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Metabolic hypothesis for human altriciality

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The classic anthropological hypothesis known as the “obstetrical dilemma” is a well-known explanation for human altriciality, a condition that has significant implications for human social and behavioral evolution. The hypothesis holds that antagonistic selection for a large neonatal brain and a narrow, bipedal-adapted birth canal poses a problem for childbirth; the hominin “solution” is to truncate gestation, resulting in an altricial neonate. This explanation for human altriciality based on pelvic constraints persists despite data linking human life history to that of other species. Here, we present evidence that challenges the importance of pelvic morphology and mechanics in the evolution of human gestation and altriciality. Instead, our analyses suggest that limits to maternal metabolism are the primary constraints on human gestation length and fetal growth. Although pelvic remodeling and encephalization during hominin evolution contributed to the present parturitional difficulty, there is little evidence that pelvic constraints have altered the timing of birth.

bipedalism | EGG hypothesis | energetics | metabolic crossover hypothesis | pregnancy

Eutherian mammals vary widely in their degree of development at birth. Altricial species (e.g., rodents and some carnivores) are characterized by a large number of littermates and short gestation lengths, resulting in relatively undeveloped brains, a lack of specialization in corporal development, and feebleness at birth. Altricial neonates are usually hairless and dependent on external sources for warmth, and their sensory organs are often closed. In contrast, precocial species (e.g., bovids, equids, cetaceans) are born when they are highly developed with fully open and operating sensory organs. Immediately after birth, precocial neonates begin behaving similarly to adults in movement, sensory perception, and communication. Neonate development is thought to reflect each species' evolved maternal investment strategy, as well as environmental pressures, such as resource availability and predation risk (1–3).

Humans differ from other primates in terms of neonatal development. Our neonates are born with the least-developed brains of any primate, with brains less than 30% of adult size (4). As a result, although human newborns are precocial in other respects, our neonates are neurologically and behaviorally altricial. Portmann (5) coined the term “secondary altriciality” to describe the distinct state of human neonates compared with the kind of primary or primitive altriciality experienced by other mammals and derived with respect to primate precociality. He estimated that instead of 9 mo, a gestation period of 18–21 mo would be required for humans to be born at neurological and cognitive developmental stage equivalent to that achieved by a chimpanzee neonate (see also ref. 6).

Human altriciality has long been seen as an important hominin trait, not just because of its departure from the other primates but because of the reproductive and social strategies that vulnerable human babies demand. With highly dependent babies that mature slowly and cannot cling to their mothers, humans care for offspring through pair-bonding, grand-parenting, and alloparenting. Thus, hypotheses for the evolution of human behavior have often hinged on the evolution of human birth and neonatal development (7–9).

Portmann (5) hypothesized that human altriciality was adaptive: that truncating gestation allowed for an “extrauterine spring” during the first year after birth, when a human infant develops cognitive and motorneural skills. However, it is more commonly proposed that human gestation length and altriciality are a solution to the uniquely human “obstetrical dilemma” (10–20), also called the “obstetric dilemma” and, henceforth, referred to as OD. The OD hypothesis proposes that Pleistocene hominins faced antagonistic selection pressures on locomotor requirements and encephalization. These competing demands pushed fetal brain size to the functional limits of hominin mothers' bipedal-adapted pelvis. With continued pressure for increased adult brain size, natural selection favored mothers who birthed babies earlier in fetal development while still small enough to escape the narrow birth canal. In other words, in an evolutionary tradeoff, natural selection favored a shorter gestation period and less developed neonates to accommodate both locomotion and encephalization.

As an explanation for altriciality, arguments for the OD often focus on the dimensions of the human pelvis and the complicated and difficult nature of childbirth. Where Cesarean sections are not performed, human pelvic morphology determines the maximum size of the neonate that can pass through the birth canal safely, as in all mammals with bony birth canals. However, in humans, the birth canal is smaller relative to neonatal size than it is in most other primates (Fig. S1), which has been partly attributed to adaptations for bipedal locomotion (13, 21–23). As a result, many humans experience rotation during childbirth to pass through the birth canal, which from inlet to outlet shifts from being widest in the mediolateral plane to widest in the anteroposterior plane. Because of the difficulties of childbirth, nearly all women in nearly all cultures have assistance during labor, and mothers sometimes die in the process (24).

The OD focus on pelvic constraint as the explanation for human gestation timing and altriciality is intuitively appealing, but is it correct? That is, given that all female mammal pelvis are under selection to accommodate neonates, are human pelvis uniquely limited and, thus, uniquely influencing life history? Using data that were unavailable when the OD hypothesis was initially proposed, here we reexamine gestational investment among humans and other primates. We then test the primary prediction of the OD hypothesis that increased pelvic breadth results in mechanically and energetically compromised walking and running in humans. As we demonstrate, current data strongly challenge components of the OD. Instead of a pelvic constraint, we propose a different explanation for the timing of human birth: human gestation length, neonatal size, and altriciality are the consequences of a constrained maternal metabolism.

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Human Gestation in a Comparative Context

Gestation Length. Gestation length among placental mammals is related to body size, but gestation length in humans is shorter than expected based on how much growth the neonatal brain must achieve to reach adult size (25). However, using adult brain size as an allometric scalar for gestation length (or any trait) will lead to relatively low values for humans simply because of our high degree of encephalization. Instead, we compared human gestation length to that of other primates using maternal body size, a reliable proxy for maternal resources and metabolism (25, 26).

At 38–40 wk, on average, human gestation is absolutely longer than that of *Pan* (32 wk) and *Gorilla* and *Pongo* (37–38 wk). Controlling for the positive relationship between maternal body mass and gestation length in primates ($n = 21$ species; $r^2 = 0.56$; Fig. 1 and Fig. S2), humans are second only to *Pongo* in their gestation length. Human gestation length is 37 d longer than expected for a primate of similar body mass, relatively longer than either *Gorilla* or *Pan*. So not only is human gestation not truncated, as comparisons controlling for adult brain size might suggest, but the data indicate that gestation has increased in the hominin lineage.

Maternal Investment. One possible interpretation of human altriciality is that human mothers invest less in fetal brain and body development than other primates, forgoing the last bit of maternal investment during gestation so neonates can negotiate the uniquely constrained birth canal. However, human neonates are large compared with other mammals (14, 27, 28), indicating that they receive more, not less, maternal investment during gestation than expected.

Compared with chimpanzees, humans have small brains at birth relative to adult brain size; humans are born with brains less than 30% their adult size, whereas chimpanzees are born with brains ~40% their adult size (4) (Fig. S3). However, as with gestation length, the use of adult brain size as an allometric scalar will always produce low values of human neonatal brain size.

Instead, we compared neonate body and brain size among humans and other primates to maternal body size (29), which is a proxy for the metabolic resources of the mother (Fig. 1). Human neonatal brains are larger than those of other apes both in absolute measures and in relation to maternal body size. Human neonates have brains 47% larger than gorillas and body masses twice that of gorillas, the primate with the next largest values. Controlling for the positive relationship between mothers' body mass and neonatal brain size among primates ($n = 21$ species; $r^2 = 0.87$) humans have neonatal brain sizes a full SD above that

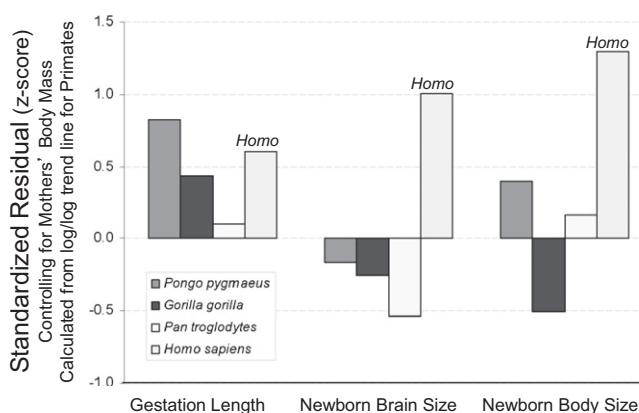


Fig. 1. Maternal investment in hominoids. Among the great apes, humans have relatively long gestation lengths, large-brained infants, and large-bodied infants. For further explanation, see Fig. S2.

expected from maternal body size (z score = 1.01), substantially larger than the other apes. Human neonatal body size is also larger than expected (z score = 1.29).

Together with the measurement of gestation cited above, these results suggest that neonatal brain and body size have increased in the hominin lineage and that human maternal investment is greater than expected for a primate of our body mass. Increased gestation length and investment in humans point to a divergent strategy for increased fetal growth relative to other hominoids. However, given the helpless nature of human neonates and the challenges of caring for them, the question remains: what limits further fetal growth?

Testing the Obstetrical Dilemma Hypothesis

As outlined above, the traditional explanation for the apparent constraint on increased fetal investment in humans is the OD hypothesis, which suggests that broadening the female pelvis beyond its current dimensions would significantly diminish locomotor performance. The OD hypothesis suggests that the sexual dimorphism evident in human pelvis evolved because childbirth in Pleistocene hominins was difficult and dangerous, and selection favored a wider pelvis to lower the risks associated with delivery by better accommodating an encephalized neonate. Indeed, females are smaller-bodied than males but have absolutely wider interacetabular breadths, and other dimensions of the pelvis, than males (30). As a complex trait, pelvic morphology experiences a variety of selection pressures in both males and females. Women's walking and running mechanics are similar to those of men, and it is widely held that selection has favored female pelvic morphology that is conducive to successful parturition but compromises locomotor efficiency (21, 31, 32). The OD hypothesis argues that further broadening of the female pelvis is evolutionarily untenable, because the concomitant decrease in locomotor efficiency would reduce fitness.

The argument linking pelvic width and locomotor efficiency centers on the function of the hip abductors during walking and running. The hip abductors (*M. gluteus medius* and *minimus*) activate during single-leg-support phase during walking and running to prevent the trunk from rotating (falling) away from the stance leg. The traditional view of hip abductor mechanics (the view integrated into the OD hypothesis) is that broader pelvises ought to increase the force required by the abductors, thereby increasing their activity and metabolic demand. This view is based on static mechanical models of the human pelvis where biacetabular breadth is expected to define the external moment arm, R , of the resolved ground reaction force generating torque about the hip (Fig. 2). Thus, the OD predicts that female walking and running should be more costly than that of males and that any additional evolutionary broadening of the pelvis would further increase the force required by the abductors and reduce walking and running economy.

We drew on recent work examining the mechanics and energetics of walking and running in humans to test these predictions. Numerous studies over the past three decades have measured the metabolic energy cost of walking and running in men and women with varying results; the majority have found no difference in cost, with some finding that females are more economical (*SI Text*). The inconsistency of these results highlights the variability in locomotor cost among humans, as well as methodological differences in calculating cost. However, taken together, these studies strongly challenge the expectation of the OD hypothesis, that wider female pelvises negatively affect locomotor economy.

Recent work on the mechanics of hip abductor muscles moves beyond the static models used by the OD hypothesis to more explicitly and dynamically address the relationship between pelvic shape and locomotor cost. A study of 15 men and women (*SI Text*) by A.G.W. demonstrated that mediolateral ground force

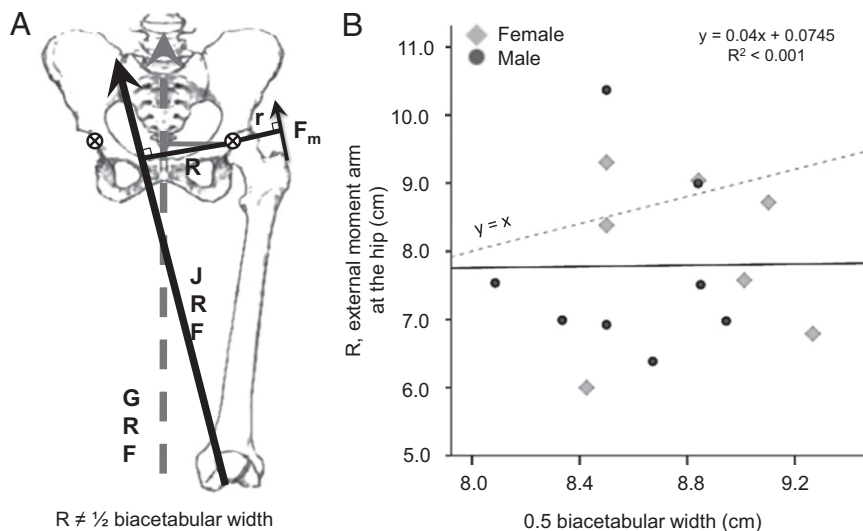


Fig. 2. Hip abductor mechanics. (A) To maintain equilibrium about the hip during single leg stance, the hip abductors must generate torque (multiple of muscle force, $F_m \times$ abductor moment arm, r) equal to the external torque rotating the pelvis away from the stance side. Previous mechanical models assumed the external ground reaction force (GRF) passes nearly vertically through the body midline; therefore, the body weight moment arm could be approximated as equal to one-half biacetabular width. However, external torque is properly measured as the multiple of joint reaction force (JRF) at the distal segment of the femur and the JRF moment arm (R). This calculation accounts for the mediolateral component of the external force and the inertial and gravitational moments acting on the more distal segments of the limb. These forces cause the resolved JRF to move away from the joint center of rotation during single leg stance. (B) As a result, there is no relationship between one-half biacetabular width and the external moment arm at the hip (R) in the coronal plane during walking. Results are similar for running (see *SI Text* and *Table S1*).

production and segmental accelerations of the foot and shank alter hip abductor force production in ways that cannot be predicted by pelvic width alone. Walking and running trials, in conjunction with anatomical data taken from lower body MRIs, showed that biacetabular width does not predict the length of the external moment arm, R , about the hip in the coronal plane (Fig. 2 and Fig. S4). These data indicate that skeletal dimensions of the pelvis do not predict the magnitude of hip abductor muscle force activation. Instead, subtle variation in walking and running dynamics counteracts the potential cost of broader pelvis. Together with studies of locomotor cost outlined above, these results indicate that broader pelvis are not less efficient and that women's locomotor economy is not reduced by virtue of having broader pelvis.

Finally, it should be noted that broadening the human female pelvis to birth a neonate with chimpanzee-like brain development would not radically change human pelvic dimensions. To birth a human baby at the same stage of brain development as a chimpanzee neonate, at $\sim 40\%$ its adult brain size (4), a human mother's pelvis would need to accommodate a fetal brain size of 640 cc. Considering the neonatal head as a sphere (33), and accounting for the layers of meninges, bone, and skin, a neonatal brain this large would have a diameter of ~ 11 – 12 cm. This diameter is less than 3 cm larger than that of the typical human neonatal head, which has a brain size of 350–400 cc after 9 mo of gestation (29), and a diameter of about 9 cm (33). This suggests that birthing a neonate with a brain size 40% that of adults would require a 3-cm increase, on average, in the mother's pelvic inlet to pass that larger fetus. A 3-cm increase is within the range of pelvic dimensions seen in modern human females (30) and has no measurable effect on hip abductor mechanical advantage (Fig. 2) or, as discussed above, on locomotor cost. In other words, the available evidence suggests that human females could adapt to accommodate a 640 cc neonatal brain without any reduction in locomotor economy (contra ref. 6). [Other aspects of neonate size morphology (e.g., shoulder breadth) can also contribute to parturitional difficulty; we do not address these here.]

In sum, biomechanical evidence fails to support the predictions of the OD hypothesis regarding locomotor cost. There is no evidence that female pelvic morphology affects locomotor cost, or that further neonatal brain expansion is evolutionarily constrained by pelvic mechanics. Instead, and as in other mammals, human pelvic dimensions have been selected to accommodate neonate dimensions, which, we suggest, are, in turn, constrained by some other aspect of maternal or fetal physiology. We propose that the primary constraint on human neonatal brain and body size is maternal metabolic throughput, as it is across mammals.

Metabolic Hypothesis for Gestation Length and Fetal Growth

Gestation places a heavy metabolic burden (measured in calories consumed) on the mother (34). During gestation, mothers must support the metabolic cost of tissue growth (both of the fetus and the mother), as well as the ever-increasing metabolic rate of the growing fetus. Comparative data from across mammals and primates suggest that there is a metabolic constraint on how large and energetically expensive a fetus can grow before it must leave the mother's body (29, 35–38). We propose that energetic constraints of both mother and fetus are the primary determinants of gestation length and fetal growth in humans and across mammals and, for ease of communication, we have named this the “EGG hypothesis” (energetics of gestation and growth). Under this hypothesis, the timing of human birth is a direct consequence of maternal metabolic constraints.

The EGG hypothesis is essentially an extension of Ellison's (39) “metabolic crossover hypothesis” for gestation length and timing of parturition in humans. According to current understanding, the normal onset of parturition in humans is governed by the balance between maternal and fetal metabolism and not by uterine or pelvic constraints. Labor begins when fetal energy demands surpass, or “crossover,” the mother's ability to meet those demands. The timing of parturition is determined by metabolic stress via hormonal signaling (*SI Text*).

The biochemical processes governing the timing of birth are different for different species, but the EGG hypothesis is consistent

with physiological evidence for metabolic constraints on reproduction across mammals. Laboratory studies of mammals consistently show that sustained (i.e., over multiple days) metabolic rate is constrained and that energy costs during pregnancy and lactation approach the metabolic ceiling for many species (40). In humans, maximum sustained metabolic rate is thought to be 2.0–2.5× basal metabolic rate (BMR) (40, 41). [Tour de France cyclists can approach 4–5× BMR, but this is not typical for humans, which generally do not exhibit sustained energy expenditures in excess of 2.5× BMR (40).] During pregnancy, metabolic rates in human mothers quickly approach this limit, with daily energy expenditures two times greater than prepregnancy BMR by the sixth month (42, 43). Throughout the rest of pregnancy and through the first months of nursing, maternal metabolic rates stay at 2.0× BMR but never climb higher, even in populations where strenuous manual labor is common among pregnant women and new mothers (40, 42, 43). Instead, among both affluent and energy-stressed populations, women commonly use a range of behavioral and physiological strategies to reduce daily energy needs during pregnancy and lactation (44). Together, these studies suggest that across human populations mothers approach a metabolic ceiling during pregnancy that constrains further energy throughput.

The length of human gestation and the timing of parturition appear to follow directly from this constraint on sustained maternal metabolic rate. As a fetus grows exponentially throughout gestation, so do the metabolic requirements for tissue growth and maintenance (Fig. 3). By 9 mo, metabolic demands of the fetus threaten to push maternal energy requirements beyond 2.1× BMR. Extending gestation by even one month would likely require metabolic investment beyond the mother's capacity. Instead, the mother delivers and the neonate's growth rate slows relative to its fetal growth rate, keeping both the offspring's and the mother's energy requirements in check.

Discussion

The combined circumstantial evidence of unique locomotion, high adult encephalization, atypical neonatal altriciality, and difficult

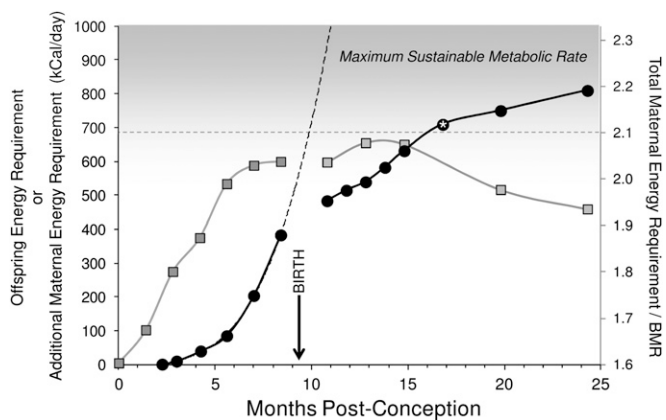


Fig. 3. Metabolic constraint on gestation length and fetal size. Fetal energy demands (black circles, kcal/d) increase exponentially during gestation. Maternal energy expenditure (gray squares) rises during the first two trimesters but reaches a metabolic ceiling in the third, as total energy requirements approach 2.0× BMR. Projected fetal energy requirements for growth beyond 9 mo (dashed line) quickly exceed the maximum sustainable metabolic rates for human mothers. After parturition (arrow), infant energy demands (black circles) increase more slowly, and maternal energy requirements do not exceed 2.1× BMR. Required maternal energy expenditure for a fetus developmentally similar to a chimpanzee newborn (7-mo-old infant; symbol with asterisk) would entail maternal energy requirements greater than 2.1× BMR. Data are from refs. 40–42 (Table S2).

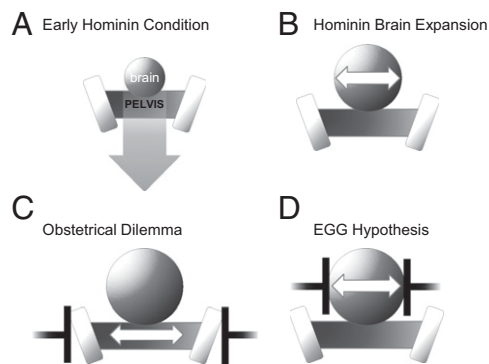


Fig. 4. Schematic of OD and EGG hypotheses. (A) Early hominins, like living apes, have little difficulty in parturition; the neonatal brain is small relative to the pelvic outlet. (B) As hominin brain size expands, neonatal brain and pelvis size become tightly coupled. (C) The OD hypothesis proposes that further neonatal brain expansion is constrained by selection acting on pelvic width: the female pelvis cannot expand further because of selection on locomotor economy. (D) The EGG hypothesis proposes that further neonatal brain expansion is constrained by the limits of maternal energy supply: larger neonatal brain and body sizes would exceed the mother's capacity to provide energy to the fetus (Fig. 3).

childbirth has long been used to support the hypothesis that human gestation and fetal growth are constrained by the passage of neonates through the mechanically constrained hominin pelvis (OD). However, the available data on maternal energy use and neonatal energy demand indicate that metabolic constraints determine the timing of parturition and degree of fetal investment for human mothers (EGG). Furthermore, the EGG hypothesis suggests that increased maternal metabolism, not increased pelvic dimensions, may be the primary target of selection for increasing fetal investment in humans. This view is consistent with recent work showing daily energy expenditures in humans are greater than those of orangutans (45), but more data on ape energy expenditure are needed to test this prediction of the EGG hypothesis.

The EGG hypothesis provides a different perspective on the evolution of hominin brain size, gestation, and pelvic anatomy. Both the OD and EGG hypotheses envision brain expansion in Plio-Pleistocene hominins leading to a tight coupling of neonatal brain and maternal pelvis dimensions (Fig. 4). The OD hypothesis proposes that further fetal brain expansion is constrained by locomotor demands on the pelvis, whereas the EGG hypothesis proposes that further fetal brain expansion is constrained by the limits of maternal metabolism (Fig. 4). In the EGG scenario, the female pelvis has adapted to the size of the fetal brain, not the other way around. This view is supported by the metabolic comparisons presented here and by the well-documented pelvic dimorphism evident in humans.

However, if the human female pelvis is adapted to the size of the neonatal head, then why is there such a tight and often problematic fit? One possibility is that female body size is under strong stabilizing selection, such that a greatly expanded pelvis, and the larger body sizes it would entail, is selected against. This scenario is consistent with the view that female body size is constrained by ecological factors (46). A second possibility is that expanding the pelvis beyond its current dimensions would diminish some unexamined, nonenergetic aspect of locomotor performance, such as speed or stability. Wider pelvises may also increase the risk of injury, either through increasing the likelihood of pelvic prolapse (47) or by increasing mediolateral stresses on the knees and ankles (48). These scenarios would suggest an OD-like mechanism acting on pelvic morphology secondarily to the metabolic limits on neonatal body and brain size. A third possibility is that the present level

of difficulty and danger in childbirth is a relatively recent phenomenon brought on by an increase in maternal energy consumption (49). In this scenario, recent changes in the diet have increased energy availability during gestation, leading to larger neonates, but selection has not had sufficient time or reason to accommodate the female pelvis to this recent dietary change. Finally, a fourth possibility, originally proposed by Portmann (5), is that the timing of human birth and degree of neonatal brain development optimizes cognitive and motor neuronal development (50). Additional work is needed to determine whether these factors, or others, might help to explain the difficulty of birth in modern human populations.

Although the development of neural circuitry, pelvic size, fetal growth rates, and other factors may be involved in the evolution of gestation length, the evidence we present here supports an energetic explanation, based on mammalian physiological constraints, for the timing of human birth. Under the EGG hypothesis, if the human reproductive system poses a dilemma between competing needs, then fetal energy needs and maternal

energy supply are the competitors, rather than encephalization and bipedalism. Thus, human neonatal altriciality is better described as prolongation of fetal brain maturation and growth irrespective of parturition (5). With a better understanding of the energetic constraints on gestation and fetal growth and a stronger grasp of all of the factors that determine human birth timing, there is greater potential to explain the evolution of the extended human childhood and to understand its biological, behavioral, and cultural consequences.

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