

## *Brains, Birth, Bipedalism, and the Mosaic Evolution of the Helpless Human Infant*

JEREMY M. DESILVA

A human infant is born into the world in a nearly helpless state, without the neuromuscular coordination necessary to actively hold on to her mother. Echoes of our arboreal past are still apparent in newborns who can grasp a parent's pinky finger with unexpected strength or reflexively throw their arms and legs into the air when they are put down on a changing table. In spite of these interesting but essentially useless vestigial behaviors, human infants must be actively carried, and mothers benefit both from the use of slings and from the help of others to balance the costs of carrying large, helpless infants. Furthermore, human newborns continue to experience prenatal rates of brain growth for the first year of life, which puts a considerable energetic burden on the mother as she attempts to gather the necessary high-quality foods to sustain her own needs and those of her infant. It therefore may be no surprise that selection has favored behaviors that mitigate some of the mother's energy burden, such as shared parental care, alloparenting, and technologies that maximize the extraction of energy from food via tools and/or cooking.

Given the exceptionally high energetic burden challenging a new mother and the overall trend of an extended life history in humans, one might expect that the interbirth interval in humans would be longer than that found in the apes. But that is not the case at all. Humans wean our young years earlier than apes typically do and consequently have a shorter interbirth interval. Even our weaned toddlers remain relatively helpless, and there is a period of extended childhood in which they are still highly dependent on their mother, even though the mother may very well become pregnant again at this time. We humans therefore have overlapping dependent offspring, meaning that

mothers (and others) have to care not only for a helpless, energetically expensive infant, but often for a toddler simultaneously (Lancaster and Lancaster 1983; Hrdy 2009).

The human condition contrasts sharply with that found in modern apes. A chimpanzee, for instance, gives birth to a small and relatively precocial infant. Although a neonate requires active support from its mother (van Lawick-Goodall 1967; Mizuno et al. 2006), it has a strong grip soon after birth (Yerkes and Tomlin 1935) and requires infrequent support during travel in the weeks following birth (van Lawick-Goodall 1967). The mother can therefore continue to navigate between the forest floor and the canopy to feed, as the infant grasps the mother's belly or rides dorsally on her back (figure 4.1). The typical chimpanzee mother is possessive of her infant and does not let another chimpanzee inspect her offspring until upward of 6 months after birth. The earliest observed case of a wild mother chimpanzee sharing her infant was documented by J. Goodall (1986), who noted that Flo allowed Fifi to inspect and hold Flint 4 months after his birth. In contrast, a typical human infant is held, cuddled, fed, poked, smiled at, and spoken to by many individuals in the first 4 months of life (Hrdy 2009). Even after chimpanzee infants can locomote on their own, mothers continue to nurse them for 4–5 years, so that when the females do have another infant, their juvenile is usually old enough to forage on its own.

Assuming that the child-rearing strategy observed in the modern apes is the ancestral state, how did the human condition evolve? When and why did human infants lose their gripping abilities? When and under what conditions did mothers begin to trust others to help rear their children? When and under what conditions did humans begin to wean their infants earlier and begin to have overlapping dependent offspring? In this chapter, I review comparative and paleontological data that help reconstruct these changes over the course of human evolution—critical changes that have helped make us human.

### **Brain Development and the Evolution of Secondary Altriciality**

The prevailing proximate explanation for human altriciality is the fact that our brains are not nearly as developed at birth as those of our ape cousins.<sup>1</sup> While brain maturation is not necessarily the same as brain growth, here I use the more plentiful data on brain size as a proxy for brain development. Still, few data exist even on brain size at birth in primates, and often these data are based



Figure 4.1. Two mothers carrying large toddlers. Bipedality turns the gravity vector  $90^\circ$  and eliminates dorsal riding in the absence of sling technology. *Left*: a female chimpanzee from the Ngogo community, Uganda, allows her toddler to dorsally ride as she knuckle-walks terrestrially. *Right*: a modern female human actively carries her toddler, who no longer possesses the anatomies required to cling to her mother. Photo of chimpanzees courtesy of Kevin Langergraber. Photo of mother and toddler courtesy of Nicole Tremblay.

on single individuals (e.g., Sacher and Staffeldt 1974). In fact, prior to Vrba (1998) and Herndon and colleagues (1999), all studies that examined chimpanzee neonatal brain size to infer life history (Sacher and Staffeldt 1974; Hofman 1983; Martin 1983; Harvey and Clutton-Brock 1985; Dienske 1986; Smith and Tompkins 1995; Fragaszy and Bard 1997), brain development and ape cognition (Holt et al. 1975; Passingham 1975, 1982, 1985; Gould 1975), and obstetrics (Leutenegger 1987; Häusler and Schmid 1995; Tague and Lovejoy 1998) were based on 1 or 2 chimpanzee infants. Some studies reported a value of 128 g at birth in chimpanzees, which was based on a single male neonate reported by Schultz (1941). Others have used a value of 150 g at birth, which is the average of the 128 g individual and another young chimpanzee that had a brain mass of 171 g (Schultz 1940). However, this latter individual was already more than 2 months old and presumably had experienced considerable postnatal brain growth already. Herndon and colleagues (1999) and DeSilva and Lesnik (2006) reported the brain masses of 24 newborn chimpanzees, which averaged 150.9 g. Therefore, previous studies that used the 150 g estimate for chimpanzee brain size at birth are supported by larger data sets, while those that used the 128 g estimate should be interpreted with caution or even revisited.

Table 4.1. Great Ape and Human Advancement Factors

Species	Adult Brain Mass (g)	Neonatal Brain Mass (g)	Advancement Factor (%)
<i>Homo sapiens</i>	1330.5	373.8 ( <i>n</i> = 729)	28.1
<i>Pan troglodytes</i>	381.7*	152.8 ( <i>n</i> = 20)	40.0
<i>Pan paniscus</i>	343.3*	154.9 ( <i>n</i> = 1)	44.9
<i>Gorilla gorilla</i>	494.8*	222.0 ( <i>n</i> = 2)	44.9
<i>Gorilla beringei</i>	474.5	208.0 ( <i>n</i> = 1)	43.8
<i>Pongo pygmaeus</i>	377.8*	158.0 ( <i>n</i> = 2)	41.8

\* Data from Yerkes National Primate Research Center; Herndon et al. 1999.

\* Cranial capacity from Isler and van Schaik 2009, converted to grams using equation in Ruff et al. 1997.

Sources: DeSilva and Lesnik 2006; DeSilva 2011; McFarlin et al. 2013.

Given an average adult brain mass of 382 g, chimpanzee neonates are born with roughly 40% of their adult brain size (DeSilva and Lesnik 2006). This percentage of adult brain size achieved by birth is equivalent to the advancement factor first used by Sacher and Staffeldt (1974) and the reciprocal of the multiplier factor used by Portmann (1990). Humans, in contrast to apes, give birth to infants whose brains average 374 g (*n* = 729; from DeSilva 2011), and thus newborn human brains are approximately the same size as adult chimpanzee brains. Human brains grow to an average of 1330 g, meaning our brains are only 28% of adult size at birth, despite the large absolute size of the neonatal human brain. While this value can vary depending on the population (DeSilva and Lesnik 2006) or even whether cranial capacity or mass is the metric of brain size (Coqueugniot and Hublin 2012), the point here is that humans have considerably less of our brain volume grown by birth than chimpanzees do. But what about the other great apes? Again, there are few data on brain size at birth in the apes. However, the existing data all indicate that the great apes achieve at least 40% of their brain growth by birth (table 4.1). But the link between brain growth and the state of development of the newborn requires a broader mammalian and avian perspective.

Barton and Capellini (2011) compiled data on neonatal brain mass, adult brain mass, and developmental state for 132 placental mammals. These are graphed in figure 4.2a. Notice that for a given adult brain mass, altricial

mammals have a smaller neonatal brain mass. In other words, they are consistently born with a less developed brain than are precocial mammals of the same size. This has long been recognized by researchers (Portmann 1990; Mangold-Wirz 1966; Sacher and Staffeldt 1974; Harvey and Pagel 1988), and the same pattern has been found in birds (Bennett and Harvey 1985), the taxonomic group for which the terms “precocial” and “altricial” were first developed (Portmann 1939). Nevertheless, larger data sets like those compiled by Barton and Capellini (2011) should always be used to retest older ideas that may have been originally proposed based on more limited data.

Figure 4.2b demonstrates that the percentage of adult brain size achieved by birth clearly separates precocial from altricial mammals. The average altricial mammal has grown only  $15.5\% \pm 12.1\%$  of its brain mass by birth. The most extreme case is the brown bear (*Ursus arctos*), which is born having grown only 1.7% of its adult brain mass. The three altricial mammals with higher advancement factors within the range of precocial mammals are all large-bodied bats: the brown long-eared bat (*Plecotus auritus*), the Indian flying fox (*Pteropus giganteus*), and the common noctule (*Nyctalus noctula*). The role that specialized locomotion may play in an otherwise altricial newborn having a relatively large brain at birth is worthy of future study.

Precocial mammals, in contrast to altricial mammals, average  $45.7\% \pm 12.8\%$  of adult brain size at birth. Eisert and colleagues (2013) claimed that the Weddell seal (*Leptonychotes weddellii*) possessed the most developed brain at birth of any known mammal with 70% of its brain grown by birth. But the data presented here suggest that two mammals may exceed this exceptionally high value: the domestic llama (*Llama glama*) grows 72% of its adult brain size by birth, and the newborn harp seal (*Phoca groenlandica*) already possesses an amazing 88% of its full brain size. Eisert and colleagues (2013) suggested that the Weddell seal is so precocial because the pups need to successfully navigate the complex under-ice world immediately after birth; the same selective pressures may have promoted such precociality in harp seals as well.

Primates are not unusual at all in terms of relative brain growth for a precocial mammal. Compared to other precocial mammals ( $n = 58$ ), primates ( $n = 34$ ) have a statistically identical ( $p = 0.49$ ) advancement factor ( $47.6\% \pm 12.1\%$ ) (figure 4.2b). This is consistent with behavioral studies that characterize newborn primates as precocial, with infants actively grasping their mothers soon after birth. The key observation in this comparative context is the position of modern humans: we possess the lowest advancement factor (28%) of

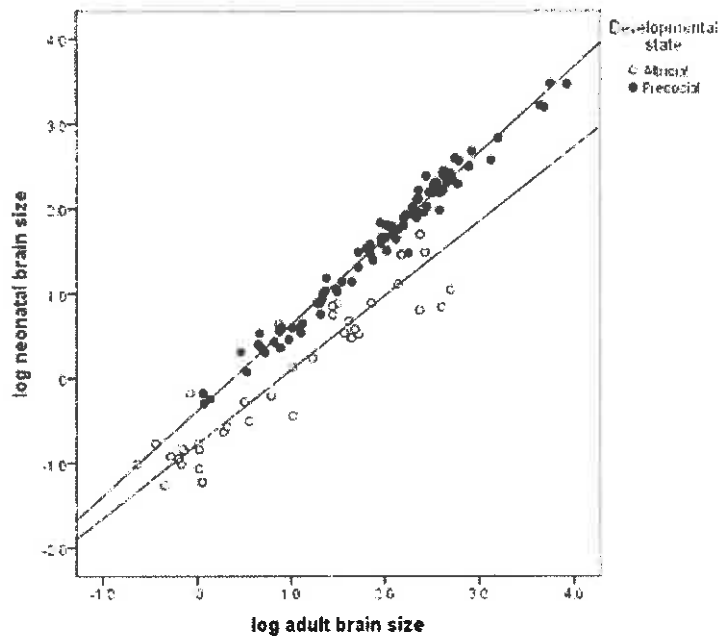


Figure 4.2a. Neonatal brain mass plotted against adult brain mass for a large sample ( $n = 132$ ) of placental mammals. As long recognized (Portmann 1990), altricial and precocial mammals can be clearly distinguished by the amount of brain development that has occurred at birth. Data from Barton and Capellini 2011, supplemented with data from Eisert et al. 2013; DeSilva and Lesnik 2008; DeSilva 2011; Isler and van Schaik 2009.

any modern primate and the fifth lowest of any precocial mammal. Based on the precocial mammal regression, humans “should be” born with brains that are 612.8 g at birth, but instead our species typically only achieves 60% of this expected value. Only four precocial mammals are known to have a smaller percentage of brain size achieved by birth than humans do: the wild boar (*Sus scrofa*), sambar deer (*Rusa unicolor*), nine-banded armadillo (*Dasypus novemcinctus*), and coypu (*Myocastor coypus*). It is not clear why these four precocial mammals—quite distinct biologically and phylogenetically—have such poorly developed brains at birth, and with such limited data on brain size at birth, there is the possibility that some of these species are being mischaracterized

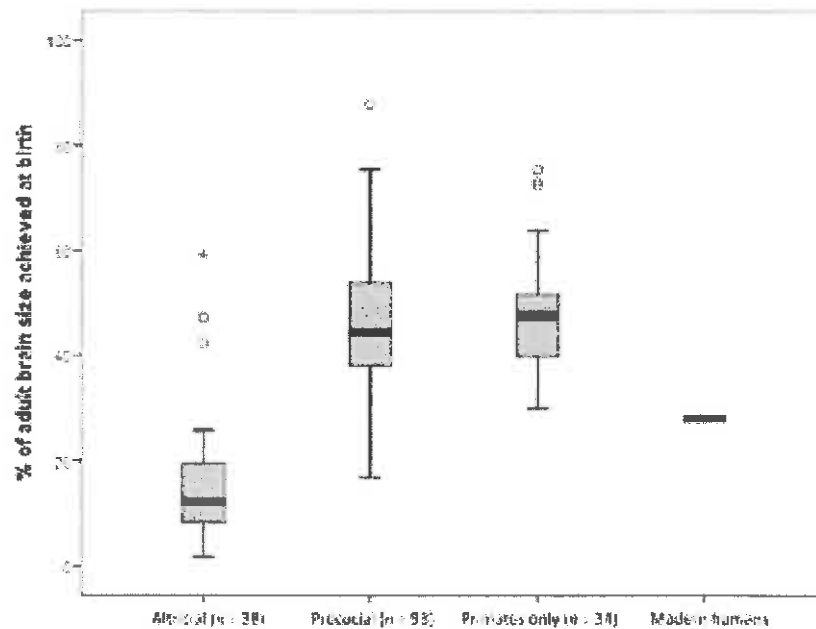


Figure 4.2b. The advancement factor (% of adult brain size grown by birth) in 132 mammals plotted by developmental state. Altricial mammals have on average less (~15%) of their adult brain mass completed by birth, whereas precocial mammals, including primates, have a larger percentage (~45%). Humans have the lowest (most altricial) advancement factor of any primate, though we do not fall within the box plot for altricial mammals. Data from sources listed in figure 4.2a.

based on the brain mass measurement of a single pathologically small-brained newborn. Regardless, modern humans are the least developed (in terms of brain growth) of the precocial primates for which brain data are currently known.

Given these data, it appears as though the proportion of adult brain size achieved by birth is a good metric for inferring the motor helplessness of an infant. Assuming that modern apes represent the primitive condition (~40% of brain size achieved at birth, well within the precocial value), when, why, and how did humans shift to having, as Portmann (1990) called it, “secondary altriciality”? To address these questions, I now turn to the human fossil record.

In order to calculate the advancement factor, or percentage of adult brain size achieved at birth, two data points are required: adult brain size and neonatal brain size. Paleontological work in eastern and southern Africa has resulted in the discovery of dozens of fossil hominin crania with reliable cranial capacities (Falk et al. 2000; Holloway et al. 2004). However, an early hominin neonate has never been discovered, and given the fragility of a newborn skeleton, the likelihood of such a discovery is extremely low. Fossil juveniles of *Australopithecus* are known (Dart 1925; Alemseged et al. 2006), and an infant *Homo erectus*, perhaps as young as 1 year old, has been described and its relative brain ontogeny explored (von Koenigswald 1936; Coqueugniot et al. 2004; Balzeau et al. 2005; O'Connell and DeSilva 2013; Cofran and DeSilva 2015). However, so much brain growth happens in the first year of life in humans that these finds cannot be used to infer much about brain size at birth in early hominins. The oldest known fossil neonate comes from the ~40,000-year-old (Pinhasi et al. 2011) Neanderthal site of Mezmaiskaya, Russia, which includes two infant burials, one of which has yielded a skull preserved well enough to calculate a brain size at birth (Ponce de León et al. 2008). Given the rarity of neonatal fossils, another method is therefore required to reconstruct brain size at birth in hominins.

It has long been recognized that in allometric studies, the slope of the regression line describing the relationship between two variables increases at higher taxonomic levels (Gould 1975). Therefore, although there is an isometric relationship between adult and neonatal brain size in precocial mammals (slope [m] = 1.013; 95% CI of slope: 0.99–1.05), within the more exclusive grouping of catarrhine primates, neonatal brains scale with negative allometry (m = 0.77; DeSilva and Lesnik 2008). As previously recognized (Martin 1983, 1990; Häusler and Schmid 1995) and more recently refined (DeSilva and Lesnik 2008), humans do not stray from the catarrhine regression and have nearly the expected brain size at birth given their large adult brain size. Therefore, for a given adult brain size, one can reasonably estimate the expected neonatal brain size in an extinct catarrhine. Since the adult brain size is known for many extinct hominin taxa, this approach was used to calculate brain size at birth throughout human evolution (DeSilva and Lesnik 2008). Since 2008, new fossils have been discovered that not only permit additional brain size at birth calculations, but provide a test of the regression-based approach. Additionally, here, I calculate neonatal brain size throughout human evolution from the ordinary least squares (OLS) regression equation, which is the



recommended approach over using reduced major axis equations as predictors (Hens et al. 2000; Smith 2009).

In 2008, Simpson and colleagues described the first nearly complete female *Homo erectus* pelvis. Though quite small, the birth canal was spacious and would have accommodated an infant with a head of 300–315 cm<sup>3</sup> (Simpson et al. 2008). Using the OLS equation and *H. erectus* crania ( $n = 13$ ) of the same geological age as the pelvis from Gona, the predicted neonatal brain for *H. erectus* is  $302.1 \pm 21.0$  cm<sup>3</sup>. This value is slightly larger than the 270.5 cm<sup>3</sup> reported in DeSilva and Lesnik (2008) because it restricts the comparison just to the *H. erectus* individuals known from 0.9–1.4 Ma (the age of the Gona pelvis). Using just the three African crania from this time period (OH 9, BOU-VP-2/66, UA-31), the predicted neonatal skull of a *Homo erectus* is  $312.3 \pm 20.4$  cm<sup>3</sup>. Given the congruence between the neonatal brain size predicted based on the size of the birth canal in a female *H. erectus* and the predicted brain size from the DeSilva and Lesnik (2008) OLS regression equation, this approach appears reasonable for inferring brain size at birth in extinct hominins. Furthermore, using the OLS equation on adult Neanderthal skulls ( $n = 29$ ) yields a predicted neonatal brain of  $405.7 \pm 39.3$  cm<sup>3</sup>, nearly identical to the 399 cm<sup>3</sup> (382–416 cm<sup>3</sup> range) of the reconstructed Mezmaiskaya Neanderthal infant (Ponce de León et al. 2008). This regression-based prediction of neonatal brain size in fossil hominins should continue to be tested as new fossils are discovered, and the equation itself should be refined as data on neonatal brain size in extant primates improve. Until then, the application of this equation to the hominin fossil record yields preliminary insight into the evolution of infant helplessness.

Because neonatal catarrhine brains scale with negative allometry ( $m = 0.77$ ), the larger an adult brain is, the *relatively* smaller the neonatal brain is. The resulting advancement factor (neonatal brain compared to adult brain, expressed as a percentage) necessarily falls as adult brains get larger. Thus, as hominin brains increased in size through human evolution, the percentage of the adult brain grown at birth became smaller and smaller, resulting in more altricial infants. Figure 4.3 graphs the change in the advancement factor of extinct hominins through time. The ardipithecines (the two crania from *Ardipithecus* and *Sahelanthropus*) are calculated to have been born with brains that were 40.6% of the adult size, well within the range of modern apes. Australopiths (*Australopithecus* and *Paranthropus*) achieved on average 37.7% of their brain growth in utero. If, as argued earlier, this advancement factor is

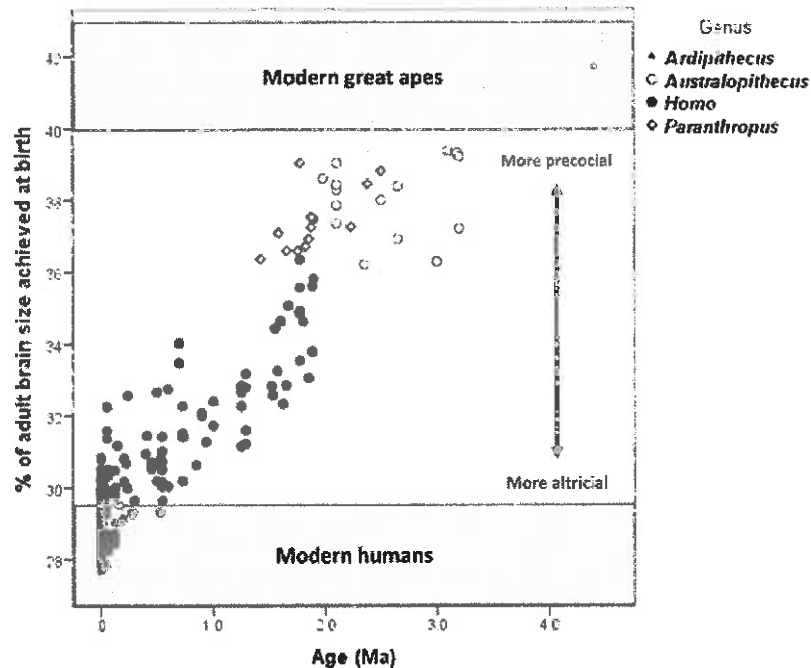


Figure 4.3. The large advancement factor gap between modern humans and modern apes (~12% difference) perhaps helps explain the difference in developmental state (precocial versus altricial) of newborn humans versus newborn apes. Using the conserved relationship between adult and newborn brain size in catarrhine primates (DeSilva and Lesnik 2008), the evolution of the altricial state in the human newborn can be reconstructed from fossil crania. Ardipithecines have apelike developmental patterns, which are presumed to be primitive. However, australopiths (both *Australopithecus* and *Paranthropus*) are more altricial at birth than modern apes are.

related to altriciality, then australopiths would have been slightly more helpless in terms of their motor skills than modern ape infants, but certainly not as helpless as a human infant. Early *Homo* at 35%, *H. erectus* at 32%, and late *H. erectus* (Heidelberg) at 30% illustrate the gradual trend toward helplessness that characterized Pleistocene hominin infants. Neanderthals and Pleistocene *Homo sapiens* are both under 30% of brain growth achieved at birth and are within the error range of modern humans. Again, assuming that the advancement factor is a reliable indicator of altriciality, the trend toward

infant helplessness began in the Pliocene, but did not reach the modern extent of helplessness present in today's newborns until the middle to late Pleistocene.

There is one final aspect of this scenario that should not be overlooked. Brain tissue is energetically expensive both to grow and to maintain (Leonard et al. 2003). Research has even suggested that the timing of birth in humans is based not on the size of the female pelvis, but on the energetic demands of the neonatal brain outstripping maternal supply (Dunsworth et al. 2012; Dunsworth, chapter 2, this volume), a hypothesis consistent with the close relationship between brain size at birth and gestation length across mammals (Sacher and Staffeldt 1974; Martin 2013). However, by birthing more altricial infants, humans have not by any means eased the energetic responsibilities of the mother. Instead, the energetic needs of a growing brain are shifted to the lactational period (see Quinn, chapter 5, this volume) and beyond, increasing the burden on the mother, who already is expending energy caring for a helpless infant. Given that modern humans approach or reach full brain volume by 6–7 years, the postnatal growth of the brain is concentrated during the infant and early childhood years and may be the driver behind our extended childhood (Kuzawa et al. 2014). Given the calories needed both to grow this much brain tissue and to maintain it, and given that this energetic burden falls almost exclusively on the mother, selective regimes that increase the maternal energy budget either directly (e.g., a higher-quality diet) or indirectly (e.g., shared provisioning) must have evolved coincident with the increase in postnatal brain growth and the gradual development of more and more helpless infants.

### **Bipedalism and the Helpless Infant**

It is tempting to look at the analysis above and regard australopiths as essentially apelike. However, I suspect that this characterization of australopiths is misleading for four reasons that are discussed below: australopiths had larger brains than modern chimpanzees; australopiths had less developed brains at birth than modern apes; australopith neonates were proportionately larger than ape newborns; and australopiths were bipedal. Thus, the paleobiology of australopiths set the stage for many of the critical social and energetic changes necessary to care for an even more helpless infant later in human evolution.

Compared to the 1330 g average of the modern human brain, the measly 450 g average of an australopith cranium is quite small and often characterized as apelike. However, compared to modern chimpanzees (or to the Miocene

hominids from which they evolved), australopiths had brains that were 20% larger, making them the most encephalized apes on the planet at the time of their existence. Additionally, given that neonatal brains scale with negative allometry, more brain tissue (~30%) was grown postnatally in australopiths compared to modern chimpanzees. Female australopiths would therefore have had elevated energy requirements compared to female chimpanzees simply in terms of helping to grow and maintain the slightly larger and therefore more energetically expensive brains of their young.

Furthermore, these early hominins had an advancement factor of 37.7%. While this value is certainly closer to the ape condition than to the modern human one, it implies that australopith infants would have been slightly more helpless than a modern ape infant. Unfortunately, there is no ape that has this advancement factor, and thus it is unclear what 37.7% of brain growth at birth would look like in terms of relative helplessness, except that australopith infants would probably have been much more precocial in motor development than modern human infants, but more altricial than a baby chimpanzee. Garwicz and colleagues (2009) have found that the time it takes for a mammal to begin to locomote is a function of adult brain size and gestation length. Assuming that australopiths had a gestation similar to chimpanzees (240 days), the Garwicz and colleagues' equation would imply that an infant australopith would take 6–7 months to begin walking on two legs. And while the appropriateness of the comparison is questionable, it may still be informative to look at another large-brained, social mammal with an advancement factor just under 38%: the African elephant (*Loxodonta africana*). While newborn elephants are quick to get on their feet and join the herd, their survival is dependent not only on their mother, but on other related females, who alloparent and even nurse the calf (Hrdy 2009).

Not only did australopiths have larger brains than do modern chimpanzees and birthed infants with less developed brains than modern chimpanzees, but these infants were proportionately large. Inspired by *Mothers and Others* (Hrdy 2009) and the birth of my own children, I began to wonder what life was like for australopith mothers and their infants. Modern humans give birth to proportionately large babies, which on average are 6% of the mass of the mother and equipped with proportionately high body fat (Kuzawa 1998); modern apes give birth to proportionately small and skinny infants, only 3% of the size of the mother (DeSilva 2011). What about australopiths? As discussed above, regression-based approaches can yield reasonable approximations

for the size of the neonatal brain in australopiths. But what about the size of their bodies? Fortunately, the relationship between brain mass and body mass in neonates is conserved in the great apes (~10% of body mass is brain), permitting a reasonable calculation of body mass in australopith neonates. Upward of 12% of the body mass in modern humans is brain, which puts a lower limit on the size of the australopith neonate. My calculations revealed that australopiths (*Australopithecus* and *Paranthropus*) gave birth to infants that were about 1.8 kg. This is considerably smaller than the modern human infant (3.1 kg; weighted average of 11,317 infants from 19 different populations) and only slightly larger than the average mass of an infant chimpanzee (DeSilva 2011). However, australopith females were quite small (average ~31.5 kg) and had smaller weight-bearing joints (hips, ankles) than do female chimpanzees. The result of australopiths having slightly larger infants and slightly smaller females than chimpanzees is an infant:mother mass ratio of 5%. Thus, australopith mothers were carrying proportionately larger infants than chimpanzee mothers do. While it is possible that this 5%–6% actually represents the ancestral condition and that apes independently reduced the relative size of their neonates to more easily and safely carry infants in arboreal contexts, the fact that *Ardipithecus ramidus* (the presumed ancestral condition) is calculated to have an infant 3% of the size of the mother (DeSilva 2011) instead suggests that the enlarged infant in australopiths and early *Homo* is derived.

The relative size of the australopith neonate has energetic consequences in terms of providing sustenance to the infant, but also in terms of transport costs. In the absence of slings, humans exert 16% more energy while walking with an infant in their arms than without (Wall-Scheffler et al. 2007). Undoubtedly, these costs were exacerbated by the fact that australopiths were bipedal. Bipedalism changes the gravity vector acting on a clinging infant by 90° (Amaral 2008). Chimpanzees and other primates experience the same vertical gravity vector when they are climbing (see DeSilva 2011:fig. S3). However, all nonhuman primates have a grasping hallux and other adaptations for clinging to their mother while she is climbing. During quadrupedal locomotion, the infant primate either clings to the underbelly of her mother with powerfully gripping hands and feet, or the infant rides on the mother's back, which is a horizontal platform that requires little effort from either the infant or the mother after the first few weeks, during which the mother does help support the infant during transport (van Lawick-Goodall 1967). Australopiths did not have either option of transport.

Because australopiths were bipedal, dorsal riding was no longer a viable option given that australopith anatomy demonstrates that both the hands and the feet had lost important adaptations for grasping. This is not to imply that australopiths did not still climb trees. They almost certainly did, both for sustenance and for safety from predators at night. However, most researchers would agree that they were less suited for climbing than are modern apes, and their climbing strategy would likely have been slow, cautious, and deliberate—as humans climb today (Venkataraman et al. 2013; Kraft et al. 2014). This mode of climbing is a by-product of the trade-offs between anatomies adaptive for bipedalism and those adaptive for climbing (Ward 2002; DeSilva 2009). Importantly, the very same anatomies that would compromise the climbing abilities of australopiths would render the infants less likely to be able to grip their mother. Furthermore, there may have been little for the infant to grab. Evidence from lice genetic studies indicate that hairlessness may have begun by 3.3 Ma (Reed et al. 2007; but see Knott 2015, who found that at least in orangutans, the infant often grips the loose skin of the mother rather than her body hair). Australopiths may have foraged terrestrially in the heat of the day to avoid the predation that would inevitably occur if they were active during the cool dusk or dawn hours, and therefore the evolution of hairlessness and enhanced sweat glands may have occurred in the Pliocene, concurrent with the drying and cooling of the African savanna, the expansion of grassland environments, and the evolution of obligate bipedality. Next I argue that this combination of features characteristic of australopiths and their environment is a recipe for alloparenting and/or shared parental care.

Consider the following: A small-bodied female australopith has given birth to a relatively large infant (5% of her body mass at birth, and this value only increases as the baby grows). The newborn australopith is more helpless in motor development than a chimpanzee infant since only ~38% of its brain has grown by birth. The mother cannot put the infant on her back since she is bipedal and the gravity vector is now vertical. Furthermore, dorsal riding on her now-vertical back is not a viable option since the infant has reduced grasping abilities both due to its altriciality and due to bipedal adaptations that have either eliminated or at the very least reduced the grasping abilities of the more adducted hallux. There may be little for the infant to grab on to anyway since australopiths may have been losing their body hair as they foraged more frequently in the heat of the day to avoid predation. Assuming a chimpanzee-like gestation of ~240 days, the infant australopith would not take its first

bipedal steps on its own for 6–7 months, meaning that the mother would have to actively carry her infant for those months while actively foraging both for herself and for her infant, who has a growing brain (20% larger than a chimpanzee's) to support. The landscape is littered with predators and (at the very least) each evening, the female will need to ascend a tree for safety. Though australopiths retained some adaptations for climbing, their anatomy was not nearly as well suited for life in the trees as an ape's, and therefore australopiths would have climbed slowly and cautiously. But how could a female australopith—already more poorly suited for arboreality than is a modern chimpanzee—get into a tree with one arm (the other arm actively holding her relatively large, relatively helpless, poorly grasping infant)?

There are three possible non-exclusive solutions to this problem. The first is that australopith females invented slings, which if true would be one of the first technological inventions in the human lineage (Tanner and Zihlman 1976; Lancaster 1978; Zihlman 1981). While this is a possibility—and perhaps even likely—it is quite difficult to test given that a sling made of vegetation would not be preserved in the fossil record. The second possibility is that female australopiths parked their infants. While they almost certainly did not do this in the evening, when the little offspring would have attracted predators, female australopiths may have employed this strategy in the daytime, a scenario that may have encouraged vocal contact between mother and child and may have seeded the first roots of language (Falk 2004). The third solution—the one emphasized here—is that the mother and infant (Hrdy 2009) may have solicited and received help from other members of her group. In considering the same set of variables facing australopiths, Stutz (2014:8) wrote, “Virtually the only theoretically plausible behavioral phenotypic compensation that would have co-evolved with the bipedal embodied niche is alloparenting: cooperative offspring care.” If true, then the origin of alloparenting and/or shared parental care has its roots not in the genus *Homo*, but in the australopiths. While group care of infants in australopiths may have taken the form of holding an infant while her mother carefully climbed into a tree at night, these simple acts would have required intragroup tolerance, trust, and cooperation, laying the foundation for the more conspicuous acts of alloparenting that likely characterized early *Homo*.

The questions that follow are twofold: Who helped? And how can we detect the presence of helpers in the fossil record? Who helped in australopiths, or even in early *Homo*, is not clear. There is little evidence that australopiths lived

long enough for grandparents to assist. While pair bonding and therefore an increased likelihood of male paternal care (see Gettler, chapter 8, this volume) have been hypothesized for australopiths (Lovejoy 1981, 2009; Reno et al. 2003), elevated body size dimorphism may instead suggest male-male competition (Plavcan et al. 2005) and a more limited role of males in caring for the young. Other possible helpers may include maternal relatives and/or older siblings. One potential problem with the maternal relative hypothesis is the possibility that australopiths had chimpanzee-like male philopatry and female dispersal (Copeland et al. 2011). If so, then a female would have had fewer related members in the group that would indirectly benefit from alloparenting her young. Using a mathematical model, Bell and colleagues (2013) have countered that even in the context of low levels of relatedness, female cooperative mothering still would have prevailed in early hominins. And, even if australopiths were patrilocal, there still may have been related female helpers available.

Emlen (1995) proposed that the delayed dispersal of females may lead to alloparenting. Given that high levels of predation are a predictor of delayed dispersal (Emlen 1995) and that australopiths almost certainly were subject to high predation (Pickering et al. 2004), young females not yet ready to leave their natal group may have been recruited as helpers. If related, these individuals would gain indirect fitness benefits. If not related, they still would benefit by learning the skills necessary to raise an australopith baby. This scenario would probably require relaxed female hierarchies (Hrdy 2009) so that the risk of infanticide was low and therefore females would be willing to share their infants with other members of the group.

I suspect that we already possess physical evidence that female australopiths were social with one another and took care of one another in times of need. Based on the size of the birth canal in australopith pelvises (AL 288-1, Sts 14, Sts 65, MH2) and on regression-based estimates of brain size in australopith infants, birth was a challenging event early in human evolution (Wells et al. 2012). Although it is not clear whether australopiths experienced the corkscrew rotation through the birth canal that characterizes most modern human births, the cephalopelvic index alone would suggest that australopiths labored during birth. Furthermore, given the width of ape and human shoulders (Trevathan and Rosenberg 2000), even when the head emerged from the birth canal, the wide shoulders still posed a problem. Australopiths probably would have benefited (in a fitness sense) by giving birth in the presence of other females, who could assist during delivery, especially in cases of head



or shoulder dystocia (Rosenberg and Trevathan 2002). Additionally, there is growing evidence for frequent conspecific care in early hominins, the most obvious of which is the 1.77 Ma edentulous skull (D4444) of an early *Homo* from Dmanisi, Georgia, which lived for several years despite full tooth resorption (Lordkipanidze et al. 2006). If early hominins were social enough to assist one another during delivery and to keep some elderly individuals from starving to death, how much of a stretch would it be for them to care for one another's offspring after delivery through a form of reciprocal altruism that would benefit all females in the group, related or not?

### Early Weaning and Overlapping Dependent Offspring

How can we tell when early hominins started to alloparent? Although the scenarios presented above are reasonable, they do not serve as confirmation of the hypothesis that australopiths and early *Homo* alloparented. To test this idea, I return to the comparative approach.

Before I joined academia, I worked as an educator at the Boston Museum of Science. There, we had on exhibit a family of cotton-top tamarin monkeys (*Saguinus oedipus*). They were in the museum's human biology exhibit to teach visitors about primates and about cooperative breeding. Like humans, tamarins share their young and take turns carrying the infants. The fathers in particular play a crucial role in infant carrying, and there are data demonstrating that male parental care is correlated with survival for infant tamarin monkeys (Garber et al. 1984). Incidentally, they very often twin. After my own twins were born and I spent many hours carrying 15 pounds of helpless babies around, I felt camaraderie with my tamarin cousins. Given the data I presented above about relative body mass, I wondered whether the relative size of the infants was a selective force driving alloparenting, or whether the behavior of alloparenting and the resulting provisioning of the infant drove the increase in body mass. In other words, there existed a chicken-and-egg problem; the arrow of causality could be in either direction.

The comparative data on fish, birds, and mammals confirmed that there was a relationship between litter mass and cooperative breeding, but it was never clear to me which was the driver and which the result. However, there is another variable that appears to be a result of cooperative breeding, not a driver: reduced weaning time. If a female reduces her weaning time and shortens her interbirth interval in the absence of alloparents, then the infant is less

likely to survive on her own. This may not be an issue for mammals with large litters, but for those with small litters (including primates), early weaning in the absence of shared provisioning makes little sense from a fitness perspective. What good is resuming the reproductive cycle if your first infant is likely to die on its own? Reduction in weaning time is contingent on some form of shared parental care or alloparenting being in place already. This contention is supported by comparative data that indicate that primates who alloparent are more likely to have shorter nursing times (Mitani and Watts 1997).

Compared to the modern apes, humans have shorter interbirth intervals and wean our infants at a younger age. Modern great apes suckle their young for approximately 4–7 years, with gorillas at the low end and orangutans at the high end of the nursing range (Knott 2001). Humans, in contrast, nurse infants for a shorter period of time. The average weaning age for seven traditional human hunter-gatherer populations is just over 3 years (Konner 2010). The traditional scholarly approach is to ask when this change occurred and why humans have evolved a shorter interbirth interval. However, given suggestions that the great apes are derived morphologically and perhaps also behaviorally (i.e., Lovejoy et al. 2009a), we have to consider the possibility that the apes have all independently extended their weaning age and that humans represent the ancestral condition. Based on body size, humans would be expected to wean infants between 2.8 and 3.7 years (Harvey and Clutton-Brock 1985; Dettwyler 2004), which is close to the actual average weaning age, though there is considerable population-level and inter-individual variation in human weaning age. We may therefore be asking the wrong question. Instead of wondering why the human nursing stage shortened, we may want to consider why the weaning age in the apes—particularly in orangutans and chimpanzees—rose.

However, while the primitive weaning age may bridge the gap between the high ape value and the lower human one, there is some evidence that the interbirth interval either shortened in the australopith clade or was variable among different australopith species. The tantalizing evidence comes from an analysis of tooth wear on two similarly aged australopith juveniles (Aiello and Montgomery 1991) who lived about a million years distant in time. The fossil LH 2 is a juvenile *Australopithecus afarensis* from ~3.6 Ma deposits of the type locality for *A. afarensis*: Laetoli, Tanzania. It possesses an erupted, but nearly unworn permanent first molar, and based on an ape schedule of first molar eruption, LH 2 was approximately 3.5–4.0 years old when it died. The wear on

the deciduous molars is minimal. It is informative to contrast LH 2 with the Taung juvenile (*A. africanus*) from ~2.5 Ma deposits in South Africa. Taung is of a similar dental age as LH 2 with a fully erupted, but unworn permanent first molar. It too would have been 3.5–4.0 years old based on an ape schedule of tooth eruption, and this has been independently supported using enamel growth lines (Lacruz et al. 2005). Unlike in LH 2, however, the Taung deciduous dentition is highly worn, with exposed dentin. Given evidence that *A. afarensis* and *A. africanus* had a similar mixture of C<sub>3</sub> and C<sub>4</sub> plants in their diets (Sponheimer et al. 2013), and the fact that these species had similarly thick tooth enamel (Haile-Selassie et al. 2010), one possible explanation for differences in tooth wear on similarly aged individuals might be that *A. africanus* was incorporating solid foods into its diet in higher frequencies earlier in childhood than *A. afarensis* did (Aiello and Montgomery 1991). While it is recognized that *A. africanus* may not have even descended from *A. afarensis* (Irish et al. 2013) and that tooth wear is at best a crude measure of assessing weaning age (Smith 2013), this comparison still illuminates a possible temporal trend toward earlier weaning in the australopiths, or perhaps suggests variability in weaning age in different australopiths. More work is clearly needed to characterize the patterns of weaning in early hominins.

Even if weaning occurred earlier in australopiths than in modern apes, they still matured rapidly, and it is unlikely that mothers would have had to provision both a nursing infant and a fully dependent toddler. Only when the elongated childhood period evolved did hominin mothers have to face the challenges of overlapping dependent offspring, and it appears likely that the elongated childhood of modern humans may be a relatively recent evolutionary phenomenon, perhaps not reaching humanlike form until the late Pleistocene (Dean 2006; Smith et al. 2010). It is possible that this final shift in human life history—the continuation of helpless infants into still-dependent children and the resultant overlapping dependent offspring—may not have been possible until the energy budgets were sufficient to sustain a mother and her multiple offspring. Food sharing and provisioning by alloparents, including grandparents (O’Connell et al. 1999), combined with the utilization of fire to cook food (Wrangham and Conklin-Brittain 2003) by at least 1.0 Ma (Berna et al. 2012) and the development of more sophisticated technology throughout the Pleistocene would have gradually provided the energetic buffer necessary to extend humans’ childhood.

## Conclusion

As with many other aspects of human evolution, the shift from an apelike strategy of child rearing to a human one was mosaic. The very earliest hominins (ardipithecines) likely birthed small-bodied, small-brained infants who could still grip their mothers with a grasping hallux. It is possible that these hominins weaned their young earlier than chimpanzees do, though this hypothesis remains to be tested with fossil and comparative evidence. The evolution of obligate bipedalism in the australopiths eliminated dorsal riding and an abducent hallux, forcing mothers to actively carry their relatively large infants. Australopiths' survival may have depended on intragroup tolerance and some degree of alloparenting given the energetic burdens and predation threats facing australopith mothers. The evolution of helpless infants had already begun by this point since the advancement factor of australopiths was lower than in modern apes, though this gradual trend toward birthing neurologically less developed infants did not reach a modern level until later in the Pleistocene. Therefore, many of the behavioral adaptations to caring for altricial infants and, eventually, overlapping dependent offspring may have taken root in the Pliocene and permitted the evolution of the large, developmentally helpless infants we birth today.

## Acknowledgments

Thank you to S. Hrdy and C. Knott for comments on an earlier draft of this chapter. Many thanks to the other SAR participants for the lively, entertaining, and thought-provoking discussions. I am particularly grateful to K. Rosenberg and W. Trevathan for organizing the "Costly and Cute" SAR workshop, for editing this volume, and for providing the SAR participants and the entire biological anthropology community with a model for how to be both great scientists and great people. Finally, many thanks to E. DeSilva, J. DeSilva, and B. DeSilva for inspiring me to think about the role of infants in human evolution.

## Notes

1. Describing the human infant as "altricial" is problematic for the reasons detailed in Trevathan and Rosenberg, chapter 1, this volume.