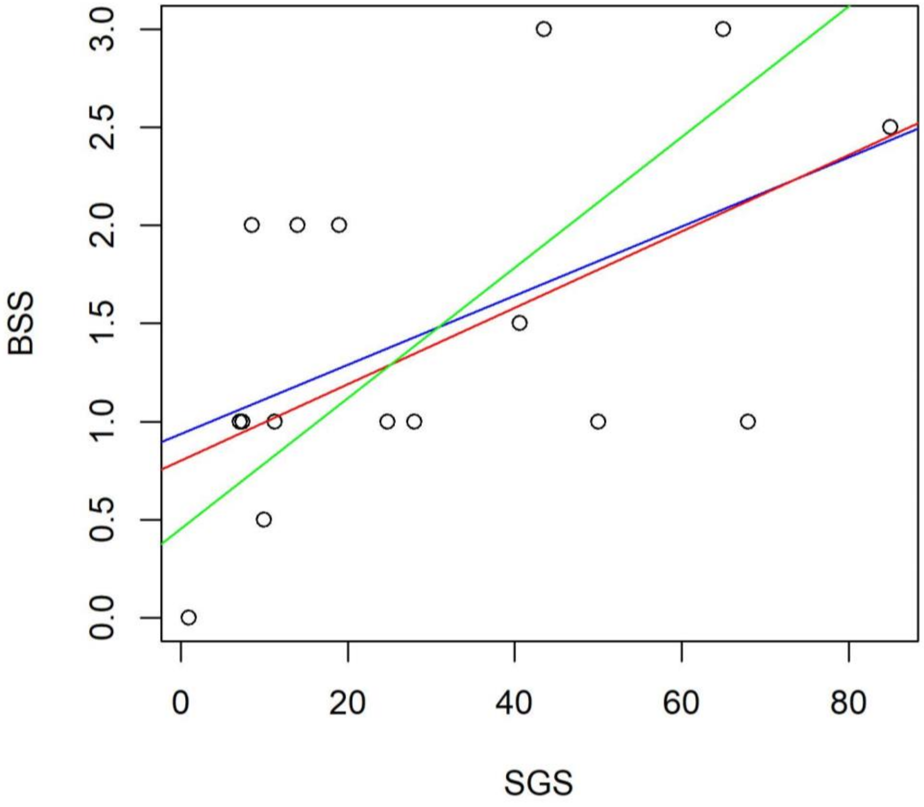


Figure 5.6. Graph depicting OLS (blue line), PGLS (red line) and phylogenetic RMA (green line) regressions for BSS and social group size in Simiformes.

Residuals	**Min**	**1 Q**	**Median**	**3 Q**	**Max**
	-1.1336	-0.4760	-0.1017	0.7502	0.7502
Coefficients	**Estimate**	**Std Error**	**t value**	**Pr(>|t|)**	
Intercept	0.937669	0.300593	3.119	0.00754	
SGS	0.017587	0.007685	2.288	0.03818	

Residual Std Error	0.7642 on 14 degrees of freedom
Multiple R-squared	0.2722
Adjusted R-squared	0.2203
F-statistic	5.237 on 1 and 14 degrees of freedom
p-value	0.03818

Table 5.8. Statistical output for OLS regression of BSS against social group size in Simiiformes.

Residuals	**Min**	**1 Q**	**Median**	**3 Q**	**Max**	
	-1.9931	-1.1129	0.1359	0.8226	2.4013	
Branch length transformations	**Kappa [Fix]**	**Lamba [ML}**	**Lower bound**	**Upper bound**	**95% CI**	**Delta [Fix]**
	1.000	0.000	0.000, p=1	1.000, p=0.007074	NA: 0.878	1.000
Coefficients	**Intercept**	**X**				
Intercept	0.45535038	0.03324263				

Residual Std Error	1.418 on 12 degrees of freedom
Multiple R-squared	0.323
Adjusted R-squared	0.2666
F-statistic	5.725 on 1 and 12 degrees of freedom
p-value	0.0.03396

Table 5.9. Statistical output for PGLS regression of BSS against social group size in Simiiformes, accounting for phylogeny.

Coefficients		**Intercept**	**X**		
		0.45535038	0.03324263		
VCV Matrix		**x**	**y**		
	X	2268.62861	40.00334		
	Y	40.00334	2.50700		
Estimates		**lambda**	**Log(L)**		
		6.610696e-05	-9.172075e+01		
Hypothesis test (after Clarke, 1980: Biometrika)		**R^2**	**t**	**df**	**p**
		0.281368	15.024166	14.273338	<0.001

Table 5.10. Statistical output for phylogenetic RMA regression of BSS against social group size in Simiiformes, accounting for phylogeny.

The statistical results of further analysis using OLS, PGLS and phylogenetic RMA (**Tables 5.8 – 5.10.**) additionally supports the conclusion that the relationship between BSS and social group size is not significantly influenced by phylogeny. The minimal estimated lambda value (≈0) for the PGLS and RMA regression demonstrates that there is very little phylogenetic signal in the observed data, where BSS is suggested by the regression to evolve independently amongst sister taxa. This is a much more realistic lambda estimate than the one produced by OLS. As we can also see, however, controlling for phylogeny again improves the fit of the data and the PGLS regression fits much closer to the phylogenetic RMA than the OLS regression. In essence, the fact that accounting for phylogeny improves the correlation of data, suggests that whilst an excess of deviation and variation around the regression is a product of phylogeny to some degree, it does not account for all of the variation between the Simiiforme samples.

Together, these results suggest social group size is a significant driver of social birthing behaviours amongst primates, with highly prosocial birthing behaviours coevolving in multiple events in distantly related taxa. However, as noted by Boyer et al (2013), in smaller samples of more closely related primate taxa, OLS and PGLS analysis yields much closer results than for larger samples. Here, the autocorrelation is seen to have a much larger effect on larger primate samples, and fits with concerns noted by Nunn (2011:71) where ML calculations utilised in PGLS struggle to disseminate variation caused by relatedness or convergent evolution. Although the PGLS regression does appear steeper, tending towards the line constructed through phylogenetic RMA, this is certainly to a much lower extent. Whether high levels of prosociality evolve in the face of selective pressure from general group size increase, or specifically the affiliative social group size, will be confirmed by the following analysis of population density.

Detecting the relative strength of phylogenetic signal in BSS and social group size

In order to further test the null hypothesis and the likelihood of a relationship between BSS and social group size, an ML model was run using the values for BSS and social group size for the sample of Simiiformes. The complex model produced by BayesTraits estimated a log marginal likelihood value of -107.982, whilst the test correlation model produced a log marginal likelihood value of -112.39. This produces a log Bayesian factor ratio of 8.815904 shown in the below calculation (after Gilks et al, 1996):

$$\begin{aligned}\log \mathit{Bayesian\ Factor} &= 2(\log \mathit{marginal\ liklihood\ complex\ model} \\ &\quad - \log \mathit{marginal\ liklihood\ simple\ model}) \\ &= 2(-107.982 - -112.39) \\ &= 8.815904\end{aligned}$$

From this data run of MCMC (using *random walk A*), the resultant Bayesian Factor of 8.8 suggests strong evidence for h_1 alternative hypothesis, rather than the h_2 null hypothesis (scale of interpretation after Jeffreys, 1961:432). This additional statistical method further confirms the relationship between birthing prosociality and social group size (see **Figures SI.3.1-2** for plots of modelled iterations). Additionally, the use of MCMC run for tree transformation analysis produced a series of lambda values which suggest that there is no significant phylogenetic signal in the birthing sociality data (see **Figure 5.7.**). Here, the lambda value estimates sit overwhelmingly close to 0 rather than 1, with 85.7% of the iterations resulting in a lambda value below 0.5.

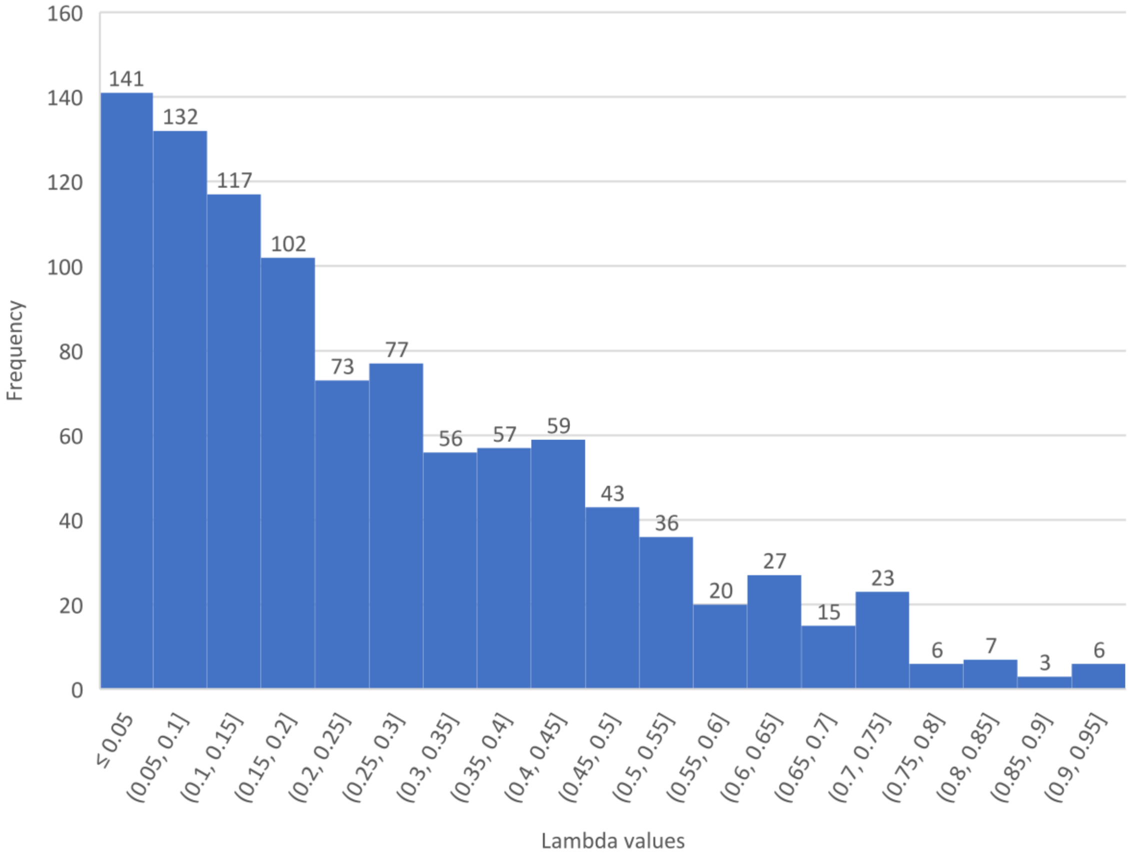


Figure 5.7. Histogram depicting the distribution of lambda values for estimated likelihood of phylogenetic signal in the sample of Simiiformes BSS values, using Bayesian MCMC analysis.

Bayesian model	Log likelihood	Lambda
ML	-19.9339	0.0000001
MCMC	-21.585	0.26043

Table 5.11. ML and MCMC Bayesian model outputs for estimation of phylogenetic signal in the BSS dataset.

This very low mean lambda estimates (see **Table 5.11**) from the iterations performed (n=1000) signifies that there is a statistically very weak signal of phylogenetic contribution towards the variation in BSS in the sample, and supports a rejection of the assumptions of the 'obstetric dilemma hypothesis' – that inherited morphological factors underpin the expression of variation in birthing sociality. Alternatively, these results support a 'social birthing hypothesis' model of birth assistance behavioural evolution where another non-heritable variable (or series of variables) causes the variation in Simiiforme birthing sociality. In this thesis, this is argued to be social group size, as the primary proximate factor in birthing prosociality expression.

Reconstructing ancestral states

Using MCMC modelling to estimate the ancestral state of the last common ancestor (LCA) for all primates sampled, this suggests that there would likely have been a degree of sociality rather than complete absence of prosocial behaviours, with a mean birthing sociality score estimate of 1.28, with the highest log maximum likelihood (-27.804498, iteration 475000) predicting a value of 1.306. The distribution of BSS value estimates, however, suggests a score for an ancestral nodal species which sits in the range of 1-2. The distribution of these estimates is presented below in **Figure 5.8**.

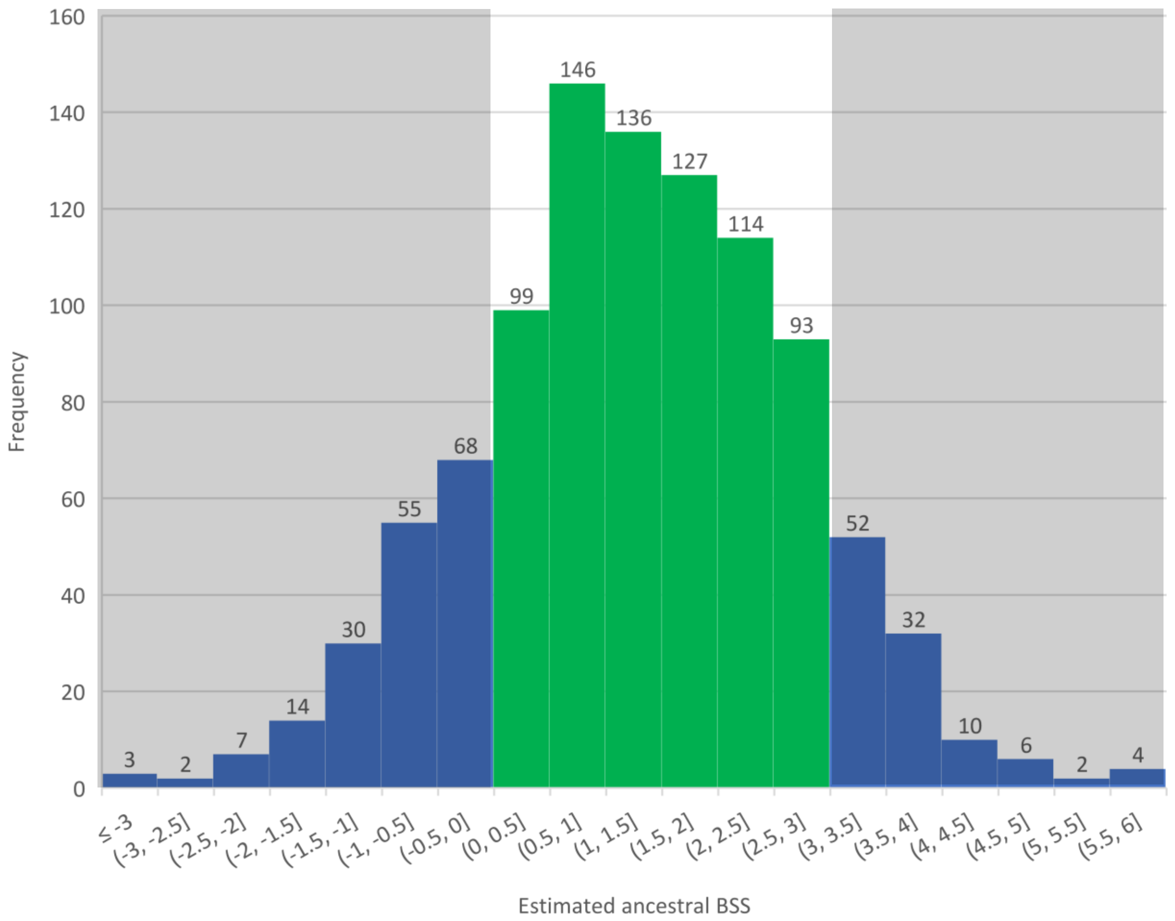


Figure 5.8. Histogram displaying the distribution of estimated ancestral trait values of birthing sociality for ancestral Simiiformes, using Bayesian MCMC analysis. The grey area signifies estimated values for which ancestral BSS scores fall beyond 0 and 3 extremes.

Bayesian model	Log likelihood	Ancestral BSS estimate
ML	-27.804496	1.303716165
MCMC	-28.37642109	1.282366254

Table 5.12. ML and MCMC Bayesian model outputs for ancestral BSS states in a Simiiforme last common ancestor. Note that the MCMC values presented above are mean values from the iterations performed (n=1000).

Here, this is confirmed by both ML and MCMC methodology within BayesTraits, where the ML model estimated a value of 1.303, and the MCMC model predicted a mean estimate of 1.282 and median value of 1.314 (see **Table 5.12.**). Together, these results fairly consistently predict a moderate BSS value for ancestral Simiiformes, at around 1.3. However, whilst the MCMC does suggest a lower value than the ML model, disparity is minimal and suggests an ancestral species to Simiiformes species would have displayed a moderate degree of prosociality during birth. With the highest frequency of iterations between 0.5 and 1 specifically, the results presented support the conclusion that the true value would sit closest to one, or rather that the ancestral Simiiforme state involved a moderate to minor degree of social interaction, with group members visible and within accessible range, but without any direct interaction. Crucially, this suggests that prosocial behaviours would not be absent from ancestral Simiiformes, contra to the consensus of primate behavioural capacity supported by the obstetric dilemma hypothesis. The ancestral history of prosocial behaviours would appear to have much deeper roots than simply recent evolution and emergence among a select few extant nonhuman primates and humans.

Estimating internal nodes in nonhuman primates

Interestingly, the results of further internal node estimation using Bayesian MCMC models suggests higher BSS values in nonhuman primates is more likely for an Old-World monkey ancestor than in apes. Of the 1000 iterations performed, 37% (n=370) of iterations estimated a higher value for an ape LCA than an Old-World monkey LCA, with a mean ancestral BSS estimate of 1.231. However, 63% (n=630) of iterations estimated a higher value for an Old-World monkey LCA than for an ape LCA, with a mean ancestral BSS estimate of 1.554. This is interesting, as it suggests high levels of birthing prosociality, such as those seen in humans and bonobos, may be more derived than similarly prosocial behaviours in extant Old-World monkeys. The significant of these results will be further discussed in the following section.

5.5. Discussion

Neonatal body mass as a proxy for neonatal cranial dimensions

Whilst this small-scale study had a small sample size, the statistical results suggest that neonatal cranial metrics can accurately be predicted by neonatal body mass. Effectively, the results demonstrated that the total body mass of the neonate does correlate significantly with most neonatal cranial dimensions, with the exception of the suboccipitobregmatic and glabella-to-glabella dimensions. Interestingly, these two dimensions are those which do not present in nonhuman primates during descent through the maternal birth canal. Whilst the occipitomental does not also represent a presenting diameter, it does determine the attitude of the neonatal head, as a longer occipitomental diameter would restrict the extension of the head and result in a lack of typical facial presentation.

With the limits of the sample size in this study, conclusions are also limited from the data set in terms of wider trends in other primate species. However, the promising results suggest that a wider study to include a larger sample of primates from other lineages would be of significant value, as an identified relationship between these variables may increase the opportunity and scope for collection of (previously sparse) primate neonatal metrics and data. Furthermore, the application of these results to estimating hominin neonatal morphology would improve the capacity for estimating ancestral hominin neonatal morphology from limited and fragmentary fossil specimens.

However, it is worth noting that within the dataset, two individuals were measured from the same species. These individuals were both Francois langurs, with estimated volumes of 61.15

and 27.18cm^3. However, the second individual was measured post-mortem and whilst the exact cause of death was not available, it is reasonable to suggest that this smaller volume combined with a body weight of less than a tenth of the live individual, indicates the neonate was a stillbirth pre-term. As this was not conclusively determine by the authors as the cause of death, this data point was included within the analysis. By utilising the methodology for recording cranial dimensions alongside body weight, this could support the conclusion of such cases of pre-term birth, with the aim of improving conservation efforts. By identifying conclusive incidents of pre-term birth, patterns of incidence may be also highlighted and mitigated once potential causes are identified.

Whilst half of the individuals were measured live and half post-mortem, the correlation between the metrics body mass, as well as endocranial volume estimate, suggests the state of the neonate does not significantly affect the relationship. This could support the reliability of conclusions drawn, not only from collected post-mortem samples in captivity and in the wild, but also from palaeontological samples of individuals long dead.

The fact that the relationship between neonatal body mass and neonatal cranial metrics crucial to successful at-term delivery exists suggests that these dimensions determining facial presentation in nonhuman primates (following Joulin, 1864) are limited by the allometric scaled size of the neonatal body. The dimensions of the neonatal cranium are limited at term by the dimensions of the maternal pelvis in order to be successfully delivered, and logically the neonatal body mass is allometrically related to the three-dimensional size of the cranium. These results therefore would support a conclusion that nonhuman primate neonatal cranial dimensions (those presenting during birth) are limited by the dimensions of the maternal pelvis. This contravenes the consensus among anthropological and anatomical work that nonhuman primates do not face a significant level of selective pressure on neonatal dimensions in response to the limitations of the maternal pelvis (see Chapter 2 for a wider discussion). Further investigation into this relationship using a wider and more extensive sample would expand on these results, and crucially test this hypothesis. However, the limits of this thesis prevent a wider and larger sale collection of morphological data.

The obstetric dilemma ultimately posits that it was pressures faced by hominin mothers on mortality as a result of increasing CPD, which drove the emergence of birth assistance behaviours. Whilst the results of this small-scale study do show a significant correlation between neonatal cranial metrics, particularly obstetrically relevant dimensions which would affect the severity of CPD, no significant relationship appears to exist between proxy values and birthing sociality. This arguably supports the conclusion that the emergence of prosocial birthing behaviour in primates did not evolve in response to pressures of maternal mortality, as a direct result of CPD. Therefore, these results do not support the predictions of the 'obstetric dilemma hypothesis'. In the absence of significant samples for the hominin lineage and known sociodemographic and life history values, it is difficult to accurately determine if the correlation would be any more or less significant among hominin species.

If neonatal size were associated with birthing sociality, and birthing sociality was driven by pressures from neonatal size and maternal obstetric morphometrics (as posited by the obstetric dilemma hypothesis), then one would also expect to see a correlation between BSS and neonatal size. However, the lack of any significant correlation supports a rejection of the predictions of the obstetric dilemma hypothesis. A brief investigation of this, no significant relationship exists either with neonatal body mass as a proportion of total adult body mass, or adult brain weight as a proportion of body mass (r=0.181, R^2=0.033, p=0.502 and r=0.179, R^2=0.032, p=0.508 respectively – see **Table SI.1.2.**). Therefore, it seems unlikely that obstetrically critical morphology, and specifically the risk of CPD, is a driver of prosocial birthing behaviour in primates. This fits with the conclusions of Kavanagh et al (2011), who found that in vervet monkeys, neonatal size did not predict birthing outcomes (i.e., did not correlate with an increase in mortality). Although many of the stillbirths recorded in the author's study were macrosomatic, with 72% of neonatal deaths a product of dystocia (Kavangh et al, 2011:30), this suggests CPD is still a significant risk to primate birthing outcomes. However, this affect does not seem to influence group behaviour. Since Kavanagh et al's (2011) study was limited to captive primates, research effort dedicated towards the study of wild primate groups could significantly improve our understanding of primate birthing risk, and in turn the understanding for our own birthing outcomes.

Evaluating the 'obstetric dilemma hypothesis'

The relatively weak signal of a relationship between BSS and neonatal body mass after accounting for phylogeny, suggests that the neonatal body mass may have some influence in driving the expression of prosocial birthing behaviour. However, this is again a very weak signal, and cannot be concluded as a statistically significant result. Therefore, this evidence arguably does not support the predictions of the 'obstetric dilemma hypothesis' – that morphological factors do not correlate with BSS, even after controlling for phylogeny. The presence of this weak negative correlation independent of phylogeny, suggests a coevolution of this link irrespective of shared ancestry among primates. Further investigation into the factors influencing this relationship may provide further clues to why smaller neonates are associated to some degree with more prosocial birthing behaviours.

If we were to explore the allometric, heritable relationship between obstetric morphology and factors such as adult body mass (Sharma, 2002; Betti and Manica, 2018; Grunstra et al, 2021) alongside birthing sociality, this may yield a correlation which aligns with phylogeny. This would of course require a larger scale study to obtain morphometric data across a wide variety of primate species. Given the variation discussed in Chapter 2 for modern human obstetric morphology, a significant sample size for each species would be needed to obtain an accurate mean for each species in order to accurately map morphological trends and predict ancestral states. This could then be mapped alongside fossil record specimens, to determine whether fossil morphology correlates with predicted birthing sociality behaviours.

Work by Fischer and Mitteroecker (2015) found that human females with larger adult head sizes were more likely to produce larger brained neonates, but also to themselves have obstetrically spacious pelvic dimensions, as the sacrum protruded less into true-pelvis. This is argued to be an adaptable heritable trait in humans, by widening the pelvic outlet and easing the passage of a larger brained neonate, theoretically requiring lower demands for birthing assistance. This morphological, heritable trait has in fact also been documented for Rhesus macaques (Kawada et al, 2020). Whilst this suggests the relationship is deep rooted within our own and indeed primate ancestry, Grunstra et al (2021) note that hybridised, interbreeding populations (such as overlapping populations of modern humans and Neanderthals), the correlation between maternal pelvic shape typology and stature may reduce after a degree of random mating, where corelation selection is weak and inconsistent (Sinervo and Svensson, 2002). This may be further observed not only in interspecies populations, but also in humans between populations of different cultures, where previous genetic drift between neighbouring populations will have produced alternate morphological means. Indeed, work by Buck et al (2021) on the effect of hybridisation between regional subspecies of macaques, found that admixture actually had a minimal effect on pelvic morphology. Their findings are argued to support the conclusion that this lack of difference, in contrast to *H.sapiens* and *H.neanderthalensis*, highlights the potential role of cultural and behavioural factors in facilitating local adaptations, and neutral genetic divergence. Investigating the relationship between heritable obstetric morphology, and the cultural trends in human behaviour would be of significant interest in understanding the challenges faced by women of alternate contemporary populations. Improving our understanding of these challenges could provide highly beneficial knowledge and aid in delivering positive outcomes for women's health irrespective of socioeconomic status and across all backgrounds.

Given the evidence for relationship between birthing outcomes and sociality, alongside maternal health (see Lowe and Moore, 2014 for review), one might expect to see a correlation increase after accounting for phylogeny. Where maternal health within a population is facilitated by uninherited social status, increased health (and by proxy, observed in correlation with adult female weight), could improve the likelihood of prosocial behaviours directed by the mother and by social group members, alongside positive birthing outcomes. However, the distinct lack of correlation, either before or after correcting for phylogeny, suggests that maternal health at the species and population level, does not correlate with levels of birthing prosociality. This could have particular bearing on improving maternal health, where further understanding of how birthing outcomes are affected by sociality could drive innovations and improvements in clinical and local services' best practice. In primates, the lack of correlation between species typical adult female weight and BSS suggests that primates of all sizes display varying degrees of sociality, and so this must be taken into account for both large and small species in captivity, in terms of provisioning for optimal social environments.

The use of stratigraphic parsimony methodology would be of particular interest additionally in mapping signals of phylogenetic emergence of obstetric morphology and physiology onto stratigraphic (or chronological) data, crucially onto the archaeological evidence of shifts in hominin obstetric morphology and the fossil record. On a finer timescale, this methodology could theoretically also be used to detect signals of inherited obstetric morphology in tandem with archaeological evidence of demographic and socioeconomic change experienced by past human populations, but also ancient and recent historical groups. This would contribute towards a greater understanding of the factors influencing our own species' obstetrical adaptations and plasticity, in response to shifts in socioeconomic status, diet and activity. This methodology was beyond the scope of this thesis, but would be of great value for future investigation.

Both weaning age and gestation length are determined by energetic demands on the mother and energetic requirements for somatic growth of the infant. It therefore would be reasonable to suggest that those species exhibiting relatively slow life histories, with later weaning ages and longer gestation lengths, could benefit from prosocial birthing behaviours which assist both the mother and infant through an energetically costly process. Again, if this prediction were true, we would expect to see a significant correlation between heritable life history factors and birthing sociality. However, there appear to be only weak correlations between these life history variables and BSS, even after accounting for phylogeny. If as predicted by the obstetric dilemma hypothesis, primate birthing behaviour was determined by obstetrical limitations on neonatal morphology, one would expect to see more prosocial birthing behaviour amongst species which exhibit slow life history strategies (with infants born relatively altricial after having gestated for a relatively longer period). Given the evident lack of significant correlation in life history variables tested with birthing sociality, the data presented in this thesis does not support the obstetric dilemma hypothesis. In order to test for a potential correlation between BSS and life history characteristics in hominins, reliable estimates of life history variables such as weaning age would be required. Weaning age and gestation length arguably may present the most stable life history variables in terms of relatively reduced variation between populations, but factors such as age at first menarche and age at first reproduction, are based on a much broader set of factors. Age at first birth, for example, varies widely with socioeconomic status (Rendall et al, 2009), as well as with cultural factors both within and between populations (Gurmu and Etana, 2014). Therefore, the results presented in this chapter do not support the prediction from the ‘obstetric dilemma hypothesis’ – that birthing prosociality does not significantly correlate with life history factors in primates.

However, it is worth noting the disparity between the strength of correlation for weaning and gestation length. Whilst gestation length appears to have a very weak correlation, weaning age does have a weak, verging on moderate level of correlation (though half of that seen for social group size). The results could be argued to suggest that weaning age may have coevolved alongside the emergence of highly prosocial birthing behaviours, both in part due to increasing social network complexity. Where species may evolve slower life histories and by extension later weaning ages, they may similarly display much more prosocial behaviours during birth. The results presented here certainly would support previous findings by Joffe (1997) and van Schaik and Isler (2012:229), where increasing social group size is suggested to facilitate increasing weaning ages. Whether this is facilitated by the increasing capacity of the ‘social brain’ (Dunbar and Schultz, 2021) to manage social networks which promote prosocial birthing behaviours, alongside the provisioning of more altricial infants requiring longer periods of maternal and allomaternal investment, is an avenue of research which requires further exploration.

Sociality and convergent prosocial evolution in primate birth

The relatively significant r and R^2 value for social group size does suggest a positive correlation exists between increasing social group size and increasing BSS, but the not all of the variance can be explained by this relationship, and warrants further investigation. Interestingly, the *G.berengei*, *S.entellus*, *P.hamadryas*, *R.roxellana*, *P.paniscus* and *C.jacchus* samples sit above the regression line based on these values. Given the relatively distant relationships across the simian tree, with three of these five species being from the family Cercopithecidae, but similarly two pairs of closely related subfamily taxa (the homininae *G.berengei* and *P.pansicus*, and the two colobinae *S.entellus* and *R.roxellana* species) being the most relatively closely related taxa. However given the distinct lack of prosociality from other members of theses clades, this may in fact indicate convergent evolution of birthing prosociality, independent of phylogeny.

Interestingly, the higher r and R^2 values for the logarithmic regression suggests that the relationship between BSS and social group size is not linear. Rather, whilst initial expansion of primate group size does increase the likelihood of prosocial birthing behaviours, this increase drops off rapidly as group size grows further still. This suggests that beyond relatively moderate group sizes social group size exerts a decreasing effect in terms of raising birthing prosociality. Instead, other factors may limit the increase of the BSS to increase much over 2.5. It is possible that the quality of these social networks reduces with the number of social group members, after which prosociality does not increase further without addition mechanisms to manage these connections. This would be supported by Dunbar and Schultz (2010), who reviewed the potential for quantifying the quality of primate social networks. The fact that humans sit above the expected social value for their social group size, would fit with the consensus that humans have evolved these necessary social mechanisms to manage such a high number of connections.

As discussed in the previous chapter, a number of factors may influence the decision by social group members to interact and remain in close proximity to the mother, and vice versa may influence the decision of the mother to remain within close proximity and facilitate or instigate prosocial interactions. The results presented above would support the hypothesis that not only does a relationship exist between sociodemographic factors and birthing prosociality (which is to be expected), but that it is the quality of the social networks rather than volume of interactions which mediates the level of prosociality. This is also consistent with the observations of primate birthing events, where those interactions between adult conspecifics are usually between closely related or highly affiliative group members, both male and female (though primarily female). The lack of a distinct correlation with population density also indicates that birthing prosociality does not appear to be influenced by the frequency of likely interactions between members of local populations. Rather, the correlation with social group size implies that it is the quality of associations between the birthing mother and social group members which influence and determine the expression of prosocial birthing behaviours. Whilst a partial correlation between BSS and social group size controlling for population density does increase the strength of the correlation and significance level, this increase is relatively minimal. Whilst population density may explain some of the variance, these results support the conclusion that it is the social group size and therefore capacity for strong affiliative bonds which influences birthing sociality, rather than the number and frequent chance of interactions. The mother may facilitate and solicit known individuals to interact, and known individuals may actively seek to engage with the mother during parturition.

Given the lack of significant correlations after correcting for morphological variables, the increased strength of the positive linear regression seen after correcting for population density, neonatal body mass and weaning age may suggest that the relative altriciality and need for post-natal care of the infant may drive the expression of prosocial birthing behaviour. Whether the capacity and drive for altricial social care and allomaternal care of the neonate is facilitated by these prosocial interactions during birth is difficult to determine. The partial correlation results presented may support the hypothesis that prosocial birthing behaviour coevolves with increased levels of allocare which allow for extended weaning periods of neonates. This extended period of weaning and development has been hypothesised to correlate with increases in neonatal body mass (Bowden et al, 2015; Samuni et al, 2020), and so it is logical to propose that prosocial birthing behaviours may directly facilitate an increase in neonatal body size.

Second, the degree of population density may negatively impact on the quality of social interactions, as the increase in population size may increase the fluidity of social group dynamics, reducing the capacity for developing strong, long-term affiliative bonds which may last until the female has become pregnant and reached full-term, and then provide the opportunity for the expression of prosocial birthing behaviours. Further direct, long-term observation of wild populations and the interactions between social group members in varying population sizes and structures would provide further clues as to the nature of these interactions between life history and sociodemographic variables.

The lack of a significant phylogenetic component in the relationship between BSS and social group size, supports the conclusion that it is most likely that prosocial birthing behaviours are learned through observed or communicated experience rather than determined by heritable traits. Furthermore, the prevalence of such behaviours despite the lack of observed or reported obstetrical difficulties, supports a ‘social birthing hypothesis’ model in which prosocial birthing behaviour facilitates an increase in obstetrical difficulty, and any emerging necessity for assistance (rather than such difficulty driving the evolution of birth assistance behaviours).

The lack of correlation with population density despite the influence of social group size is particularly interesting, as the results presented suggest it is not the density and by extension chance of social interactions which determines the sociality of birthing behaviour. This correlation could indicate that the quality of social networks, rather than the frequency of potential interactions which influence the expression of prosocial birthing behaviour. In this scenario, strong, affiliative social networks which factor into individual decisions to proactively react to birth and engage with the parturient mother, rather than individuals encountering a birthing female and interacting reactively to parturition. Further observational research into the nature of these interactions would provide greater understanding of the role of quality social networks in birthing, both in terms of proximate causes for individuals to interact with the mother, and conversely what influences the mother to accommodate such interactions.

Such a model of birth assistance behaviour emergence further supports the need for provisioning of social birth environments for both human and nonhuman primate mothers, with of course a level of ad-hoc clinical or veterinary support where appropriate for emergencies (and in some cases for assurance). In our own evolution, the provisioning of supportive birth environments would surely have been routine in closely bonded groups, with high levels of allocare and intergenerational support for nulliparous and parturient females. From the linear regression through OLS, PGLS and phylogenetic RMA, we can also see that for all social group sizes, the regression predicts some level of birthing sociality, never estimating a value of zero. Whilst this is unlikely to be the case in real-world observations, the lack of social group members would of course minimise the opportunity for such interactions to occur, and therefore result in low BSS scores for the species. It is therefore arguably the case that the relationship between BSS and social group size is exponential rather than simply linear, with a threshold and optimal peak for prosociality to occur.

Whilst maximum parsimony was not utilised within this study, the application of this methodology to modelling the emergence of the presence or absence of obstetric morphology in tandem with social birthing behaviours would be of merit. As discussed in Chapter 3, cetaceans in particular have also demonstrated prosocial birthing behaviours, despite their highly divergent morphology from primates (McBride and Kritzler, 1951; Beland et al, 1990; Notarbartolo-di-Sciara et al, 1997; Stacey and Baird, 1998). Where sufficient birthing observations are possible to similarly quantify BSS, then these potential outgroups could provide a reliable sample necessary for parsimony methods, and deeper insight into the phylogenetic trajectory and history of obstetrically relevant morphology in mammals. Whether the correlation between birthing prosociality and larger group size is a product of natural selection (in the face of selective pressure from an extrinsic or intrinsic factor), or the product of behavioural drift, remains unclear. Any conclusive models of costs and benefits to birthing prosociality would serve to provide a context on which to map prosocial behavioural traits, and potentially identify coevolutionary relationships between morphology and behaviour.

Social transmission of prosocial birthing behaviour

Given what we know of variation between human birthing behavioural variation between cultures (see Selin and Stone, 2009), evidence for culture in other nonhuman primates could imply that birthing behaviour may be subject to variation in cultural memes. An ever increasing body of evidence clearly demonstrates the systems and mechanisms by which cultures emerge in nonhuman primates (Matsuzawa, 1993; Perry et al, 2003; van Schaik et al, 2003; Leca et al, 2007; Watson et al, 2018:213), and indeed in other animals (Krutzen et al, 2005; Allen et al, 2013; Whiten, 2021), where group-typical patterns of behaviour are shared by members of the same community and are socially learned and transmitted (Reader and Laland, 2003:148). What perhaps defines human culture as ‘exceptional’ is the capacity for cumulative culture (Dean et al, 2014), whereby the transmission of knowledge builds upon previous experience and knowledge by others. Whiten (2005) referred to this social transmission as a form of ‘second inheritance’ where individuals may gain the benefits of transmitted information while minimising potential cost and risks. Although this form of learning can be detrimental, where newcomers to social groups may adopt and conform to the customs and behaviours of their new group, even if previous behaviours conferred greater benefit (Leeuwen and Haun, 2013). Whether cultural variation, if identified, confers adaptive benefits to external pressures on birth in nonhuman primates, or indeed among humans, remains to be seen. Cultural patterns of behaviour may be identified through long-term study of neighbouring wild populations, with the potential for shared and unique behaviours exhibited by primate groups. Whilst this thesis is limited in terms of studying multiple neighbouring wild populations, the evidence highlighted for variation within species in behavioural expression, could indicate the conditions necessary for social birthing behaviours to be culturally influenced.

As reviewed in Chapter 4 and observations shown in this chapter, juveniles appear in the wild to be afforded many opportunities to observe births in social primates. This opportunity for observation and experience is of course crucial for the formation of individual experience of birth, as well as building stable cumulative cultures within social networks. However, the transmission of potential birthing cultural traits may be difficult between groups, in the absence of strong philopatric and matrilineal associations. In species where females transmit from natal groups, we may expect to see higher variation in birthing behaviours, where patterns of behaviour are not transmitted with exiting females, and instead stay within the collective culture of the natal groups. Therefore, any identified trends between individuals displaying prosocial behaviours and genetic affiliations on a finer, population level would be of significant interest, in terms of detecting the potential transmission of primate birthing behaviour through populations.

Whilst much of the focus on primate cultural expression has been on foraging techniques, numerous instances of 'medical' behaviours have been observed, whereby primates are seen to inspect wounds and in rare instances self-medicate with local flora and even fauna (Huffman, 2001; de Roode et al, 2013; Morrogh-Bernard et al, 2017). Interesting, a recent study by (Mascaro et al, 2022) found that wild chimpanzees at Loango National Park in Gabon, would inspect and insert crushed insects into the wounds of injured group members. This highly prosocial display of behaviour, considered to be a firm example of primate culture by the authors, would support the theoretical potential for birth assistance behaviours to be added to the suite of primate cultures.

The evidence of a lack of phylogenetic signal presented in this chapter may suggest a lack of a genetic component, however, a genetic signal between populations of the same species, may indicate a cultural transmission of the behaviour. The use of mitochondrial DNA may be of great interest in identifying the transmission of birthing behaviour along matrilineal lines. Theoretically, the transmission of cumulative knowledge between closely related females would be the most obvious method for the conservation for birthing behavioural norms in wild populations. However, in captive populations the maintenance of matrilineal affiliative networks for this specific reason is likely not well founded in guidance and policy. Alternatively, close affiliative non-kin relationships are at least promoted for social primate species, where possible. In order to maintain effective cumulative knowledge and understanding of birthing among primates in captivity, it should be strongly encouraged to maintain strong affiliative networks for females, ideally along matrilineal lines or at least through ensuring females are paired with sociable non-kin.

An important aspect of previously observed births among both wild and captive populations of primates and summarised in **Table 5.3.**, is the description of juvenile behaviour and the proximity of juveniles to the birth event. Of the 17 narrative observations presented in this chapter, 10 birth events involved interactions with juvenile group members, with two of the seven observations involving juvenile interactions occurring in captivity. These observations in the data was unexpected, though perhaps not surprising if the juveniles were previous offspring of the parturient mother. The mother may have intended to still remain able to guard these individuals, however the observations do not suggest this to be the case. Rather, juvenile interest seems to be the active component in these results, particularly since these interactions appear in wild samples with a lack of potential enclosure restriction influencing proximity decisions. Whether these are previous offspring of the birthing multiparous mother, or those of another conspecific, the fact that over half of these birth events involved juveniles raises an interesting implication for understanding how primates may acquire birthing knowledge and understanding, prior to becoming pregnant themselves or without the capacity for personal experience.

Much like the accepted consensus for how social play can help prepare individuals for future social interactions (see Mayhew et al, 2019), direct observation and interaction with birthing mothers and neonates is surely crucial to the future understanding of group birth. Whilst many captive institutions will attempt to emulate similar group structures as documented and typical for wild populations, limits of size, resources and other factors prevent the reconstruction of sociodemographic environments experienced by their wild counterparts. Reproductive rates are therefore likely to differ from wild populations, and with intergenerational overlap uncommon, juvenile females born in captivity are unlikely to have experienced a birth prior to the point at which they themselves give birth. It’s therefore reasonable to assume that in captivity, exposure and opportunity to learn about birth from observation even in its most simple terms are minimal. This lack of first-hand experience and opportunity for learning is a potential factor driving the expression of antagonistic and detrimental behaviour by primates towards neonates and birthing mothers. If we were to assume a similar scenario among humans where a female was raised to adulthood without having experienced birth or any knowledge of the process, and was subject to either a group member going through labour or experiencing it themselves, is it at all surprising that individuals would react with shock, anxiety, and hostility to the neonate?

With regard to the bearing of juvenile learning and exposure to the birth event, and the transmission of birthing knowledge among humans, the results of this chapter highlight a number of areas for further discussion which have previously been absent from the literature. In particular, the longevity of human females is widely theorised to have resulted in intergenerational populations being commonplace among early hominins. Therefore, as seen amongst wild primate groups, juveniles would have had considerable exposure to the birth event, and opportunities to gather information from direct observation, and with the advent of more sophisticated communication and language, this could be supplemented with verbal transmission of knowledge and expectations. This may have been a significant factor facilitating the increase in social complexity and brain size seen in hominins, and certainly cannot be discounted. Whilst this is difficult to test, research into the source of birthing knowledge and experience among humans today may shed light on the potential effect of group structures on birthing outcomes during our ancestral history.

It would be of particular interest to observe more births to species which typically live in relatively solitary groups or pairs, where the opportunity for observing birth is rare (e.g. for many lemur and loris species, and orangutans which typically live solitary or single familial pair groups). Although with species such as *Microcebus murinus* which typically forage alone at night, females will nest with and ‘park’ infants in communal nesting sites with other females during the day, as a form of cooperative breeding (Eberle and Keppler, 2006). These communal sites, while spending much of their time in isolation, may provide juveniles opportunity to observe births where females return to labour at these safe nesting sites.

Lastly, given the large body of research dedicated to primate experiences, social dynamics, bonding, and learning, it seems strange that any real understanding of the experience of primate mothers is significantly lacking (though see Hrdy, 2016 for a review of postpartum behaviour). As birth forms a crucial and primary focus for breeding and conservation efforts, understanding the behavioural and psychosocial aspects of the birth event for both mother and group members is key to ensuring the survival of endangered species, as well as providing optimal and enriching environments for captive populations. Further research into levels of stress among primates with varying group structures, around the timing of birth, will help inform on appropriate and supportive care for females and neonates in captivity among breeding populations, as well as in ensuring positive social dynamics across captive groups essential to conservation efforts.

Applications to understanding human social evolution

Together, these results suggest that more prosocial birthing behaviours are most likely to have co-evolved across multiple lineages independently, rather than through common descent. Given the lack of any evidence of phylogenetic signal in the birthing sociality score, this suggests that the predictions of the ‘obstetric dilemma hypothesis’ (that obstetric morphological demands drove the evolution of prosocial birthing behaviour in humans) are not supported by the primatological evidence presented. Birthing sociality does not coevolve alongside phylogenetically determined traits such as obstetrical adequacy, but rather relative prosociality evolves independently amongst taxa. An alternative ‘social birthing hypothesis’ is therefore argued to portray the likely evolutionary scenario more accurately for the emergence of highly prosocial birthing behaviour in humans and nonhuman primates. The preceding high degree of sociality and formation of closely affiliated social networks allowed for the expression of these prosocial, interactive behaviours on the part of both the mother and social group members, in turn facilitating increasing difficulty of birth and increasing CPD observed in the hominin lineage.

Given the aforementioned lack of phylogenetic signal in the data for prosocial birthing behaviour, it would seem likely that the reconstructed estimate of Simiiforme ancestral state (of around 1.3) is unreliable. As the correlations between social group size and birthing sociality suggest, other variables are better predictors for the level of prosociality observed in primates. However, the interesting findings of internal node analysis, where the results support a higher level of birthing prosociality in an Old-World monkey LCA than for apes. Whilst this certainly fits with estimates of higher birthing prosociality and larger social groups sizes, which are typical monkey populations exist in large social networks (Chapman and Teichroeb, 2012), the high degree of prosociality and assistance seen in humans and bonobos therefore presents an interesting puzzle. If these estimates can be considered reliable, then this would suggest BSS values in humans are more derived from an ape LCA than for similarly prosocial Old-world monkeys from their respective LCA. For primates such as spider monkeys, where infanticide risk also increases with social group size (Dunbar, 1984; Borries, 1997; Crockett and Jackson, 2000; Steenbeek and van Schaik, 2001), this may explain why prosocial birthing behaviour emerges, as a strategy to mitigate against infanticide risk by increasing 'social guarding'. Further exploration through the collation of further sociodemographic variables for a wider sample of primate taxa will aid in uncovering the exact costs and benefits of prosocial birthing behaviours, and in turn model the potential ancestral states in extinct primates.

In order to theorise what birthing behaviour would have looked like for the LCAs of extant primate taxa, social group size would be best place to predict this based on the results presented in this thesis. Social group size in itself is determined by a number of external and internal factors (see Dunbar and Schultz, 2021 for a review of social group size predictors), and further research could provide further clues to model and predict ancestral states of birthing behaviour among extinct primates, as well as for extant taxa for which direct observations are lacking (i.e. amongst Strepsirrhines and Tarsiers). Given the variety of social dynamics across the Strepsirrhine and Tarsier clades, it is reasonable to assume a vast array of social birthing behaviours and species typical patterns of behaviour. For example, many nocturnal prosimians are solitary (Williams, 2015:295) and would likely display minimal to no prosociality during birth. However, given the highly affiliate and complex social dynamics of many lemur species, such as *Lemur catta*, it is surely highly likely that individuals will display highly prosocial birthing behaviours – particularly given their matriarchal group structures. Although in *L.catta*, female-female competition is also relatively high (Sauther, 1993:141; Ichino and Koyama, 2006:233), and so sociality during birth may be restrictive compared with sister taxa with lower between-female competition, similar to the differences observed between closely related but socially dichotomous chimpanzee and bonobo groups (Gruber and Clay, 2016).

In order to apply this line of reasoning and investigation to our own hominin ancestral lineage, we must first identify the most likely model of social structure and affiliation amongst extinct hominin species. Luckily through the advent of significant steps in mtDNA and ancient DNA sequencing inferences on population modelling, we can theorise and glimpse the sociodynamic nature of early human social structure (e.g. Neanderthal patrilocality reported by Lalueza-Fox et al, 2011). By utilising the methods employed in this study, we can similarly reconstruct the sociodemographic characteristics of ancient populations, in tandem with predicted species-typical behaviours. However, whether these behaviours were highly variable in their expression between populations and even local social groups, would require a much deeper understanding of other human-exclusive factors determining the expression of birthing behaviour. This could include the complexities of social dynamics and language, or cultural norms and taboos.

Given the lack of phylogenetic signal in the data presented in this chapter, ancestral reconstruction using ML and MCMC is unlikely to be an accurate determination for the ancestral state of Simiiformes birthing sociality. Alternatively, the emergence of prosocial behaviours among extant primate taxa (both at the species and local population levels) with larger social group sizes, suggests that ancestral species with typically large, close-knit social groups would also most likely have displayed highly prosocial birthing behaviours. Whilst this is difficult to test for archaeologically, in hominin evolution the evidence of social networks from lithic assemblages (Gamble, 2008; Aubrey et al, 2012; Rios-Garaizar, 2020; Aubry et al, 2022) would indicate the necessary social networks for the expression of prosocial birthing behaviours. However, given the evidence presented in this thesis for the evolution of highly prosocial behaviour in multiple clades, it is reasonable to assume that early hominins, likely also forming large and closely bonded social groups (Gamble et al, 2011), would have typically demonstrated highly prosocial birthing support. Moreover, the variation between different populations, would also have followed similar trajectories of cultural diversification and divergence. Further analysis of the common and differentiating facets of contemporary human birthing behaviours across cultural boundaries, would provide a significant insight into the factors driving alternate cultural traits. Whilst this was beyond the scope of this thesis with a specific focus on primate behaviour, future exploration of anthropological and ethnographic data could begin to answer the question of what drives the uniqueness of human birthing cultures across the globe.

With the lack of evidence for a phylogenetic component for birthing behaviour prosociality, learning through observation and knowledge exchange seems the most likely explanation for the transmission of birthing behaviour between generations and across populations. As discussed in Chapters 2 and 3, practices of course vary between contemporary human populations, with varying understandings of and attitudes towards the birthing process. A wide body of work in anthropology has demonstrated links between socioeconomic status (Kutty et al, 1993), local food traditions (Ramulondi et al, 2021), shared religious rights and beliefs (Magana and Clark, 1995), and even modern popular culture and social media (Dekker et al, 2016). Therefore, we should expect similar patterns of variation to have occurred between and even within ancestral hominin groups. Any shared behavioural traits would have arguably formed the basis of birthing ‘culture’ among our ancestors, and the factors driving this variation in culture would be of particular interest to evolutionary anthropologists.

Going back to the results of internal ancestral node analysis, the suggestion that ape birthing prosociality may be more derived than for Old-World monkeys, may suggest that humans and bonobos may indeed have faced unique and directed pressures driving the emergence and establishment of highly prosocial behaviour, and in particular for hominins, a morphological link with birthing assistance. Here, the framework for the evolution of specifically medicalised birth assistance, a level of prosociality beyond that of other primates as suggested by the obstetric dilemma hypothesis, may explain the more derived emergence of birthing sociality in humans and prosocial apes. Where the establishment of higher and more socially inclusive events may have characterised early hominin births, the increasing cost from CPD risk (due to increasing neonatal brain size and restricted maternal birth canals) faced by early *Homo* could have been the effective catalyst for more interactive and dependant social birthing behaviours, such as midwifery. However, the result of this chapter, and previous results within this thesis, underpin the fact that prosocial birthing behaviours are present in nonhuman primates, and were likely present in ancestral hominin and primate species. The evolution of birthing assistance is therefore argued by thesis to be most accurately modelled by an alternate ‘social birthing hypothesis’.

It is reasonable suggest that, given the evidence of extensive social networks throughout human evolution (Hill and Dunbar, 2003; Fehl, 2011; Dunbar, 2012; Atkisson et al, 2020), that prosocial birthing behaviour would have been a characteristic feature of birth in our ancestral history. The establishment of deep rooted and diversified cultural norms with regard to birthing practices across populations today, may indeed be the product of sustained cultural evolution of birthing prosociality, with the divergence coupled to sociodemographic context. Given the intricacies of human social networks, it is reasonable to suggest that kin selection alone may not explain this relationship, as many of the prosocial interactions do not appear to have been between kin, but rather close affiliative group members. This would place these findings within the predictions of the ‘cooperative breeding hypothesis’, whereby prosocial birthing behaviours by group members benefit maternal reproductive success. Relying on kin for the provision of birthing support would be evolutionarily restrictive, whereas the more flexible and responsive nature of affiliative group networks could provide the necessary support as needed for females leaving their natal groups. Moreover, soliciting social support on top of potential kin support would of course increase the level of support for birthing mothers, and therefore provides additional reproductive fitness from facilitating the support.

In addition, a previously undiscussed topic in previous discourse involves the integration of pyrotechnology and origins of fire-use among early humans. With the extension of daylight hours and ability for individuals to observe one another at night or in dark places such as caves or constructed shelters, other groups members previously unable to witness births (which are widely demonstrated to occur primarily at night) would now be able to witness and share in the event itself. Assuming positive reception, this may have further encouraged cultural development of prosocial birthing practices between and within human groups, as entire social groups would now be able to witness and in theory take part in the social birth event, with the use of fire and artificial lighting. With the use of lighting during birth, this would also have the added benefit of allowing more direct birthing assistance and proto-medical intervention, in order to assist the mother and infant in the event of any complications. However, with the absence of evidence for fire use prior to ~1.5Ma (Gowlett, 2016), we must assume that this practice would not have been widespread in species preceding the emergence of *H.erectus*. Therefore, any reduction in maternal and neonatal mortality from intervention during difficult births would not have been until after the establishment of significant fire management technology, and once such behaviours were common enough to effect survival rates of both mothers and neonates. From an archaeological perspective, evidence for this would only be indirect at best, as such behaviour would leave no trace within site floors and only involve minimal artefacts prior to the advent of more culturally significant tools and artefacts among modern human populations. Therefore, we must rely on examples of behaviour from extant primates to theorise scenarios for the emergence and establishment of the diverse examples of social birthing behaviour and culture among human populations today.

A deeper cross-cultural analysis of the trends and patterns of behaviour between and within human cultures existing today, and within historical ethnographic literature, would provide further insight on the factors driving the expression of elements of prosocial birthing behaviour and the diversification of these elements among populations of our species. Whether these factors include geography, diet, ecology, inherited morphology, or socio-normative heritage and tradition, or even superstition, could be tested through a diverse investigation, again utilising a methodology similar to that employed in this thesis. However, given the scope of this variation, this falls beyond the limits of this thesis.

Contemporaneously, the findings of this analysis of primate behaviour suggest a deep-rooted capacity for highly prosocial birthing behaviour within our shared ancestry, and therefore have a bearing on understanding the necessity of sociality in our own successful birthing experiences. The commonality of such behaviour across multiple distinct lineages would indicate that multiple shared ancestors in human and primate lineages would have expressed similarly prosocial birthing behaviour. Potentially, ancestral and branching species would have experienced similar factors driving convergent evolution and selection for the expression of these traits. By understanding these proximate and ultimate factors driving prosocial birthing behaviour, whether inherited or learned, we can better understand the conditions needed to ensure we ourselves experience the best possible outcomes for both parent and child and both in terms of reducing mortality risk and providing the best possible social care and development.

Limitations

To test the underlying prediction of the obstetric dilemma hypothesis – that birthing sociality should correlate with obstetrically relevant morphology – this thesis relied on a series of proxy variables for (specifically) metrics of obstetrical capacity in primates. Chiefly, the use of neonatal body mass as a proxy for neonatal cranial morphology which presents during birth. The distinct lack of available obstetrical metric data for a wide variety of primate species hampers any direct assessment of the correlation between predicted birthing difficulty (chiefly CPD) and primate birthing behaviour. With the limited species for which data is available, coupled with the limited observations of primate behaviour, few taxa have data available on both variables. This necessitates the use of analogous data for morphology – in particular, the measurement of neonatal cranial morphology in extant primates. As the sample was limited to include New World and Old World monkeys, the conclusions drawn on wider primate taxa are hampered by this species bias. However, given the obvious need in primates for neonatal dimensions to conform to limitations of the maternal pelvis, it would be safe to assume that a similar trend between neonatal cranial dimensions and maternal birthing dimensions would exist. Therefore, neonatal morphology would reasonably be assumed to correlate closely with maternal dimensions. However, the degree of standard deviation in this, whilst potentially minimal, would have significant impact at an individual and species level (in terms of the degree of CPD). The heritability of morphological traits likely contributes a significant amount of variation of the sample, and future analysis would benefit from further phylogenetically independent modelling of the relationship. However, the limitations of this thesis in terms of sample size and scope prevent further investigation here.

The limitations in this study are also acknowledged to include the nature of the study in relying on secondary observations of primate birthing behaviour. This secondary analysis consequently would be limited by the variables and measures of the original studies, as relying on second-hand data for the analysis could also arguably be a limitation on the reliability of the measured BSS values. Determining the BSS value relies on an accurate recording of the proximity of group members and the number of individuals, as well as interpreting their published description of events. Furthermore, the sample size of published birthing observations where social context was described remains small and variable in terms of detail and methodology. By utilising a standardised and generic method for determining BSS from observations published by multiple authors from multiple sources, this approach has attempted to limit the impact on the reliability and credibility of the values central to this thesis.

The limited sample size is also a possible source of discrepancy in the results presented in this thesis. Given the difficulties of gathering direct observations of species which for the most part give birth at night, there is an inherent restriction in opportunities for data collection which is difficult to overcome. Whilst an attempt was made to observe further birthing events in captive primates, this ultimately provided a significant challenge and did not yield successful observations (this is further explored and discussed in the Appendix). Future deep and extensive research following a more homogenous and standardised methodology to collect primary data would improve the validity of these qualitative observations, but would require a long-term study able to identify pregnant individuals, estimate due dates, provide accurate and substantial information on social network dynamics, and of course to observe birth events during non-daylight hours. This research programme would also need to be caried out on numerous species to ensure that a useable comparative database is established.

One limitation of the study is the collation of social group size data – in terms of what defines a social group. This feeds into Nunn's (2011:56) observation that mathematically, the use of such phylogenetic methods are only estimates based upon existing data, theory and assumptions of evolutionary process, and are not observable data themselves. These estimates also may rely on statistical and gathered data, which may themselves be tentative in accounting for error. In attempting to measure social group size, this interestingly relies on a consistent and repeatable method for identifying members of the same social group, and what constitutes a social group member rather than a population level, unaffiliated group members. However, given the strength of the correlation observed between social group size and birthing sociality independent of phylogeny, it would seem unlikely that this correlation is generated by chance.

The majority of data were obtained from the PanTHERIA (Jones et al, 2009) database of social group sizes, collated from other prior sources in turn, and supplemented with data where missing from the PanTHERIA dataset. These values themselves are often mean values from multiple samples of observed data, and wild or captive primate social groups are unlikely to have the exact same number of individuals. Moreover, the use of social group size and other variables from wild primates, compared with scoring social birthing behaviour observed from both captive and wild species, may present some unreliability in the correlation observed. As this research aims to identify any patterns of species-typical behaviours in order to inform on the evolutionary trajectory and ancestral state of primate birthing norms, this assumption of similarity between wild and captive primate birthing is arguably justified. Moreover, this assumption follows on from the assumption of the obstetric dilemma hypothesis in assuming that such behaviour is the product of innate, heritable mechanisms, rather than a culturally transferred and learned behaviour between primate individuals, both with and between social groups. Given the widely observed variation in cultural birthing practice among human groups across the globe both in space and time, it is likely that extant primate species and certainly our hominin ancestors would have also displayed a degree of variation in practiced birthing behaviour. Further study of course could investigate the level of heritability or learned influence of birthing behaviour between primates, but the limitations of sample size prevent further investigation here.

The relatively small sample size of the data also may have introduced bias in error produced by ML and MCMC models. However, given the lack of observed data available on group and individual responses to birthing, this was unavoidable and therefore attempts to model the evolution of birthing behaviours must rely on relatively small sample sizes to date. As previously discussed in Chapter 3, primate birthing primarily occurs during nocturnal hours, and many of the observations are a product of good fortune in observing a live birth. Whilst captivity may provide greater opportunity to observe pregnant females and their conspecifics, it is difficult to maintain both a holistic and ethically compliant environment alongside guaranteeing the exact location of the birth and therefore placement of observers or camera equipment. This will be further discussed in the Appendix, however it must be noted that future study of primate birthing behaviour will greatly benefit from meticulous observation and recording of individual and group behaviours in both the wild and in captivity.

Nunn (2011:55) notes that among the limitations of phylogenetic reconstruction is the inability of phylogenetic methods to predict the changes which occur along reconstructed branches (between the nodes). Rather, phylogenetic models predict a beginning and end state between emergent species or populations. Secondly, without evidence of extinct lineages or clades, phylogenetic analyses will only reconstruct trees of known relationships. In which case, extinct lineages are usually "pruned" from estimated trees (Nunn, 2011:55). This pruning can unfortunately create sampling biases affecting the outcomes of analyses, as the outcomes of reconstruction are determined by estimated values for node species. Where data are unavailable, extant species branches may also be pruned, further skewing branch construction for species with known values. With some values missing for certain species (in particular for *Alouatta guariba* and *Gorilla berengei*), this omission from the models would likely have had an effect on the estimation of phylogenetic signal in the data sets, as well as the prediction of nodal values of a hypothetical Simiiforme LCA. Further modelling which can utilise regressed values of birthing sociality from social group size or other potential correlating variables could improve the reliability of these models, however due to the limitations of the available data, such modelling was not performed. Additionally, Fortunato and Mace's (2009) study of Indo-European marriage practices using ML comparative analysis noted that within this methodology, if societies share cultural traits along ancestral lineages, these may not be picked out by ML models as independent data points. The authors suggest that the use of comparative samples from genetically diverse populations may mitigate this potential issue, for which comparisons between primate taxa may be unaffected, but comparisons between populations may be affected. Within the methodology utilised in this thesis, the sampling of populations with relatively distant ancestry would avoid this bias in ML comparative analysis.

Lastly, branches are constructed as displaying a single variant of a trait for that period of branching as a single snapshot in time (Nunn, 2011:56). However, in reality this may not be the case, as populations of a branching species trait may display a broad array of variations along that event, with a species typical average shifting between discrete or continuous values. In particular from the data presented in this chapter, the modelling of birthing behaviour has utilised methods which treat birthing sociality scores as both continuous and discrete values. Interestingly, both methods result in conclusions that birthing sociality is not determined by phylogeny, but rather appears to coevolve with social group size. This does reflect the predictions of evolutionary variation argued by Nunn (2011), as it would be reasonable to assume that throughout the primate family trajectory, social group size was highly dynamic, and therefore would have resulted in a vast array of primate birthing behaviours and strategies.

5.6. Conclusion

The clear evidence of prosocial, human-like birthing behaviours by nonhuman primates suggests that not only is the emergence of highly prosocial birthing behaviour not driven by birthing difficulty (as the product of obstetric morphology), but that prosociality and assistance during birth has likely evolved across multiple primate species deep in the evolutionary past. However, the lack of significant correlations between morphological variables and birthing sociality questions the implications of the obstetric dilemma – that it was an emergence of obstetrical difficulty which in turn drove the emergence of birthing prosociality uniquely in the hominin lineage. However, the results do suggest that nonhuman primates face selective pressures on neonatal cranial dimensions which present during labour, and suggest that similar evolutionary pressures and mechanisms by which to minimise CPD are shared with other primate taxa. Together, the results presented in this chapter support the central prediction 'social birthing hypothesis' over that of the 'obstetric dilemma hypothesis' – that sociodemographic factors, not morphological or life history factors – which correlate with BSS. The lack of significant correlations between BSS and morphological or life history variables, even after correcting for phylogeny of species, supports the conclusions that the 'obstetric dilemma hypothesis' does not accurate model the evolutionary emergence of prosocial birthing behaviours in primate, and indeed hominin evolution. The correlation between BSS and, specifically social group size over population density, suggests that affiliative networks play a significant role in influencing social birthing behaviours.

The results presented in this chapter further highlight the unique and significant role of social group size as a factor driving the expression of prosocial birthing behaviours, both in nonhuman primates and humans. Whether this relationship is determined by heritable genetic factors or coevolves independently among primate species alongside a suite of prosocial behaviours requires further investigation. Given the widely accepted conclusion that such heritable factors do influence the evolution and ontological development of obstetric morphology and are evident through hominin ancestry (as discussed in Chapter 2), it is safe to conclude that if the ‘obstetric dilemma hypothesis’ were accurate, we would expect to see a phylogenetic signal in the correlation between birthing sociality and social group size. Is the degree of birthing prosociality a product of common ancestry or has BSS evolved independently in sister taxa?

Of the potential factors tested which may influence social birthing behaviour evolution in primates, the results presented suggest that social group size is the primary factor which significantly influences birthing sociality. After controlling for phylogenetic contributions towards the variance, the results of this chapter further highlight the significant primary influence of social group size in determining the degree of prosociality during birth in primates. Whilst the sample was limited to Simiiforme species, for which data was available, this chapter has sought to demonstrate the implications of these findings for hominin evolution, and the emergence of our own highly prosocial and cultural birthing events.

In attempting to utilise Bayesian statistical models to predict likely ancestral BSS states for a Simiiforme LCA, the emergence of prosocial birthing behaviours in multiple clades, irrespective of phylogeny, suggested that birthing prosociality may have deeper roots within the primate evolutionary tree. The results of the Bayesian MCMC methodology support this conclusion, with an estimate indicating that birthing in a Simiiforme LCA would have included a moderate degree of sociality, with group members in proximity of the birth event, without directly intervening. Social group size appears the strongest predictor, and therefore those ancestral species which formed large social networks, would likely have additionally displayed highly prosocial birthing behaviours. From a palaeoanthropological perspective, the evidence presented of a distinct lack of phylogenetic and inherited contribution to the variation in birthing sociality, overwhelmingly supports an alternative model of birth assistance evolution to the previous ‘obstetric dilemma hypothesis.’ The proposed ‘social birthing hypothesis’ presented in this thesis, is supported by the results presented here, and should be considered as a viable alternative model of human birthing behaviour evolution, with significant implications for a variety of other aspects of our ancestral history.

The evidence for potential coevolution of birthing sociality with weaning ages in primates merits further future investigation, not only for understanding the implications for primate conservation and breeding efforts, but additionally for understanding optimal birthing outcomes for women today. Further testing of the relationship between prosocial and supportive environments, and potentially the extension of weaning periods indicative of slower life histories and healthier infants, will enhance the provisioning of support services and healthcare to achieve improvements and innovation in maternal and paediatric health internationally.

Chapter 6: Challenges in studying birthing behaviour in captive zoological populations.

6.1. Introduction

This chapter will discuss and explore the prevalence and causes of neonatal mortality amongst captive primates over a 19-year period, alongside five separate birthing events covering nine individuals born at Twycross Zoo between December 2002 and June 2019. Seven records were identified from ZIMS, and two further individual births were identified from supplementary notes and from correspondence with zoo staff. These events will be discussed in terms of recorded observations by zoological and veterinary staff, and recorded through the ZIMS database, which will be explored in terms of any previously recorded birthing events amongst individuals of the same species, and any possible correlation with species typical behaviours.

To further explore this data, qualitative study of these available cases at Twycross Zoo will be discussed, in terms of their potential relance in understanding proximate and ultimate causes of prosocial birthing behavioural expression. Additionally, this chapter will highlight current problems in the use of observations of birthing behaviour amongst primates in captivity. This will discuss the variability of ZIMS data collection, and the need for greater clarity and consistency in the data to be collected relating to birthing events and outcomes. This will further include a draft protocol for the recording of birthing related data in zoos, which could also be applicable in semi-free ranging and wild settings. This protocol will provide a significant contribution to the development of a more standardised qualitative and quantitative data set for birthing-related research and be a concrete, application for future studies.

6.2. Background

Whilst reviews of neonatal mortality in captivity are numerous (e.g., Kavanagh et al, 2018), no studies appear to investigate the potential risk to primate maternal health from birth in captivity. It is commonly observed that primates face risks of dystocia during birth, but this is framed in terms of the risk to the neonate rather than any risk, physical (e.g. infanticide) or psychological (e.g. increased stress levels) to the mother. In humans, dystocia is widely associated with a number of fatal risks (Alijahan and Kordi, 2014), but the incidence of this in primate mothers is not well documented. Whether this is due to the rarity of such maternal mortality, or a lack of published material, is difficult to confirm. Given the focus on breeding effort for the successful delivery and health of the neonate, it is understandable that the focus on improving birthing outcomes shifts to the neonate rather than maternal health. However, successful birthing outcomes and socialisation of the neonate require optimal conditions for the mother (e.g. conditions which minimise risks to maternal health). Therefore, understanding the potential risks to nonhuman primates in captivity are essential to developing consistent methods to identify factors to record with regard to group responses to birth.

Given the evolutionary scenario presented by the ‘obstetric dilemma hypothesis’, where rising maternal mortality and neonatal mortality drove the emergence of birth assistance behaviours, the presence of high neonatal and maternal mortality coupled with prosocial birthing behaviours would support this hypothesis. However, given the evidence presented in Chapter 4 of a lack of a significant relationship between birthing behaviour and obstetrically relevant morphology, this scenario is not supported by primate behavioural and morphological evidence. Yet the importance of understanding the risk to maternal and neonatal health is still critical to the survival of both generations, and the continuation of primate reproductive success. Within our own species’ evolutionary trajectory, any primate-wide trends in maternal and neonatal risk occurring as a direct result of parturition would have a significant impact on reproductive fitness where heritable factors are conserved. The exploration of nonhuman birthing risk is crucial to understanding the evolutionary conditions faced by hominin species experiencing increasing risk during birth from increasing levels of CPD. Therefore, this chapter will provide an essential contribution to the understanding of primate birthing outcomes, specifically on primates in captive environments. The implications of this study will provide a greater insight into optimal birthing conditions for primate conservation and breeding efforts, as well as the implications for hominin evolution and the impact of negative birthing outcomes on our evolutionary trajectory.

6.3. Methodology

Data for case studies were collected from records maintained by staff at Twycross Zoo in Leicestershire, UK, and stored within the Zoological Information Management System (ZIMS) Species360. This information was accessed by staff at Twycross to facilitate the current research. Physical records prior to 1990 were investigated for potentially useable data, however no records were considered applicable to the research. From ZIMS, the total number of incidents of primate neonatal death between 1/1/1990 and 19/2/2019 were extracted from the ZIMS data base for Twycross Zoo. Of the 962 recorded births to primates at Twycross Zoo during this period, 205 incidents of neonatal death were recorded with sufficient Relative Death Index (RDI) information attached. Here, RDI categorised unspecified fetal death or premature birth (determined to be the cause of death) as neonatal issues. The sex of the neonate was recorded as unidentified where births were recorded before staff were able to confirm the sex of the new-born, where infants were consumed, or when staff were otherwise prevented from determining the sex of the neonate.

A selection of incidents recorded on ZIMS also featured more detailed information, including species neonatal ID, the date of birth, sex, cause of death, and any further notes. In order to maintain consistency in identification, incidents were categorised as neonatal incidents where the infant died within one month of birth. No incidents of mortality as a direct result of parturition (e.g. dystocia) were noted and recorded within the obtained ZIMS and veterinary records during the period of data collection, nor from historic records.

6.4. Results

From the relevant Death Information (RDI) data presented below (**Figure 6.1.**, for detailed figures see **Table SI.3.1.**), it is clear that the most common cause of neonatal death listed on ZIMS records was 'neonatal issues' (46%, n=94). This itself is divided between 'fetal death' and 'premature birth', for which 73% of cases (n=68) were a result of fetal death, and 27% (n=25) were as a result of premature birth.

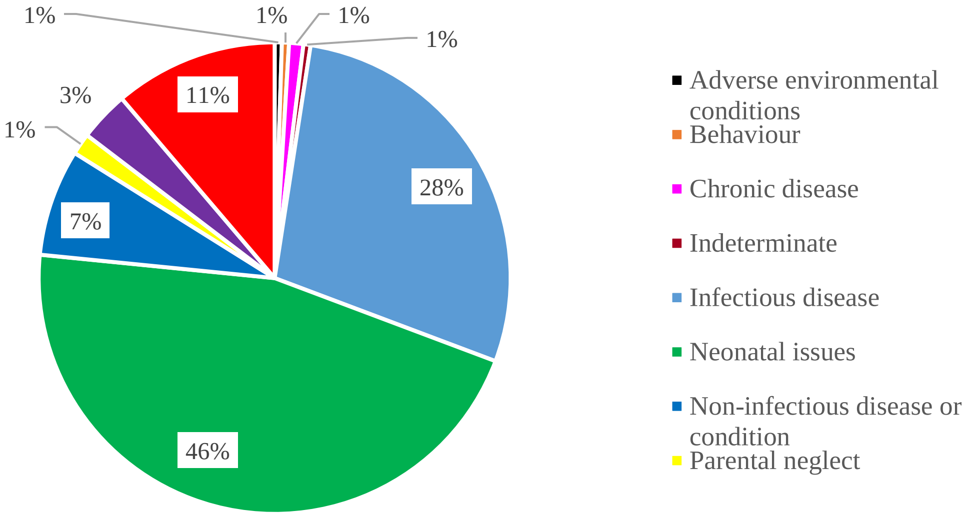


Figure 6.1. Chart showing the proportion of RDI factors listed as the cause of neonatal mortality in primates born at Twycross Zoo (UK) between 1990 and 2019. Figures are a proportion of the overall total number of times a factor is listed, including incidents with single and multiple RDIs.

Over of a quarter of incidents of neonatal mortality were also recorded to be the result of infectious disease (28%, n=58). The remaining 26% of cases were divided between trauma (n=23), other non-infectious diseases or conditions (n=15), restraint complications (n=7), parental neglect (n=3), chronic disease (n=2), and single incidents of adverse environmental conditions, behavioural causes, an indeterminate cause. However, these causes were not all mutually exclusive, with some incidents of neonatal mortality noting multiple RDIs. In particular, behaviour, chronic diseases, indeterminate causes, infectious disease, neonatal issues, and non-infectious disease or condition were listed in tandem with other factors (outlined below in **Figure 6.2.**).

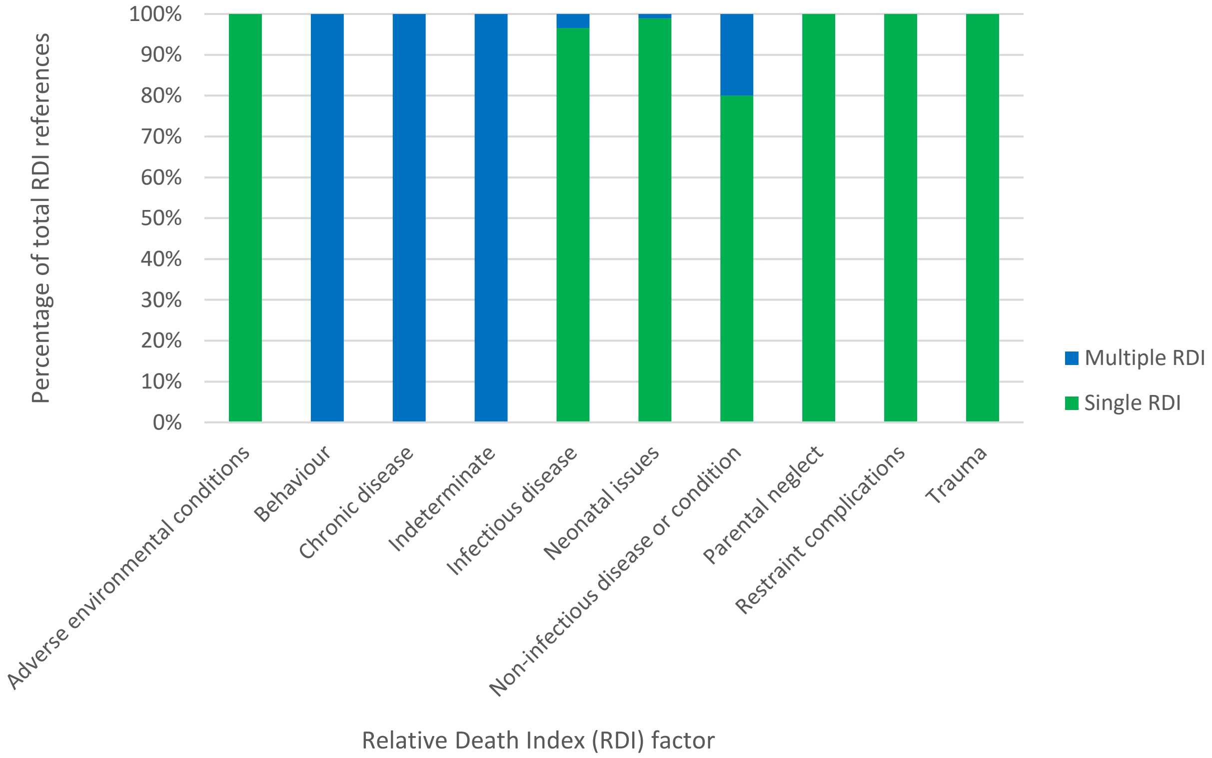


Figure 6.2. Figure representing the total proportion of single and multiple RDIs according to RDI description. Percentages represent the proportion of times each factor RDI is reported relative to the total number of times each RDI was listed on a record of mortality on ZIMS.

Whilst it was not possible to obtain the records directly to qualitatively investigate the events in detail, it is interesting to note that diseases were solely coupled with other causes of neonatal mortality. Given the presence of records with multiple RDIs for diseases and conditions with only neonatal issues (of a single fetal death or premature birth), it is reasonable to argue that maternal behaviour was not a quantitatively significant factor in neonatal mortality. A significant proportion (11%) of incidents listed as resulting from trauma is also worth noting. The descriptive term trauma is stated to include antagonistic actions by group members, whether accidental or malicious, and could be considered an indicator of detrimental social interactions and potential risk of birthing within a social context in captivity. Given the relatively low representation of trauma as a cause of neonatal mortality, it is therefore an unlikely source of risk to neonates and an unlikely predictor of maternally driven social behaviour during parturition. However, this is difficult to confirm as the trauma rate may be minimal where mothers in captivity take measures to avoid such incidents. Interestingly, a single incident of dam trauma (trauma caused by the mother) was against a female neonate. For the incidents listed as malicious trauma, a single incident was against a male neonate, with the other two against neonates of unknown sex. Neglect was seen against two male neonates, and a further single neonate of known sex.

Fetal death appears to be the largest categorisation of neonatal mortality at Twycross Zoo during the period, with 68 total incidents recorded. This as a proportion of the overall number of incidents is 33-35% (n=195 single RDI records and n=205 total ZIMS records respectively). This lack of specified categorisation perhaps highlights the lack of resources available to full assess causes of death in captivity. Second to fetal death, premature birth occurs at a similar rate to trauma, accounting for approximately 12-13% of neonatal mortality. This rate of around 1 in 8 births being premature in captivity at Twycross, is interesting and on the whole relatively high risk, as around 1 in 10 human births are premature globally (Liu et al, 2016:3027).

Case Study 1: *Eulemur coronatus* (Crowned lemur)

Over the 29 year period, 14 births of *Eulemur coronatus* were recorded at Twycross. Of these, 64% (n=9) were male and 29% (n=4) were female, with 1 undetermined neonate. This event concerns the birth of a single *Eulemur coronatus* infant on 10/6/2012 (ID 6528). The individual was a female, who was 1580g at the time of death. The circumstance of death was recorded as 'Dam', which follows additional notes describing an attack by the mother after 24 days on the infant, whilst it was being held by the sire (who was also attacked and injured). Whilst this mortality event was not directly a result of the birth, it was instead a result of the mother's post-natal behaviour within the first month, and a subsequent birth by the mother to an un-sexed infant on 19/6/2019 did not show the same level of aggression. However, on the second day, the infant was euthanised as it was not suckling and was described as having some physical deformity.

In the wild, the species typically persists in multimale, multifemale groups (Gould et al, 2011) of 5-9 individuals (Wilson et al, 1989). However, at Twycross the female was housed with a single male (the infant's sire). This may potentially be a cause of aberrant behaviour, with the female spending a significant amount of time without the presence of other females and without chance for first -hand experience of birth or maternal caregiving. Whilst of course some elements of intuitive maternal 'instinct' would be induced by hormonal shifts through pregnancy and labour, the mediation and production of behaviours by the mother are highly likely to be a product of learned experience. If this female did indeed lack any opportunity for learned behaviour prior to her first nor second birth, it is possible that such aggressive, disinterested and neglectful behaviour may be the product of no understanding of maternal caregiving. It is also possible that, whilst the cause of neonatal mortality was listed by staff as 'Dam' (death by the hand of the mother), this action may have been accidental. In context, the male was observed handling the infant when the female was seen to strike at the male, causing him injury and in the process fatally injuring the neonate. It is possible the infant here was not the primary target of maternal aggression but may have been accidentally grievously injured during the attack on the sire. The subsequent death of the mother's second infant seven years later was not a direct result of birth but was a result of 'neonatal issues'. Whilst the birth was initially successful, the infant was not seen to suckle well and was eventually found dehydrated and critically ill on the floor of the enclosure, and a decision within 48 hours of birth was taken to euthanise the individual. Whilst the mother did not behave aggressively towards the infant, the mother was not considered attentive and again this may be a product of reduced exposure to normalised maternal and allomaternal care.

From observations prior to birth in 2019, it is clear the female did not typically display any particularly anti-social tendencies towards the male (*pers. comm*). The lack of interaction with the neonate post-partum in 2019 may also have been in response to its apparent deformity, with the mother choosing to reject it out of a perceived lack of suitability. However, in many cases in wild populations, other primate species are observed to provide highly dedicated care to infants with increased need and indeed are often seen attempting to care for stillborn infants or will carry their offspring long after their death (Matsumoto et al, 2016). It is therefore more likely that it was a lack of normalised socialisation in captivity which influenced the mother's behaviour in both cases. If other group members with allomaternal care experience had been present, they may also have intervened to care for the infant or prevented the mother from attacking the male after the first birthing event. In relation to the question of the social aspects of birth amongst *Eulemur coronatus*, these two birthing events to a nulliparous mother with minimal (if any) interactions and experience with birth amongst other crowed lemurs, and lack of normal (wild) multifemale group members, demonstrate a highly likely need amongst the species for social experiences. In particular, for socially mediated experience of birth. The distinct lack of any opportunity to learn how to give birth, what birth is and how to appropriately handle and care for neonates would likely have contributed to the expression of aggressive tendencies and lack of care for her neonates.

It is commonly observed amongst Eulemur that males will provide allomaternal care in carrying the neonate (Curtis and Zaramody, 1997; Overdorff, 1993a; Mittermeier et al, 1994). Therefore, this should be a lowered source of tension amongst wild populations. In terms of any influence of the sex of the neonate as a factor, the larger proportion of male births (more than double) suggests male-male competition is minimal among the individuals at Twycross. Given the sub-optimal group size of the *E.coronatus* pair at Twycross (where groups usually contain five to six group members in the wild [Burrows, 2015:205]), the lack of maternal and birthing experience and socialisation of the female may have contributed towards her aggressive behaviour in this case, resulting in the death of her infant, and lack of maternal care displayed towards her second infant.

Case Study 2: *Lagothrix lagotricha* (Brown woolly monkey)

Over the 29 year period, 22 births were recorded to *Lagothrix lagotricha* females. Of these births, over half (55%, n=12) were male whilst 27% (n=6) were female, with a further 18% (n=4) remaining unidentified. This event concerns the birth of a single *Lagothrix lagotricha* infant on 19/6/2011 (ID 6346). The individual was a male, and was not weighed at the time of death. The circumstance of death was described as malicious, with additional notes stating that the infant was born alive, but was later observed to have been half eaten by the mother on the day of birth, with only the lower half of the body remaining.

Di Fiore et al (2011:184) note that captive Lagothrix populations experience 93.7% infant survivorship to 12 months. This high figure observed amongst atelines (53-100% among Alouatta, 67% among Ateles, and ~100% among Brachyteles), suggests that this incidence of malicious infanticide in Lagothrix is not species typical. Given the fact that woolly monkeys are described as having a more hierarchical yet promiscuous mating system than seen in Brachyteles, male-male competition could be a likely driver of infanticide in wild Lagothrix social groups. However, the individuals at Twycross were not living in a group size approaching those seen in the wild (of 13-45, Nishimura, 1990a; Defler, 1989), with four individuals at that point of study.

Whilst wild born females experience lower reproductive success than captive females (see Nishimura, 2003), woolly monkey species are known to be difficult to successfully breed in captivity (Ange-van Heugten et al, 2010; Zewdie, 2017). They commonly experience high infant mortality rates (see Barnes and Cronin, 2012), coupled with long interbirth intervals and relatively short reproductive periods. Indeed, Mack and Kafka (1978:117) observed that only 55% of 49 births survived within a captive population between 1965 and 1974. Given the resulting expected and observed low intrinsic reproductive rate (Ange-Van Heugten et al, 2008), it is likely that captive females very rarely have opportunity to observe births to other females. This may explain the aberrant behaviour seen in this case, as no other instances of cannibalism for woolly monkeys can be found in the literature. As with previously discussed incidents of cannibalism amongst non-carnivorous species, no recorded examples of meat consumption were found to suggest any innate urge to consume for nutritional reasons amongst this population of woolly monkeys. It therefore must constitute an example of aberrant behaviour, as a result of learned behaviour or rather a lack of learned, typical response to neonate births.

Case Study 3: *Saguinus imperator subgrisescens* (Bearded emperor tamarin)

Over the 29 year period, 47 births were recorded to *S.imperator subgriscens* females. Of these, 45% (n=21) were male and 32% (n=15) were female, with a further 23% (n=11) undetermined. Three recorded events of neonatal mortality were observed between 2002 and 2019. The first event concerns the birth of a male on 29/3/2016 (ID 7269), who was 34g at the time of death. The circumstance of death was described as 'neglect', with additional notes detailing that the decision was taken to euthanise the infant at two days old, as it was suffering severe dehydration likely after maternal neglect and was found abandoned on the enclosure floor. Additional specimen IDs show the infant was the first triplet born. The second of these triplets was also a male born on 29/3/2016 (ID 7261) and was 38g at death. 'Neglect' was also listed as the cause of death for this second infant, although it survived for 18 days before the decision was taken to euthanise. It was noted that the infant was found weak and had been dropped multiple times on the date of death. The notes for this record also mentioned that all three triplets were rejected and died, however the only other available record is for 7269. The final *S.imperator subgriscens* individual described concerns an unknown infant born on 15/3/2019 (24g at death). As is common amongst tamarins and marmosets, the infant was one of a set of triplets, but was the only one to perish, listed as a result of 'neglect'. This individual was noted as being the smallest of three but was found dead on the floor of the enclosure at four days old. The weight of the individual at death (two-thirds of the previously listed weights at death) seems a particularly low weight for the species, and is perhaps indicative of *in utero* development issues (such as fetal growth restriction [Miller et al, 2008]). Given the survival of the other two infants, it seems unlikely that this was the result of a premature birth.

Of the incidents of neonatal mortality detailed for *S.imperator subgrisescens*, two of the three neonates were male. With regard to any potential influence of sex on maternal and group behaviours, it seems reasonable to suggest males were targeted. However, as the sex of the individuals was only determined for a single event, this conclusion is tenuous.

What is evident from the observations presented for this species, is the need for further detailed recording of complete group structure and social context, in order to determine the potential antagonists and actors in fatal incidents. As is often observed in similarly cooperatively breeding species (Burkart and van Schaik, 2010), dominant females may actively disrupt the reproductive activities of subordinate females, something which may have occurred within this group. However, given the fact that the death appears to have been the result of neglect, this suggests a lack of interest from the mother for which an exact reason was not determined by the observers. Work by Johnson et al (1991) demonstrated a clear link in a captive population of *S.oedipus*, where the rejection of neonates whose parents were raised with siblings, was significantly lower. Crucially, Jonson et al (1991) demonstrated that the high survival of infants was possible in captivity, where infants were born to family groups with higher maternal parity status and older ages of both parents. Here, the experience of parents in captive primates was shown to play a primary role in determining neonatal mortality.

Case Study 4: *Saguinus midas* (Red-handed tamarin)

Over the 29 year period, there were 23 births to *Sagiunus midas* females at the zoo. Of these births, 26% (n=6) were male, 30% (n=7) were female and a further 43% (n=10) were undetermined. The first described incident of neonatal mortality concerns a single event, but in fact involves the birth of twin *S.midas* infants on 21/12/2002 (ID 4040 and 4041). The sex of both individuals was not determined, and no weight was obtained at the time of birth. The circumstance of death was recorded as ‘malicious’, as the notes for both individuals show that both were found on the day of birth partially eaten. The record also shows attachment to five individuals, suggesting the twins were part of a group of five *S.midas* (including the twins).

The most obvious explanation for series events leading to the death of the twins is that a single or multiple members of the group attacked and cannibalised the infants. Given the lack of any predatory species within the enclosure, cannibalism is the only possible explanation for the circumstance of death. Furthermore, given the typically distinct pattern of allocare seen amongst wild callitrichids from all members of the group (Garber, 1997; Schaffner and Caine, 2000), the reported incident of malicious destruction and cannibalism of an infant in captivity should be considered highly unexpected. Whilst multiple factors can be attributed to cannibalism in the wild, such as period of ecological stress and lack of resources (Elgar and Crespii, 1992), the managed supply of food provided by zoo staff means a lack of resources would not have driven this incident of cannibalism. Elgar and Crespi (1992) note that one social factor influencing acts of cannibalism is competition. For many mammal species including primates, infanticide may bring the mother back into oestrus and provide a competing male with a breeding opportunity. However, given the likelihood the group consisted of five members including the mother, twin neonates, and father, the final member would have been unlikely to have been seen as significant competition (assuming it was even a male).

Furthermore, the cannibalism of the infant was a secondary choice on behalf of the destructive individual, and so it is of interest to question the possible motive of the responsible group members. It is perhaps worth noting that within captivity, evolutionary selection pressure is oft removed (such as wider reproductive fitness), given the lack of overlapping generations within enclosures. Therefore, if this were indeed infanticide of kin and potentially of own progeny, experience and selective pressure would not have influenced the expression of infanticidal and cannibalistic behaviour. Moreover, comparative data from Harcourt et al (1981) suggests that, given the relatively smaller testes size with body size in marmosets, marmosets experience relatively low male-male competition. Therefore, it is even more unlikely that this incident was the product of male-male perceived competition.

However, a previous observation of cannibalism of a neonate within hours of birth among a group of red tamarins (*S.nigricollis*) by Mallinson (1965), shows that certainly this behaviour is not unique. Digby et al (2011) note that whilst Hrdy's (1979) sexual selection hypothesis observes an evolutionary functionality for infanticide, amongst callithricines, the limited influence of lactation means that infanticide is highly unlikely to bring females back into oestrus. This lack of affect from lactation of the mother is likely an evolutionary by-product of increased allomaternal care and reduced pressure on maternal lactation. Instead, Digby et al propose that competition for access to this allomaternal care is a more likely driver of enforced neglect or infanticide (see Digby, 1995a, Digby and Saltzman, 2009). An apparent rise in reported incidents of infanticide by females amongst wild *Callithrix jacchus* (Saltzman, 2003; Saltzman et al, 2008) and captive groups of *Leontopithecus chrysomeas* (De Vleeschouwer et al, 2001), in particular by dominant females, suggests a common pattern of competition for allomaternal care driving this behaviour among callithricidae.

In relation to the question of the origins and relevance to social birthing behaviour, the capacity for such behaviour presents a possible risk of neonatal mortality as a result of infanticide by the neonate's own social group, even amongst seemingly protected captive populations. In the wild, neonates may find themselves at risk from predation or intergroup aggression, whereas at the zoo the infants perished as a direct result of intragroup aggression. Interestingly amongst wild populations, it is further observed in multiple instances (see Digby 1995a; Roda and Medes Pontes, 1998; Lazaro-Perea et al, 2000) that perpetrators of infanticide often gave birth within a few weeks or days of the attack. Digby et al (2011) argue that this increased chance of infant loss when the births to dominant and subordinate females are closely spaced, supports a hypothesis that infanticide by females in a response to resource competition. Whilst this may vary between species of callitrichidae according to rates of reproductive skew, population densities, and food availability, the cost to dominant females for both survival and reproductive fitness are demonstrated by such evidence and likely influence the expression of aggressive behaviours toward the offspring of subordinate females.

Given the solely frugivorous and gumnivorous diet of *S.midas* both in the wild (Digby et al, 2011) and in captivity (*pers. comm.*), the cannibalism of the infant again seems highly aberrant. To explain this aberrant behaviour (as discussed in further detail in Chapter 3), it may be reasonable to suggest that the expression of such behaviour in context is the product of sub-optimal group-composition and socialisation conditions faced in captivity. As individuals raised in captivity are less likely to have experienced birth via observation in captivity as a result of living in typically smaller groups facing lower reproductive rates, the small group composition at Twycross and likely lack of exposure by females to multiple births among previous generations, may have contributed to a lack of normalisation of birth and awareness of relatively altruistic maternal care.

6.5. Discussion

Absence of maternal mortality

No records of maternal mortality as a direct result of birth were observed within the captive population records from Twycross Zoo, which would suggest that nonhuman primates do not suffer similar levels of maternal risk as seen in birthing humans. Whilst the observations by Kavanagh et al (2018) suggest a high level of neonatal mortality in captive vervet monkeys, anecdotal discussion with zoological teams (pers. Comm) suggests this variation between captive environments may be the result of captive environment stress on mothers. Given that the disturbance effect on captive primates is demonstrated to impact on health and wellbeing, it seems possible that the conditions faced by the primates in Kavangh et al's (2018) study were detrimental to maternal health and resulted in increased mortality. These conditions included the separation of the mother from group members during labour, regular fasting, blood sample extraction and ultrasounds, all of which may have been habituated to individuals, but likely would have raised stress levels among particularly nulliparous females with minimal concept of pregnancy and labour. Such invasive practices, whilst compliant under US laws, would not be compliant under UK laws, and thus would not be experienced by individuals at Twycross Zoo.

If the 'obstetric dilemma hypothesis' were to implicate prior high risk of maternal mortality as a direct driver of birth assistance behaviours, then the presence of previously discussed prosocial birthing behaviours in primates would suggest primates should also experience high levels of maternal mortality. The evidence presented above shows that across multiple primate species, this is not the case. However, it could be argued that the clear inconsistencies in recording and observation of captive behaviour on the part of both mother and (where applicable) the social group, and the absence of context to these observations, limits any conclusions drawn on proximate causes for behavioural expression. Ultimately, this inconsistency between contexts for the case studies in captive environments, highlights the need for a more rigorous methodology for ensuring accurate and consistent data collection for future review.

Implications for understanding the expression of birthing behaviour in captivity

Together, the observations collected from Twycross Zoo's ZIMS records (seven identifiable individuals from ZIMS, and a further two from supplementary notes and observation) supports the 'social birthing hypothesis' over the predictions of the 'obstetric dilemma hypothesis', as the prevalence of neonatal mortality amongst primate populations is not recorded at a level sufficient to influence birthing behaviour. The lack of any mention of birthing behaviour by the mother or group, and any direct reference to the delivery of the neonate as a direct cause of death in mothers or infants, suggests a low mortality risk to primates in captivity at Twycross. Therefore, it is reasoned to be unlikely for birthing behaviour to be influenced by morality risk in this captive environment.

The restrictive nature of the enclosures in captivity arguably enforces some level of social interaction during labour. With enclosures legally obliged to be suitable for the species concerned (i.e. to allow for suitable normal mobility [DEFRA, 2009:13]), the lack of specific size guidelines means that enclosure dimensions likely vary according to the financial and spatial limitations of the site owners. Despite having outdoor and indoor sections, it seems that the individuals still were unable to avoid instances of aggression by other group members. Interestingly, work by Kurtycz et al (2014) found that among chimpanzees, the choice of indoor and outdoor enclosures increased the frequency of prosocial interactions and reduced inactivity levels, although the opposite was seen for captive gorillas. However, whilst the incidence of aggressive interactions presented in this thesis was relatively low, the limitations of the enclosure could be contributing towards the incidence of aggressive interactions where females are unable to avoid conflict successfully. What was observed was a high potential incidence of maternal destructive actions against the neonate, for which the captive conditions could be a significant factor driving the expression of birthing behaviour – in particular, of maternal infanticide.

In the observations detailed here for Saguinus species, the lack of observed direct aggression towards neonates suggests that the deaths of the neonates were not intentional. Whilst the majority of deaths were against male infants, sexual competition and malicious interactions by males seem unlikely, given that males of these species are typically observed to display highly protective care on neonates (Epple, 1975; Hershkovitz, 1977). Among both Callithrix and

Saguinus, males are shown to display high prosocial and intensive caretaking behaviours within the first hour of neonate birth, ranging between 1% to 96% of observed interactions between males and neonates (Whitten, 1987:349). Therefore, an attack by a male group member on the neonate would go against observed wild behaviour. If this was however the case, then such behaviour would arguably constitute an example of non-species typical behaviour. Whilst the behaviour of the *S.midas* group was implicated in the death of two neonates, this was not directly observed. The recording of the cause as ‘malicious’ may be misleading, as the cannibalism may have taken place post-mortem after death by disease, malnourishment, or other non-aggressive or malicious factors.

Of the recorded RDIs, the overwhelming majority were as a result of neonatal issues, or other factors not the result of direct maternal or group behaviours. Only 11% of interactions were as a result of trauma, which may include accidental falls or other non-malicious actions. Therefore, it is unlikely that aggressive or malicious intentions across the captive primate species at Twycross present a significant threat to neonatal mortality, and would not constitute species-typical patterns of behaviour. However, the capacity to accurately determine the incidence rate of malicious RDIs in wild populations is severely limited. Ideally, a wild population would need to have a significant proportion of births observed both during parturition and for a period postnatally to monitor group interactions. This would be difficult to maintain, as observations at night or in forested environments with high vegetation cover would make monitoring extremely difficult. Whilst the value of the potential results of continued monitoring of wild populations would be high, in reality the process of capturing the data would be unfeasible without significant logistical resources and an extended period of observation in order to capture a large enough sample over successive breeding seasons.

Together, these case studies suggest that aggressive interactions towards neonates are relatively uncommon in captivity, whether as a lack of observation and recording of such behaviours or as a result of species typical drives for reduced aggression towards infants. However, these interactions do sometimes occur and, as noted above, they include incidents in which the neonate is cannibalized. It is possible the cannibalisation of neonates may follow similar cues to expression as seen with placentophagy. Placentophagy is seen amongst a number of primate species irrespective of typical dietary patterns, with species normally solely frugivorous or folivorous still commonly consuming the placenta after birth (as discussed in overview within Chapter 4).

The discussed incidence of consumption of the neonate by one or more group members in *S.midas* is something which has further implications, depending on whether the perpetrator was a member of the group or the mother. If this was by a member of the group, this could have been driven by intragroup competition which is in turn dependant on differences in benefits to inclusive fitness between sexes. Amongst primates, this behaviour observed in captivity may be an example of species typical behaviours seen amongst red-handed tamarins in wild populations with typical co-operative breeding systems. However, the mother may have been the perpetrator, given the evident effect of captivity on expressions of primate behaviours. If this is the case, it highlights an obvious need in captivity for primates to be housed in social contexts that closely resemble those seen in the wild.

In the case of consumption of the neonate by the brown woolly monkey mother, provided with a folivorous and frugivorous diet as observed in the wild (Di Fiore et al, 2011), the carnivory observed is highly unusual and not predicated by any other instance of meat consumption. How this relates to the question of drivers of birthing behaviour, it should be considered that in captivity, conclusions on species typical patterns of behaviour are sceptical. What is possible to conclude however, is a capacity for such behaviour, and that the notion of an overriding sense of maternal instinct to protect and care for a mother’s own infant, can be overridden by other factors and drivers of cannibalistic and seemingly evolutionarily maladaptive behaviours.

Whilst cannibalism and infanticide may be a viable evolutionary strategy in wild populations facing resource stress, or as a result of a social structure related driver, the expression of this behaviour in captivity can only be considered maladaptive. Individuals housed should not be experiencing resource stress, and any additional costs to the mother from infant care should be compensated for by zoological staff.

Van Schaik (2000) notes that although cannibalism of neonates amongst nocturnal prosimians by both males and females is not uncommon, this behaviour is primarily observed in captivity. As suggested by Izard and Simons (1986), the expression of such behaviour in activity may likely be the product of induced 'stress' under abnormal conditions and confinement. Therefore, observations of such behaviour in captivity haze conclusions on any functional explanation for such behaviour (van Schaik, 2000). However, the capacity for such behavioural expression in captivity and a lack of observations in wild populations, suggests a difference in individual learned experience and in situ conditions rather than an innate impulse in response to external stimuli.

The observation of filial cannibalism (cannibalism by the mother) among a wild bonobo troop by Fowler and Hohmann (2010) is argued to suggest filial cannibalism is in fact not a behavioural aberration, given the social acceptance of behaviour by the troop. The fact that the mother participated in the consumption of her infant (a two and a half-year-old infant) along with the group, is perhaps indicative of socially mediated expression of such behaviour. In this case, the mother may have participated as a form of social compliance. If this were the case, this would further support the notion that such behaviours are the product of social stimuli rather than any innate or physiologically mediated response (i.e. nutritional stress). Such behaviour is also of course relevant to understanding perceptions of death amongst primates, but this is something for future discussion and investigation.

The consumption of neonates by conspecifics is a topic which requires deeper investigation and research. From a greater understanding of direct and indirect causes of such behaviour, more preventative measures can be taken to reduce incidence among captive and breeding populations and ensure a more sustained conservation effort among at-risk species in captivity.

Implications for conservation and breeding efforts in captivity

These potentially fatal interactions with group members may be difficult to predict, yet the reported small proportion of fatal interactions relative to the number of successful births suggests that the benefits of social inclusion outweigh the costs, particularly the inclusion of parturient females and juveniles within social groups during expectant periods. This opportunity for birthing observation is argued within this thesis to be instrumental in the effective transference of adequate maternal and allomaternal behaviours between group members, both horizontally between peers and vertically between generations (where groups contain cross-generational females). By excluding males proactively, this may serve to increase female stress in species where male affiliative bonding is common, and additionally serve to remove any chance of normalised behaviour and learning by males.

Of the observed aggressive interactions amongst the group toward neonates, females are solely identified to have displayed malicious behaviours (directly or indirectly) resulting in neonatal mortality. In particular, the *E.coronatus* mother's actions would fit a species typical pattern of female-female sexual coemption observed in the wild as a matriarchal species (Marolf et al, 2007). If this was indeed a direct attack, then this would suggest the infant was perceived as a competitor for either resources or sexual partners by the mother. However, given the reported aggressive behaviours between the female and male, it is also possible that this was an accident and that a lack of experience of typical maternal behaviour resulted in aggressive displays around the neonate (where care would usually be taken around more vulnerable infants). This lack of experience of maternal and allocare is something which is concerning for future primate conservation efforts. Ensuring that captive females and males (where males are housed with females) are exposed to birthing events in order to acquire understanding and observational 'knowledge' is surely critical to providing females with an understanding of birth and mitigating potential future stress and anxiety from their own pregnancy and labour, and for males to similarly provide an awareness of labour and what the signs of labour mean. This would ideally minimise antagonistic responses by group members and reduce stress levels for the labouring mother. In turn, the ideally improved birthing outcomes and positive responses from group members would provide an optimal environment for post-natal development in captivity, and ensure the future longevity of captive populations.

The importance of minimising stress in captive primates is crucial in optimising birthing conditions for females. Numerous studies have documented the effects of stress on captive animals and primates in particular (Crockett et al, 2000; Davis et al, 2005; Olsson and Westlund, 2007; Morgan and Tromberg, 2007; Novak et al, 2013; Baker and Dettmer, 2017), but few papers have explicitly investigated the effect of human disruption and intervention on birthing outcomes. Interestingly some studies have found an association between routine exposure to human caretakers for extended periods, and an offset of birth timing, where births occurred exclusively during non-monitored periods (McGrew and McLuckie, 1984; Alford et al, 1992). Waitt et al (2002) suggest this is due to the perception of caretakers and a predatory risk, where female stress levels elevate in the presence of unfamiliar humans. This would fit with evidence presented in Chapter 2 of the link between elevated stress hormones such as cortisol, and arrest of normal labour and contractions. Together, the evidence supports a conclusion that observations of high neonatal mortality risk in captive primates are the result of increased stress levels of primates in captivity, which directly effects a safe progression of labour, leading to fatal dystocia and foetal death.

Given the volume of available recordings by members of the public and other sources published online through social media and other streaming platforms (e.g. YouTube and Twitter), a potential avenue for obtaining birthing observations would be to review and collate recordings on these platforms. While recordings may lack sufficient contextual details in terms of definitive species names, location for wild observations or captive, the behaviour observed could serve to provide a broader collection of data for identifiable taxa. Furthermore, this could be a logistically minimal methodology for collecting data, where data collection does not require observers to travel to sites, habituate primate colonies nor risk equipment and technical issues from recordings – as the data has already been recorded. However, the prevalence of public observations does not constitute an exact quantification of just how typical prosocial birthing behaviour is among primates. What is often lacking from these observations are, again, consistent, and methodological recording of context and potential variables influencing the expression of these behaviours.

Implications for understanding evolutionary significance of human social birthing

With no significant evidence of maternal mortality from the records at Twycross Zoo, it would support the conclusion that maternal risk is minimal in primates. Whilst this is of course limited in providing reliable conclusions on wild populations, the evidence provided can at least suggest a minimal species-level trend, in terms of obstetrical morphological capacity for mortality as a direct result of obstetrical adequacy. The implications of these results for our own evolution, are limited but crucial – neonatal risk is likely a higher critical factor in evolutionary terms than is maternal risk. Any increase in risk to maternal health in humans is more likely to be a derived feature rather than conservative, primate trend. What does appear from the data presented in this chapter, is the impact of social behaviour on mortality of neonates, and highlights the importance of understanding it’s impact on models of primate and hominin demography, alongside models of behavioural evolution. The previously outlined model of a ‘social birthing hypothesis’ proposed by this thesis, would predict a strong relationship between birthing behaviour and neonatal mortality. Whilst previous chapters do not suggest a relationship between birthing sociality and obstetric morphology crucial to minimising the risk of mortality from delivery, primates may alternatively face significant pressure directly after birth from conspecifics. The capacity for prosocial birthing behaviours evolving within our primate ancestors, may have led to an evolutionary scenario where the increasingly prosocial births reduced the risk of antagonistic interaction between group members and the infant, but also an increasing awareness of birth for mothers reduced the incidence of infanticidal tendencies.

It is possible that the low rate of maternal mortality reported is a result of higher levels of care and practices at Twycross Zoo, as opposed to colonies housed in institutions with the express purpose of increasing population yield (e.g. US laboratory breeding colonies). Kavanagh et al’s (2018:4) study for example found a high historic neonatal mortality rate of 39% among a mixed sample of African green and vervet monkey breeding colonies, significantly higher than the proportion typically observed in the species (Kushner et al, 1982; Kirkwood et al, 1986; Else, 1985; Seier, 1986). However, this appears to conform with reported mortality rates in other captive species of primate, with even higher proportions reported for pigtailed Macaques (Sackett, 1990) and tamarins (Kirkwood et al, 1983). What this variation shows however is the significant deviation in neonatal mortality between populations of the same species in captivity, which Kavanagh et al (2018) attribute to maternal physiology and status mediated behaviour. With regards to maternal physiology, the risk of maternal gestational diabetes was shown to increase risk of neonatal mortality, something which also contributes to a significant proportion of human neonatal deaths (Metzger et al, 2008; Riskin-Mashiah et al, 2009). Therefore, given the link found between neonatal death in captive vervet monkeys and glycaemic index, it should be highly advised to avoid fasting pregnant females rather than fasting prior to sample collection as used in Kavanagh et al’s (2018) methodology. The author’s results also suggests that the risk of gestational diabetes is a significant risk factor in all primates and is not unique to humans, occurring at a high enough frequency in nonhuman primates so as to dramatically increase the incidence of neonatal mortality. Hominins would also have likely faced such issues, however the process of natural selection would likely have minimised the emergence of high-risk genes across populations, given the significant detriment to reproductive fitness.

Interestingly in this study, one of the primary causes noted in neonatal mortality incidents were kidnappings by other females. These incidents were observed to occur in 70% of all fatal cases of severe dehydration and malnutrition (Kavanagh et al, 2018:5), and were significantly correlated with social rank where higher ranking females would kidnap lower ranking offspring. The practices observed and recorded by staff at Twycross appear are less invasive and disruptive for primates, and likely minimises stress levels at the zoo compared with laboratory subjects. Whilst impossible to detect within the archaeological record, the degree to which kidnappings by females may have occurred, would not have been insignificant, given the incidence reported for primate populations. With the contribution towards neonatal mortality high, this behaviour is something which should be factored into a suite of potential interactions between overlapping hominin populations.

Towards a systematic methodology for recording birthing behaviour in primates

As previously discussed, the inconsistency in observational data collection during birth in primates limits the reliability of conclusions drawn on proximate and ultimate causes. Whilst ZIMs provides a framework for the recording of clinical data on individuals involved, minimal consideration is made for qualitative additions to these records. Furthermore, the inconsistency in behavioural observations of birth in examples discussed within Chapter 4 further signify the need for a rigorous, systematic and consistent framework for recording birthing context and behaviours in primates, both in captivity and in the wild. The development of a single method of recording is challenging in application to these contexts, but not impossible. Here, this thesis proposes a series of crucial variables necessary for understanding responses and behaviours on the part of the mother and, where mothers live in social groups, the part of social group members. Together, the data should be recorded in a consistent manner, openly accessible to researchers to facilitate broader opportunities for study.

Group composition

These variables should on a basic level, the number of social group members, and a summary of the affiliative network structure – are they kin, closely bonded, typically antagonistic? Prior to the observational study period, relations between study group members should be established, to facilitate greater insight into how social networks may influence individual behavioural choices during birth.

Socioecology

In addition, an estimation of population density, and the context of captive restrictions limiting density, would aid in providing sociodemographic context. As is outlined in previous chapters, the use of group member proximity as a proxy for prosocial interactions in the birth event presents a broadly applicable methodology for quantifying the degree of birthing prosociality across subject settings consistently. Additionally, if scaled with population density, this would provide a consistent framework between captive and wild settings, accounting for restrictions of population density. In all cases, all-occurrence scan sampling should consider responses by all group members to the birth event, whether prosocial or antagonistic, or null.

Clinical context

Additionally, context and observations should be provided of both the mother and neonate and fully as possible. Given the varying access to veterinary staff on-site for opportunistic observations or study periods, researchers should familiarise themselves with subject obstetric morphology and species typical birthing mechanics. Timings and the orientation of the neonate during delivery should be recorded to provide potential observations of correlation between birth abnormalities and group behaviour.

6.6. Conclusion

The rate of neonatal issues occurrence, and overwhelming contribution of neonatal mortality at Twycross, indicates that further investigation is needed as to potential drivers of still births and other incidents. As discussed throughout this thesis, the influence of stress factors likely contributes to the incidence of fatal neonatal issues in both human and nonhuman primates. For the benefit of optimising primate conservation efforts, as well as optimising human maternal and neonatal health outcomes, it is recommended that practices and policies address speculative and identified causes of stress as a high priority.

The behaviours observed and discussed in this chapter demonstrate a clear complexity for maintaining effective breeding populations in captivity. Whilst birth may be successful in delivery, the behaviour of primates even typically believed to display highly prosocial and alloparental care, may display unpredictable aggressive or neglectful behaviours towards neonates. The results discussed in this chapter and from the case studies presented, support a recommendation for optimising the social group sizes, encompassing evidence for typical group sizes in wild populations. The aim of this optimisation would be to minimise the incidence of aggressive or malicious interactions, through intergenerational opportunities for learning and experience of birth.

Further to this, additional research and investigations utilising observations of primate in captive and wild primates, while difficult to obtain, are crucial aiding our understanding of birth in nonhuman primates and ourselves. Additionally, the proposed variables required for consistent methodological recording of birthing events in primates, would significantly aid in expanding on our understanding of both human and non-human primate birth.

The application of the methodologies used in this thesis to a wealth of available recorded observations on public platforms would aid in future research, and serve to broaden our understanding of species typical patterns of behaviour, and the potential optimal conditions for healthy births in primates. In understanding hominin evolution, extant primate models undoubtedly provide a glimpse into the conditions and mechanisms which our hominin ancestors would have faced, and must be factored into our understanding of ancient human demography, behaviour and evolutionary trajectory.

Chapter 7: Conclusions

The primary aim to identify, investigate and untangle the factors which exist and have driven or facilitated the evolution of highly prosocial birthing behaviours in humans and nonhuman primates, has been approached from multiple avenues within this thesis. This has included a novel approach to quantifying the degree of prosociality of primate birthing behaviour, in order to determine potential statistical relationships between sociodemographic factors, morphological variables and life history traits, and potential phylogenetic determinants.

The previous literature has maintained much of the consensus initially outlined during the mid-20th Century, where the highly interventionist birthing behaviour seen in humans, underlies our uniqueness in having mechanically difficult births. Under the 'obstetric dilemma hypothesis', the emergence of birth assistance behaviours and midwifery is modelled to be driven by mortality pressure from increasing CPD risk. Whilst archaeological evidence indeed suggests an increasing degree of disparity between mechanically constricted maternal pelvic morphology, and increasing neonatal cranial dimensions, evidence of birth assistance behaviours is near impossible to detect from archaic hominin species. Whilst the onset of written language may suggest early understandings of possible medical support, prior behavioural evidence is certainly lacking. Furthermore, with evidence for similar levels of CPD, and in some cases more extensive levels in primates and other mammals, this suggests that the evolution of social birthing behaviours is not determined by morphological factors as suggested by the 'obstetric dilemma hypothesis.' In fact, evidence for high levels of CPD in nonhuman primates suggests that, under a 'social birthing hypothesis' framework, prosocial birthing behaviour was already a feature of many ancestral primate species prior to the emergence of the hominin lineage.

A primary goal of this thesis was to highlight the capacity for highly prosocial birthing behaviours among nonhuman primates. Through the collation of multiple published sources across a wide variety of primate taxa, the evidence overwhelmingly supports a rejection of previous consensus amongst anthropologists and wider audiences, that in fact we are not alone in seeking social support during birth. The overarching theme of the obstetric dilemma, in our uniqueness in provisioning social support during birth, is not supported by the primatological behavioural data and observations. Whether this has evolved in other primates in response to morphological constraints from CPD, or socioecological and demographic factors requires further investigation in addition to that performed in this thesis.

The results of the primary methodology utilised in this thesis, through quantifying the relative degree of prosociality of primate birthing behaviours, demonstrates a clear sociodemographic relationship above other variables tested. The strong signal of correlation detected between BSS and social group size over population density, supports a conclusion that strong affiliate bonds between social primate groups drive the expression of these prosocial behaviours. These initial results support a model of birth assistance evolution within the framework of a ‘social birthing hypothesis’, rather than that of the ’obstetric dilemma hypothesis.’ The emergence of prosocial behaviours in populations with larger social group sizes, rather than among species with morphological or life history constraints, suggests that birthing assistance may have deeper roots in primate ancestry, and was likely a feature of early hominin birth events.

From further investigation of the potential phylogenetic contribution towards variation in birthing sociality, the evidence reported in this thesis suggest that highly prosocial behaviour is not inherited. The weak correlation between BSS and variables other than social group size, even after accounting for phylogeny, does not support the ‘obstetric dilemma hypothesis’, as characteristic birthing prosociality does not appear to follow ancestral routes. Rather, birthing prosociality appears to evolve in events, in tandem with higher group sizes. The high likelihood estimates from Bayesian statistical analysis for ancestral Simiiforme species, suggests a moderate degree of prosociality would have been present in historic primate populations. Given the evidence of prosocial birthing behaviours in cetaceans alongside primates, this seems highly plausible, and again supports a model of birth assistance evolution under the 'social birthing hypothesis' proposed in this thesis.

From the available mortality data accessible from Twycross Zoo, neonatal mortality as a result of birth or at birth, seems far more prevalent than maternal mortality. Therefore, it is suggested that the evolutionary benefits of social birthing behaviours, may serve to mitigate this high risk to neonatal health. What is argued in particular, in conjunction with evidence presented in Chapter 4 for the high juvenile tolerance by birthing females, is the key role played by birthing experience in nonhuman primates. Whilst experience and shared knowledge is well documented in humans as a factor influencing birthing outcomes, this is not the case for our closest living relatives. The consequences for understanding optimal social group structure necessary for learning opportunities key to ensuring positive birthing outcomes, are numerous and crucial in maintaining effective conservation and breeding efforts in captivity. Additionally, this suggests social group structures with multiple overlapping generations, coupled with experience shared under the 'grandmothering hypothesis' model of female affiliate group structures in hominins, has been key in maintaining the persistence of birth assistance behaviours in hominin evolution.

What this thesis has demonstrated, is a systematic lack of correlation with morphological variables as predicted by an 'obstetric dilemma hypothesis' model. Instead, the expression of prosocial birthing behaviours in nonhuman primates seems to most strongly correlate with the size of species typical social group sizes. These findings in turn support an alternate 'social birthing hypothesis' model of evolution of prosocial birth assistance and support in hominin evolution proposed by thesis. Further exploration of factors within this, such as kin networks or further signals of social ‘support’ during birth, will provide further clues as an exciting avenue for future primatological and palaeoanthropological research. However, the implications of these findings arguably have ramifications and implications much more relevant to the healthcare challenges faced by women today.

Appendix: Primate Husbandry and the effect of the Coronavirus Pandemic on Zoos.

Introduction

One of the initial methodological aims of my research was to utilise camera traps housed in primate enclosures, in order to try and capture primate birthing events and record group responses to birth first-hand. This would have been coupled with a more extensive collection of available ZIMs records of maternal and neonatal deaths in captivity from multiple institutions outside of an initial study at Twycross Zoo.

The initial aims of this behavioural data collection were threefold. Firstly, to provide further evidence and behavioural observations to broaden the scope of initial data analysis for other nonhuman primates outside of previously published data. Second, to provide a more detailed observation of social group and maternal behaviour during the birth event in captivity, and to determine where possible if this behaviour differed from that observed in wild populations. Lastly, the final aim was to investigate whether patterns of behaviour existed across captive populations where nulliparous females with no experience of birth in captivity, behaved in a detrimental way towards offspring or showed significant signs of stress during an immediately after the birth event compared with those who would likely have had previous experience of births to conspecifics.

However, this data collection was severely hampered by technological, logistical and restrictions imposed by response to the coronavirus pandemic in 2020. The effect of these restrictions and the issues faced during the data collection period will be discussed within this appendix, as well as a brief discussion of the wider impact of the coronavirus pandemic on zoos and zoological research.

Issues with camera trap data collection

The initial methodology for collecting primary behaviour observations of birth in captivity relied on the use of several camera traps setup to capture the moment of birth in captive primates, or at least behaviour significantly close to the timing of the birth. The cameras used were two Apeman 12 MP 1080P camera traps **(Figure A.1.)**, and two Toguard 14 MP 1080p trail cameras. Both were set to record 30 second bouts of footage on activation, with infrared modes allowing for recording throughout the night. Practical concerns played a role in the selection of captive species, where primates were not induced into labour. Group behaviour during birthing events in captive primates were to be observed through all-occurrence sampling from reviewed footage, to ensure a full assessment of group behaviour and context for maternal behaviour. This observation period for recording aimed to last until the neonates were born, or the conclusion was drawn of a false pregnancy or miscarriage. Materials would then have been removed from enclosures at the most convenient and least intrusive point i.e. so as not to disturb the new-born mothers and infants.

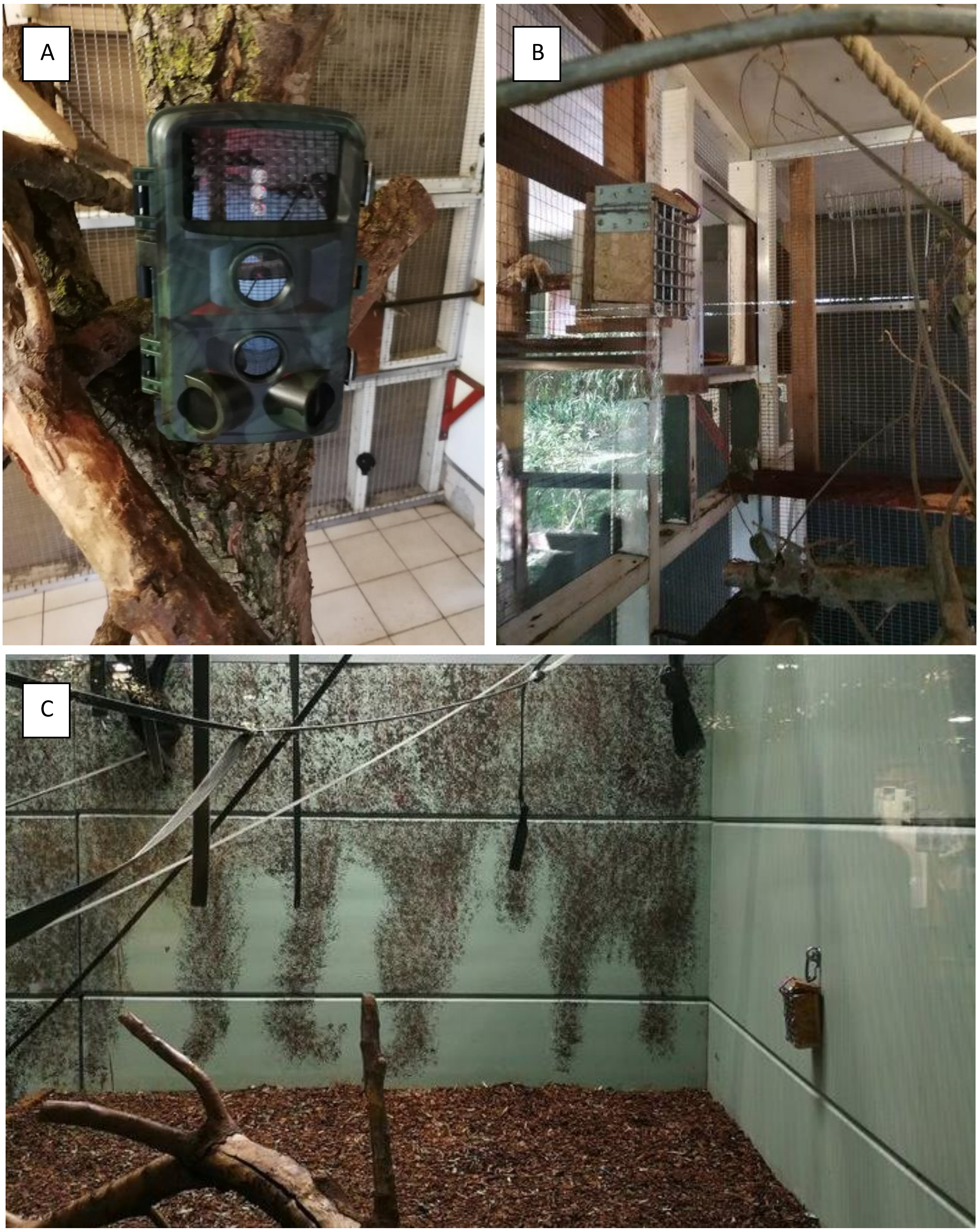


Figure A.1. Example of one of the Apeman camera traps placed within alternate primate enclosures. (A) the crowned lemur enclosure, (B) Brazzer’s monkey enclosure, (C) gibbon enclosure. The initial attempt with the crowned lemur’s did not require protective housing, however for the Brazzer’s and gibbon attempts, boxed housing was constructed to reduce the risk of damage and potential harm to the animals.

The species observed were limited to those with accurate visual and observation signals of pregnancy, such as weight gain, ano-genital swelling reduced mobility, changes in behaviour (personal comms., Wolfensohn and Honess, 2008:139), and for which birth dates could be estimated to begin camera set-ups. This meant that observations for smaller species would be difficult, given the minimal signs of pregnancy to observers without intrusive or chemical testing of urine or faeces. This method would have required significant further resources and was beyond the methodological capacity for this thesis (however the use of pregnancy testing to detect pregnant individuals would be a significant avenue for future methodology).

For the first attempt in early 2019 (**Figure A.2.**), a primiparous female crowned lemur (*Eulemur coronatus*) (a previous birth was recorded, although the infant was killed by the mother, and is discussed in Chapter 5) was identified as displaying signs of pregnancy, with a notable rapid increase in abdominal dimensions indicative of a near-term foetus, an increase in aggressive male interactions towards keepers, and a reduction of female mobility (personal commentary). However, it was believed that a miscarriage occurred as blood was found in the enclosure and pregnancy did not appear to continue.

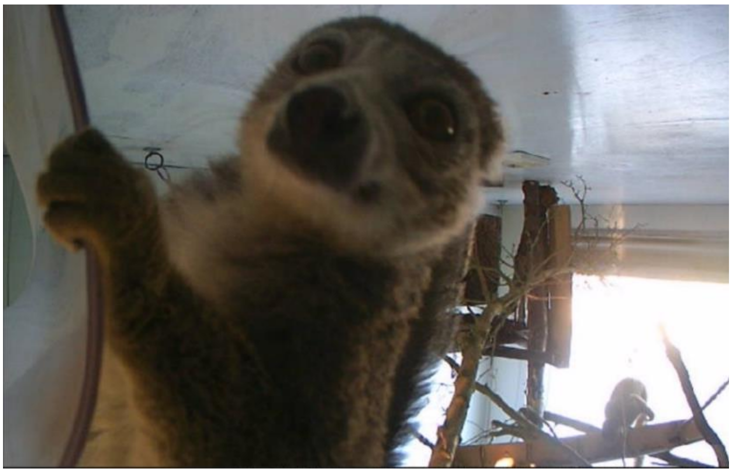


Figure A.2. Still from initial capture footage prior to birthing event at Twycross Zoo to a female crowned lemur (*Eulemur coronatus*). The female is pictured above, with the male on the back right of the indoor section of the enclosure.

Later in the year however, a similar pattern of signals was identified as well as significant weight gain, and a birth to the female did occur. However, several issues arose with the use of camera traps utilising limited data storage. As video observations were required, this necessitated regular changes to check both battery use and memory card free-space. Given the relatively mobile activity cycle of the lemurs, this meant a high number of videos were recorded even on lowered sensitivity. These meant that the memory cards were rapidly filled before it was possible to re-enter to enclosure weekly to swap to new batteries and free memory cards. Unfortunately, this resulted in the cessation of recording the day prior to the birth itself. It is perhaps worth future study for understanding maternal and conspecific behaviour during the gestation period in captivity, but the observations were no longer relevant without the observations close to the liming of delivery. The neonate did not survive long after birth, with zoo staff removing it from the enclosure owing to signs of poor health and dehydration, taking the decision to euthanise it for humane reasons.

The second attempt to record births in another multiparous female were set-up for a Diana’s monkey group. This time, an issue occurred where the camera which would have been able to observe the birth (which was believed to have been within an indoor section of the enclosure) had its video data corrupted. More frequent trips and attempts to change memory cards and batteries were made, specifically given the larger group size and larger proportion for time spent indoors during the colder period during the autumn of 2019. However, the rate at which the memory was used significantly increased and coupled with the corrupted data, the other camera traps would also stop recording prior to storage and power change-overs.

Lastly, just prior to the onset of the pandemic in early 2020, a multiparous female gibbon was identified as showing signs of pregnancy and an addition two cameras (four total) were set-up throughout the indoors gibbon enclosure. Given the increase in frequency needed to reduce the chance of memory and power running out, and the camera set-up which required keepers to climb high posts and trees, this changeover was handled by zoo staff. However, this frequency was limited by the need to minimise intrusions into the enclosure, which in turn again resulted in a cessation of the footage capture just a few hours short of the birth event.

The use of continuous recording devices such as web camera theoretically could provide a solution to the issue of memory and power issues encountered, whilst also minimising the intrusions into the enclosure. However, this set-up would require adequate internet connection to maintain continuous recording and uploading of footage for later viewing. However, due to the financial limitations of this thesis, combined with the onset of the pandemic, prevented the acquisition and trial of such equipment.

None of the previous studies discussed in this thesis have utilised camera trap or other continuous recording footage, as observations recorded were captured ad-hoc as researchers were present at the moment of birth. It seems that the difficulties of capturing the event attempted as part of this research highlight the difficulties in the logistics of observing birth events first-hand in primates in captivity, with wild births significantly more challenging to capture. Together, this explains the small sample available to draw conclusions from. Yet these observations are not without merit, and when achieved can provide a significant benefit to our understanding of primate behaviour, production, and evolution, and in turn the implications for understanding our own species. Therefore, future research should continue to explore this avenue of observation and investigation, given its significance.

Limitations to ZIMs data

Unfortunately due to the variation in captive breeding and veterinary record keeping between UK institutions, records necessary to track prior group composition necessary to test the third aim were severely limited. Therefore, a wider investigation of a potential correlation between birthing experience and birthing behaviour was not possible within the limits of this research project, which would have required a longer-term study of group composition and observation of each birth during that period, as well as determining the extent of experience gained by group member from births during this period. Any group members who were moved to other institutions would also need to have been tracked and studied and new host institutions. Future long-term study would be able to provide a significant understanding of the effect of experience on birthing behaviour and outcomes in primates, with a significant contribution to our understanding of primate breeding and conservation efforts.

Financial pressures of the pandemic on zoos

Whilst initial attempts to record birthing behaviour were unsuccessful due to technical issues, the scope for attempting with an alternate equipment setup was cut short. With the onset of the pandemic and the closure of all UK zoological institutions, some temporarily and some permanently (Kirby, 2021), the scope of the data collection for this thesis and many other's research was put either severely hampered or rendered unfeasible.

The UK government provided a series of relief packages aimed to provide basic £114 million relief fund to cover the keeping costs (such as food, heating and security), but the true loss of income through visitor attendance (from not only ticket sales but cafes and restaurants, gift shops, and donations) due to the closure between 16th March 2020 and 15th June (4th July for indoor areas) incurred “long term financial problems” (Department of Environment, Food & Rural Affairs and Goldsmith, 2020). Indeed the Independent estimated that the 207-day lockdown had cost UK zoos, aquariums and safari parks upwards of £200 million (Kirkby, 2021), with a letter by leading BIAZA figures describing the impact of lockdowns during busy periods as “crippling” (Morris et al, 2021).

Effect on research

Due to the capacity for the COVID-19 virus to transmit between human primate species, as well as many other animals (Hobbs and Reid, 2020; Nova, 2021), not only entering the enclosure to set-up cameras but entering and communicating with staff was made near impossible. This was in order to prevent the transition to captive individuals, but also due to the economic impact of zoo closures on staff. In many cases, zoos lost major ad primary sources of income through the loss of ticket sales, and the accompanying further visitor related sales. Instead institutions had to rely on government support and charitable support, simply to feed those housed in enclosures but also to support those staff on furlough or those not made redundant through budget cutbacks. This meant in many cases support for research and non-core activities at the zoos were cut-off.

For myself, this meant that contact with zoo staff became minimal if at all, with some institutions unreachable due to staff shortages. Twycross Zoo remained responsive in remote communication, but this capacity was not shared by many institutions contacted. In this regard, this meant that not only were camera setups no longer feasible at Twycross, but ZIMs animal husbandry data was only obtainable from Twycross between 1990 and 2019 (when the initial pilot data was sourced). Attempts to contact and obtain further data from other zoos was not possible with the affect of the pandemic.

Studies on the impact of reduced visitors on animal behaviour

Interestingly, some limited studies were able to record and investigate the effect of closures and reduced visitor attendance on animals housed in zoos. Williams et al (2021) found that for some species changes were not significant, but some did as expected show increased ‘comfort’ and environmental ‘interactive’ behaviours in the absence of visitors, and the authors suggest that species will demonstrate varying re-habituation capacity to increased human presence. Whilst the small sample size of the study (in terms of the number of individuals studies and range of species) reflects the limitations of research at UK zoos during the pandemic, the authors do note the frequency of chimpanzee individuals seeking increased keeper contact during closures (Mack, 2020). Given the evidence for the benefits for prosocial interactions by keepers towards housed primates (Baker, 2004, Davis et al, 2005; Funnel, 2021), it seems that human visitors may in fact be crucial in providing social and psychological enrichment for species which typically display relatively social tendencies. However conversely for some primates the increase in human presence may in fact reduce activity and be detrimental to physical health (Waitts et al, 2002; Caravaggi et al, 2018). The findings of Waitt et al (2002) suggest that in the absence of habituated and familiar humans in captive environments, primates will display significant signs of stress. Furthermore, the elevation of cortisol from increased visitor density has been documented in captive primates (see Davis et al, 2005). It is therefore reasonable to suggest that the return of visits to zoos after period of hiatus, would raise stress levels in captive primates, with potentially detrimental effects on birthing outcomes. Here, the impact of returning visitors on breeding and birthing behaviour would be of particular interest for future research, with substantial implications for conservation effectors for better or worse as part of guidance for evidence-based best-practice.

Conclusion

One of the initial data collection methods attempted as part of this thesis was unfortunately unsuccessful, with issues caused by a myriad of factors, compounded by the onset of a global pandemic. However, this impact was not only felt by myself, but zoological institutions housing animals were critically impacted by the loss of a substantial source of revenue necessary for not just staffing and animal husbandry, but also support for researchers.

In terms of the future for zoos after the impact of the COVID-19 pandemic, support has trickled in for zoos to keep many in operation, but the closure and reduction in capacity to care for and maintain normal operations and research will have repercussions for the long-term. It is hoped that the alternate methodology used within this research, and understanding of the limited sample size has still provided substantial support for the principal arguments of the thesis. Given adequate research conditions and a more rigorous methodology, the potential for the use of camera traps to record birth in a wider sample of primate taxa in captivity, will provide a significant contribution to the understanding of maternal and neonatal health in captivity.

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Supporting Information

SI.1. Estimating neonatal cranial volumes

Date	Animal ID	Species	Common name	Live/ PM	a	b	c	d	e	f	g	h	Estimated brain volume (cm^3)
10/10/2019	7632	*Cercopithecus neglectus*	De Brazza	Live	6.0	8.0	6.0	1078.0	23.0	10.0	10.0	-	56.16
05/11/2019	7489	*Trachypithecus francois*	Francois langur	Live	18.0	12.0	11.0	4500.0	24.0	12.0	10.0	-	61.15
17/12/2019	7478	*Ateles fusciceps*	Black headed spider monkey	Live	10.0	13.0	9.0	5850.0	27.0	11.0	10.5	-	77.39
22/01/2020	-	*Cercopithecus diana*	Diana monkey	PM	7.0	10.5	6.5	-	21.0	11.0	10.5	-	46.82
30/01/2020	7688	*Trachypithecus francois*	Francois langur	PM	5.0	6.0	4.0	428.0	16.0	9.0	8.0	-	27.18
04/02/2020	7689	*Trachypithecus obscurus*	Dusky leaf langur	PM	6.5	8.0	5.5	572.0	19.0	10.0	10.0	46.0	38.32

Table SI.1.1. Neonatal cranial metric data obtained from primate samples at Twycross Zoo.

Neonatal metric	a	b	c	d	e	f	g
r	0.555	0.872	0.800	0.886	0.997	0.708	0.714
R^2	0.308	0.761	0.640	0.785	0.993	0.501	0.510
n	6.000	6.000	6.000	5.000	6.000	6.000	6.000
t	1.334	3.571	2.666	3.311	23.994	2.005	2.039
df	4.000	4.000	4.000	3.000	4.000	4.000	4.000
p	0.253	0.023	0.056	0.045	0.000	0.115	0.111

Table SI.1.2. Statistical analysis of BSS against neonatal cranial volume estimate. **PM** – Post-mortem. (**a**) true and/or reduced true and/or reduced suboccipitobregmatic diameter (cm), (**b**) true and/or increased occiptomental diameter (cm), (**c**) true and /or reduced occipitofrontal diameter (cm), (**d**) total body weight (g), (**e**) total head circumference (cm), (**f**) ear-to-ear measurement (cm), (**g**) glabella-to-opisocranion measurement, (**h**) cranial weight (g).

SI.2. PICS data outputs

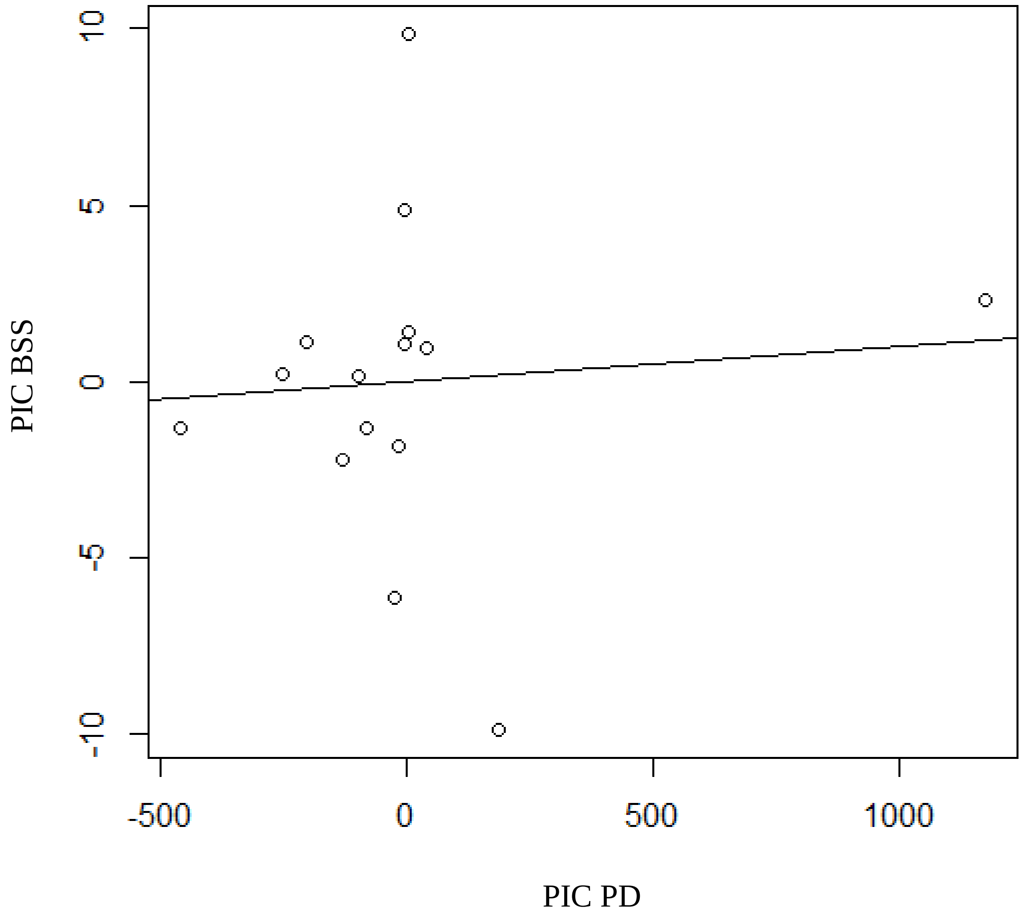

Figure SI.2.1. PIC plot of BSS against population density.

Residuals	**Min**	**1 Q**	**Median**	**3 Q**	**Max**
	-10.0337	-1.5228	0.4948	1.2332	9.8458
Coefficients	**Estimate**	**Std Error**	**t value**	**Pr(>|t|)**	
PIC PD	0.001018	0.003345	0.304	0.765	

Residual Std Error	4.439 on 14 degrees of freedom
Multiple R-squared	0.006572
Adjusted R-squared	-0.06439
F-statistic	0.09261 on 1 and 14 degrees of freedom
p-value	0.7654

Table SI.2.1. Statistical output for PIC of BSS against population density.

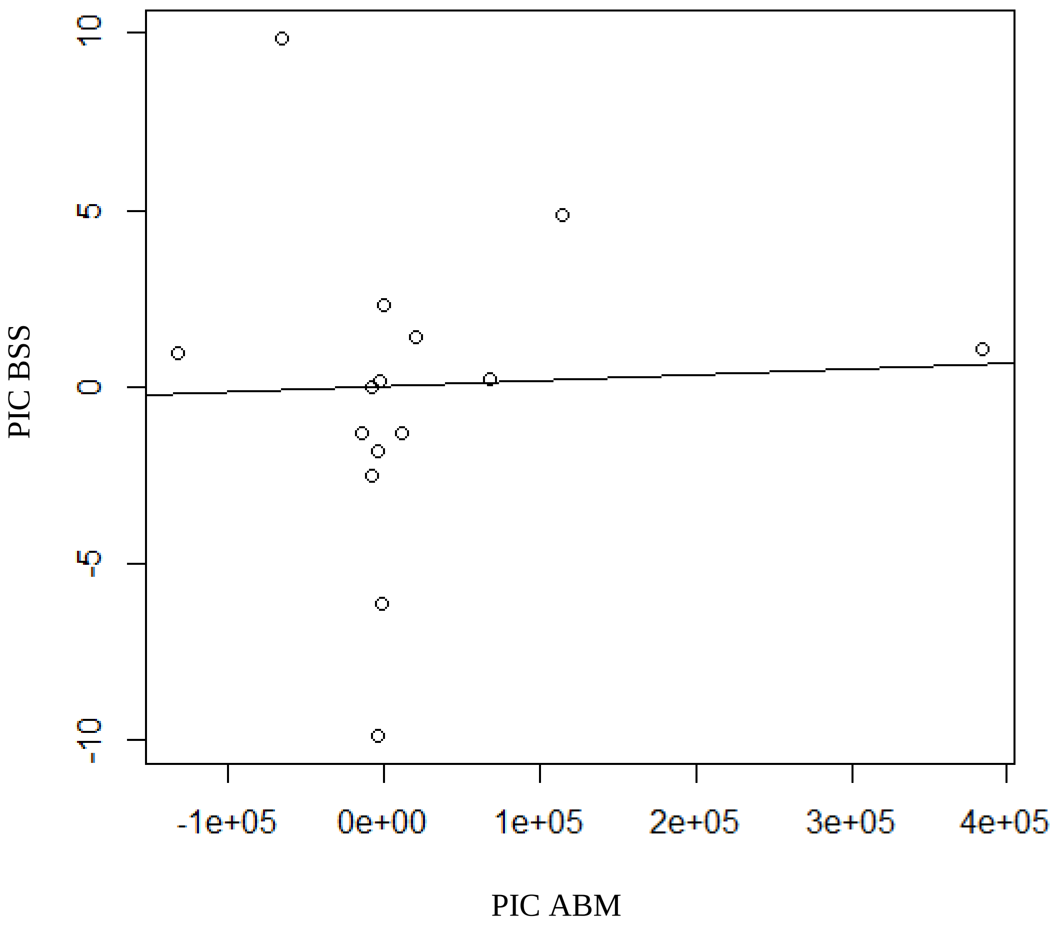

Figure SI.2.2. PIC plot of BSS against adult body mass.

Residuals	**Min**	**1 Q**	**Median**	**3 Q**	**Max**
	-9.8373	-1.5696	0.1232	1.2819	9.9591
Coefficients	**Estimate**	**Std Error**	**t value**	**Pr(>|t|)**	
PIC ABM	1.693e-06	1.026e-05	0.165	0.871	

Residual Std Error	4.449 on 14 degrees of freedom
Multiple R-squared	0.001939
Adjusted R-squared	-0.06935
F-statistic	0.0272 on 1 and 14 degrees of freedom
p-value	0.8714

Table SI.2.2. Statistical output for PIC of BSS against adult body mass.

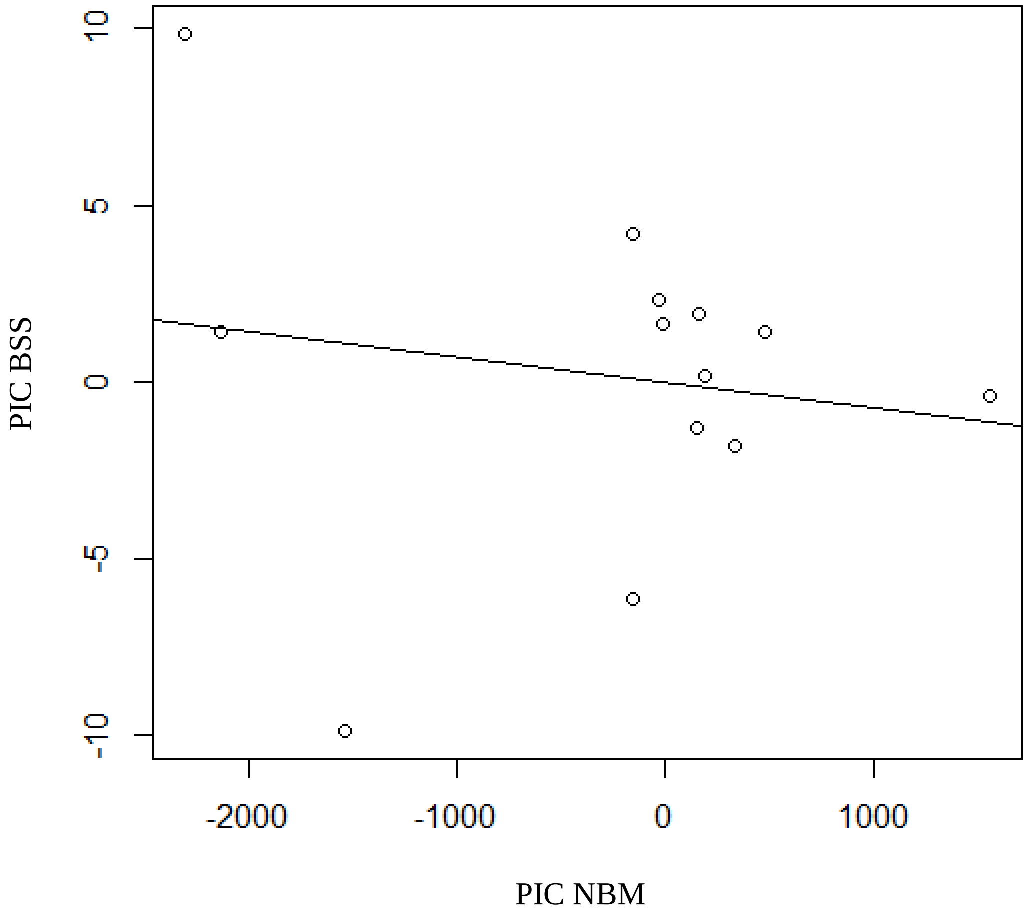

Figure SI.2.3. PIC plot of BSS against neonatal body mass.

Residuals	**Min**	**1 Q**	**Median**	**3 Q**	**Max**
	-10.9395	-1.2173	0.6993	2.0220	8.2055
Coefficients	**Estimate**	**Std Error**	**t value**	**Pr(>|t|)**	
PIC NBM	-0.0007139	0.0012025	-0.594	0.564	

Residual Std Error	4.671 on 12 degrees of freedom
Multiple R-squared	0.02853
Adjusted R-squared	-0.05242
F-statistic	0.3525 on 1 and 12 degrees of freedom
p-value	0.5637

Table SI.2.3. Statistical output for PIC of BSS against neonatal body mass.

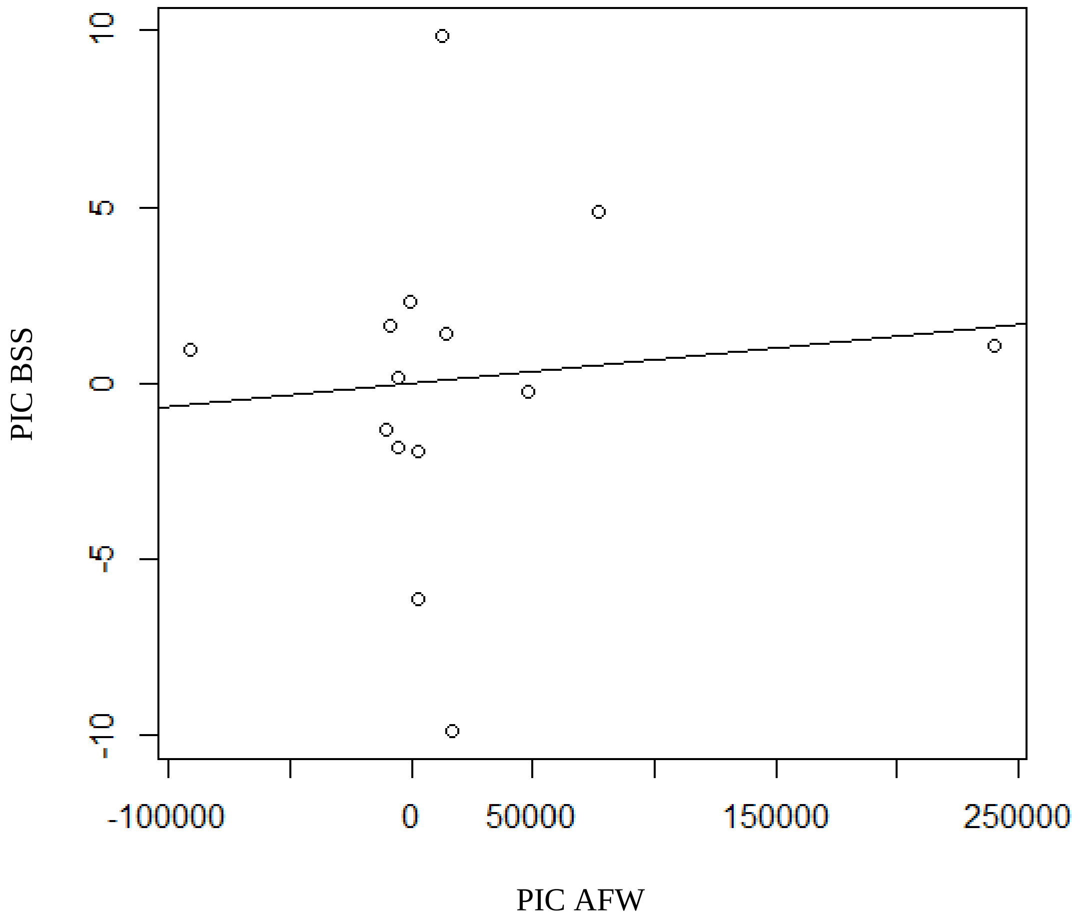

Figure SI.2.4. PIC plot of BSS against adult female weight.

Residuals	**Min**	**1 Q**	**Median**	**3 Q**	**Max**
	-9.9537	-1.6511	-0.1512	1.6621	9.7649
Coefficients	**Estimate**	**Std Error**	**t value**	**Pr(>|t|)**	
PIC AFW	6.674e-06	*1.671e-05*	0.399	0.696	

Residual Std Error	4.58 on 13 degrees of freedom
Multiple R-squared	0.01213
Adjusted R-squared	-0.06386
F-statistic	0.1596 on 1 and 13 degrees of freedom
p-value	0.696

Table SI.2.4. Statistical output for PIC of BSS against adult female weight.

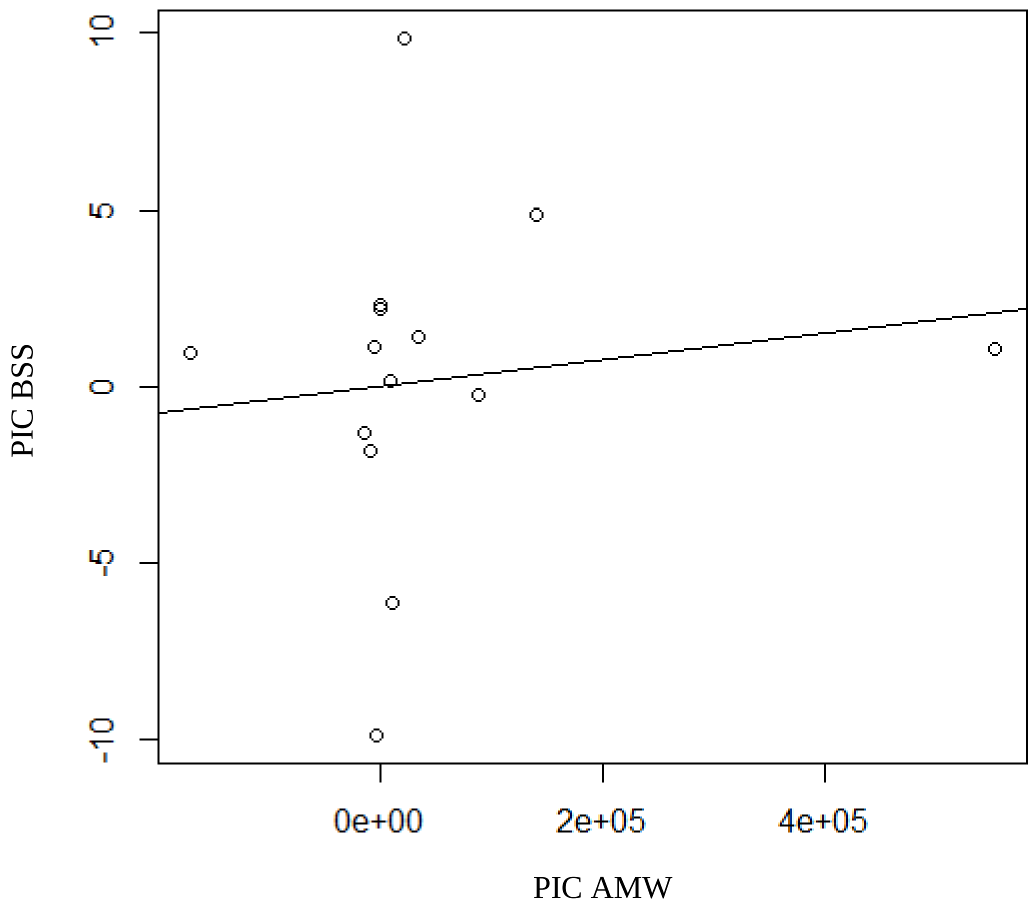

Figure SI.2.5. PIC plot of BSS against adult male weight.

Residuals	**Min**	**1 Q**	**Median**	**3 Q**	**Max**
	-9.8284	-1.2016	0.6463	2.0800	9.7640
Coefficients	**Estimate**	**Std Error**	**t value**	**Pr(>|t|)**	
PIC AMW	3.771e-06	7.548e-06	0.5	0.626	

Residual Std Error	4.564 on 13 degrees of freedom
Multiple R-squared	0.01884
Adjusted R-squared	-0.05664
F-statistic	0.2496 on 1 and 13 degrees of freedom
p-value	0.6257

Table SI.2.5. Statistical output for PIC of BSS against adult male weight.

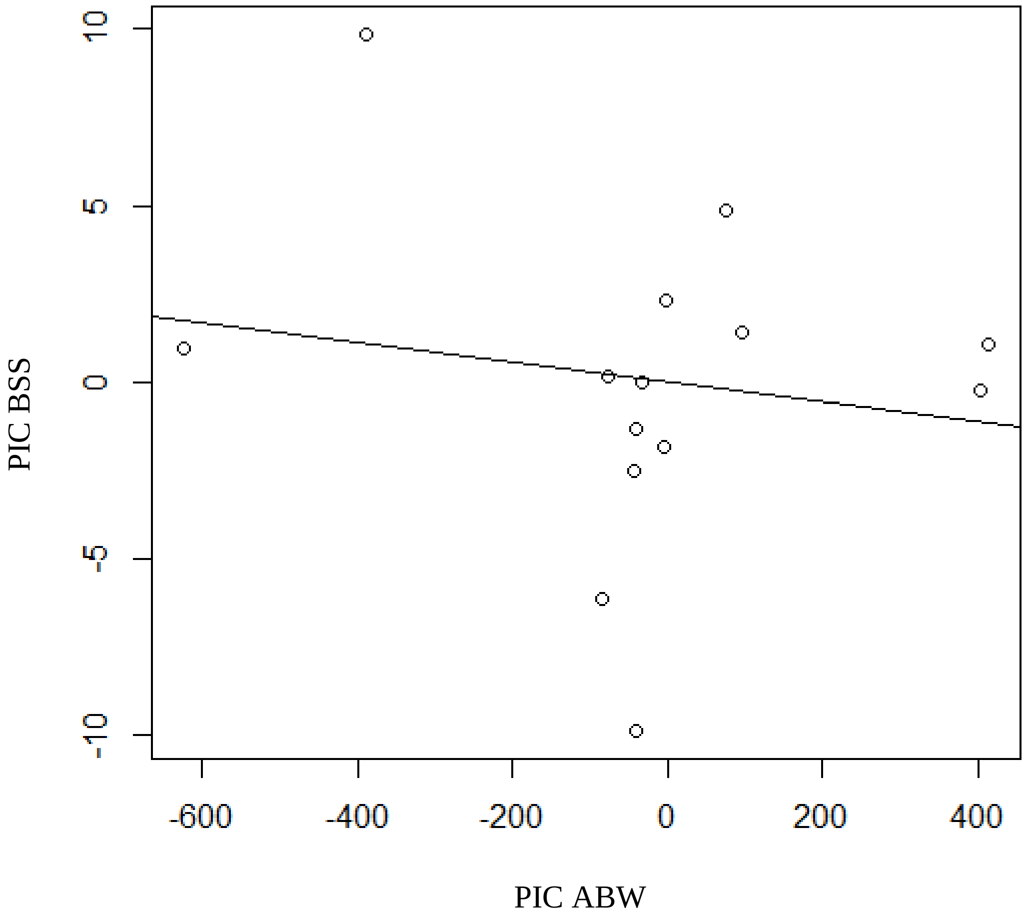

Figure SI.2.6. PIC plot of BSS against adult brain weight.

Residuals	**Min**	**1 Q**	**Median**	**3 Q**	**Max**
	-9.9590	-1.7360	-0.0705	2.0954	8.7687
Coefficients	**Estimate**	**Std Error**	**t value**	**Pr(>|t|)**	
PIC ABW	*-0.002773*	*0.004775*	-0.581	0.571	

Residual Std Error	4.549 on 13 degrees of freedom
Multiple R-squared	0.02528
Adjusted R-squared	-0.0497
F-statistic	0.3371 on 1 and 13 degrees of freedom
p-value	0.5714

Table SI.2.6. Statistical output for PIC of BSS against adult brain weight.

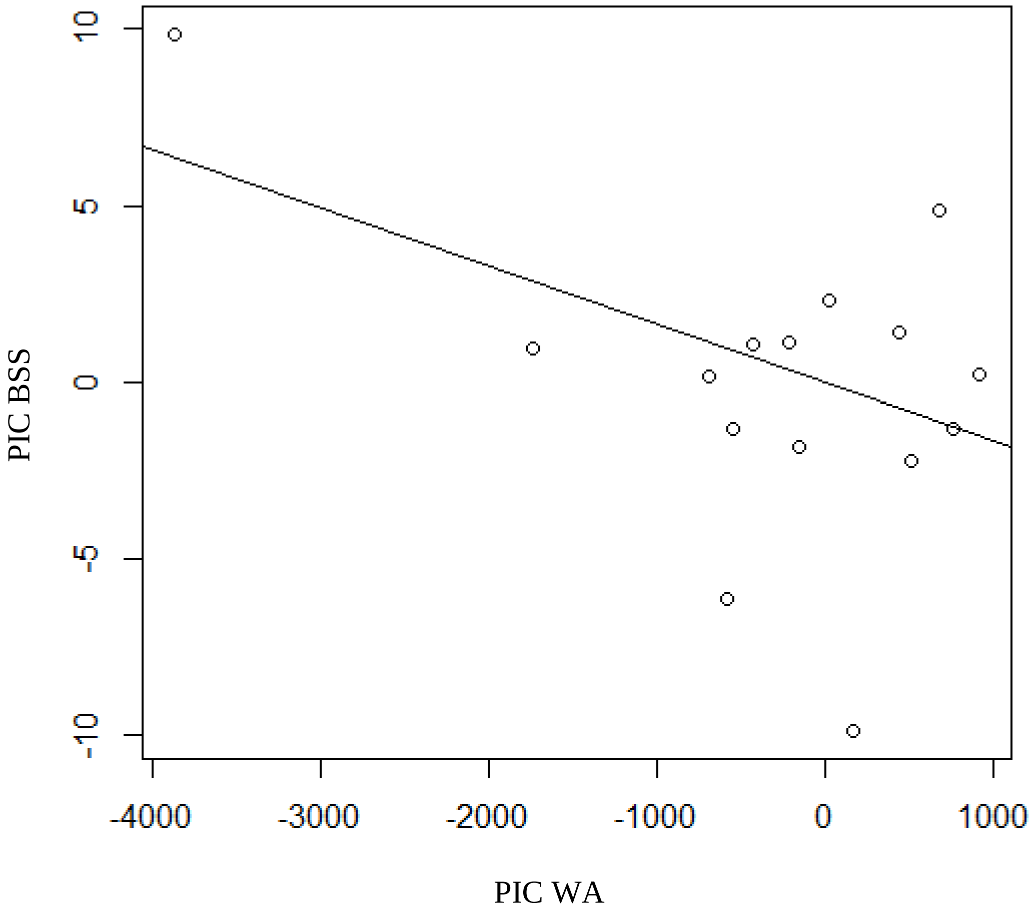

Figure SI.2.7. PIC plot of BSS against weaning age.

Residuals		**Min**	**1 Q**	**Median**	**3 Q**	**Max**
		-9.5681	-1.9745	-0.0687	1.9277	5.9975
Coefficients		**Estimate**	**Std Error**	**t value**	**Pr(>|t|)**	
	PIC WA	-0.001640	0.000849	-1.931	0.074	

Residual Std Error	3.958 on 14 degrees of freedom
Multiple R-squared	0.2103
Adjusted R-squared	0.1539
F-statistic	3.729 on 1 and 14 degrees of freedom
p-value	0.07397

Table SI.2.7. Statistical output for PIC of BSS against weaning age.

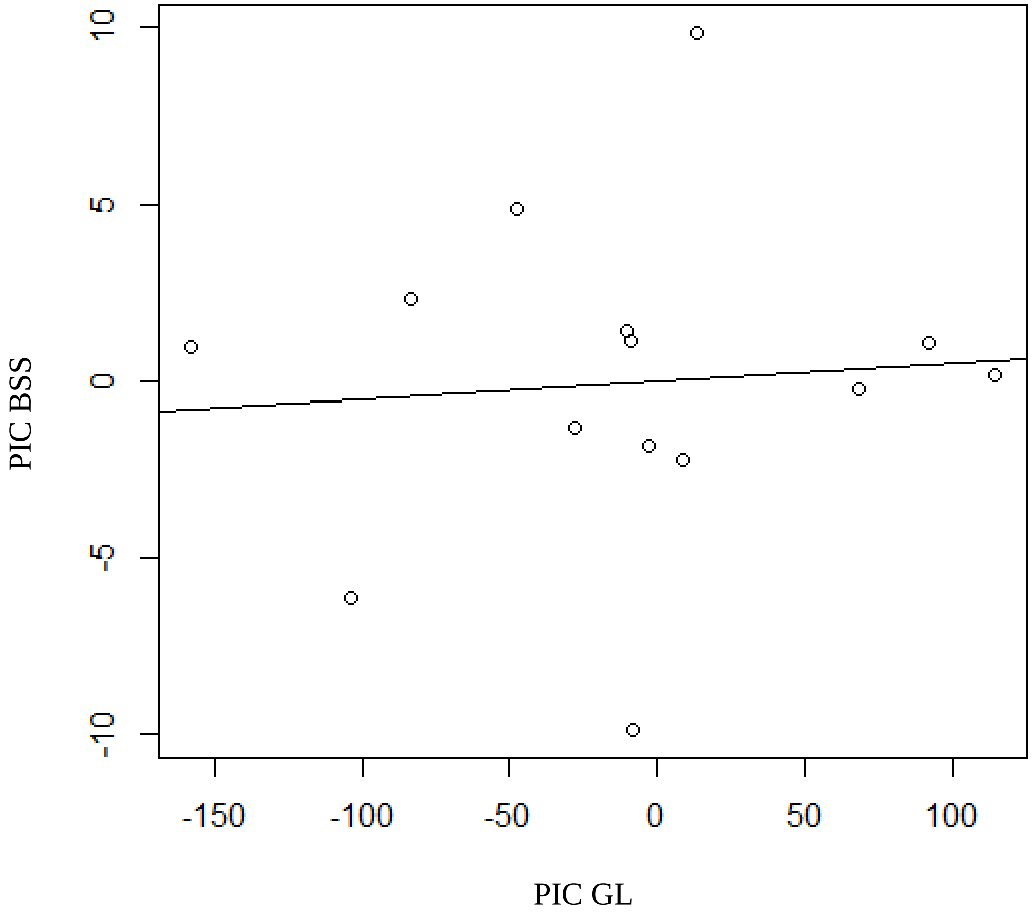

Figure SI.2.8. PIC plot of BSS against gestation length.

Residuals	**Min**	**1 Q**	**Median**	**3 Q**	**Max**
	-9.8037	-1.6493	0.1123	1.6926	9.7822
Coefficients	**Estimate**	**Std Error**	**t value**	**Pr(>|t|)**	
PIC GL	0.005027	0.017071	0.294	0.773	

Residual Std Error	4.592 on 13 degrees of freedom
Multiple R-squared	0.006625
Adjusted R-squared	-0.06979
F-statistic	0.086 7on 1 and 13 degrees of freedom
p-value	0.7731

Table SI.2.8. Statistical output of BSS against gestation length.

SI.3. Bayesian modelling analysis

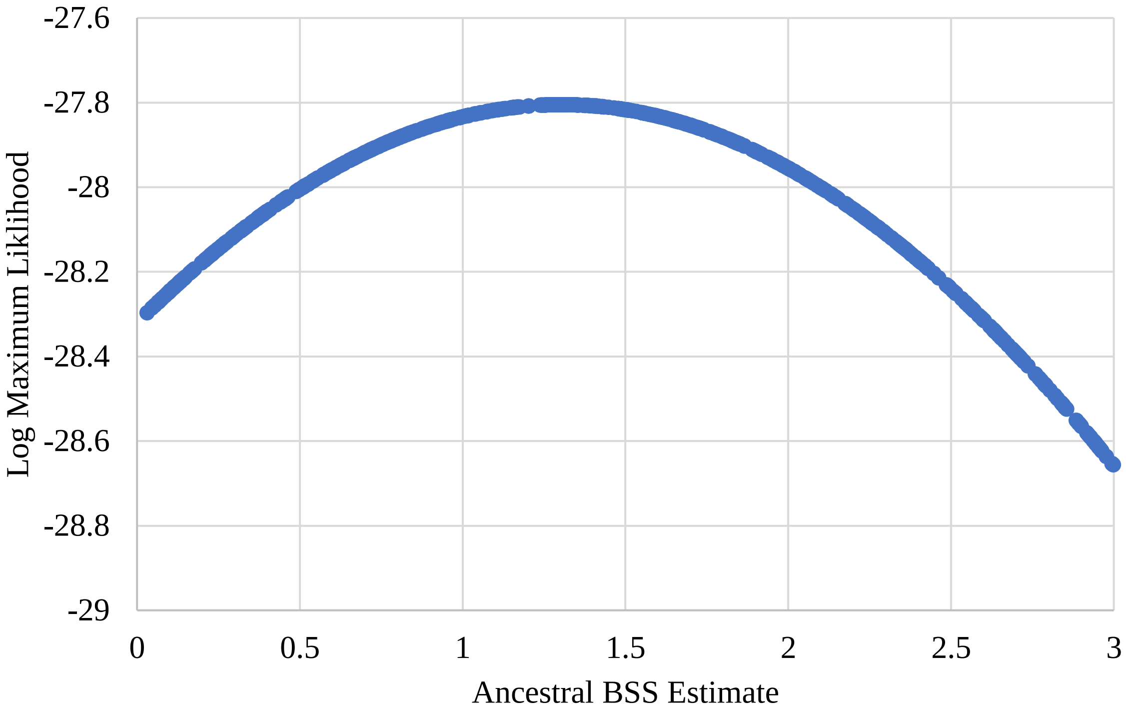

Figure SI.3.1. Plot of Log maximum likelihood estimates for Simiiforme ancestral BSS. As we can see, the curve peaks at a BSS estimate of 1.306, which suggests a degree of sociality during the birth of Simiiforme LCA infants.

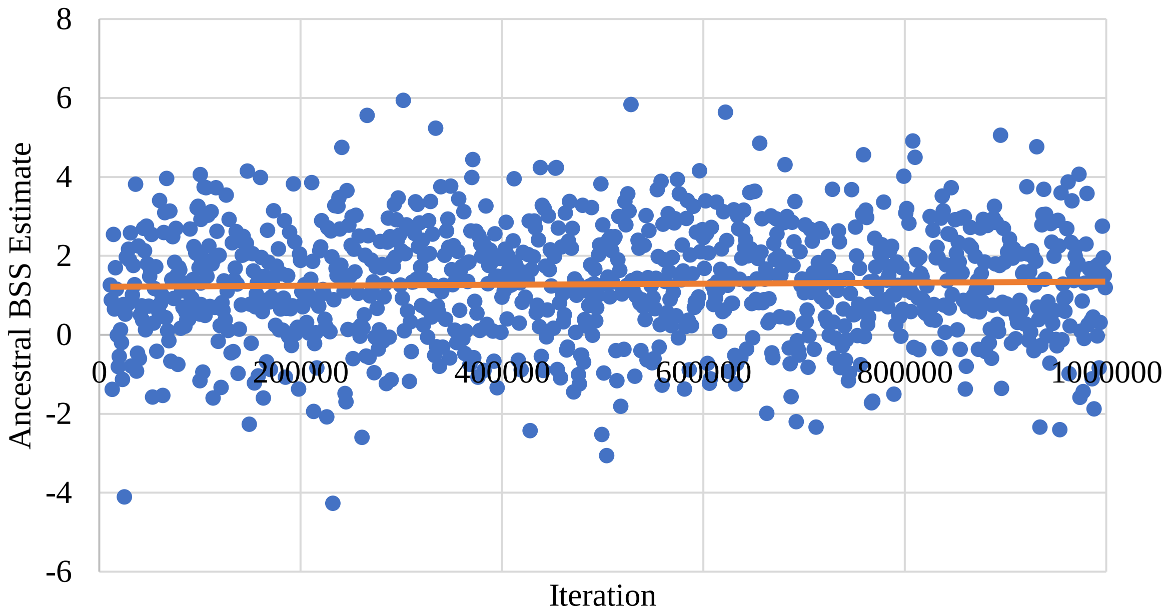

Figure SI.3.2. Plot of all iteration estimates for Simiiforme ancestral BSS. Here we can see the linear regression estimates a value of ~1.21, where the equation of the line is estimated at y=1E-07x+1.2171.

SI.4. Case study RDI data

Relevant death information (RDI)	Overall	Single RDI	Multiple RDI
Adverse environmental conditions	1	1	0
Behaviour	1	0	1
Chronic disease	2	0	2
Indeterminate	1	0	1
Infectious disease	58	56	2
Neonatal issues	94	93	1
Non-infectious disease or condition	15	12	3
Parental neglect	3	3	0
Restraint complications	7	7	0
Trauma	23	23	0
Total	205	195	10

Table SI.4.1. RDI figures provided by Twycross Zoo for primate births between 1990 and 2019. Here, single RDI refers to a recorded death where only one RDI was identified, whereas multiple RDI refers to a recorded death where multiple RDIs were recorded.