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The Derived Features of Human Life History

Shannen L. Robson, Carel P. van Schaik,
and Kristen Hawkes

SUMMARY

This chapter compares and contrasts the life histories of extant great apes in order to construct a hypothetical life history of the last common ancestor of all great apes and to identify features of human life history that have been derived during the evolution of our lineage. Data compiled from the published literature indicate some variation across the living taxa, but all great apes have relatively long lifespans and late maturity. Therefore, we infer that a slow life history is the ancestral state of all great apes.

We examine variation in the timing of brain growth and aspects of dental development and find that they are not correlated in the life history variation across these species. We conclude that adjustment in growth and development, though constrained by life history, are imperfect predictors of life history variables.

Our comparisons show that humans have the slowest life history of the great apes, with a notably longer adult lifespan and an older age at first birth. We investigate the two important features of human life history that deviate from the expected great ape pattern: shortened interbirth intervals and vigorous postmenopausal longevity. Human infants are weaned earlier than

expected for their age at maturity and before they are capable of independent feeding. Because females conceive soon after weaning an infant, women typically have multiple dependent offspring simultaneously. The pattern of human age-related fertility decline appears to be conserved. Reproductive senescence occurs at essentially the same age among all great apes, suggesting that the marked postmenopausal survival of human females is a derived trait resulting from selection for slower rates of somatic aging. The human pattern of shortened interbirth intervals and "stacking" dependents could have evolved only if human mothers had reliable sources of help. Related postmenopausal and prereproductive females, without infants of their own, likely gained inclusive fitness benefits from supplying that help.

Despite variability in the statistics of deaths and births, every species shows strong central tendencies in demographic variables as a result of underlying, biologically anchored, individual predispositions for growth, development, reproduction, and aging (Harvey and Clutton-Brock 1985). Our species is no exception. Although there have been frequent allusions to dramatic changes in human life history as a result of changes in sources of mortality (Olshansky, Carnes, and Cassel 1998), our species shows all the hallmarks of one designed for slow development and long life, with female fertility declining to menopause well before aging advances in other physiological systems. Thus, like any other species, humans possess a clearly delimited life history. And, for other species, it is a productive working hypothesis to regard these features as adaptations that evolved through natural selection.

To set the agenda for the rest of this volume, it is essential that we obtain a clear picture of the changes that have taken place in hominin life history since the point of departure: the origin of the very first bipedal ape, five to seven million years ago. Ideally, we would also estimate when the major changes or novelties evolved during hominin evolution, associating the shifts with adaptations to the new habitats colonized and lifestyles adopted by new hominid species. This task is fraught with difficulties, however, because values for extinct species tend to be reconstructed through processes with many steps, each with a particular uncertainty, or through relationships of unknown validity for the species involved (Skinner and Wood, chapter 11, this volume).

We can map the similarities and differences between modern

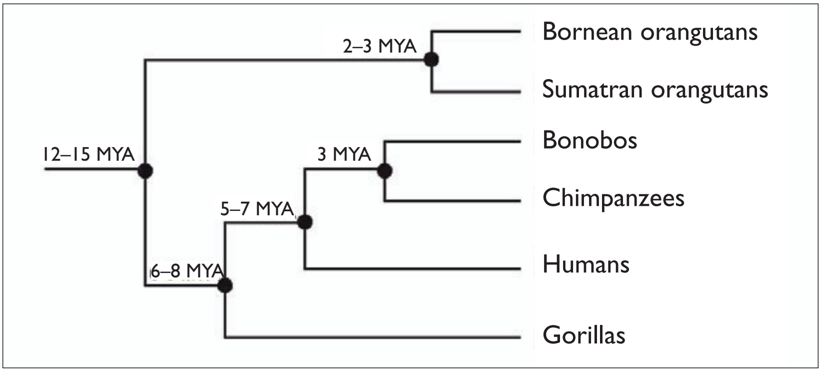

FIGURE 2.1
Phylogenetic relationships of the great ape species. Estimated time of divergence of the orangutan, gorilla, and chimpanzee/bonobo lineages from the hominid lineage (Glazko and Nei 2003). Estimated time of bonobo/chimpanzee divergence (Wildman et al. 2003). Estimated time of Bornean/Sumatran orangutan divergence (Zhang, Ryder, and Zhang 2001).

humans and our closest living relatives, the great apes, with much less uncertainty and use these comparisons to infer the likely changes in life history over the radiation of our own lineage.

DERIVED HUMAN LIFE HISTORY TRAITS

Humans are part of the wider radiation of great apes. As shown in figure 2.1, our closest relatives are the two species of chimpanzee (genus *Pan*): the common chimpanzee (*P. troglodytes*) and the bonobo (*P. paniscus*). There is one other extant African great ape, the gorilla (*Gorilla gorilla*), which comes in various distinct subspecies. In Asia, a separate lineage of great apes evolved, of which two species of orangutan (*Pongo pygmaeus* and *P. abelii*) are the only living representatives (Zhang, Ryder, and Zhang 2001).

Which Apes Resemble the First Hominin?

Using some composite estimates based on the living great apes to reconstruct the common ancestor at the root of the hominin lineage would be permissible only if these taxa have changed little since then. On one hand, there is some support for this assumption: the molecular and morphological similarities among the great apes suggest that they have been more conserved than the hominin radiation (Moore

1996). On the other hand, many assume that some parallel evolution has taken place in the African hominoid lineages, especially with respect to their locomotion. Because chimpanzees and gorillas are terrestrial knuckle walkers, it has long been considered parsimonious to assume that our common ancestor was too. However, Schmitt's (2003) recent examination of the locomotor biomechanics among extant primates suggests that human bipedalism most likely evolved independently from an arboreal ancestor. Because this change implies that the African great apes became more terrestrial over time, it may be argued that their late Miocene arboreal ancestors had slower life histories, given the general correlation between terrestriality and faster life history (van Schaik and Deaner 2003). If such parallel evolution is important to life history, then the still strictly arboreal orangutan may provide the best estimate for the earliest hominins. Therefore, if the African apes did not change independently, then the earliest hominins had a life history similar to our closest living relatives, the chimpanzee and bonobo, or if they did, one closer to the more arboreal orangutan. The utility of reconstructing a common ancestor from shared patterns and similarities between phylogenetically close extant relatives is obvious, but caution should be used in assuming that shifts in hominin life histories always favor one direction. The recently discovered *Homo floresiensis,* a "hobbit"-size hominid (Brown et al. 2004; Falk et al. 2005) may exemplify how selection can favor a faster life history from a slower ancestor within our genus.

Gorillas require special consideration because they are unusual among the great apes in that they achieve the largest body size in the shortest time. Adult body size is the result of both the duration and the rate of growth before maturity. Relative to other primates, all great apes grow for a longer time and achieve larger adult body sizes. Gorillas, however, grow much faster than the rest of us. On average, primates grow more slowly than other mammals and are therefore smaller at adulthood than nonprimate mammals of similar ages at first birth. Humans, chimpanzees, bonobos, and orangutans grow even more slowly than the primate average (Blurton Jones, chapter 8, this volume). But this is not true of gorillas. Variation in growth rate across the mammals is closely tied to variation in the rate of offspring production (Charnov 1991; Charnov and Berrigan 1993). Gorillas grow more quickly and also produce babies at shorter intervals than the other great apes (table 2.1). The reasons gorillas exhibit rapid growth are debated, but analyses by Leigh (1994) show that growth rates among primates co-vary with diet.

Leigh (1994) examined the diet ecology and growth rates of forty-two anthropoid primate species and found that those with more folivorous diets tend to grow faster than those with more frugivorous ones. All great ape species, including gorillas, favor fruit when it is abundant, but chimpanzees and orangutans specialize on fruit and extractive foods (such as insects) and sometimes vertebrate meat (chimpanzees more so). To some extent, bonobos (and gorillas, in particular) fall back on vegetative foods that tend to be abundant but of lower quality (Malenky et al. 1994; Conklin-Brittain, Knott, and Wrangham 2001). The first australopithecines were thought to have diets dominated by fruits and seeds (Schoeninger et al. 2001). If diet ecology influences growth trajectories, then we would expect the earliest hominins to have growth and reproductive rates closer to those of chimpanzees and orangutans than to gorillas. Also, fossil evidence suggests similarities between chimpanzees and australopithecines (versus gorillas) in body sizes (McHenry 1994). Average growth rates for living humans are close to the rates for chimpanzees, bonobos, and orangutans (Blurton Jones, chapter 8, this volume). For these reasons, we consider the values of chimpanzees and orangutans as the endpoints of the range of estimates for the first hominins and refer to gorillas only when relevant.

Data Sources

To develop proper comparisons between people and living great apes, we primarily rely on the life history parameters estimated from hunter-gatherers, because their diets, mobility, foraging styles, and population densities most likely resemble those of modern humans before the invention of agriculture. Although we note estimates for some of these variables from a broader range of human populations in the text, in table 2.1 we used composite estimates from different detailed studies of extant hunter-gatherers whenever possible. This reduces concern about possible effects of improved diets and medical care on rate of development and senescence. It can be argued that the estimates are conservative in that ethnographically known populations

TABLE 2.1

Primary Life History Parameters of Female Great Apes (Arranged by Phylogenetic Distance from Humans), Mainly for Wild Populations, Compared with Those of Humans, Mainly Foragers

Great Ape Species	Maximum Lifespan (Years)	Age at First Birth (Years)	Adult Female Weight (kg)	Gestation Length (Days)
Orangutan (*Pongo pygmaeus* and *P. abelii*)	58.7[a]	15.6[d]	36.0[i]	260[m]
Gorilla (*Gorilla gorilla*)	54.0[a]	10.0[e]	84.5 (71–98)[j]	255[m]
Bonobo (*Pan paniscus*)	50.0+[b]	14.2[f]	33.0 (27–39)[j]	244[n]
Chimpanzee (*Pan troglodytes*)	53.4[a]	13.3[g]	35.0 (25–45)[j]	225[m]
Human (*Homo sapiens*)	85.0[c]	19.5[h]	47.0 (38–56)[k]	270[m]

Sources: a. Judge and Carey (2000), b. Erwin et al. (2002), c. Hill and Hurtado (1996); Howell (1979); Blurton Jones, Hawkes, and O'Connell (2002), d. Wich et al. (2004), e. Alvarez (2000); for humans, only data from two foraging populations, the Ache and !Kung, f. Kuroda (1989), g. Average age at first birth for five *P. troglodytes* populations: Bossou, 10.9 years (Sugiyama 2004); Gombe, 13.3 years (Wallis 1997); Mahale, 14.56 years (Nishida et al. 2003); Tai, 13.7 years (Boesch and Boesch-Achermann 2000); and Kibale, 15.4 years (Wrangham in Knott 2001), h. Average age at first reproduction from four human foraging groups: Ache, 19.5 years (Hill and Hurtado 1996); !Kung, 19.2 years (Howell 1979); Hadza, 18.77 years (Blurton Jones, unpublished data); and Hiwi, 20.5 years (Kaplan et al. 2000), i. Smith and Jungers (1997); mean of subspecies, j. Average (range reported in parentheses) compiled from Smith and Jungers (1997); Zihlman (1997a); and Smith and Leigh (1998), k. Average of range (reported in parentheses) of ethnographic samples from Jenike (2001:table 5), m. Harvey, Martin, and Clutton-Brock (1987), n. Median gestation length for bonobos in captivity reported by de Waal and Lanting (1997:190) from Thompson-Handler (1990), o. Average of range (reported in parentheses) compiled from Smith and Jungers (1997); Zihlman

of hunter-gatherers occupied only a subset of habitats initially colonized by modern people, mostly environments that are marginal for agriculture.

The nonhuman great ape data primarily come from long-term field studies, and these data are improving over time (see table 2.1 for source references). In all the reports of wild studies, the ages of many adults were estimated; all maximum lifespans were based on estimates with unknown errors. Maximum lifespans in the table are therefore

Neonate Weight (kg)	Neonate as a % of Maternal Weight	Age at Weaning (Years)	Interbirth Interval (Years)	Age at Last Birth (Years)
1.56 (1.31–1.81)[o]	4.3%	7.0[e]	8.05[d]	>41[d]
1.95 (1.6–2.3)[o]	2.3%	2.8[e]	4.40[e]	–
1.38 (1.30–1.45)[o]	4.2%	–	6.25[r]	–
1.90 (1.4–2.4)[o]	5.4%	4.5[e]	5.46[s]	42[u]
3.00 (2.4–3.6)[p]	5.9% [q]	2.8[e]	3.69[t]	45[v]

(1997a); and Smith and Leigh (1998), p. Average neonatal weight of seventy-eight groups worldwide (range reported in parentheses) from Meredith (1970), q. Calculated from data reported by Poppitt and colleagues (1994) on linked maternal/neonatal weight for eight populations, r. Average of two *P. paniscus* populations: Wamba, 4.5 years (Takahata, Ihobe, and Idani 1996), and Lomako, 8.0 years (Fruth in Knott 2001), s. Average interbirth interval of six *P. troglodytes* populations: Bossou, 5.3 years (Sugiyama 2004); Gombe, 5.2 years (Wallis 1997); Mahale, 5.6 years (Nishida et al. 2003); Tai, 5.7 years (Boesch and Boesch-Achermann 2000); Kanywara, Kibale, 5.4 years (Brewer-Marsden, Marsden, and Emery-Thompson n.d.); and Budongo, 5.6 years (Brewer-Marsden, Marsden, and Emery-Thompson n.d.), t. Average human interbirth interval of three foraging groups: Ache, 3.2 years (Hill and Hurtado 1996); !Kung, 4.12 years (Howell 1979); and Hiwi, 3.76 years (Kaplan et al. 2000), u. Average of latest recorded age at last birth in four *P. troglodytes* populations: Gombe, 44 years (Goodall Institute); Mahale, 39 years (Nishida et al. 2003); Tai, 44 years (Boesch and Boesch-Achermann 2000); and Bossou, 41 years (Sugiyama 2004), v. Hill and Hurtado (1996); Howell (1979); and Martin and colleagues (2003).

taken from individuals of known ages in captivity. The mortality profiles constructed for wild populations do not indicate stable or growing populations for any of the species, which implies that observed mortalities are higher than they have generally been until quite recently.

LIFE HISTORY CONTRASTS

Comparisons of data in table 2.1 show that extant humans evolved the following changes in character states from the other great apes.

Maximum Potential Lifespan

The maximum potential lifespan of humans is clearly longer than that of the other great apes by several decades. Even among human foragers without access to any medical support, some people live into their 70s and 80s (R. B. Lee 1968; Howell 1979; Hill and Hurtado 1996; Blurton Jones, Hawkes, and O'Connell 1999, 2002). In contrast, chimpanzees in the wild usually die before they reach 45 (Hill et al. 2001), and orangutans before age 50 (Wich et al. 2004). This difference in lifespan remains even under captive and modern medical conditions; maximum recorded longevity for great apes is around 60 years (Erwin et al. 2002), whereas the oldest human on record died at 122 (Robine and Allard 1998). These data show that humans have gained an increase in maximum lifespan relative to the ancestral state of at least twenty to thirty years. Maximum lifespan and average adult lifespan are correlated variables (Sacher 1959; Hawkes, chapter 3, this volume). Chimpanzee (Hill et al. 2001) and orangutan (Wich et al. 2004) females in the wild who survive to age 15 can expect to live only an additional fifteen to twenty more years (probably more for orangutans), whereas hunter-gatherers at age 15 can expect to live about twice that long (Howell 1979; Hill and Hurtado 1996; Blurton Jones, Hawkes, and O'Connell 2002).

Longer adult lifespans reflect lower adult mortality. When extrinsic adult mortality is as low as it is among great apes, adults can live long enough to display signs of declining physiological performance and eventually die from age-specific frailty. Ricklefs (1998) showed that in species with adult lifespans similar to chimpanzees, about 69 percent of adult deaths result from age-related causes. Selection can favor slower rates of aging if the fitness benefits of extending vigorous physical performance exceed the costs of increased somatic maintenance and repair. Slower rates of aging may account for the difference between human and nonhuman great ape maximum lifespans (Hawkes 2003). There is little systematic evidence documenting age-specific declines in physical performance in nonhuman great apes, but qualitative descriptions suggest that, as expected from their relatively shorter lifespans, chimpanzees do age faster than humans. Goodall (1986) classified chimpanzees at Gombe as old aged beginning at age 33. Finch and Stanford (2004:4) report that individuals age 35 or more years "show frailty and weight loss" and the "external indications of senescence include sagging skin, slowed movements, and worn teeth." As chimpanzees in the wild reach their mid-30s, they appear to age rapidly and die within a decade. In contrast, studies of physical performance among people who hunt and gather for a living show that vigor declines more slowly with age. Measures such as muscle strength in hunter-gatherer women decrease slowly over many decades (Blurton Jones and Marlowe 2002; Walker and Hill 2003). Comparable systematic performance data on great apes are needed to test whether they do, in fact, age more quickly than people.

Age at First Birth

As expected from an extension in lifespan, age at first reproduction among humans is much later than among other great apes and has increased from the ancestral state by four to six years. The age at first birth of female chimpanzees and bonobos in the wild, while variable, shows a central tendency toward 13 and 14 years, respectively. For gorillas, the mean age at first birth is 10 years, and orangutans bear their first offspring around age 15.6 years. Mean age at first birth among human foraging populations is 19.5 years.

These central tendencies persist for all great ape species in spite of differences in environment and ecology among populations in the wild. The affluence of captivity seems to have only a modest effect on age at first birth. It is often assumed that superabundance enhances physical condition, accelerates the timing of first birth, and extends longevity. However, there is evidence that the husbandry practices and socioecological conditions of many captive colonies do not always maximize the welfare of great apes and often increase incidents of vascular disease, obesity, and stress (DeRousseau 1994; Finch and Stanford 2003). Captive chimpanzees and bonobos bear their first offspring when they are around 11 years old (Bentley 1999; Knott 2001; Sugiyama 2004). Even though this mean is earlier than the central tendency of age at first birth among their wild counterparts, it is within the age range of at least one wild population. Age at first birth for gorillas in captivity is virtually identical for those in the wild (9.3 versus 10 years). Captive orangutan females show the largest shift in age at first birth from their wild counterparts. Markham (1995) reports age at first birth for orangutans in captivity as 11.5 years, almost four years earlier than orangutans in the wild. Whether in the wild or captivity, though, orangutans have the latest age at first birth and remain the "slowest" of the nonhuman great ape species.

Similar to captive great apes, there is also surprisingly little variation in average age at first birth among humans. Even under current conditions of ample food supply and medical care, human females, on average and cross-culturally, bear their first offspring after they are 18 years old (Bogin 1999a; Martin et al. 2003). Data from historic human records indicate that average age at first birth occurred even later, in the early to mid-20s (Le Bourg et al. 1993; Westendorp and Kirkwood 1998; Korpelainen 2000, 2003; Low, Simon, and Anderson 2002; Smith, Mineau, and Bean 2003; Grundy and Tomassini 2005; Helle, Lummaa, and Jokela 2005; Pettay et al. 2005). These data emphasize the limited plasticity of life history traits even in light of resource abundance.

Maternal Body Size

Later age at first birth enables energy to be invested in growth over a longer juvenile period, so most mammals with slower life histories also have larger body sizes (Purvis and Harvey 1995). Of all the primates, great apes are the longest-lived and latest maturing, as well as the largest-bodied. As previously discussed, gorillas are unusual in that they grow faster than the other great apes, including humans, achieving a much larger adult size. The remaining great ape species share a similar growth rate and achieve body sizes that generally vary with the duration of growth before maturity (Blurton Jones, chapter 8, this volume).

Chimpanzees, bonobos, and orangutans bear their first offspring between the ages of 13 and 16 and have similar body weights, around 35 kg. Human females have a later average age at first birth, 19.5 years, increasing the duration of growth four to six years longer than *Pan* or *Pongo* species. As a result, human females in extant foraging societies are about 10–15 kg larger than chimpanzee, bonobo, or orangutan females. Modern foragers are generally smaller than the estimated body sizes for people before the Mesolithic (Ruff, Trinkhaus, and Holliday 1997; Jenike 2001). Ethnographic hunter-gatherer means may therefore underestimate the average maternal-size differences between humans and our common ancestor.

Gestation Length and Size at Birth

Larger mothers have greater resources for offspring production, and great ape mothers translate this energy into larger, more expensive babies (Stearns 1992; see Hawkes, chapter 4, this volume:figure 4.7). As noted above, the rate of offspring production co-varies with growth rate (Charnov and Berrigan 1993); gorillas grow faster and produce babies at shorter intervals than the other great apes. Chimpanzees, bonobos, orangutans, and humans grow more slowly, more slowly even than the average primate but for a longer period of time, resulting in large mothers who produce large babies. Human females, with the longest duration of growth, have the largest maternal body sizes and produce the largest offspring.

Larger human neonatal size is achieved through a comparably longer length of gestation, ten to thirty days longer than the other great apes (Haig 1999; Dufour and Sauther 2002). Although this difference seems slight, human newborns spend the last weeks before parturition accumulating remarkably large adipose fat stores (Southgate and Hey 1976), and these fat stores likely account for the comparatively larger size of human neonates. Across the mammals, neonatal fat stores scale allometrically with body size (Widdowson 1950). Human neonates, however, are more than three times fatter than expected for a mammal of their size (Kuzawa 1998). At birth, 12 to15 percent of human neonatal body weight is adipose tissue (Fomon et al. 1982). Although there are no data documenting the body fat of great ape infants, the qualitative difference in the amount of body fat between human and great apes is apparent. Schultz (1969:152) made the general observation that "most human babies are born well padded with a remarkable amount of subcutaneous fat, whereas monkeys and apes have very little, so that they look decidedly 'skinny' and horribly wrinkled."

Estimating neonatal size relative to maternal size is difficult because there is extreme variation in adult body size both inter- and intra-individually and within and among populations (see table 2.1 for ranges). Nevertheless, graphing data reported by Poppitt and colleagues (1994) show that neonatal weight scales allometrically with maternal weight (figure 2.2). Bigger mothers bear larger infants, but the increase in the ratio of neonatal mass to maternal mass declines allometrically (slope of 0.746) with maternal size—6.4 percent for the

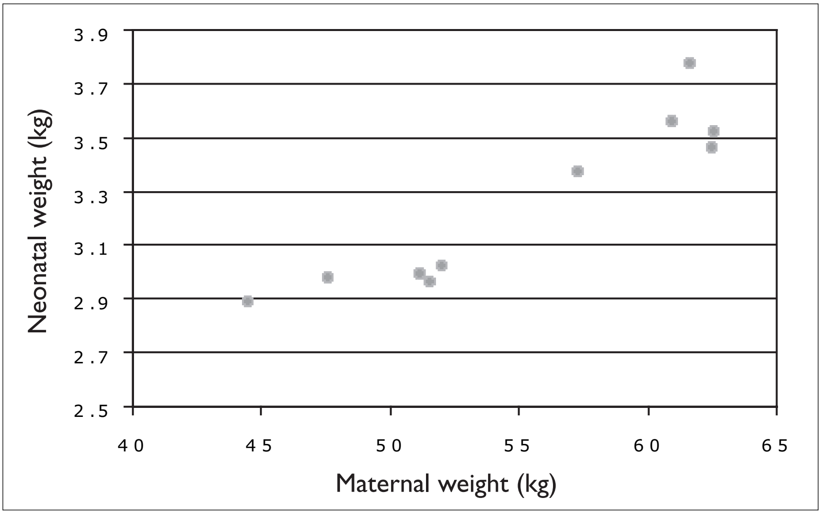

FIGURE 2.2

Neonatal weight relative to maternal weight (data from Poppitt et al. 1994). Neonatal weight scales allometrically with maternal weight at a slope of 0.746.

smallest mothers and 5.8 percent for the largest mothers in Poppit and colleagues' sample. Among extant human populations, neonatal size is somewhat larger relative to maternal body weight than other great ape species (Leuttenegger 1973). This difference is inflated when ethnographic hunter-gatherers are used to represent maternal size and may result from late Pleistocene decreases in adult size. Using two methods to estimate body mass, Ruff, Trinkhaus, and Holliday (1997) determined that adult individuals in our genus were about 10 percent larger during the Pleistocene.

Age at Weaning and Interbirth Intervals

Species with slow life histories generally have later ages at weaning and longer interbirth intervals. Great apes exemplify this pattern. They wean their dependent offspring relatively late, especially the frugivorous chimpanzees and orangutans (around ages 4.5 and 7 years, respectively), and have long interbirth intervals (5.5 and 8 years, respectively). Humans, however, have the slowest life history in many respects, but we wean our infants comparatively early. Human foragers typically wean their infants by age 3 and have mean interbirth intervals of around 3.7 years. Like age at first birth, human weaning ages are similar across a broad range of ecologies. Weaning age for humans is consistently "between 2 to 3 years and generally occurs about midway in that range" (Kennedy 2005:7).

Many ways have been proposed to estimate expected ("natural") weaning age from other human life history variables, and most predict later weaning age than practiced (Sellen 2001a). Harvey and Clutton-Brock (1985) predicted an average weaning age of 3.36 years based on a correlation between maternal and infant body size, but Charnov and Berrigan (1993) noted that mammalian infants are generally weaned when they achieve one-third of maternal body weight (Lee, Majluf, and Gordon 1991), which for humans occurs around 6.4 years. B. Smith (1992), following Schultz (1956), found that across a sample of primates, weaning age correlated with the eruption of the first permanent molar, around 6.5 years in humans. It is clear that the observed human weaning age of 2 to 3 years is earlier than these predictions. This is all the more remarkable because other aspects of our life history have slowed down relative to the ancestral state (Smith and Tompkins 1995).

Age at Last Birth and Menopause

Among mammals, oocytes are produced in the fetal ovaries until the third trimester of gestation, when the mitosis of germ cells ends. At this point, females have a fixed initial store of oocytes that is then subject to a process of continual depletion, or atresia, over their lifetime until the number of remaining follicles nears zero (vom Saal, Finch, and Nelson 1994; O'Connor, Holman, and Wood 2001; A. Cohen 2004). In humans, the cycle of ovulation and menstruation is generated by an endocrinological feedback loop that requires a sufficient oocyte store (J. Wood 1994). When there are too few oocytes remaining to stimulate ovulation, estimated at around one thousand follicles (Richardson, Senikas, and Nelson 1987), cycling ceases. All menstruating primates can potentially experience the senescent cessation of menses, or menopause, if they live long enough. In nonhuman species, however, reproductive senescence usually corresponds with somatic senescence, and few species live beyond the depletion of their oocyte store.

This is well documented in captive populations of macaques (for example, *M. fuscata,* Nozaki, Mitsunaga, and Shimizu [1995]; *M. mulatta,* M. Walker [1995]; *M. nemestrina,* Short et al. [1989]), where individuals live longer with senescent impairments than they can in the wild. Data on reproductive senescence in great apes is scant, but histological examination of captive chimpanzee females' ovaries suggests that the process of oocyte reduction is similar to that in humans (Gould, Flint, and Graham 1981). The few captive females that survived to menopause exhibited the same pattern of declining fecundity and variable cycling experienced by women (Tutin and McGinnis 1981) and around the same age (Gould, Flint, and Graham 1981).

Several years before menopause in women, the hormonal system that regulates menstrual cycles, the hypothalamic-pituitary-ovarian (HPO) axis, begins to break down because the number of oocytes necessary for ovarian steroid production is reduced below a necessary threshold. During this period of "perimenopause," cycle lengths become long and irregular, and many are anovulatory. Inconsistent functioning of the HPO axis and the increase in pregnancy failure during perimenopause result in a steep decline in the fertility of human females (Holman and Wood 2001). In noncontracepting human populations, average age at last birth precedes average age at menopause by about ten years (Gosden 1985). There are few data documenting the pattern of age-specific fertility decline in nonhuman great apes, but those available for chimpanzees suggest that fertility nears zero at 45 years of age (Nishida, Takasaki, and Takahata 1990; Boesch and Boesch Achermann 2000; Sugiyama 2004), as it does in humans (Howell 1979; Hill and Hurtado 1996; Muller et al. 2002; Martin et al. 2003). It appears that the age at which fertility declines in the other great apes is similar to that of humans (see Wich et al. 2004 on orangutans). This similarity suggests that we all share the ancestral pattern of ovarian ontogeny and what is derived in humans is not an unusual rate or timing of reproductive decline but a slowed rate of somatic aging and a vigorous, postmenopausal lifespan.

EFFECTS OF DERIVED HUMAN LIFE HISTORY

Many characteristics of growth and development depend on life history but are not, themselves, life history traits. The contrasts described above for females, excluding body size—maximum potential lifespan (or average adult lifespan), age at first birth, gestation length, interbirth intervals and age at weaning, and age at last birth—are directly linked to population vital rates. In this section, we discuss links between the derived features of human life history and aspects of human growth, development, and sociality.

Altriciality and Brain Growth

The postnatal growth requirements of human brains have long been seen as the source of our slow maturation. Compared with infants of the other great apes, human infants have been considered "helpless and undeveloped at birth" (Gould 1977:369), incapable of independent movement until at least 6 months of age; neonatal great apes are able to cling to their mothers from a very early age. This relative altriciality (Portmann 1941) has been attributed to the relatively small size of the human neonate's brain, under the assumption that a rapidly growing and developing brain is incapable of coordinating fully developed locomotor behavior (R. Martin 1990). There have been objections to both primary aspects of this widely accepted perspective. First, Schultz (1969:154) pointed out that the minimal locomotor development of humans at birth is not unusual, that, in fact, "the apes are born as helpless and immature as the exceptionally large human newborn." Because chimpanzee and gorilla infants are carried by their mothers for approximately twenty postnatal weeks, Schultz (1969:157) concluded that this "flatly contradicts the frequently heard vague claim that man is unique in his being born utterly helpless in such a very immature state as is very exceptional among primates." In addition, human babies are born with strong grasping reflexes equal to that of other primates (Konner 1972) and use sophisticated behavioral strategies to maximize their survival (Hrdy 1999). Together, these observations suggest that the motor skills of human neonates are no more altricial than those of other great apes and that infants are not behaviorally underdeveloped.

Second, human altriciality is said to be the result of a smaller relative brain size at birth due to an obstetrical constraint imposed by a pelvis shaped for bipedality. For most mammals, the rapid rate of fetal brain growth ends at, or just after, parturition. For humans, however, the fetal pattern of brain growth is comparably steeper and continues for almost a year after birth. The continuation of rapid fetal brain growth rates during the first twelve postnatal months led Portmann (1941) to suggest that humans really have a twenty-one-month gestation span: nine months in utero and twelve extra-uterine months that R. Martin (1990) termed “exterogestation.” This suggests that human infants are born “early” because continued brain growth in utero would result in a head size too large for successful parturition (R. Martin 1983). Recent analyses comparing the patterns of brain growth in chim-pan-zees and humans (Leigh 2004) invite doubts about the uniqueness of rapid postnatal brain growth. We examine these data below.

There are few published data sets of brain sizes for individuals of known ages. Most authors present their original data in figures and report averages instead of original values, making intraspecies comparisons difficult (Jolicoeur, Baron, and Cabana 1988; Cabana, Jolicoeur, and Michaud 1993). Of the complete data sets published, most are derived from autopsy and necropsy records, a unique sample of individuals with various pathologies that possibly misrepresents the “normal” population. These are cross-sectional data, not longitudinal, repeated measurements on the same individual to assess individual variation in brain size and growth. However, these data currently provide the only opportunity for quantifying brain growth and development. Technological advances in brain imaging should make longitudinal data sets available for future comparison and analyses.

We calculated human brain measures from Marchand’s (1902) data set, which reports brain weight (wet, including meninges, in grams), stature (in centimeters), sex, and known or estimated chronological age. Marchand assembled these data from German autopsy records documented between 1885 and 1900. The original data include a total of 716 human males and 452 females from birth to more than 80 years old. The variation in brain size with age and sex compares favorably with other reports (Dekaban and Sadowsky 1978; Kretschmann et al. 1979), indicating that Marchand’s series can serve as a representative sample. Our calculations use his data on all individuals 3 years old and younger.

Brain weights for chimpanzees (*Pan troglodytes*) of known ages were drawn from necropsy data reported by Herndon and colleagues (1999). Brain weights were obtained fresh at Yerkes Regional Primate

Center from 76 captive individuals (33 females and 43 males) who died from natural causes or were euthanized when natural death was imminent. We used a subset of these data to calculate percent of adult brain weight at birth and to graph brain size from birth to 3 years.

These data, summarized in table 2.2 and plotted in figure 2.3, challenge three common assumptions about the uniqueness of human brain growth. First, chimpanzee and human infants are more similar in their percent of adult brain size at birth than usually assumed. It is conventionally reported that human neonatal brain weight is only 25 percent of adult size at birth whereas chimpanzee neonates have 50 percent of their adult brain weight at birth (Dienske 1986). But chimps are twice as close to adult size at birth as are humans; instead of a large interspecific difference in relative neonatal brain size, the difference is only about 10 percent. A larger sample of chimpanzee neonates may close this interval even more. This revision results from slightly lower percentage values for humans but primarily from the much smaller neonatal value for chimpanzees. Until now, relative chimpanzee neonatal brain size has been repeatedly based on the estimated cranial capacity of a single cranial specimen, known to be 74 days old at death (Schultz 1941). When plotted against Herndon and colleagues' (1999) values, this specimen is larger than neonatal size and falls where it should in the scatter, given its age of 2.5 months.

Second, we find that chimpanzees and humans share a very similar pattern of relative brain growth (see figure 2.2). Leigh (2004:152), using the same data to calculate brain growth trajectories for chimpanzees and humans, concluded that "after the first 18 months of life, *Pan* and *Homo* are not substantially different in terms of growth rates." Third, humans reach adult brain size much earlier than widely claimed, some individuals by 3 years of age. Kretschmann and colleagues (1979) used the Marchand (1902) data to show that, on average, males achieve 95 percent of total brain size by 3.82 years old and females reach 95 percent values by 3.44 years old. This is much earlier than assumed by most researchers.

Analyses indicate similarities in brain growth, relative neonatal brain size, and motor and behavioral skills at birth between humans and chimpanzees, challenging the characterization of humans as distinctively altricial. The similarities between chimps and humans do

TABLE 2.2

Human and Chimpanzee Brain Size at Birth and Adulthood by Sex

Species	Sex	Average Neonatal Brain Weight (g)[1]	Average Adult Brain Weight (g)[2]	Percent of Adult Total at Birth
Homo sapiens[3]				
	Males	371 (n = 16)	1404 (n = 150)	26.4
	Females	361 (n = 8)	1281 (n = 116)	28.2
Pan troglodytes[4]				
	Males	125 (n = 3)	406 (n = 17)	30.8
	Females	146 (n = 4)	368 (n = 17)	39.7

1. *Neonate* is defined as an individual between birth and 10 days old.

2. Average adult brain size was calculated as the mean of individuals between 20 and 40 years old by sex for humans and the mean of individuals between 7 and 30 years old for each sex in chimpanzees because this range safely precedes a known trend toward declining brain weight with age (Dekaban and Sadowsky 1978; Herndon et al. 1999).

3. References: Marchand (1902).

4. References: Herndon and colleagues (1999).

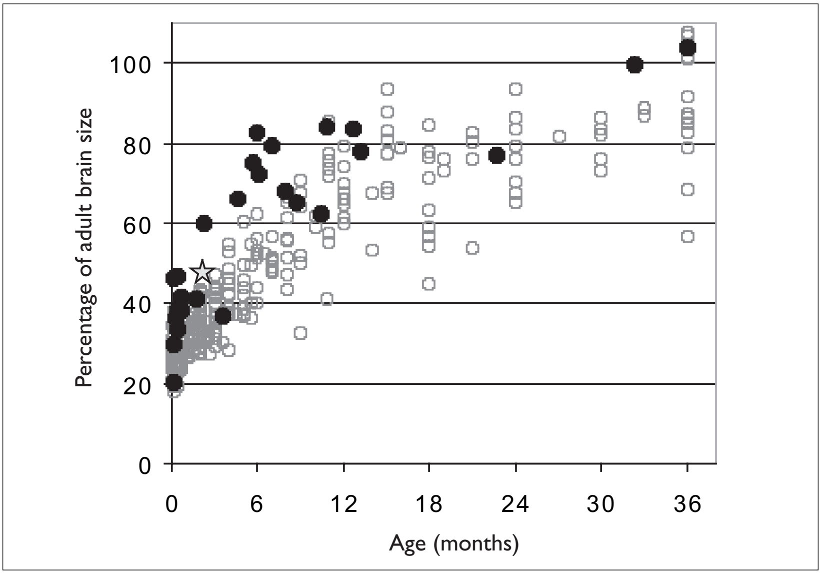

FIGURE 2.3

Percent of adult brain size achieved by age. Black dots are chimpanzees (Herndon et al. 1999; n = 26; males = 16, females = 10); open circles are humans (Marchand 1902; n = 160; males = 111, females = 49). The star represents Schultz's (1941) 74-day-old specimen.

not support the view that our juvenility is longer because of the growth requirements of our large brains.

Dental Development

Like brain growth and development, the pattern of dental growth and development is commonly used as a marker of life history events. Efforts have primarily focused on uncovering correlations between the timing and sequence of eruption of the permanent dentition and age at weaning and maturity. Relationships between dental markers and life history would provide a means to make direct interpretations of maturation schedules during hominin evolution based on fossil teeth. Given the systematic relationships among life history traits, establishing the timing of one would provide grounds for hypothesizing others. Teeth are less sensitive than other tissues to developmental insults and short-term ecological fluctuations (Nissen and Riessen 1964; Garn et al. 1973; Liversidge 2003), making them relatively reliable maturation markers. Schultz's often reprinted graph depicting variation in timing of life stages across the primates (for example, in Schultz 1969) used the emergence of the first permanent teeth to mark the end of infancy and the emergence of the last permanent teeth to mark the beginning of adulthood. Comparing primate species, Schultz (1949) also observed variation in the sequence of tooth eruption across the order. In species that are weaned relatively early, molars erupt before the deciduous teeth are lost and the emergence of the anterior permanent dentition. Schultz presumed that permanent molars erupted first so that infants would be prepared to masticate food when weaned, a generalization that B. Smith (2000) calls "Schultz's rule." Slower-developing humans show a distinctive eruption sequence: the permanent anterior dentition emerges before the molars. Schultz speculated that the human shift in eruption sequence is directly connected to slower human life history and, in particular, our much longer period of juvenility.

Building on Schultz's recognition of a connection between dental development and life history, B. Smith (1989a) showed that across the primates there is a strong correlation between the eruption of the first permanent molar (M1), weaning age and eruption of the third molar (M3), and age at first birth. In addition to eruption schedules, crown and root formation increments have been used to assess developmental age (Moorrees, Fanning, and Hunt 1963). The daily growth of

TABLE 2.3

Eruption and Crown Formation Schedules for Permanent Teeth

Species	Sex	M1 Eruption Mean (Years)	Age at Weaning (Years)[i]	M3 Eruption Mean (Years)[a]
Orang	Unknown	4.20 (~3.5–4.9)[a] ~3.5[a]	7.0	~10 ~10
Gorilla	Unknown	3.50 (3.0–4.0)[b] 3.50 (3.0–4.0)b	2.8	11.40 (9.70–13.10) 10.38 (8.70–12.10)
Chimp	Female	3.27 (2.75–3.75)[b] 3.19 (2.67–3.75)[b]	4.5	11.30 (9.75–13.08) 10.71 (9.00–13.08)
Chimp	Male	3.38 (3.00–3.75)[b] 3.33 (3.00–3.58)[b]	4.5	11.36 (10.00–13.58) 10.27 (9.00–11.08)
Chimp	Unknown	3.323 (2.2–4.1)[c] 3.218 (1.9–4.1)[c]	4.5	
Human	Female	6.35 sd 0.74[b] 6.15 sd 0.76[b]	2.8	20.50 20.40
Human	Male	6.40 sd 0.79[b] 6.33 sd 0.79[b]	2.8	20.50 19.80
Human	Unknown	5.84 (4.74–7.0)[d]	2.8	

Top values represent maxillary teeth, and lower line, mandibular teeth. Ranges are reported in parentheses.

a. Smith, Crummett, and Brandt (1994) and Kelley and Schwartz (2005)

b. Smith, Crummett, and Brandt (1994)

c. Conroy and Mahoney (1991) and Zihlman, Bolter, and Boesch (2004) report maxillary M1 at alveolar margin (estimating four months from gingival emergence) at 4.1 years in a wild chimpanzee; they report dental characteristics of seventeen immature wild chimps of known ages and conclude that "emergence of permanent teeth in wild chimpanzees is consistently later than 90 percent of captive individuals" (Zihlman, Bolter, and Boesch 2004:10541).

d. Liversidge (2003); mean (range) of fifty-six worldwide populations

e. Macho (2001); Kelley and Schwartz (2005)

f. Macho (2001)

g. Reid et al. (1998)

h. Liversidge (2000)

i. See table 2.1 for references.

Age at First Birth (Years)[i]	M1 Crown Formation (Years)	Average Molar Crown Formation (Years)[f]	I1 Crown Formation (Years)	I2 Crown Formation (Years)
15.6	3.01 (2.90–3.12)[e] 2.81[f]	3.13		
10.0	2.70[f] 2.90[f]	2.85		
13.3				
	2.85[f] 2.73[f]	3.39	4.00[g] 4.90 (4.45–5.35)[g]	4.50[g] 5.07 (5.00–5.15)[g]
19.5				
	3.03[f] 2.62[f]	3.07	4.29 (3.33–4.54)[h] 3.90 (3.12–4.50)[h]	4.42 (4.17–5.40)[h]

dental microstructures, primarily crown formation and enamel deposition, is an especially promising line of evidence that can link aspects of dental development to absolute calendar time (Bromage and Dean 1985; Benyon and Dean 1987). Like eruption schedules, crown formation is also broadly correlated with life history variation across the anthropoid primates (Macho 2001). This correlation fails, however, within the narrow phylogenetic range we consider here. Table 2.3 shows that the patterns of dental maturation and eruption in great apes do not always correspond with one another, nor with the order of fast-to-slow life histories among these species.

A comparison of age at weaning in table 2.1 with M1 eruption in table 2.3 illustrates this lack of correspondence. M1 eruption follows weaning age in gorillas and chimpanzees by nine months to one year, but by more than three years in humans, whereas it precedes weaning by a similar span in orangutans. Although the age of M3 eruption is much older in later breeding humans, M3s do not erupt at an older age in the later breeding chimps and orangutans, compared with gorillas. M3 eruption misestimates age at first birth in all the nonhuman great ape species by 1–5.5 years, erupting at around 11 years in gorillas and chimpanzees and 10 years in orangutans, whereas age at first birth occurs around 10, 13.3, and 15.6 years, respectively. These data show that the life history variation among the living great apes is not closely reflected in their molar eruption schedules.

Comparison of crown formation rates in table 2.3 shows that microstructure development and life history variables correspond even less well. Not only are crown formation times quite similar among the nonhuman apes, failing to track variation in either weaning ages or age at maturity, but also there is "considerable overlap among great apes and humans" in the formation rates of both incisors and molars (Macho and Wood 1995b:23). The data show that researchers must temper expectations that individual aspects of dental development (such as anterior crown formation times) are tightly tied to age at first birth (Ramírez Rozzi and Bermúdez de Castro 2004) and age at weaning (Macho 2001).

The timing of tooth eruption, crown maturation, and other aspects of dental development (Godfrey et al. 2003) varies among great ape species. Although the range of this variation is not independent of life history, the evidence reveals that the link is not a tight one. The robust associations among life history traits themselves reflect the necessary interdependence of population vital rates (Hawkes, chapter 3, this volume), but the demographic constraints on growth and development are quite indirect. Life histories may change without concomitant shifts in all aspects of development, and, conversely, selection might favor developmental adjustments within immature stages because of particular problems faced by infants and juveniles in each species (Godfrey et al. 2003).

Interbirth Intervals and Juvenile Foraging

A primary life history difference between human and nonhuman great apes is the faster rate of offspring production in human females. For large-bodied mammals that produce large-bodied babies, the span between two offspring (the interbirth interval) is typically long, resulting in slow female reproductive rates (Harvey and Clutton-Brock 1985). In primates, conception closely follows weaning of the preceding offspring (Pusey 1983; Graham and Nadler 1990; Watts 1991; Lee and Bowman 1995), suggesting that interbirth intervals end when an infant can successfully feed itself. Weaning is strictly defined as the cessation of infant suckling, but this definition conceals the fact that weaning is primarily a transitional process, a gradual reduction in the portion of milk ingested and a concomitant increase in solid food consumption, not an abrupt cessation of lactation (Sellen, chapter 6, this volume). From the start of transitional feeding, primate infants forage for the solid food they ingest, although they occasionally obtain nonmilk resources through passive food sharing (Feistner and McGrew 1989). The period of transitional feeding and the interbirth interval generally end when mothers have less fitness to gain from continuing their investment in the growing offspring than from beginning another pregnancy (Trivers 1974), usually at a time when an infant can successfully obtain all its own daily calories.

Offspring dependence is generally defined as the period during which the offspring drinks milk from its mother, that is, the time from birth to weaning. Some suggest a broader definition of dependence, noting that the mother provides services in addition to lactation that contribute to offspring survival (for example, Pereira and Altmann

1985). Primate orphans provide a good measure of the timing of independence from the mother. The available data, although largely anecdotal, suggest that suckling infants generally do not survive the death of their mother. Great ape orphan survival approaches that of no orphans if the mother is not lost before weaning age (Pusey 1983; Goodall 1986; Nishida, Takasaki, and Takahata 1990; Watts and Pusey 1993). In contrast, human infants are weaned at an age when they are still largely incapable of independent foraging and therefore continue to depend on provisioning by older individuals (Lancaster and Lancaster 1983). Data for humans show that offspring suffer poor survivorship if the mother dies during the first years of a child's life (Hill and Hurtado 1991; Sear et al. 2002; Pavard et al. 2005). Thereafter, death of the mother has less effect, not because the child is independent but because others supply support (Mace and Sear 2005).

Weaning and nutritional independence are not synonymous in humans as they are among the other apes. Children are weaned earlier yet are nutritionally dependent much longer than expected for a primate with our age at maturity. It is generally assumed that children require provisioning because they lack the ecological knowledge and complex foraging skills to forage independently. Gaining these skills is thought to require a long period of learning and practice during juvenility, an "apprenticeship," in order for human children to forage competently for themselves (Kaplan et al. 2000; Kaplan, Lancaster, and Robson 2003).

Recent studies challenge two common assumptions about the limitations of children's foraging efforts and capabilities. First, many foraging skills do not require substantial time and practice for children to master (Bliege Bird and Bird 2002; Blurton Jones and Marlowe 2002). Rather, children's foraging strategies appear to be more strongly constrained by their diminutive size, strength, and speed than by age and experience (Bird and Bliege Bird 2005; Tucker and Young 2005). Because children cannot acquire resources that require adult size, they forage from a different diet breadth. Calculations of juvenile foraging returns in child-accessible patches reveal that children are optimal foragers, targeting resources that yield the maximum immediate return rate (Bird and Bliege Bird 2002, 2005). These studies show that when evaluated within the constraints of their small size and strength, children are strategic and skilled foragers.

Second, Hawkes, O'Connell, and Blurton Jones (1995) have shown that foraging children can contribute more to their own subsistence than is widely assumed. Hadza children actively participate in food acquisition soon after weaning and throughout childhood, and these efforts make important contributions to their own nutrition. A mother often incorporates the productivity of her offspring when selecting foraging locations or resources, by choosing the strategy "that maximizes the *team rate* she and her children earn collectively, *even if the rate she earns herself is less than the maximum possible*" (Hawkes, O'Connell, and Blurton Jones 1995:695, italics original). Nevertheless, even though human juveniles can forage on their own behalf, they reside in habitats selected by adults and rarely ideal for independent juvenile subsistence. Thus, human children, unlike other ape juveniles, remain dependent upon supplemental provisioning long after they are weaned.

Stacking and Cooperative Breeding

With an earlier age at weaning and shorter interbirth intervals, human mothers shoulder the simultaneous nutritional dependence of multiple sequential offspring, a phenomenon we may call "stacking": mothers move on to bear another baby before the preceding one is nutritionally independent. This characteristic of humans is absent among nonhuman great apes. Great ape mothers may be accompanied by weaned subadult offspring while carrying a dependent infant, but they do not provision their offspring once weaned. Sumatran orangutans (van Noordwijk and van Schaik 2005) tolerate the presence of weaned juveniles, but these juveniles feed themselves and tend to leave their mother before the next infant is 2 years old (although there may be a longer association in the eastern subspecies *P. pygmaeus morio* of the Bornean orangutans [Horr 1975; M. Ancrenaz, personal communication 2005]). Maternal association with multiple immature offspring is more apparent in chimpanzees when a just-weaned juvenile and an older juvenile approaching adolescence may travel with their mother but, again, feed themselves. Orangutan immatures develop foraging competence at about the same age chimpanzees do, and their later weaning ages may be a response to the low productivity of the Southeast Asian rainforest, in which mothers cannot afford to travel with both a new baby and a weaned juvenile (van Noordwijk and van

Schaik 2005). This finding highlights the benefits that juveniles gain from association with adults. In more gregarious species, mothers may have shorter interbirth intervals because their weaned offspring need not make independent ranging choices yet. Comparing weaning ages in orangutans, chimpanzees, and gorillas, interbirth intervals vary inversely with gregariousness, and intervals are shortest in our own, especially gregarious species.

Human juveniles not only remain in association with their mothers but also continue to depend on provisioning after the birth of a younger sibling. The caloric returns necessary for multiple dependents may exceed the abilities of a single individual forager and require contributions from helpers other than the mother (Kaplan et al. 2000).

Fathers have long been assumed to be the primary source of help. Men differ from the males in other great ape species by regularly acquiring food that is consumed by women and children, and it is assumed that paternal benefits to improved nutrition and survival of their own offspring account for the evolution of men's work (Kaplan et al. 2000). Forager men sometimes provide a substantial component of food for their own children (for example, Marlowe 2003); among hunter-gatherer societies, higher average subsistence contributions from men are associated with higher average female fertility (Marlowe 2001). But the motives for men's contributions and the benefits they earn are disputed. Social benefits may be more important than parenting benefits in shaping these male activities. The returns from men's hunting are unpredictable, making it an unreliable strategy for family provisioning among low-latitude foragers (Hawkes, O'Connell, and Blurton Jones 2001b). When a hunter is successful, the meat is widely shared, so his family gets little more than others (Hawkes, O'Connell, and Blurton Jones 2001a). As in primates generally, the association of adult males with youngsters can sometimes serve as mating effort, mate guarding, or social bridging (Flinn 1992; Smuts and Gubernick 1992; Kuester and Paul 2000). Nevertheless, even if competition for social standing is the main motivation for men's food acquisition, especially big game hunting, the result does provide benefits for mothers and their children (Hawkes and Bliege Bird 2002).

Features of our distinctive life history, long postmenopausal lifespans and late age at first birth, provide two more reliable sources of potential help to mothers with multiple dependents. Postmenopausal and adolescent females lack newborns of their own and are therefore inclined to provide allomaternal assistance to gain inclusive fitness benefits (Hrdy 1999). Ethnographic and historic data show that the presence of a grandmother (especially the maternal grandmother) increases the welfare of her grandchildren (Sear, Mace, and McGregor 2000, 2003; Jamison et al. 2002; Sear et al. 2002; Voland and Beise 2002; Lahdenpera et al. 2004; Ragsdale 2004; Tymicki 2004). When circumstances permit (Hames and Draper 2004), older adolescents provide important help to their mothers through the caretaking of younger siblings (Tronick, Morelli, and Ivey 1992). The fact that human mothers stack nutritionally dependent offspring points to the evolutionary importance of help from provisioners other than the mother in the evolution of our life histories (Hrdy 1999).

CONCLUSIONS

We have compared the life histories of humans and the living great apes to develop a hypothetical life history for a common ancestor and identify changes in our lineage. A general feature of living great apes is a slow life history, so we infer that this was also true of our common ancestor. Human life histories are even slower. Humans have a significantly longer lifespan, with adults living at least twenty-five years longer than the other great apes. Human age at first birth is four to six years older than for orangutans and chimpanzees, increasing the period of juvenility and opportunity for growth. Additional time to grow results in larger human mothers who produce absolutely and relatively larger babies.

Two striking deviations have shaped the pattern of slowing in human life histories: our short interbirth intervals and our vigorous postmenopausal longevity. First, slower life histories typically include longer interbirth intervals. Although humans have the longest subadult period, attain the largest body size, and produce the largest infants, we have the shortest interbirth intervals. Human infants are weaned several years earlier than might be expected of an ape with our age at maturity. Also, because women (like most primate females) conceive soon after a child is weaned, they bear another baby before the preceding one is capable of independent foraging. Second, women stop bearing offspring by their early 40s. The age at which fertility declines to menopause appears to be essentially the same in women as in the other apes, indicating that this trait may be conserved across the great ape radiation. The distinctively early weaning of human infants and stacking of dependent offspring could evolve only if human mothers had a reliable source of help. Postmenopausal grandmothers and adolescents, because they themselves did not have infants, likely supplied that help.

We have also highlighted the imperfect correspondence among various aspects of growth and development in brains and teeth and between those developmental variables and the life history traits that are tied to population vital rates. Our exploration of the cross-species variation among great apes and humans in these dimensions is only a beginning. More is clearly in order.

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