Primate pelvic anatomy and implications for birth

Wenda Trevathan

Department of Anthropology, New Mexico State University, Las Cruces, NM 88003, USA

The pelvis performs two major functions for terrestrial mammals. It provides somewhat rigid support for muscles engaged in locomotion and, for females, it serves as the birth canal. The result for many species, and especially for encephalized primates, is an ‘obstetric dilemma’ whereby the neonate often has to negotiate a tight squeeze in order to be born. On top of what was probably a baseline of challenging birth, locomotor changes in the evolution of bipedalism in the human lineage resulted in an even more complex birth process. Negotiation of the bipedal pelvis requires a series of rotations, the end of which has the infant emerging from the birth canal facing the opposite direction from the mother. This pattern, strikingly different from what is typically seen in monkeys and apes, places a premium on having assistance at delivery. Recently reported observations of births in monkeys and apes are used to compare the process in human and non-human primates, highlighting similarities and differences. These include presentation (face, occiput anterior or posterior), internal and external rotation, use of the hands by mothers and infants, reliance on assistance, and the developmental state of the neonate.

1. Introduction

A universal characteristic of almost all mammals is that birth takes place through the pelvis. Unlike the knee, where there is much homogeneity in morphology across many orders [1], the pelvis (and thus, the birth canal) is highly variable depending on both locomotor habits, and neonatal size and shape. The need for a rigid and stable pelvis for walking in mammals places limits on the size of the neonate that can successfully pass through the pelvis, and thus an upper limit on brain size at birth. This poses challenges for all mammalian orders characterized by having large brains in adulthood relative to body size, a description that fits most primates [2]. In a well-known diagram, Schultz [3] first depicted the relationship between neonatal head size and maternal birth canal as a series of rectangles (modified here as ovals) that showed a tight fit in monkeys, gibbons and humans in contrast to relative spaciousness in great apes (figure 1).

Although our knowledge of the birth process in monkeys and apes is somewhat limited and largely restricted to captive populations, it appears that the tight fit in monkeys leads to longer labour and slower delivery, and greater potential challenges than have been reported for great apes. This suggests that the large-headed neonate has more difficulty traversing the more constricted birth canal and, indeed, birth-related mortality is not uncommon in small-bodied monkey species. As an example, the small-bodied squirrel monkeys have one of the closest ratios among non-human primates; stillbirths owing to cephalopelvic disproportion have been reported to be as high as 50% in one captive population [5].

Beyond relative maternal–fetal size dimensions, however, there are shape differences between quadrupedal and bipedal pelves that have an impact on the birth process. In this paper, I first review the birth process in humans, with a focus on how adaptations for bipedalism have impacted birth, and the clinical consequences of those changes in the context of modern obstetrics. This is followed by a consideration of similarities and differences between human and non-human primate birth and factors that may account for those differences. Finally, I argue that the recently contested ‘obstetric dilemma’ [6],
stability and support. In contrast to the parallel planes of the ilium articulates with the sacrum is wider, providing greater is shorter, wider and expanded front-to-back. Where the bipedal pelvis, the ilium anterior–posterior (A–P, sagittal, front-to-back) dimension at the sacrum before entering the pelvic canal [3] (figure 2). The greatest dimension of the quadrupedal birth canal is the transverse, whereas the exit is greatest in the A–P or sagittal dimension. In between these two planes is the midplane, which usually presents the smallest diameter of the bipedal birth canal. Furthermore, the bipedal pelvic basin is compressed from top to bottom bringing the top of the sacrum directly opposite the public symphysis in the same plane [3]. This means that the neonatal head and body must pass these bony protuberances at the same time, as can be seen in figure 2. In summary, the most obstetrically relevant result of bipedalism is a pelvis that is a long-curved passageway with three alternating planes, in contrast to the much shallower quadrupedal birth canal with only two planes. Both quadrupedal and bipedal pelvises are bounded in several dimensions by bony protuberances that provide resistance to the neonate during parturition.

Because the bipedal pelvis of humans is twisted in the middle, the infant itself must ‘twist’ as it passes through the pelvis, a movement known as fetal rotation. Most frequently, the infant enters facing side-to-side (or slightly oblique) and rotates mid-way to emerge facing front-to-back. In obstetric texts, this process is described as the ‘seven cardinal movements of labour’ (i.e. engagement, descent, flexion, internal rotation, extension, external rotation and expulsion) [10,11]. Rotation is a passive movement that results when the presenting part of the neonate comes in contact with the bony portions of the pelvis and the highly resistant muscles of the pelvic floor. The head of the human neonate begins labour flexed after encountering the bony pelvis and tissues of the pelvic floor. It remains flexed throughout labour until the occiput contacts the lower border of the pubic symphysis; the head is then born by extension as the head rotates around the pubic symphysis [12]. This flexion allows the smallest diameter of the fetal head (the suboccipito-bregmatic diameter, measured from the lowest posterior point of the occipital bone to the centre of the anterior fontanel) to lead the passage through the pelvis. Stoller has suggested that birth with the head flexed until it emerges from the birth canal may be a uniquely human characteristic [13], perhaps owing to the potential for excessive neck torsion that would be required to pass through the deeper pelvis of bipedalism if it were extended throughout the birth process.

Additional pelvic modifications with bipedalism resulted in the top of the sacrum (the sacral promontory) protruding into the birth canal, so that the front of the human pelvis is more spacious than the back. As noted, the fit between neonatal head and maternal pelvis is so tight that all dimensions must line up with each other for birth to be successful. This means that the larger back of the human neonatal head (the occiput) usually fits best against the larger anterior portion of the birth canal, with the baby almost always emerging facing towards the mother’s buttocks (occiput anterior in obstetric terminology) [14]. Possible consequences of this presentation are discussed below.

Much of the preceding discussion has focused on the size of the neonatal head in presenting challenges to the birth process. For humans, however, the shoulders may provide greater obstacles than the head, and their greatest dimension (transverse) is perpendicular to the greatest dimension of the head (A–P). The cranial vault bones of human infants do not fuse until several years after birth and they can slide over each other (referred to as moulding), thus reducing the

while no longer seen as unique for humans, is a relevant challenge for almost all primates, with particular exacerbation for bipedal humans.

### 2. Human birth: anatomy, evolutionary history and modern consequences

The bipedal mode of locomotion evolved in the human lineage approximately 5–7 million years ago [7,8]. Few aspects of human evolutionary history have had a greater impact on human anatomy, not the least of which is the impact on parturition. Evolution from a putative ancestral quadruped to a biped had an impact on the shape of the human pelvis, thus affecting the passageway through which the baby is born [9]. In a quadrupedal pelvis, the ilium lies lateral to and parallel to the vertebral column and the ischium extends dorsally. Three sacral vertebrae are fused and lie high above the pubic symphysis so that during birth, the neonatal head passes the sacrum before entering the pelvic canal [3] (figure 2). The greatest dimension of the quadrupedal birth canal is the anterior–posterior (A–P, sagittal, front-to-back) dimension at both the entrance and the exit. In a bipedal pelvis, the ilium is shorter, wider and expanded front-to-back. Where the ilium articulates with the sacrum is wider, providing greater stability and support. In contrast to the parallel planes of the quadrupedal birth canal entrance and exit, the bipedal birth canal is ‘twisted’ in the middle, so that the entrance is greatest in the transverse dimension, whereas the exit is greatest in the A–P or sagittal dimension.

![Figure 1](image1.png) Redrawing of Schultz’s classic diagram relating the size of the maternal pelvic inlet (outline) and the size of the neonatal head (dark circles) in selected primate species. From Rosenberg & Trevathan [4].

![Figure 2](image2.png) Comparison of the entry of the fetal head (seen in lateral view) into the birth canal in a baboon (left) and a human (right). Note the location of the pubic bones and the sacrum in both species. The infant head passes the sacrum before it reaches the pubis in the monkey and passes both at the same time in the human. From Rosenberg & Trevathan [4].
circumference of the fetal head temporarily to allow easier passage through the birth canal [15]. The shoulders of the human infant lack that degree of flexibility, however, and may actually provide more obstruction to the birth process than the head and the rest of the body. If the rigid shoulders get stuck in the birth canal (shoulder dystocia), serious complications can result for both mother and infant, including fetal brachial plexus injury, fractures of the fetal humerus and clavicle and postpartum haemorrhage, uterine rupture and severe perineal lacerations for the mother [16]. Shoulder dystocia is more common with gestational diabetes, the lithotomy position for delivery and other phenomena of modern life and medical intervention [17], but it should not be discounted as a factor in the evolution of close correspondence between neonatal size and maternal pelvis size and shape.

The adoption of upright posture of bipedalism in the hominin line affected the way in which the upper body is supported. Rather than the torso weight being somewhat evenly distributed and slung beneath the vertebral column as it is in quadrupedal animals, more than half of the body weight of a biped must be supported by the muscles and bones of the pelvic basin. In quadrupeds, the weight of the abdominal organs (and the developing fetus in pregnancy) is distributed along the vertebral canal, where the abdominal wall acts to carry the contents, as in a hammock. In humans, abdominal contents (including the fetus during pregnancy) are carried by muscles of the pelvic floor, which are supported by the ischial spines. These spines often present the greatest challenges to delivery because they form the most restricted part of the birth canal, in the pelvic midplane [18]. If they are too far apart, the muscles can weaken with pregnancy and birth, contributing to pelvic organ prolapse (POP), a disorder that affects as many as 25% of women in the United States today [19–21]. In women with transversely wide birth canals (and potentially easier births), the risk of POP is greater than it is for women with pelves characterized by closely spaced ischial spines [18], suggesting a selective advantage of closely spaced spines that may override the advantage of large birth canals. (It should be noted, however, that POP is somewhat common in domesticated animals and captive primates, so it cannot be uniquely linked to bipedalism.)

The challenge to the supporting muscles of the pelvic floor becomes even greater in later pregnancy when the fetus ‘spills out’ into the abdomen beyond the bony support of the pelvis, altering a woman’s centre of gravity. To some extent, pregnancy length may be constrained by the physical limitations of carrying a large fetus as it expands into the abdominal cavity. Although humans have evolved adaptations that enable them to weaken efficiently and bipedalism in the late stages of pregnancy [22,23], most contemporary women find it challenging to move during the last week or two of pregnancy; it is possible that, in the past, their ability to keep up with the group and escape predators may have been compromised in late pregnancy.

3. Birth in monkeys and apes
The descriptions above of the hypothesized birth process in ancestral, non-bipedal primates are based on observations of pelvic anatomy and the birth process in monkeys and apes. For most primate species, the entrance and exit of the birth canal are longer in the sagittal dimension than in the transverse dimension, as noted for generalized quadrupeds above. The neonatal cranium is largest in the sagittal dimension in most primates species, including humans [2]. Furthermore, the back of the infant cranium presents the greatest dimension of the skull at birth, so that it fits best against the more roomy back of the human pelvis, as noted above. Monkey shoulder breadth is no greater than the head breadth, so the monkey head and body can pass through the birth canal without rotation (but see §4). With the back of the baby’s head lined up with the back of the mother’s birth canal and the shoulders providing little resistance, the monkey infant usually passes through to emerge facing in the same direction as the mother and the infant is born (figure 3).

In 1987, [14] Trevathan proposed that human and non-human primate births differed in three primary ways: (i) birth in non-human primates tends to be non-rotational, whereas human neonates almost universally rotate during birth and (ii) non-human primate infants tend to emerge from the birth canal facing the same direction as the mother (OP), whereas human neonates are usually born facing away (OA) and (iii) non-human primate births typically occur in isolation, whereas human births most often occur with assistance (but see reference [24] for a critique). These conclusions were based on my own observations of more than 250 out-of-hospital human births and a literature search of a very limited set of
observations of non-human primate births, including only a few from non-captive populations. Fortunately, the number of pri-
mat births reported in the literature has almost quadrupled since I first consulted the literature on the subject in the mid-
1980s, and many of the reports specifically challenged some of
my conclusions. Nevertheless, observations of births in both cap-
tive and wild populations are extremely rare, so caution is urged
in interpreting the descriptions discussed below. Monkeys com-
monly deliver at night in the trees, making it very difficult if not
impossible to have clear views of the process. Even in captivity,
births often occur at night or when attendants are not present.

4. Is rotational birth unique to humans?
The short answer is ‘no’. As noted, internal rotation within the
birth canal occurs in almost all human births in order for the
large-headed, large-shouldered infant to pass through the per-
pendicular pelvic planes. It was thought that rotational birth
would not occur in monkeys because of the parallel dimen-
sions of the quadrupedal pelvis and the smaller breadth of
the shoulders. This view was altered, however, when Stoller
[13], using radiographs, observed internal rotation in seven
squirrel monkeys and four baboons as the mandible passed
under the pubic symphysis; external rotation after the head
emerged from the birth canal to free the shoulders did not
occur, most likely because this was not necessary. Stoller’s
observations suggest that internal rotation during birth is not
uniquely human, nor is it uniquely related to bipedalism.

5. Do humans routinely deliver infants in the
occiput anterior position and is this distinct
from other primates?
Almost all human births occur with the head flexed and occi-
cut anterior, and the infant emerging by extension facing the
mother’s back and buttocks. Human infants occasionally
enter the birth canal with the occiput posterior, but they
usually rotate to emerge occiput anterior. Persistent occiput
posterior births are estimated to represent about 8% of all
deliveries [25]. They are associated with an increased likeli-
hood of perineal lacerations, labour and delivery are longer,
and there is more extensive moulding of the neonatal head
[25,26]. Contractions tend to be weaker, because the fetal
head does not fit as well against the dilating cervix, providing
less stimulation to the nerves in the area [12]. For the mother,
backache is much more severe in persistent posterior presen-
tations. For all of these reasons, delivery with the occiput
posterior is regarded with concern in hospital settings. This
presentation is often associated with pelvic shapes described
in the medical literature as ‘anthropoid’ and ‘android’ [10]. It
is important to note that with some pelvic shapes, the OP
may be the best fit and is thus ‘normal’ for some women [24].

Recent observations of chimpanzee births suggest that
occiput anterior, deliveries are more common than pre-
viously reported and may well be the usual presentation in
great apes. In three chimpanzee births, the neonate emerged
in the occiput anterior presentation with the head and body
rotating after the head had emerged. In two of these births,
the infant fell to the ground without any guidance from the
mother [27]. This provides evidence that occiput anterior
presentations are not unique to humans.

Although many monkey births are reported to occur with
the occiput posterior, it is possible that, for some species, the
infants may actually emerge with a face presentation and
then flex the head as the body emerges with the head occiput
posterior. In one monkey birth that was carefully observed
and includes video, the infant’s head is extended as it first
emerges from the birth canal [28]. As with humans, it is
important that the smallest diameters of the fetal head pass
through the smallest diameters of the birth canal. In the
case of the squirrel monkey and baboon births observed
radiographically by Stoller [13], the mean submentobreg-
ematic diameter (measured from below the chin to the top of
the head) was significantly smaller than the mean occipito-
frontal diameter (measured from the back of the skull to the
most anterior point, in the area between the eyebrows). This
suggests that a face presentation provides the best fit in
these monkeys and it may be far more common than has
been reported in small-bodied primates who give birth to
large-headed infants. Stoller proposes that it is the typical
presentation for monkeys and may be the ancestral pattern.
Face presentations are considered problematic in human
deliveries and occur in fewer than 1% of births [10]. It
should be noted that the dimensions for a face and an occiput
anterior presentation in human infants are similar and,
although they are considered abnormal, face presentations
usually deliver with little difficulty. The only significant
differences are that the extended neck with a face presen-
tation is not as efficient for cervical dilation as the flexed
head with occiput presenting, and there is more torsion on
the neck. In contemporary human populations, infants born
with face presentations are more likely to be preterm [29].

6. Are humans unique in having assistance at
birth?
The way in which the infant emerges from the birth canal
may explain an important difference between human and
non-human primate births: human birth almost always
occurs with assistance. When the infant is born facing the
mother, as it is in most non-human primate births, the
mother can reach down and guide it up towards her breasts
along the normal flexion of its body. Almost all monkey and
ape deliveries that occurred in the trees were reported to
occur with manual assistance from the mother. The import-
ance of this is obvious, because infants could fall from the
trees if their mothers failed to hold them until they were
able to maintain contact with her body with their own
hands and feet. As an example, in a howler monkey breech
birth, the mother did not use her hands and her infant fell
6 ft to the ground upon emergence from the birth canal
[30]. In terrestrial monkeys, maternal use of hands to assist
delivery is more variable, and sometimes the infants fall a
short distance to the ground as they are born, but the mothers
retrieve them immediately.

If the baby emerges facing away from the mother, as it
most commonly does in human deliveries, I have proposed
that the mother may risk injuring the nerves and muscles
of the neck if she attempts to guide it from the birth canal
and pulls it against the normal flexion of its body [14]. Fur-
thermore, if the infant is born with fluids around its face
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If the umbilical cord is wrapped around the neck (referred to in medical texts as a nuchal cord) as it is in approximately 23–33% of births [31], she may also find it difficult to remove it before the baby is expelled further (and possibly strangled) with the next contraction. For humans, others are almost universally present at human births and provide some form of assistance [14,32].

While not as routine as it is in humans, the presence of others at birth has been reported for a number of primate species. Several of the small New World primate species (e.g. Callicebus, Callithrix, Saguinus) form pair bonds, in which case the males are often present at birth and typically take a direct interest in the process. In some cases, males have been observed licking and holding the infants soon after birth [33]. In monkeys, interest in the birth on the part of troop members is reportedly high, although direct assistance is not reported [29,34–36]. Nearby troop members probably provide a more safe environment for the mother at a vulnerable time. When a langur mother delivered her infant on the ground (in trees is more common), two females sat by her side and remained there until the delivery was complete and all three returned to the trees [37]. Intervention and assistance may occur more commonly in unusual circumstances. A male hamadryas tried to intervene to catch an infant born over the edge of a cliff to a primiparous female, although she was able to retrieve it before he got there [38]. A multiparous Rhinopithecus monkey was observed assisting a primipara by pulling the infant from the birth canal with her hands and breaking the amniotic sac [39]. As soon as the infant’s shoulders were born to a primiparous white-headed langur, another female quickly intervened and pulled the infant out of the birth canal towards her own ventrum. According to the authors, the mother did not appear to need assistance and the ‘midwife’ seemed far more interested in the infant than in the parturient [40]. There are several reports of orangutans assisting their mates during delivery, at least in captivity [41].

Although direct assistance with birth appears uncommon in primates, females may seek the company of other members of their social group for safety, as with the langur described above who gave birth on the ground. In species in which infanticide occurs, having a male [42,43] or other females nearby at birth may reduce the chances of a mother losing her infant and place an advantage on social birth. This proposal is particularly interesting in the light of the high degree of sociality at birth among langurs, species for which infanticide has been frequently reported [44,45].

Perhaps it is not unique to humans, but routinely seeking assistance at birth is widely distributed among human cultures and comes close to being a human ‘universal’. Of the 296 cultures in which mention of attendance at birth is made, only 24 report that delivery may and does take place unattended [14]. Even in the groups that report unattended delivery as the norm, the first birth often occurs in the presence of family members. Among the !Kung, for example, the cultural ideal is to give birth alone, but most women have others with them when they give birth [46]. Solitary delivery is the accepted way to give birth among the Bariba of West Africa and assistance is sought only in unusual or difficult circumstances [47].

7. Birth and the state of the newborn infant

In addition to those reviewed above, there are a number of other ways in which births in non-human and human primates differ beyond the significant and obvious effects of human consciousness and culture. For example, most non-human primate neonates have motor skills that enable them to play active roles in the birth process by using their hands to help themselves out of the birth canal and up towards the mother’s ventrum. Strepsirrhine primate neonates appear to play more active roles in birth than their mothers in many reported cases. In observations of lorises, newborn infants actively delivered themselves, whereas their mothers simply used their hands to provide support as the babies emerged. Even in a breech birth, the infant was observed to pull itself out in a ‘somerault-like movement’ [48, p. 569]. In a free-ranging sifaka birth, the infant was expelled and climbed up to its mother’s nipple with no apparent assistance on her part [49].

Newborn marmosets were observed to climb from the birth canal to the nipples unaided by the mother [50]. Titi monkeys were observed climbing up the mother’s ventrum without assistance [33], as were mantled howling monkeys [51], white-headed langurs [52] and Japanese macaques [53]. Squirrel monkeys, whose neonatal heads are among the largest in the order relative to the mother’s pelvis, are reported to pull themselves out of the birth canal once the shoulders are freed. Within minutes of birth, the infant is crawling around her body, eyes open and searching for the nipples [54]. An infant macaque that presented the breech attempt to pull itself from the birth canal with its legs, but died before it was born [55]. Infants in many monkey species are reported to cling within minutes of birth with little or no assistance.

There are no reports of human neonates using their hands to assist in their own deliveries, although their grip strength is unusually strong in the first few hours of life, a characteristic that disappears soon after birth. Evidence of motor skills that soon disappear includes the primary walking and Moro reflexes, which have been interpreted by some to indicate vestiges of clinging ability [56]. Of course, the absence of maternal body hair precludes gripping even if the reflexes were retained. The lack of neonatal motor skills for clinging may be related to the relatively low percentage of brain growth completed at birth: 29% in humans compared with an average of 50% in monkeys [57]. Chimpanzees are somewhat intermediate in both brain development (39.5%, [58]) and motor skills.

Haplorhine primates have been described as ‘preocial’ to describe the state of the newborn infant. Like other precocial mammals, they are born as singletons (usually) after relatively long gestations, with eyes and ears well developed, and the ability to cling to their mothers in a way that enables them to access the comparatively dilute milk with high frequency. Similarly, humans have a long gestation period, give birth to one infant at a time (usually) with eyes and ears open, and have dilute milk requiring their infants to nurse frequently. They differ from other haplorhines, however, in their motor development and the relative percentage of brain growth that has occurred by the time of birth, only about a quarter in contrast to the average half in most mammals, including most primates. Because of their state of brain and motor development, human newborn infants have been described as ‘secondarily atricial’ [59], although the term has recently come under fire as misleadingly implying a lower level of maturity than is actually true when other aspects of infant state are measured (e.g. visual acuity, cognitive development).

Why is the human infant brain so undeveloped in motor skills at birth, leading to greater need for locomotor assistance
from parents and allopairs for at least the first year of life? For more than 50 years, the most common explanation has been that of the ‘obstetric dilemma,’ a phrase first used by Washburn [6] to describe the conflicting demands of selection for bipedalism concurrent with selection for expanded brain size. In his view, the only way for a large-brained infant to pass through the constricted bipedal pelvis is for it to be born before the brain had completed even half of its growth. At some level, the claim that the human infant reaches its maximum brain size that can be delivered through the birth canal is true, as it is for all terrestrial mammals. There are other factors operating to lead to the birth of a somewhat developmentally delayed infant, however. Chief among these is energetics—the mother’s metabolism simply cannot keep pace with the increasing demands of the infant body and brain growth towards the end of pregnancy [60,61]. The deeply invasive human placenta and compromised immune system of the mother during pregnancy also likely play roles in determining the nine-month gestation period and relatively undeveloped brain.

Oxygen is of utmost importance to metabolism and brain growth, of course, and the amount of oxygen available to the infant outside the womb increases fivefold in comparison with what is available in utero [62]. Prolonging time in utero may lead not only to the infant ‘starving to death’ with regard to energy, but also oxygen starvation. Clearly, continued brain growth requires adequate oxygen; in one view, birth occurs when the fetal lungs are mature enough to use the higher levels of oxygen in the environment outside the womb. Furthermore, there are advantages to having neurologi- cal development occur in the stimulating environment of the outside world and a dense social network. These advantages are not unique for humans, of course, but they are facilitated by extensive commitment from mothers and others [63–65].

### References


