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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 pelvises are under selection to accommodate neonates, are human pelvises 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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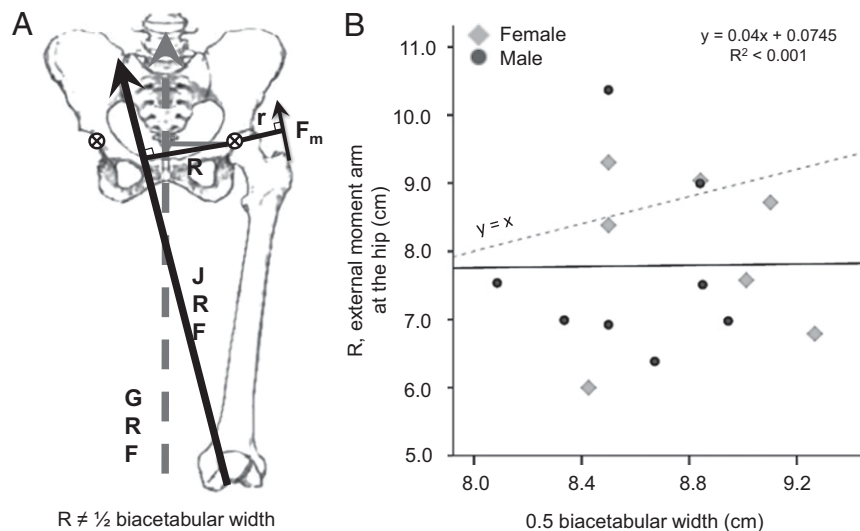


Fig. 2. Hip abductor mechanics. (A) To maintain equilibrium about the hip during single leg stance, the hip abductors must generate torque (multiple of muscle force, $F_m \times$ abductor moment arm, r) equal to the external torque rotating the pelvis away from the stance side. Previous mechanical models 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

ANTHROPOLOGY

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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1. Stearns SC (1983) The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos* 41:173–187.
2. Harvey PH, Clutton-Brock TH (1985) Life history variation in primates. *Evolution* 39:559–581.
3. Read AE, Harvey PH (1989) Life history differences among the eutherian radiations. *J Zool (Lond)* 219:329–353.
4. DeSilva J, Lesnik J (2006) Chimpanzee neonatal brain size: Implications for brain growth in *Homo erectus*. *J Hum Evol* 51:207–212.
5. Portmann A (1969) Biologische Fragmente zu einer Lehre vom Menschen [A Zoologist Looks at Humankind] (Schwabe, Basel, Germany); trans Schaefer J (1990) (Columbia University Press, New York). German.
6. Gould SJ (1977) *Ontogeny and Phylogeny* (Harvard Univ Press, Cambridge, MA).
7. Washburn S, Lancaster CS (1968) *Man the Hunter*, eds Lee RB, Devore I (Aldine, Chicago), pp 209–303.
8. Hawkes K, O'Connell JF, Blurton-Jones NG (1997) Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. *Curr Anthropol* 38:551–577.
9. Hrdy SB (2009) *Mothers and Others: The Evolution of Mutual Understanding* (Belknap Press, Harvard Univ, Cambridge, MA).
10. Krogman W (1951) The scars of human evolution. *Sci Am* 185:54–57.
11. Washburn SL (1960) Tools and human evolution. *Sci Am* 203:63–75.
12. Lovejoy CO (1981) The origin of man. *Science* 211:341–350.
13. Leutenegger W (1982) *Primate Brain Evolution*, eds Armstrong E, Falk D (Plenum, New York), pp 85–95.
14. Rosenberg KR (1992) The evolution of modern human childbirth. *Yearb Phys Anthropol* 35:89–124.
15. Small M (1999) *Our Babies, Ourselves: How Biology and Culture Shape the Way We Parent* (Anchor, New York).
16. Fisher H (2004) *Why We Love* (Henry Holt, New York).
17. Weiner S, Monge J, Mann A (2008) Bipedalism and parturition: An evolutionary imperative for cesarean delivery? *Clin Perinatol* 35:469–478, ix.
18. Trevathan WR (2008) *Evolutionary Medicine and Health*, eds Trevathan WR, Smith EO, McKenna JJ (Oxford Univ Press, Oxford).
19. Trevathan WR (2010) *Ancient Bodies, Modern Lives: How Evolution Has Shaped Women's Health* (Oxford Univ Press, Oxford).
20. Plunkett J, et al. (2011) An evolutionary genomic approach to identify genes involved in human birth timing. *PLoS Genet* 7:e1001365.
21. Schultz AH (1949) Sex differences in the pelvis of primates. *Am J Phys Anthropol* 7:401–423.
22. Rosenberg K, Trevathan WR (2002) Birth, obstetrics and human evolution. *BJOG* 109:1199–1206.
23. Kibii JM, et al. (2011) A partial pelvis of *Australopithecus sediba*. *Science* 333:1407–1411.
24. Rosenberg KR, Trevathan WR (1995) Bipedalism and human birth: The obstetrical dilemma revisited. *Evol Anthropol* 4:161–168.
25. Martin RD (1990) *Primate Origins and Evolution: A Phylogenetic Reconstruction* (Princeton Univ Press, Princeton, New Jersey).
26. Charnov EL, Ernest SK (2006) The offspring-size/clutch-size trade-off in mammals. *Am Nat* 167:578–582.
27. Leutenegger W (1972) Newborn size and pelvic dimensions of *Australopithecus*. *Nature* 240:568–569.
28. DeSilva JM (2011) A shift toward birthing relatively large infants early in human evolution. *Proc Natl Acad Sci USA* 108:1022–1027.
29. Martin RD (1983) Human brain evolution in an ecological context. *52nd James Arthur Lecture on the Evolution of the Human Brain* (American Museum of Natural History, New York).
30. Simpson SW, et al. (2008) A female *Homo erectus* pelvis from Gona, Ethiopia. *Science* 322:1089–1092.
31. LaVelle M (1995) Natural selection and developmental sexual variation in the human pelvis. *Am J Phys Anthropol* 98:59–72.
32. Correia H, Balseiro S, De Areia M (2005) Sexual dimorphism in the human pelvis: Testing a new hypothesis. *Homo* 56:153–160.
33. Epstein HT, Epstein EB (1978) The relationship between brain weight and head circumference from birth to age 18 years. *Am J Phys Anthropol* 48:471–473.
34. Wood JW (1994) *Dynamics of Human Reproduction: Biology, Biometry, Demography* (Aldine de Gruyter, New York).
35. Martin RD (1981) Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* 293:57–60.
36. Martin RD (1996) Scaling of the mammalian brain: The maternal energy hypothesis. *News Physiol Sci* 11:149–156.
37. Martin RD (1998) *The Origin and Diversification of Language*, Wattis Symposium Series in Anthropology: Memoirs of the California Academy of Sciences, eds Jablonski NG, Aiello LC (California Academy of Sciences, San Francisco) No 24.
38. Sacher GA, Staffeldt EF (1974) Relation of gestation time to brain weight for placental mammals: Implications for the theory of vertebrate growth. *Am Nat* 18:593–615.
39. Ellison P (2001) *On Fertile Ground: A Natural History of Human Reproduction* (Harvard Univ Press, Cambridge, MA).
40. Hammond KA, Diamond J (1997) Maximal sustained energy budgets in humans and animals. *Nature* 386:457–462.
41. Peterson CC, Nagy KA, Diamond J (1990) Sustained metabolic scope. *Proc Natl Acad Sci USA* 87:2324–2328.
42. Butte NF, King JC (2005) Energy requirements during pregnancy and lactation. *Public Health Nutr* 8(7A):1010–1027.
43. Butte NF (2000) Fat intake of children in relation to energy requirements. *Am J Clin Nutr* 72(5 Suppl):1246S–1252S.
44. Dufour DL, Sauter ML (2002) Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. *Am J Hum Biol* 14:584–602.
45. Pontzer H, Raichlen DA, Shumaker RW, Ocobock C, Wich SA (2010) Metabolic adaptation for low energy throughput in orangutans. *Proc Natl Acad Sci USA* 107:14048–14052.
46. Gaulin SC, Sailer D (1985) Are females the ecological sex? *Am Anthropol* 87:111–119.
47. Schimpf M, Tulikangas P (2005) Evolution of the female pelvis and relationships to pelvic organ prolapse. *Int Urogynecol J Pelvic Floor Dysfunct* 16:315–320.
48. Alentorn-Geli E, et al. (2009) Prevention of non-contact anterior cruciate ligament injuries in soccer players. Part 1: Mechanisms of injury and underlying risk factors. *Knee Surg Sports Traumatol Arthrosc* 17:705–729.
49. Roy RP (2003) A Darwinian view of obstructed labor. *Obstet Gynecol* 101:397–401.
50. Neubauer S, Hublin J-J (2012) The evolution of human brain development. *Evol Biol*, 10.1007/s11692-011-9156-1.
51. Winter DA (2005) *Biomechanics and Motor Control of Human Movement* (Wiley, New York), 3rd Ed.