HUMAN LIFE HISTORIES IN AN EVOLUTIONARY AND COMPARATIVE CONTEXT

by

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ABSTRACT

This dissertation utilizes life history theory to describe traits that are derived in humans through comparisons with other primate species. Modern human life histories are unique in that they are slower, exhibiting distinctly long postmenopausal life spans and later ages at sexual maturity as a result of a reduction in adult mortality since the evolutionary split the last Pan-Homo ancestor. Faster reproduction with shorter than expected interbirth intervals and earlier weaning ages are likely the result of cooperative breeding featuring postmenopausal grandmothers. Life history traits are distinguished from life history related variables (LHRVs) which are used to makes inferences about life history variables in extinct taxa. Body mass LHRV is a strong predictive life history proxy, but brain size and dental development are only weakly associated and inferences using them should be made with caution. Age at first birth is a central variable in demographic life history models as it identifies the beginning of fertility. For most mammals, age at first birth is closely aligned with the timing of physiological maturity. Humans live in varying ecologies that influence maturation rates and have marriage institutions that can constrain sexual access to fecund females. With few exceptions, the floor of the range of human age at first birth is remarkably consistent at about 17-18 years. Women who experience their first births before this age suffer maternal and infant costs. Heterogeneity, the inherent variation in individual quality, may have an important impact on the timing of life history events. Individuals of lower quality in severe conditions are prone to culling, leaving a subset of robust individuals who thrive in measurable ways. A test of this heterogeneity hypothesis is conducted using a subset of historic vital records from the Utah Population Database. Results show that mothers of twins have a more robust phenotype with lower postmenopausal mortality, shorter average interbirth intervals, later ages at last birth, and higher lifetime fertility than their singleton-only bearing counterparts. Thus, bearing twins may be a useful index of maternal heterogeneity.

This dissertation is dedicated to Ann Kelsey and Dr. Lois Alexander Merkler.

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INTRODUCTION

This dissertation describes the pattern of human life history in an evolutionary context and highlights the empirical advantages of comparisons between humans and nonhuman primates for identifying distinctively human features. Researchers interested in reconstructing human evolutionary history traditionally focus on fossil, archaeological, developmental, and ethnographic studies. Comparative primatology provides an additional complimentary line of evidence. Examination of interspecific variation from a phylogenetic perspective reveals the evolutionary history of derived and ancestral traits across the order, highlighting those specialized human traits that require explanation.

Most life history studies focus on females, because female fertility and mortality determine population growth and age structure. Following Schultz's original illustration, the major life events of a female mammal are age at weaning, age at sexual maturity, the pace and timing of reproduction, age at end of fertility and lifespan. The timing of these variables are correlated, responding invariantly to shifts in extrinsic adult mortality rates.

Herein I first compare modern human life histories to those of other great apes species to identify those traits that are derived in humans and which are likely to be shared by our closest ancestor. Life history variables are distinguished from life history-related variables (LHRVs), traits that are linked with, or can be used to make inferences about, life history but are not life history traits themselves. LHRVs are important to evaluate as they provide an opportunity for estimating life history events that are difficult to measure directly as well as providing proxy life history parameters for extinct taxa.

All great apes exhibit slow life histories but compared to other primates human life histories are the slowest, exhibiting long postmenopausal lifespans and later ages at first birth, pointing to a reduction in human adult mortality since we shared a last common ancestor. Gorillas, though the largest of the great apes, have relatively fast life history pace, likely the result of a specialized folivorous diet. Humans also exhibit a faster than expected reproductive rate with distinctively shorter interbirth intervals and early weaning, a pattern likely derived from a unique form of cooperative breeding featuring vigorous postmenopausal grandmothers.

Three LHRVs – body mass, brain growth trajectories, and dental development – were compared to the timing of life history variables to determine their usefulness as proxies for extinct taxa. Body mass proved to be the best predictor of life history events, while brain growth and dental development are weakly related proxies and inferences from them should be made with caution.

Many researchers claim that the human brain grows at a faster rate and for a much longer post-natal period than chimpanzees, resulting in a significantly larger absolute and relative adult brain size. However, few studies have demonstrated this pattern empirically. A common assumption is that human brain growth extends beyond weaning, perhaps even until maturity, and accounts for the extended human subadult period. In Chapters 1 and 2, I compile and plot several age-specific brain size datasets for humans and chimpanzees. These data show that chimpanzees and humans have a similar percentage of adult brain size at birth, relative rates of brain growth, and achieve adult brain size at similar ages, around 3-4 years old. Both chapters discuss how these data challenge many of the assumptions about human altriciality and its influence on delayed juvenility.

Similarly, paleoanthropologists have high expectations for dental development patterns as proxies for life history events. However, evaluation of life history-related variables for extinct hominins in chapter two shows that there is no evidence of any hominin taxa possessing a body size, brain size, or dental development pattern reflecting the modern human pattern.

Age at first birth is a central variable in demographic life history models because it identifies the beginning of fertility. For most mammals, age at first birth is closely aligned with the timing of physiological maturity. Humans, however, live in varying ecologies that influence maturation rates and have marriage institutions that can constrain sexual access to fecund females. Using data from the published literature, in Chapter 3 I examine the human pattern of age at menarche, age at first birth, and age at marriage to characterize relationships among them. I identify the observed variation in each of these variables and review the proximate mechanisms that influence their timing. These data show that, with few exceptions, the floor of the range of human age at first birth is remarkably consistent at about 17-18 years old across space and time. Women who experience their first births before this age suffer maternal and infant costs. I investigate the effect of age at marriage on age at first birth and find that, although there is broad variation in age at marriage across cultures, there is a strong tendency for marriage age to just precede female sexual maturity. I propose that, in general, female sexual maturity determines martial age rather than the reverse. Comparisons with nonhuman great ape species confirm relatively late ages for all aspects of human sexual maturity, a pattern consistent with our slow life history. Finally, I consider the contribution of demographic heterogeneity to secular shifts documented in reproductive timing of women.

While humans usually give birth to singletons, dizygotic twinning occurs at low rates in all populations worldwide. In Chapter 4, I consider two hypotheses that might account for the persistence of twinning. One hypothesis is that maternal depletion reduces the effectiveness of controls on embryo number, so that older mothers in poorer condition are less able to reject second embryos. Alternatively, twinning, while costly, may indicate mothers with greater capacity to bear that cost. Drawing from the vast natural fertility data in the Utah Population Database (UPDB), we compared the reproductive and survival events of 4,603 mothers who bore twins and 54,183 who had not. These mothers were born between 1807 and 1899, lived to age 50, and married once to men who were alive when their wives were 50. Results from proportional hazards and regression analyses are consistent with the second hypothesis. Mothers of twins exhibit lower post-menopausal mortality, shorter average interbirth intervals, later ages at last birth, and higher lifetime fertility than their singleton-only bearing counterparts. We conclude that bearing twins is more likely for those with the robust phenotype and a useful index of maternal heterogeneity.

CHAPTER 1

THE DERIVED FEATURES OF HUMAN LIFE HISTORY

by
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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

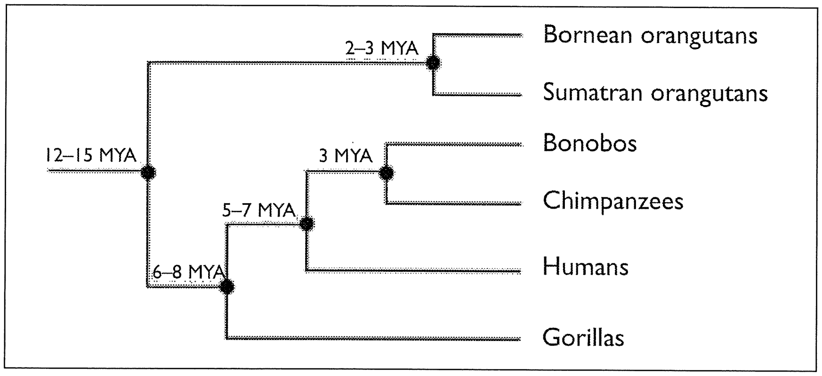

FIGURE 2.1

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

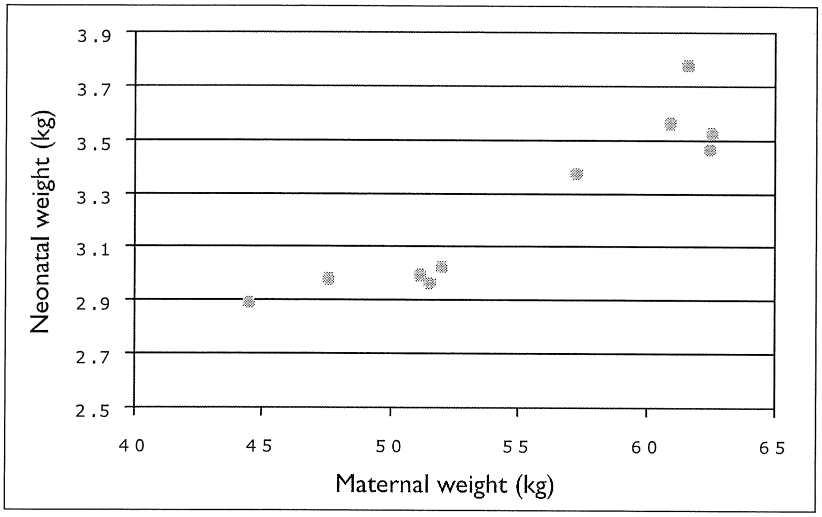

FIGURE 2.2

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 chimpan-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).

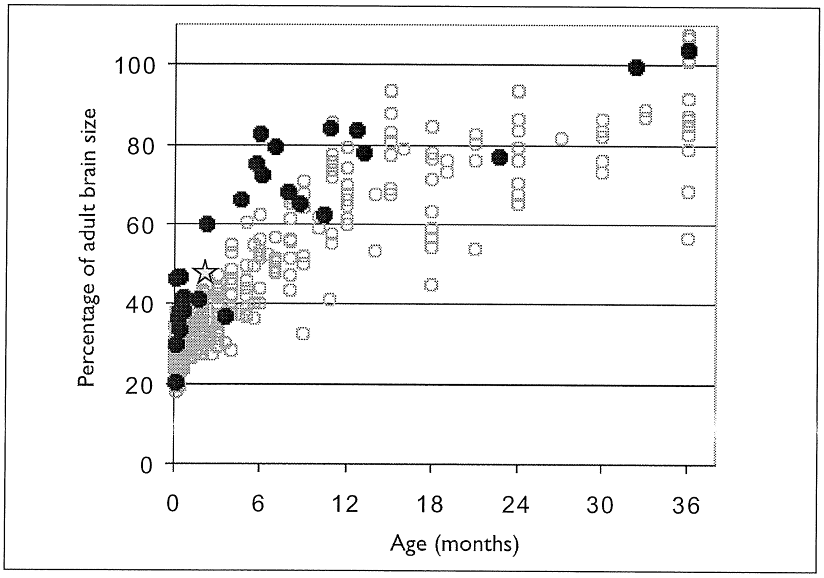

FIGURE 2.3

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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CHAPTER 2

HOMININ LIFE HISTORY: RECONSTRUCTION AND EVOLUTION

by
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REVIEW

Hominin life history: reconstruction and evolution

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Abstract

In this review we attempt to reconstruct the evolutionary history of hominin life history from extant and fossil evidence. We utilize demographic life history theory and distinguish life history variables, traits such as weaning, age at sexual maturity, and life span, from life history-related variables such as body mass, brain growth, and dental development. The latter are either linked with, or can be used to make inferences about, life history, thus providing an opportunity for estimating life history parameters in fossil taxa. We compare the life history variables of modern great apes and identify traits that are likely to be shared by the last common ancestor of *Pan-Homo* and those likely to be derived in hominins. All great apes exhibit slow life histories and we infer this to be true of the last common ancestor of *Pan-Homo* and the stem hominin. Modern human life histories are even slower, exhibiting distinctively long post-menopausal life spans and later ages at maturity, pointing to a reduction in adult mortality since the *Pan-Homo* split. We suggest that lower adult mortality, distinctively short interbirth intervals, and early weaning characteristic of modern humans are derived features resulting from cooperative breeding. We evaluate the fidelity of three life history-related variables, body mass, brain growth and dental development, with the life history parameters of living great apes. We found that body mass is the best predictor of great ape life history events. Brain growth trajectories and dental development and eruption are weakly related proxies and inferences from them should be made with caution. We evaluate the evidence of life history-related variables available for extinct species and find that prior to the transitional hominins there is no evidence of any hominin taxon possessing a body size, brain size or aspects of dental development much different from what we assume to be the primitive life history pattern for the *Pan-Homo* clade. Data for life history-related variables among the transitional hominin grade are consistent and none agrees with a modern human pattern. Aside from mean body mass, adult brain size, crown and root formation times, and the timing and sequence of dental eruption of *Homo erectus* are inconsistent with that of modern humans. *Homo antecessor* fossil material suggests a brain size similar to that of *Homo erectus s. s.,* and crown formation times that are not yet modern, though there is some evidence of modern human-like timing of tooth formation and eruption. The body sizes, brain sizes, and dental development of *Homo heidelbergensis* and *Homo neanderthalensis* are consistent with a modern human life history but samples are too small to be certain that they have life histories within the modern human range. As more life history-related variable information for hominin species accumulates we are discovering that they can also have distinctive life histories that do not conform to any living model. At least one extinct hominin subclade, *Paranthropus*, has a pattern of dental life history-related variables that most likely set it apart from the life histories of both modern humans and chimpanzees.

Key words dentition; encephalization; evolution; growth and development; hominin life history.

Introduction

Compared to other great apes modern humans have a higher rate of survival, live longer, start reproducing later, and have shorter interbirth intervals (reviewed in Leigh 2001; Robson et al. 2006). To reconstruct the recent evolution of these characteristics of modern human life history we review the life histories of closely related extant and fossil taxa. We also discuss the probable life histories of

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(1) the hypothetical last common ancestor (LCA) of the chimpanzee/bonobo and modern human (*Pan-Homo*) clade, (2) the hypothetical stem hominin taxon, (3) the taxa that make up the major grades within the hominin clade, and (4) the evolution of life history within the major subclades within the hominin clade. Comparing the life history of the living primates most closely related to modern humans enables researchers to generate hypotheses about what modern human life history traits are conserved and which are derived.

Direct evidence about non-human great ape life history has been gleaned by meticulous observation both in the field and from captive animals (see Kappeler & Pereira, 2003; van Schaik et al. 2006). These data, combined with molecular and other information about how their phylogenetic histories are related (see Bradley, 2008), contributes to reconstructing the life history of the LCA of the *Pan-Homo* clade. But in order to investigate the more recent evolutionary context of modern human life history, researchers must examine whatever evidence is available about the life history of closely-related extinct animals. If we make the untested assumption (see below) that the common ancestor of the *Pan-Homo* clade had a life history that is more like that of modern chimpanzees than that of modern humans, we must look at the fossil evidence of creatures that are more closely related to modern humans than to *Pan* (that is the hominin clade) to investigate the recent evolution of modern human life history.

Inferences about the life history of extinct hominin taxa must be extracted from fossilized remains of the hard tissues. Even this indirect information about the life history of fossil hominins is useful. If the taxon is directly ancestral to modern humans (but see Wood & Lonergan, 2008; for the reasons why this hypothesis is difficult to test and verify for most early hominin taxa) it provides evidence about an earlier stage in the evolution of modern human life history. If the taxon belongs to an extinct hominin subclade it might help throw light on the factors that determine and constrain how life history is configured more widely within the hominin clade.

In this contribution we have two primary aims: first to reconstruct the recent evolutionary history of hominin life history from extant and fossil evidence, and second to assess when, in what taxon or taxa, and at what pace, the distinctive components of modern human life history appear within the hominin clade. In the first section of our contribution we compare the life histories of the living great apes (orangutans, gorillas, chimpanzees, bonobos and modern humans) to identify traits that are likely to be derived in hominins, and thus suggest the likely life history of the *Pan-Homo* LCA, and the stem hominin. We distinguish life history variables (LHVs), traits such as age at weaning, age at sexual maturity, and life span that can only be measured in living populations, from life history-related variables (LHRVs). The latter are variables that can be used to make inferences about life history. Given the inability to collect standard life history data from fossil material, we evaluate how well three LHRVs, body mass, brain size and dental development, serve as accurate proxies for the timing of life history events in the extant great apes.

In the second section we address how different taxonomic schemes influence the analysis of hominin life history patterns by using both a relatively speciose (or 'splitting') taxonomy, as well as a less speciose (or 'lumping') taxonomy (see Wood & Lonergan, 2008). We then summarize what can be deduced about the evolution of the major elements of life history within the hominin clade. This includes an assessment of when, and in which taxa, the distinctive aspects of modern human life history make their appearance.

Finally, we consider the implications of these data for hypotheses about the first appearance of a modern human-like life history and evaluate how well the hominin fossil evidence supports the predictions made using comparative primate data. Specifically, we address three key questions: (1) Did the unique features of modern human life history appear suddenly as one integrated package, or did the components evolve independently and incrementally? (2) Did the onset of modern human life history coincide with the appearance of larger-bodied hominins with a modern human skeletal proportions, or did it appear later in hominin evolution? (3) Are modern human and modern chimpanzee life histories the only ways that life history has been configured within the *Pan-Homo* clade, or is there evidence within the fossil hominin record of creatures that have a different life history pattern?

Part I. Life history and life history-related variables of extant hominids

All organisms pass through major life stages and life history theory seeks to explain cross-species differences in the timing and covariation of these stages. It has been well established across a broad array of species that the timing of major life events tends to be correlated, even when the effects of body size are removed (Harvey & Read, 1988; Read & Harvey, 1989). A shift in the timing of one event results in a concordant extension or compression in the span between the occurrence of other events (Charnov, 1991). Primates in general, and great apes in particular, have slow life histories, with comparatively long life stages: late ages at maturity, low birth rates with small litter sizes, and long adult life spans (Charnov & Berrigan, 1993). The pace of life history is largely determined by age-specific mortality rates. Generally, species that suffer high rates of adult mortality, that is, a high probability of dying during one's reproductive years, tend to have fast life histories, whereas those with low adult mortality exhibit slower life histories (Harvey et al. 1989). Shifts in adult survival or mortality risk alter the pace of linked life

Table 1 Life history and life history-related variables and their present availability for extinct taxa

	Available for extinct taxa*
Life history variables (LHVs)	
Gestation length	No
Age at weaning	No?
Age at first reproduction	No
Interbirth interval	No
Mean life span	No
Maximum life span	No
Life history-related variables (LHRVs)	
Body mass	
Adult	Yes
Neonatal	Yes???
Brain mass†	
Adult	Yes
Neonatal	Yes???
Dental crown and root formation times	Yes?
Dental eruption times	Yes?

*Availability designated as 'Yes' means that reasonable sample sizes (but not necessarily reliable estimates) are available for most taxa; 'Yes?' means that it is possible to collect data for this variable from the fossil record but sample sizes are currently too small to be meaningful for many taxa; 'Yes???' means that it is theoretically possible to get data for this variable in the fossil record, but sample sizes may never be large enough to make meaningful inferences.
†Estimated from endocranial volume in extinct taxa.

history events, and also the constraints important for optimizing growth and development (Hawkes, 2006a).

Many published lists of life history variables are conflations of two different categories of information (Skinner & Wood, 2006), which we distinguish in Table 1. The first category (A) consists of variables such as gestation length, age at weaning, longevity, interbirth interval, and age of first and last reproduction. These variables reflect population vital rates and the timing of life history events, and we will refer to these as 'life history variables' (or LHVs). With the possible exception of weaning (Humphrey et al. 2007), we cannot yet make direct observations about life history variables on extinct taxa and thus we are reduced to making inferences about life history from qualitative or quantitative information about ontogeny gleaned from the hominin fossil record. This second category (B) consists of variables such as body mass and brain size (e.g. Sacher, 1975; Martin, 1981; Martin, 1983; Hofman, 1984; Smith, 1989, 1992; Smith & Tompkins, 1995; Smith et al. 1995; Godfrey et al. 2003) that have been shown empirically within extant primates to be constrained by, or correlated with, LHVs. To distinguish them from first-order life history variables we follow Skinner & Wood (2006) and refer to the second-order category B variables as 'life history-related variables' (LHRVs).

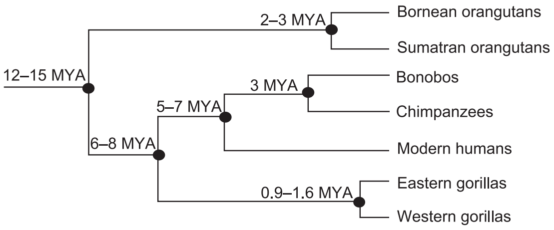

Fig. 1 Phylogenetic relationships of the extant great ape species. Estimated time of divergence of the hominid lineage from Glazko & Nei (2003), for chimpanzee/bonobo from Wildman et al. (2003), for the Bornean/Sumatran orangutans from Zhang et al. (2001), and for the eastern/western gorillas from Thalmann et al. (2007).

We examine first what LHV data are available for the extant great apes, focusing solely on females for several reasons. Female fertility rates and mortality rates determine population growth and age structure and are typically slower than male potential reproductive rates. Males must compete for paternity opportunities set by female fertilities, a limitation that has important consequences for male life histories, especially with respect to reproductive strategies (Kappeler & Pereira, 2003). In addition, many important life history variables are either restricted to females (such as gestation length, lactation, and interbirth intervals) or are difficult to ascertain for males (such as parity). We then consider in more detail how (and, more importantly, how reliably) LHRVs can be inferred from the evidence provided by the hominin fossil record.

Which apes resemble the first hominins?

Modern humans are part of the wider radiation of great apes as shown in Fig. 1. We follow the standard two species taxonomy for our closest living relatives in the genus *Pan*: the common chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*). Although differences between the three chimpanzee subspecies are small (Fischer et al. 2006), recent evaluation of genetic differences among chimpanzees supports the traditional taxonomic designation of three geographically distinct lineages (Becquet et al. 2007). The two other non-human great apes, gorillas and orangutans, are currently in a state of taxonomic flux. Gorillas were traditionally classified as a single species with various distinct subspecies, but recently the eastern and western gorilla populations have been accorded species status as *Gorilla gorilla* and *Gorilla beringei*, respectively (Groves 2001, 2003; Thalmann et al. 2007). Similarly, two species are recognized within the orangutan genus *Pongo*, *Pongo pygmaeus* from Borneo and *Pongo abelii* from Sumatra (Zhang et al. 2001). While these revisions recognize important species differences within orangutans and gorillas, there are insufficient species-specific long-term life history data to justify us distinguishing them for the purposes of our review, so we pool available life history data on chimpanzees, gorillas and orangutans and deal with these taxa at the generic level.

To use empirical data about the life history of the living great apes to reconstruct the life history of the most recent common ancestor of the *Pan-Homo* clade, or the life history of the stem hominin, we must make the untested assumption that the life histories of the non-human great apes have undergone relatively little evolution of their own. There is some support for this assumption, for the molecular and morphological similarities among the great apes suggest 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 consider our common ancestor was, too. The wrist morphology of early hominins apparently displays features similar to those seen in our knuckle-walking great ape relatives (Richmond & Strait, 2000), thus supporting this assumption, but a recent examination of the locomotor biomechanics among extant higher primates suggests that hominin bipedalism may have evolved independently from an arboreal ancestor (Schmitt, 2003; Thorpe et al. 2007; Crompton et al. 2008). Given the general correlation between terrestriality and faster life history (van Schaik & Deaner, 2003), and the evidence that the African great apes became more terrestrial over time, it may be argued that the late Miocene ancestors of the *Pan-Homo* clade probably had slower life histories. If this is the case, the still strictly arboreal orangutan may prove the best extant model for the life history of the earliest hominins. If the African apes did not evolve independently, then the earliest hominins most likely had a life history similar to that of our closest living relatives, the chimpanzee and the bonobo. If they did evolve independently, the best living model would be closer to that of the more arboreal orangutan.

Adult body size is the result of both the duration and rate of growth prior to maturity. Primates on average grow more slowly than other mammals and are therefore smaller compared to non-primate mammals of similar ages at first reproduction. Modern humans, chimpanzees, bonobos, and, orangutans grow even more slowly than the primate average (Blurton Jones, 2006). But this is not true of gorillas; they grow faster than the other great apes, including ourselves. Differences in growth rates across mammals are closely tied to differences in the rate they produce offspring (Charnov, 1991; Charnov & Berrigan, 1993). Gorillas grow more quickly and produce offspring at shorter intervals than do the other non-human great apes (Table 2, see Robson et al. 2006 for discussion).

The rapid growth of gorillas may be related to their diet. Leigh (1994) examined the diet, ecology and growth rates of 42 anthropoid primate species and found that those with more folivorous diets tend to grow faster than those with more frugivorous diets. This association may simply reflect nutritional adaptations, but it is also likely to be influenced by the lowered ecological risks and intraspecific feeding competition associated with a folivorous diet (Janson & van Schaik, 1993). Without these constraints, folivores are able to have faster infant and juvenile growth rates (Leigh, 1994). 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 chimpanzees favor vertebrate meat. In contrast, bonobos to some extent, and gorillas in particular, fall back on vegetative foods that tend to be abundant, but are of lower quality (Conklin-Brittain et al. 2001; Malenky et al. 1994). The diets of archaic hominins are generally reconstructed as being dominated by vegetative items, such as fruits and seeds (e.g. Schoeninger et al. 2001), so if diet influences growth trajectories, then these early hominins would be expected to have growth and reproductive rates closer to those of chimpanzees and orangutans than to gorillas. Also, the available fossil evidence suggests that the body size of archaic hominins is more similar to that of chimpanzees than to gorillas (McHenry, 1994). Average growth rates for modern human females are close to the rates for chimpanzees, bonobos and orangutans (Blurton Jones, 2006). For these reasons, we suggest that chimpanzees and orangutans provide the most appropriate models from which to reconstruct the life history variables of archaic hominins and we refer to data for gorillas only when relevant.

Comparing great ape life history estimates

To develop proper comparisons between modern humans and the other extant great apes we primarily rely on life history parameters estimated from modern human hunter-gatherers, because their diets, mobility, foraging styles, and population densities most likely resemble those of modern humans prior to the introduction of agriculture. While we refer to estimates drawn from a broader range of modern human populations for some of the variables in the text, in Table 2 whenever possible we use estimates derived from detailed studies of extant hunter-gatherers. This reduces concern about possible effects of improvements in diet and medical care on rates of development and senescence. We are aware, however, that it can be argued that the estimates are conservative in that ethnographically known populations of hunter-gatherers mostly occupy environments that are marginal for agriculture, thus these data are likely to sample only a subset of the habitats initially colonized by modern humans.

The non-human great ape data primarily come from long-term field studies and these data are constantly being revised and improved. In all the reports of studies of

Table 2 Primary life history variables of female great apes, mainly for wild populations compared to those of modern humans, mainly foragers

Species	Maximum life span (years)	Age at first birth (years)	Gestation length (days)	Age at weaning (years)	Interbirth interval (years)	Age at last birth (years)	Adult female body mass (kg)
Orangutan (*Pongo* sp.)	58.7*	15.6§	260§§	7.0¶	8.05§	> 41§	37.81‡‡‡‡
Gorilla (*Gorilla* sp.)	54*	10.0¶	255§§	4.1***	4.40¶	< 42¶¶¶	95.2‡‡‡‡
Bonobo (*P. paniscus*)	50.0+†	14.2**	244¶¶		6.25†††		33.35‡‡‡‡
Chimpanzee (*P. troglodytes*)	53.4*	13.3††	225§§	4.5¶	5.46‡‡‡	42****	35.41‡‡‡‡
Modern human (*H. sapiens*)	85‡	19.5‡‡	270§§	2.8¶	3.69§§§	45††††	45.5§§§§

*Judge & Carey (2000).
†Erwin et al. (2002).
‡Hill & Hurtado (1996); Howell (1979); Blurton Jones et al. (2002).
§Wich et al. (2004).
¶Alvarez (2000); for modern humans, only included data from two foraging populations, the Ache and !Kung.
**Kuroda (1989).
††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); Kibale (15.4 years) Wrangham in Knott (2001).
‡‡Average age at first reproduction from four modern human foraging groups: Ache (19.5 years) Hill & Hurtado (1996); !Kung (19.2 years) Howell (1979); Hadza (18.77 years), Blurton Jones (unpublished data); Hiwi (20.5 years) Kaplan et al. (2000).
§§Harvey et al. (1987).
¶¶de Waal & Lanting (1997): 190 report median gestation length for bonobos in captivity from Thompson-Handler et al. (1990).
***Average of median age at last suckle of both species: *G. gorilla* (4.6 years) Nowell & Fletcher (2007); *G. beringei* (3.6 years) Fletcher (2001).
†††Average of two *P. paniscus* populations: Wamba (4.5 years) Takahata et al. (1996); Lomako (8.0 years) Fruth in Knott (2001).
‡‡‡Average interbirth interval of five *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 & Boesch-Achermann (2000); Kanywara, Kibale (5.4 years) Brewer-Marsden et al. (2006); Budongo (5.6 years) Brewer-Marsden et al. (2006).
§§§Average modern human interbirth interval averaged from three foraging groups: Ache (3.2 years) Hill & Hurtado (1996); !Kung (4.12 years) Howell (1979); Hiwi (3.76 years) Kaplan et al. (2000).
¶¶¶Maximum reported age at last birth reported in captivity: Atsalis & Margulis (2006).
****Average of maximum 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 & Boesch-Achermann (2000); Bossou (41 years) Sugiyama (2004).
††††Average age at last birth: Hill & Hurtado (1996); Howell (1979); Martin et al. (2003).
‡‡‡‡Body mass reported for wild populations Plavcan & van Schaik (1997).
§§§§Average of ethnographic sample reported in Jenike (2001; Table 5).

wild populations, the ages of many adults were estimated and maximum life spans were all based on estimates with unknown errors. The maximum life spans given in Table 2 are therefore taken from captive individuals of known ages. The mortality profiles constructed for wild populations do not suggest either stationary or growing populations, implying that the observed mortalities are higher now than they have been until quite recently.

Comparisons of data in Table 2 show that modern humans differ in the following ways from the other extant great apes.

Maximum potential life span

The maximum potential life span of modern humans exceeds that of the other extant great apes by several decades. Even among modern human foragers with no access to medical support, some individuals live into their 70s and 80s (Blurton Jones et al. 1999, 2002; Hill & Hurtado, 1996; Howell, 1979; Lee, 1968). 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 life span persists under the best captive conditions; maximum recorded longevity for great apes is around 60 years (Erwin et al. 2002), while the oldest modern human on record died at 122 (Robine & Allard, 1998). These data show that modern humans have an increased maximum life span relative to the inferred ancestral state (i.e. around 45–50 years in non-human great apes) by at least 20–30 years, and maximum life span and average adult life span are correlated (Charnov 1993; Hawkes, 2006a; Sacher, 1959). 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 15–20 years (probably more for orangutans), whereas modern human hunter-gatherers at age 15 can expect to live about twice that long (Howell, 1979; Hill & Hurtado, 1996; Blurton Jones et al. 2002). Among modern human foragers about 30% of those over the age of 15 are past the age of 45, while this is true of less than 3% of wild chimpanzees (Hawkes & Blurton Jones, 2005).

Longer adult life spans 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 life spans similar to chimpanzees, about 69% 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 differences between modern human and non-human great ape maximum life spans (Hawkes, 2003). While there is little systematic evidence documenting age-specific declines in physical performance in the non-human great apes, qualitative descriptions suggest that, as expected from their relatively shorter life spans, chimpanzees do age faster than modern humans. Goodall (1986) classified chimpanzees at Gombe as 'old' when they reached the age of 33 years. Finch & Stanford (2004) report that chimpanzee individuals aged 35 years or more 'show frailty and weight loss' and the 'external indications of senescence include sagging skin, slowed movements, and worn teeth' (*ibid*, p. 4). Thus, when 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 hunters and gatherers show that vigor declines more slowly with age. Measures such as muscle strength in hunter-gatherer women decrease slowly over many decades (Blurton Jones & Marlowe, 2002; Walker & Hill, 2003). Comparable data on the physical performance of the 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 life span, Table 2 shows that age at first reproduction among modern humans is later than in the other great apes, and has increased from what is inferred to be the ancestral state (see below) by 4–6 years. The age at first birth of chimpanzees and bonobos in the wild, while variable, shows a central tendency toward age 13 and 14, respectively. This is the inferred ancestral state for the *Pan-Homo* and the hominin clades. For gorillas the mean age at first birth is 10 years and orangutans bear their first offspring at around 15.6 years old. Mean age at first birth among modern 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. Captivity seems to have only a modest effect on age at first birth (Bentley, 1999). It is often assumed that superabundance of food 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, indeed, often increase the incidence of vascular disease, obesity, and stress (DeRousseau, 1994; Finch & Stanford, 2003). Captive chimpanzees and bonobos bear their first offspring when they are around 11 years old (Bentley, 1999; Knott, 2001; Sugiyama, 2004) and while 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 to those in the wild (9.3 versus 10 years, Harcourt & Stewart, 2007). 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 4 years earlier than orangutans in the wild. However, whether in the wild or captivity, orangutans have the latest age at first birth and are the 'slowest' of the non-human great ape species.

There is surprisingly little variation in average age at first birth among modern humans. Even under conditions of ample food supply and medical care, cross-culturally modern human females, on average, bear their first offspring after 18 years of age (Bogin, 1999; Martin et al. 2003). Data from historic records indicate that the average age at first birth occurred even later than at present (LeBourg et al. 1993; Westendorp & Kirkwood, 1998; Korpelainen, 2000, 2003; Low et al. 2002; Smith et al. 2003; Grundy & Tomassini, 2005; Helle et al. 2005; Pettay et al. 2005). These data emphasize the limited plasticity of life history traits even when resources are abundant.

Later age at first birth allows energy to be invested in growth over a longer juvenile period and thus most mammals with slower life histories also have larger body sizes (Purvis & Harvey, 1995). Larger mothers have greater resources for offspring production and great ape mothers translate this energy into larger, more expensive babies than is the case for other primates (Stearns, 1992; Hawkes, 2006b).

Gestation length

Larger primate mothers have larger babies (Robson et al. 2006). The large size of modern human neonates is achieved through a gestation that is between 10 to 30 days longer than for the other great apes (Haig, 1999; Dufour & Sauther, 2002). While this difference appears slight, modern human newborns spend the weeks prior to parturition accumulating large adipose fat stores (Southgate & Hey, 1976) and it is these fat stores that account for the relatively larger size of modern human neonates. Across mammals neonatal fat stores scale allometrically with body size (Widdowson, 1950). Modern human neonates, however, are over three times fatter than expected for a mammal of their size (Kuzawa, 1998). At birth, 12–15% of modern human neonatal body weight is adipose tissue (Fomon et al. 1982). While there are no data documenting the body fat of non-human great ape infants, the qualitative difference in the amount of body fat between modern humans and the other great apes is apparent. Schultz (1969) 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' (*ibid,* p. 152).

Age at weaning and interbirth intervals

Species with slow life histories generally have relatively later ages at weaning and longer interbirth intervals. Great apes, especially the frugivorous chimpanzees and orangutans, wean their offspring relatively late (around ages 4–5 and 6–8, respectively) and have long interbirth intervals (around 5–6 and 7–9 years, respectively). However, while modern humans have the slowest life history in many respects, we wean our infants comparatively early. Modern human foragers typically wean their infants by 3 years of age and have mean interbirth intervals of around 3.7 years. Like age at first birth, modern human weaning ages are consistent across a broad range of ecologies, so that weaning in modern humans occurs 'between 2–3 years and generally occurs about midway in that range' (Kennedy 2005: p. 7).

Many different ways have been proposed to estimate expected ('natural') weaning age from other modern human life history variables and most predict later weaning ages than have been observed (Sellen, 2001). Harvey & Clutton-Brock (1985) predict an average weaning age of 3.36 years based on a correlation between maternal and infant body size, but Charnov & Berrigan (1993) note that mammalian infants are generally weaned when they achieve one-third of maternal body weight (Lee et al. 1991), which for modern humans occurs around 6.4 years. Smith (1992), following Schultz (1956), found that across a sample of primates weaning age correlated with the eruption of the first permanent molar, an event that occurs around 6 years in modern humans (see Table 4). The observed modern human weaning age of 2–3 years is substantially earlier than these predictions, and this is all the more remarkable because other aspects of our life history have slowed down relative to the ancestral state (Smith & Tompkins, 1995).

Age at last birth and menopause

In mammals, oocytes are produced in the fetal ovaries until the third trimester of gestation when mitosis of germ cells ends. This fixed store of oocytes is subject to a process of continual depletion, or atresia, over the individual's life time (vom Saal et al. 1994; O'Connor et al. 2001; Cohen, 2004). In all higher primates, including modern humans, the cycle of ovulation and menstruation is generated by an endocrinological feedback loop that requires a sufficient store of oocytes (Wood, 1994). When insufficient oocytes remain to stimulate ovulation (estimated at around 1000 follicles, Richerson et al. 1987) cycling ceases. All menstruating primates can potentially experience the senescent cessation of menses, or menopause, if they live long enough. However, in non-human species reproductive senescence usually corresponds with somatic senescence and few species live beyond the depletion of their oocyte store.

Menopause has been well documented in captive populations of macaques (e.g. *Macaca fuscata*, Nozaki et al. 1995; *Macaca mulatta*, Walker 1995; *Macaca nemestrina,* Short et al. 1989) where individuals with senescent impairments live longer than they can in the wild. Data on reproductive senescence in great apes are scant, but histological examination of captive chimpanzee ovaries suggests that the process of oocyte reduction is similar to that in modern humans (Gould et al. 1981). The few captive chimpanzee females that have survived to menopause exhibited the same pattern of declining fecundity and variable cycling experienced by women (Tutin & McGinnis, 1981) and they did so around the same age (Gould et al. 1981). Counts of primordial oocytes for a sample of chimpanzees from 3 months to 47 years show the same exponential rate of decline as the rate documented in modern humans (Jones et al. 2007).

Several years prior to menopause in modern human women, the hypothalamic-pituitary-ovarian (HPO) axis begins to break down due to the number of oocytes falling below the level necessary for ovarian steroid production. During this period of 'perimenopause', cycle lengths become long and irregular, and many are anovulatory. The age at menopause, the permanent cessation of menstruation, is assessed retrospectively, after 1 year of no menstrual bleeding. Inconsistent functioning of the HPO axis and the increase in pregnancy failure during perimenopause results in a steep decline in the fertility of modern human females (Holman & Wood, 2001). Though age at menopause varies, Treloar (1981) found in his classic prospective study an average age of 50–51 for the complete cessation of menses. In non-contracepting modern human populations the average age at last birth precedes the average age at menopause by about 10 years (Gosden, 1985) and this pattern is similar globally. 'With few exceptions the means [of age at last birth] fall in the 39–41-year range even when subpopulations with different ages at marriage, occupations of husbands, and numbers of infant deaths are considered' (Bongaarts & Potter, 1983: p. 43).

There are few data documenting the pattern of age-specific fertility decline in non-human great apes, but the data available for chimpanzees suggest that fertility is close to zero at 45 years of age (Nishida et al. 1990; Boesch & Boesch-Achermann, 2000; Sugiyama, 2004; Emery

Thompson et al. 2007), much as it is in modern humans (Howell, 1979; Hill & 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 in modern humans (see Wich et al. 2004 on orangutans). This similarity suggests that all higher primates share the ancestral pattern of ovarian ontogeny. What is derived in modern humans is not an unusual rate, and thus an unusual timing, of reproductive decline, but a slowed rate of somatic aging, distinctively low adult mortality, and, in females, a vigorous post-menopausal life.

Life history-related variables

Many characteristics of growth and development that depend on life history are not life history traits themselves. The first-order life history variables (LHVs) described above – maximum potential life span (or average adult life span), age at first birth, gestation length, interbirth intervals and age at weaning, and age at last birth – directly summarize rates of survival and reproduction across the life span. In this section we discuss three attributes that are strongly linked with life history – body mass, brain size, and the timing and sequence of tooth formation and eruption – and evaluate how well these variables correspond with the timing of major life history events in the extant higher primates. These life history-related variables (LHRVs) are particularly relevant to palaeoanthropology because, unlike first-order life history variables, they are attributes whose values can potentially be derived from hominin fossil evidence.

Body mass

Body size plays an important role in mammalian life histories (Charnov, 1993, see Hawkes, 2006a for discussion of Charnov's model) and is positively correlated with many life history variables across a range of mammalian taxa (Harvey & Read, 1988). Specifically, there is a strong correlation across subfamilies of primates between body size and LHVs such as gestation length, weaning age, age at first reproduction, interbirth interval and maximum life span (Harvey & Clutton-Brock, 1985).

Great apes are the longest-lived and latest maturing as well as the largest of all primates. Chimpanzees, bonobos, orangutans, and modern humans all have late ages at first birth, and this allows energy to be invested in growth over a longer juvenile period and thus most mammals with slower life histories are also large (Purvis & Harvey, 1995). As previously discussed, gorillas are unusual in that they grow faster than the other great apes, including modern humans, and thus they achieve a larger adult size. The remaining great ape species share a similar growth rate (Table 2) and, as expected, achieve body sizes that generally vary with the duration of growth before maturity (Blurton Jones, 2006). Chimpanzees, bonobos, and orangutans bear their first offspring between 13 and 16 years of age, and they have similar body weights around 35 kg. Modern human females have a later average age at first birth (19.5), and grow 4–6 years longer than either *Pan* or *Pongo*. As a result, modern human females in extant foraging societies are about 10–15 kg larger than chimpanzee, bonobo, or orangutan females. Modern human foragers are generally smaller than body sizes estimated for pre-Mesolithic people (Jenike 2001; Ruff et al. 1997). Ethnographic hunter-gatherer means may therefore underestimate the average maternal size differences between humans and the hypothetical common ancestor of the *Pan-Homo* and hominin clades.

Brain growth trajectories and adult brain size

Encephalization is often linked to the slow pace of modern human life history because adult brain size has been shown to be correlated with many life history variables (Sacher, 1975; Harvey & Clutton Brock, 1985; Deaner et al. 2003). Having a larger than expected adult brain size for a given body size can be achieved either by extending the period of brain growth, increasing the rate of brain growth, or both (see Vinicius 2005 for review). Because most relatively large-brained mammals also have slow life histories, and because large brain size is strongly correlated with many life history events, most researchers assume that brain size and the pace of life history are physiologically linked and that encephalization causes a slowdown in life history. The idea that large brain size slows life history implies that subadulthood is extended because it takes a longer time to grow a larger brain (Kaplan et al. 2000). However, few studies have systematically examined the rate and timing of brain growth between modern humans and the other great apes to test this assumption.

There are few published datasets of brain sizes for modern human individuals of known ages. Most authors summarize their original data in figures and report parameters instead of original values, making intraspecies comparisons difficult (Jolicoeur et al. 1988; Cabana et al. 1993). Of the complete datasets published, most are derived from autopsy and necropsy records. Because these samples are made up of individuals with various pathologies it is more than likely that they do not represent the 'normal' population. These are cross-sectional data, not longitudinal, repeated measurements on the same individual, but these data currently provide the only opportunity to quantify brain growth and development in modern humans.

We used Marchand's (1902) dataset that reports brain weight (wet, including meninges, in grams), stature (in centimeters), sex, and known or estimated chronological age, assembled from German autopsy records documented between 1885 and 1900. The original data include a total of 716 modern human males and 452 females from birth to over 80 years old and the variation in brain size with

Table 3 Comparison modern human and chimpanzee absolute and relative brain size

	Average neonatal brain size (g)*	Average adult brain size(g)†	% adult brain size at birth	Age 90% of adult brain size attained	Age at sexual maturity (years)	Years from adult brain size to maturity (years)	% subadult pd left after reaching adult brain size
Modern human‡	364	1352	27%	5	19.5	14.5	74%
Chimpanzee§	137	384	36%	4	13.3	9.3	70%

*Neonate defined as individuals from birth to 10 days old.

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

‡Modern human brain data from Marchand (1902).

§Chimpanzee brain weight data from Herndon et al. (1999).

Table 4 Eruption and crown formation schedules for permanent teeth of extant great ape species

	I^1	I_1	I^2	I_2	M^1	M_1	M^3	M_3
(A) Chronological age at crown completion (years)								
Orangutan (*Pongo* sp.)					2.9–3.1‡	2.81§		
Gorilla (*Gorilla* sp.)				2.7§	2.9§			
Chimpanzee (*P. troglodytes*)	4.0*	4.5–5.4*	4.5*	5.0–5.2*	2.1–2.3¶	1.69–3.05¶		6.9–8.0¶
Modern human (*H. sapiens*)†	4.2–5.0	3.4–3.8	4.8–5.1	3.8–4.2	3.0	3.1–3.3	9.3–9.4	11.2–11.3

	M^1	Age at weaning	M^3	Age at first birth
(B) Chronological age at molar eruption and corresponding life history event (years)				
Orangutan (*Pongo* sp.)	~3.5–4.9**	7.0	~10**	15.6
Gorilla (*Gorilla* sp.)	3.0–4.0**	4.1	8.7–13.1**	10
Chimpanzee (*P. troglodytes*)	2.66–4.08††	4.5	8–14††	13.3
Modern human (*H. sapiens*)	5.84 (4.74–7.0)‡‡	2.8	19.8–20.4**	19.5

*Reid et al. (1998).

†Reid & Dean (2006). Initiation ages: UI1 = 128 days, UI2 = 383 days, LI1 = 90 days, LI2 = 146 days, M1 = birth, M3 = 8 years old.

‡Macho (2001); Kelley & Schwartz (2005).

§Macho (2001).

¶Smith et al. (2007c): Ranges reported from radiographic and histological studies of wild-born, captive-born, and unknown provanence samples. M1 initiation age = 1–2 months prior to birth.

**Smith et al. (1994); Kelley & Schwartz (2005).

††Smith et al. (2007b; consensus range from Table 11).

‡‡Liversidge (2003): mean (range) of 56 world-wide modern human populations.

age and sex compares favorably with other reports (Dekaban & Sadowsky, 1978; Kretschmann et al. 1979), indicating that Marchand's series can serve as a representative sample. Brain weights for chimpanzees (*Pan troglodytes*) of known ages were drawn from necropsy data reported by Herndon et al. (1999). Brain weights were obtained fresh, from 76 captive individuals (33 females and 43 males) at Yerkes Regional Primate Center who died from natural causes or were euthanized when natural death was imminent.

Using these two datasets, shown in Fig. 2 and summarized in Table 3, we examined how well the timing of brain growth and development corresponds proportionately with life history events. More specifically, we investigated whether a longer period of postnatal brain growth is associated with a longer subadulthood, whether a longer period of postnatal brain growth is associated with a smaller portion of adult brain size at birth, and whether a longer subadult period is commensurate with a slower rate of brain growth. We find that none of these predictions are supported. Firstly, although modern human subadulthood is over 6 years longer than that of chimpanzees (19.5 vs. 13.3 years), only one additional year is spent growing a larger brain. The outlined portion of the shaded bands in Fig. 2a highlights the length of brain growth during subadulthood and shows that, compared to modern humans, chimpanzees devote a relatively longer period of their subadulthood to brain growth. Modern humans

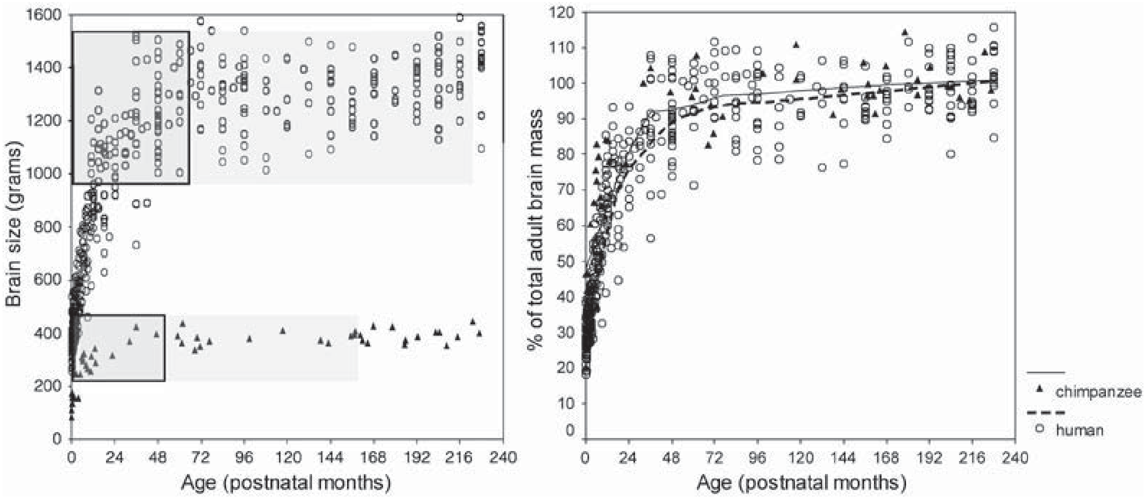

Fig. 2 Comparison of modern human and chimpanzee absolute (panel A) and relative (panel B) brain growth trajectories. Black triangles are chimpanzees (Herndon et al. 1999; $n = 26$; males = 16, females = 10); open circles are modern humans (Marchand, 1902; $n = 160$; males = 111, females = 49). Shaded bands in panel A represent the period of subadulthood with the duration of brain growth outlined and darkened.

reach adult brain size much earlier than widely claimed, some as early as 3 years of age. Kretschmann et al. (1979) used the Marchand (1902) data to show that on average modern human males achieve 95% of total brain size by 3.82 years old and females by 3.44 years old. On average, modern humans in this dataset achieve 90% of adult brain size by 5 years old, only 1 year later than the chimpanzee average (around 4 years) and much earlier than widely assumed for our long subadulthoods and slower life history.

Second, chimpanzee and modern human infants are more similar in the percentage of adult brain size achieved at birth than previously assumed. It has conventionally been reported (e.g. Dienske, 1986) that modern human neonatal brain weight is only 25% of adult size at birth, whereas chimpanzee neonates have achieved 50% of their adult brain weight at birth. But this estimate of relative chimpanzee neonatal brain size is based on the estimated cranial capacity of a single specimen (Schultz, 1941). A recent re-examination of that specimen has revealed that it was not a neonate, but was 74 days old at death (Vinicius, 2005). When plotted against the Herndon et al. (1999) values, this specimen falls in the scatter where it should be given an age of 2.5 months (Robson et al. 2006). Thus, the interspecific difference in relative brain size at birth is reduced from 25% to only 10% (see Table 3). Additional data may shrink the difference even further, weakening any remaining association between relative neonatal brain size and the length of subadulthood.

Third, chimpanzees and modern humans share a similar pattern of relative brain growth trajectories (Fig. 2b). The large brain size of modern human adults is primarily achieved by a faster rate, and not by a longer relative duration, of post-natal brain growth. Leigh (2004) conducted similar analyses using the same data and concluded that ‘after the first 18 months of life, *Pan* and *Homo* are not substantially different in terms of growth rates’ (p. 152).

These similarities between chimpanzees and modern humans do not support the view that our juvenility is longer because of the growth requirements of our large brains. Whereas adult brain size is strongly correlated with the length of subadulthood (Leigh, 2004), age at brain growth cessation is not. These data show that encephalization in primates is achieved through an increased velocity, not longer relative duration, of brain growth and challenge the widely held assumption that the length of brain growth is linked to, and sets the pace of, life history. Rather, external adult mortality and demographic profiles probably determine the pace of mammalian life history schedules and patterns of growth and development adjust to these life history constraints (Dean, 2006). From this perspective, slower life history provides an opportunity for shifts in the rate and timing of brain growth.

This analysis is important because recent studies have drawn conclusions about the developmental patterns and cognitive abilities of fossil hominins based on comparison of modern human and chimpanzee brain growth trajectories (Coqueugniot et al. 2004; Alemseged et al. 2006). We and others (Leigh, 2004; Vinicius, 2005) show that there is substantial overlap in brain growth trajectories between modern humans and chimpanzees, thus undercutting the usual basis for inferences about cognition and development.

Dental development

Any consistent relationships between dental growth and development and life history would provide a means for making direct interpretations of maturation schedules within the hominin clade. Teeth are less sensitive to developmental insults and short-term ecological fluctuations than other tissues (Nissen & Riessen, 1964; Garn et al. 1973; Liversidge, 2003), thus making them relatively reliable maturation indicators. We evaluate two forms of dental data. Firstly, we examine the potential of dental microstructure, the rate and pattern of crown and root formation, as a means of comparing life histories. Second, we evaluate the information available about the timing and sequence of tooth eruption into the jaws in the same light. Because the timing and pattern of overall dental development are considered proxies for somatic growth, and this is constrained by life history, it should in theory be possible to make inferences about shared or distinct life history patterns from these data.

Crown and root formation times. Enamel and dentin formation are especially promising lines of evidence for linking dental development with absolute calendar time (Moorrees et al. 1963; Bromage & Dean, 1985; Beynon & Dean, 1987). Because the rhythms of the incremental growth of the dental hard tissues are regular, it is possible to use those cycles of cellular activity as clocks to time the onset, duration and offset of the cellular activity responsible for the deposition of dental hard tissues (Dean, 1987; Macho & Wood, 1995b; Schwartz & Dean, 2000; Wood, 2000; and Dean, 2006 all provide reviews of the cellular basis of dental ontogeny). Specifically, the crystalline matrix secreted by enamel-forming cells (ameloblasts) and dentin-forming cells (odontoblasts) shows two discrete periodicities, a 'short period' (c. 24 h) and a 'long period' (c. 6–9 days). In enamel these physical manifestations are called 'cross-striations' and the 'brown striae of Retzius', respectively (Schwartz & Dean, 2000.) Their equivalents in dentin are 'von Ebner's' and 'Andresen's lines', respectively (Dean, 1995b, 1998; Fitzgerald, 1998; Dean, 2000).

Macho (2001) found that crown formation is broadly correlated with life history across the anthropoid primates. However, several studies have found similarities between the molar formation times of modern humans and chimpanzees (Reid et al. 1998; Smith et al. 2007a), and preliminary data suggest that this is also true for bonobos (Ramirez-Rozzi & Lacruz, 2007). We show, below, that the broader correlation of crown formation variables with life history does not operate within the narrower confines of the extant great apes.

Comparison of crown formation rates in the extant higher primates (Table 4a) shows a poor correspondence between dental microstructure and life history variables, such as age at weaning and age at first birth. Whereas the timing of life history events among the great apes fall along a continuum, crown formation times for these species are quite similar, and thus fail to track weaning ages or age at maturity. There is 'considerable overlap among great apes and humans' in the formation rates of both incisors and molars (Macho & Wood, 1995b: p. 23). These 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 weaning (Macho, 2001), or to age at first birth (Ramirez-Rozzi & Bermudez de Castro, 2004).

Timing of tooth formation and eruption. Schultz's much reproduced graph depicting differences in the timing of life stages across primates (e.g. 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. Schultz (1949) also observed differences in the sequence of tooth eruption across primates. In species that are weaned relatively early, molars erupt before the deciduous teeth are lost and prior to the emergence of the anterior permanent dentition. Schultz suggested that permanent molars erupted first so that infants would be prepared to masticate food when weaned, a generalization that Smith (2000) has called 'Schultz's rule'. Slower developing modern humans show a distinctive eruption sequence, with the permanent anterior dentition emerging before the molars. In the non-human great apes the first molar is the first permanent tooth to erupt, followed by the incisors and premolars, the second molar, and then the canine. In modern humans the first molar and first incisor erupt close together, followed by the second incisor, with the canine, premolars and second molar subsequently erupting close together (Mann et al. 1990; Conroy & Vannier, 1991a).

Dean & Wood (1981) published a provisional chart comparing modern human, chimpanzee and gorilla tooth crown and root development, and with subsequent important modifications by Anemone, Conroy and Kuykendall (summarized in Kuykendall, 2002) the chart is still used today. However, the proximate cause of these differences in eruption sequence has more to do with the roots than with the crowns. For example, one of the main differences between the dental development of modern humans and chimpanzees and gorillas, the late eruption of the first molar in the former, is caused by a temporal retardation in the final stages of root formation so that first molar eruption in modern humans occurs long after the crown and most of the root are formed (Dean, 1995a; Macho & Wood, 1995b).

Schultz speculated that the shift in eruption sequence seen in modern humans is directly connected to our slower life history and in particular to our much longer period of juvenility. Building on Schultz's recognition of a connection between dental development and life history, Smith (1989) showed that across the primates there is a correlation between the eruption of the first permanent molar (M1) and weaning age, and between the eruption of the third molar (M3) and age at first birth. However, a narrower (*sensu* Smith (1989) re. allometry) examination of just the great apes (Table 4b) shows that the patterns of dental maturation and eruption do not always correspond with one another, nor with the pace of life histories among these species. A comparison of age at weaning with M1 eruption and age at first birth with M3 eruption in Table 4b illustrates this lack of correspondence. The eruption of M1 *precedes* weaning age in gorillas and chimpanzees for a period that varies from several months to more than 1 year and in modern humans by more than 3 years. In orang-utans, M1 eruption *lags behind* weaning by 3 years. The age of M3 eruption is later in modern humans, but M3s do not erupt later in the later-breeding chimps and orangutans compared to gorillas. The eruption of M3 inaccurately estimates age at first birth in all the non-human great ape species by one to 5.5 years. For example, the M3 erupts at around 11 years in gorillas and chimpanzees and 10 years in orangutans, while age at first birth occurs around 10, 13.3, and 15.6 years, respectively, in these animals. These data show that among the living great apes differences in life history are not necessarily reflected in their molar eruption schedules.

The timing of tooth eruption, crown maturation, and other aspects of dental development (Godfrey et al. 2003) varies among great ape species. While 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, 2006a), but the demographic constraints on growth and development are indirect. Life histories may change without concomitant shifts in all aspects of growth and development, and conversely selection might favor ontogenetic adjustments that are adaptations to particular problems faced by infants and juveniles in each species (Godfrey et al. 2003).

Summary

There is a distinction between first order life history variables such as age at weaning, age at sexual maturity, and life span, and second order life history variables such as body mass, brain size, and dental development. The latter, which we refer to as life history-related variables (LHRVs), are not life history variables as such, but are either linked with, or can be used to make inferences about life history variables. Life history variables can only be recorded from observations of individual living animals, which can then be pooled to generate species parameters. To the extent that LHRVs correspond with LHVs, they offer an opportunity to estimate life history parameters for fossil taxa.

A general feature of living great apes is a slow life history, so we infer this was also true of both the hypothetical *Pan-Homo* LCA and the stem hominin. Within the great apes, there is a distinct species order in the pace of life history. Modern humans have the slowest life history, followed by orangutans, chimpanzees and bonobos, and gorillas. Compared to chimpanzees (see Table 2), modern humans live at least 25 years longer and become sexually mature more than 6 years later. Late age at maturity results in larger mothers who then bear absolutely and relatively larger, fatter babies. These characteristics point to a lowering in adult mortality rates in the *Homo* lineage since the *Pan-Homo* split. The age at which female fertility declines to menopause appears to be the same in women as in the other extant apes, indicating that this trait has been conserved. However, modern humans have the shortest interbirth intervals and experience an earlier age at weaning than expected for an ape of our age at maturity. The distinctively fast rate of modern human reproduction results in 'stacking' weaned but nutritionally dependent offspring. This unique pattern is likely a derived feature of our genus and could only have evolved if mothers had a reliable source of help with food acquisition for provisioning dependent youngsters. Vigorous, postmenopausal grandmothers and adolescents, without infant dependants of their own, are unique age stages of modern human life history, and likely provided that help (Robson et al. 2006).

Constructing life histories for extinct hominin species is problematic because it depends on the extent to which LHRVs are correlated with life history. We evaluated three LHRVs, body mass, brain growth and dental development, and found that many aspects of these variables correspond imperfectly with a species life history. Previous research has shown that aspects of life history strongly correlate with these LHRVs across broad primate taxonomic groups. Our evaluation shows that these correlations do not hold within the narrow range of taxa we examine here. Many aspects in the timing of growth and development do not accurately correspond with the timing of life history in the higher primate clade.

Of the three LHRVs we examined, body mass is the best predictor of great ape life history events. While adult brain size has been found to strongly predict aspects of life history (Deaner et al. 2003), we show that the timing of brain growth is a less effective measure because it does not match up with the length of subadulthood between modern humans or chimpanzees. Both species complete brain growth between 4–5 years old and, despite their significantly larger adult brain sizes, modern humans spend relatively less time during subadulthood growing a large brain. Similarly, dental development and eruption is also a weakly related proxy for the timing of life history events and inferences about the latter from tooth formation and eruption times should be made with caution.

Part II. Inferring the life history of extinct hominin taxa

Organizing the hominin fossil record

The classification of the hominin fossil evidence is controversial, nonetheless a sound taxonomy is a prerequisite for any paleobiological investigation, including one that addresses the evolution of modern human life history. This is because the allocation of individual fossils to each hominin taxon determines the inferences drawn about the life history of that taxon. There is lively debate about how to define living species (for a discussion see Wood & Lonergan 2008), so we should not be surprised that there is a spectrum of opinion about how the species category should be applied to fossil evidence.

One of the many factors that paleoanthropologists must take into account is that the fossil record they have to work with is confined to the remains of hard tissues (bones and teeth). We know from living animals that many uncontested species (for example, *Cercopithecus* species) are difficult to distinguish using bones and teeth, thus there are logical reasons to suspect that a hard tissue-bound fossil record is always likely to underestimate the number of species. This has recently been referred to as 'Tattersall's Rule' (Antón, 2003). When discontinuities are stressed (as in so-called 'taxic' interpretations), and if a punctuated equilibrium model of evolution is adopted along with a branching, or cladogenetic, interpretation of the fossil record, then researchers will tend to split the hominin fossil record into a larger rather than a smaller number of species. This should be the preferred approach for life history studies for the results will be less prone to producing 'chimeric' life histories (Smith et al. 1994). Conversely, other researchers emphasize morphological continuity instead of morphological discontinuity, and see species as longer-lived and more prone to substantial changes in morphology through time. When this philosophy is combined with a more gradualistic or anagenetic interpretation of evolution, researchers tend to resolve the hominin fossil record into fewer, more inclusive, species. This will also be the case if researchers think in terms of allotaxa (e.g. Jolly, 2001; Antón, 2003) and allow a single species to manifest substantial regional and temporal variation.

For the reasons given above the taxonomic hypothesis we favor is the relatively speciose taxonomy in Table 5A, but in Table 5B we also provide an example of how inferences about life history would map onto the less speciose taxonomy (both taxonomies are set out in Wood & Lonergan 2008). While some researchers might contest the specific details of each of these taxonomies, we offer them as a pragmatic way to address whether and how differences in taxonomic hypotheses affect the way we interpret the evolution of modern human life history. Further details about most of the taxa and a more extensive bibliography can be found in Wood & Richmond (2000), and more recent reviews of many of these taxa can be found in Hartwig (2002), Wood & Constantino (2004) and Henry & Wood (2007).

We use the same six informal grade-based groupings (Table 5; Fig. 3) of hominin taxa that are used by Wood &

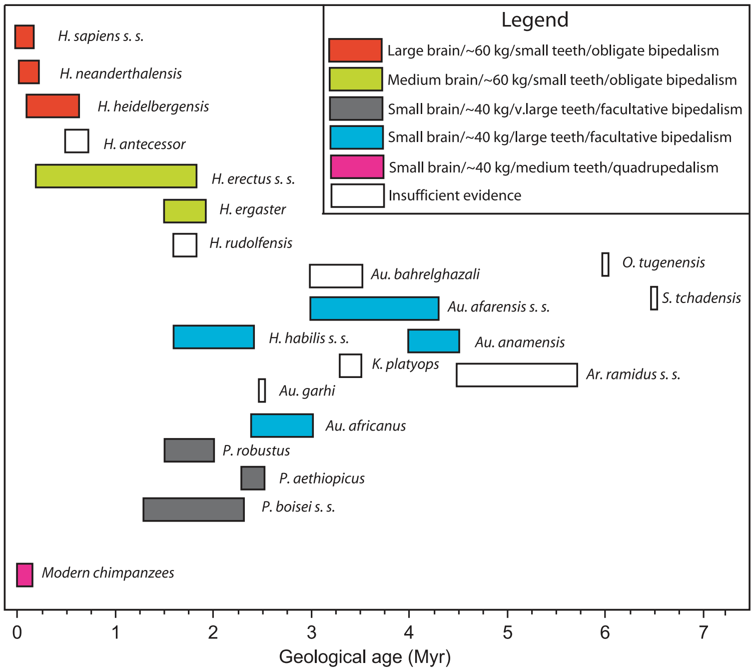

Fig. 3 The more speciose (splitting) taxonomy. Informal groupings are based on brain size, body mass, postcanine tooth-size estimates, and locomotor mode. No ancestor-descendant relationships are implied among taxa.

Table 5 (A) Splitting and (B) lumping hominin taxonomies and skeletal representation***** within the taxa in the more speciose taxonomic scheme

(A) Splitting taxonomy

Informal group	Taxa	Age (Ma)	Type specimen	Crania	Dentition	Axial	Upper limb	Lower Limb
Possible and probable primitive hominins	*S. tchadensis*	7.0–6.0	TM 266-01-060-1	X	X			
	Orronin tugenensis	6.0	BAR 1000′00		X		X	X
	Ar. ramidus s. s.†	5.7–4.5	ARA-VP-6/1	X	X		X	ff
Archaic hominins	*Australopithecus anamensis*	4.2–3.9	KNM-KP 29281	ff	X		X	X
	Australopithecus afarensis s. s.	4.0–3.0	LH4	X	X	X	X	X
	Kenyanthropus platyops	3.5–3.3	KNM-WT 40000	X	X			
	Australopithecus bahrelghazali	3.5–3.0	KT 12/H1		X			
	Au. africanus	3.0–2.4	Taung 1	X	X	ff	X	X
Megadont archaic hominins	*Au. garhi*	2.5	BOU-VP-12/130	X	X		?	?
	P. aethiopicus	2.5–2.3	Omo 18.18	X	X			
	P. boisei s. s.	2.3–1.3	OH 5	X	X		?	?
	P. robustus	2.0–1.5	TM1517	X	X		X	X
Transitional hominins	*H. habilis s. s.*	2.4–1.6	OH 7	X	X	X	X	X
	H. rudolfensis	2.4–1.6	KNM-ER 1470	X	X			?
Pre-modern *Homo*	*H. ergaster*	1.9–1.5	KNM-ER 992	X	X	X	X	X
	H. erectus s. s.	1.8–0.2	Trinil 2	X	X		X	X
	H. floresiensis‡	0.074–0.012	LB1	X	X	ff	X	X
	H. antecessor	0.7–0.5	ATD6-5	X	X			
	H. heidelbergensis	0.6–0.1	Mauer 1	X	X		ff	X
	H. neanderthalensis	0.2–0.03	Neanderthal 1	X	X	X	X	X
Anatomically modern humans	*H. sapiens s. s.*	0.19-present	None designated	X	X	X	X	X

(B) Lumping taxonomy

Informal group	Taxa	Age (Ma)	Taxa subsumed from the splitting taxonomy
Possible and probable primitive hominins	*Ar. ramidus s. l.*	7.0–4.5	*S. tchadensis, O. tugenensis, Ar. ramidus s. s.*†
Archaic hominins	*Au. afarensis s. l.*	4.2–3.0	*Au. anamensis, Au. afarensis s. s., Au. bahrelghazali, K. platyops*
	Au. africanus	3.0–2.4	*Au. africanus*
Megadont archaic hominins	*P. boisei s. l.*	2.5–1.3	*Au. garhi, P. aethiopicus, P. boisei s. s.*
	P. robustus	2.0–1.5	*P. robustus*
Transitional hominins	*H. habilis s. l.*	2.4–1.6	*H. habilis s. s., H. rudolfensis*
Pre-modern *Homo*	*H. erectus s. l.*	1.9–0.018	*H. erectus s. s., H. ergaster, H. floresiensis*
Anatomically-modern humans	*H. sapiens s. l.*	0.7-present	*H. antecessor, H. heidelbergensis, H. neanderthalensis, H. sapiens s. s.*

*Skeletal representation key: X = present, ff = fragmentary specimens, ? = taxonomic affiliation of fossil specimen(s) uncertain.

†Recently, some specimens included in the *Ar. ramidus s. s.* have been raised to a separate species, *Ar. kadabba* (Haile-Selassie et al. (2004); however, this taxonomic distinction has not been incorporated into our analyses.

‡Given the recent and limited publication of this taxon and its current interpretation as an isolated endemic dwarf descendent of *H. erectus s. s.*, *H. floresiensis* is not included in our comparisons or analyses of life history patterns in fossil hominins.

Lonergan (2008). The first group, possible and probable primitive hominins, comprises Late Miocene/Early Pliocene taxa that are temporally relatively close to the estimated 5–8 Ma split between hominins and panins (taxa more closely related to modern chimpanzees than to modern humans). In the early stages of hominin evolution it may be either the lack of panin synapomorphies, or relatively subtle derived differences in the size and shape of the canines, the detailed morphology of the limbs or some unique combination of such traits, which mark out the creatures that are more closely related to modern humans than they are to chimpanzees and bonobos. This group contains a mix of taxa, some of which may belong in the hominin clade, and others of which may belong to clades that have no living representatives. The second grade grouping, archaic hominins, includes Pliocene taxa from East and southern Africa that exhibit morphology consistent with facultative bipedalism, but cranially these taxa are broadly similar to chimpanzees with regards to brain and body size. The third group, megadont archaic hominins, includes Plio-Pleistocene taxa from southern and East Africa. This group includes taxa many researchers include in the genus *Paranthropus*, and the distinctive cranial and dental morphology of *Paranthropus* includes large and robust mandibular bodies and extremely large postcanine teeth. Few, if any, postcranial fossils are unambiguously linked with any of the three taxa concerned. The fourth group, transitional hominins, includes Late Pliocene/Early Pleistocene taxa from East and southern Africa, which exhibit morphology consistent with facultative bipedalism, and some individuals in this grade have a slightly larger brain and postcanine teeth that are absolutely smaller than those of archaic hominin taxa. We place the two taxa concerned, *Homo habilis sensu stricto* and *Homo rudolfensis* in their own grade to recognize the ongoing debate about whether they should be included in the genus *Homo* (see Wood & Collard, 1999b). The fifth grade grouping, pre-modern *Homo*, includes Pleistocene taxa present in Africa and Asia, which possess morphology that is consistent with obligate bipedalism, brains that range from medium to large, and small postcanine teeth. This is the grade to which we allocate the recently reported taxon *Homo floresiensis* from the island of Flores, Indonesia (Brown et al. 2004; Morwood et al. 2004). This species appears to represent a late surviving hominin descendant; however, given its unique morphology and probable life history within the hominin clade it is not included in comparisons among hominin taxa. The final, sixth grade grouping, referred to as anatomically modern *Homo*, includes specimens located across the globe which exhibit morphology that is similar to, if not identical with, that of modern *Homo sapiens* (the only extant hominin taxon).

Readers should be aware of two caveats with respect to the speciose taxonomy illustrated in Fig. 3. First, the age of the first and last appearances of any taxon in the fossil record (called the ‘first appearance datum’, or FAD, and ‘last appearance datum’, or LAD, respectively) almost certainly underestimates the temporal range of each taxon. It is very unlikely that we have a complete record of hominin taxonomic diversity, particularly in the pre-4 Ma phase of hominin evolution. This is because intensive explorations of sediments of this age have only been conducted for less than a decade, and because these investigations have been restricted in their geographical scope. Thus, the dataset we are working with in the early phase of hominin evolution is almost certainly incomplete. We should bear this in mind when formulating and testing hypotheses about any aspect of hominin evolution, including the evolution of modern human life history. Nonetheless, FADs and LADs provide an approximate temporal sequence for the hominin taxa. Second, we made a deliberate decision not to use lines to connect the taxa in Fig. 3. This reflects our view that within the constraints of existing knowledge there are only two relatively well-supported subclades within the hominin clade, one for *Paranthropus* taxa and the other for post-*Homo ergaster* pre-modern *Homo* taxa. Without well-supported subclades in the early part of the hominin fossil record it is probably unwise to begin to try to identify specific taxa as ancestors or descendants of other taxa.

Body mass

How reliably can we estimate body mass using skeletal fragments sampled from extinct taxa? Did increases in hominin body mass occur gradually within the history of species, or did it increase relatively quickly with the appearance of new species? When in hominin evolution did body mass reach the levels we see in contemporary and subrecent modern humans?

The most reliable estimates of body mass are made when the skeletal fragment is known to belong to a group for which regressions can be determined using actual body masses and skeletal measurements. This is clearly not the case for fossil hominins, for the regressions used have to be generated using data from extant, more or less, closely related groups such as the hominids, hominoids, anthropoids or simians (e.g. Aiello & Wood, 1994). In addition to this potential source of error, Richard Smith (1996) has cautioned that because paleontologists have to rely on proxies for body mass in fossil-only taxa this inevitably introduces additional error into attempts to estimate the body mass of fossil hominin taxa.

Traditionally, the most reliable body mass estimates for living taxa have come from the postcranial skeleton. But, reliably associated postcranial remains are rare in most of the hominin fossil record, and some early hominin taxon hypodigms (e.g. *Paranthropus boisei*) include little, or no, postcranial evidence. This has led to attempts to use cranial variables as proxies for body mass (e.g. Aiello & Wood, 1994; Kappelman, 1996; Spocter & Manger, 2007). We have compiled body mass estimates from the literature using both postcranial and cranial methods for taxa in the splitting and lumping hominin taxonomies (Table 6B,C). The published body mass estimates for *H. rudolfensis* used in Table 6 are more speculative than most because they are based on postcranial fossils whose links to *H. rudolfensis* are tentative and questionable. However, when Aiello & Wood (1994) used orbit dimensions to predict body mass directly from the KNM-ER 1470 cranium (the lectotype of *H. rudolfensis*), the 95% CIs (confidence intervals) they derived for its body mass (c. 43–67 kg) (Aiello & Wood, 1994, Table 8: p. 421) are very similar to the species 95% CIs given in Table 6.

The 95% CIs around the means show that the body mass estimates vary greatly in their reliability, and there are (as one would expect) differences in the parameters of those

Table 6 Body mass estimates for extant great ape species, modern humans and the hominin taxa as defined in the splitting and lumping hominin taxonomies

	Species adult average					
	Mean (kg)	95% CI†	Male mean (kg)	Female mean (kg)	Sexual dimorphism‡	Method§
A) Extant apes						
Orangutans (*Pongo* sp.)	64		80	38	2.12	A
Gorillas (*Gorilla* sp.)	128		160	95	1.68	A
Bonobos (*P. paniscus*)	39		45	33	1.35	A
Chimpanzees (*P. troglodytes*)	41		46	35	1.31	A
Modern humans (world-wide)	49		53	46	1.16	A
(B) Splitting taxonomy						
S. tchadensis	?	?	?	?		
O. tugenensis	?	?	?	?		
Ar. ramidus s. s.†	40	?	?	?		E
Au. anamensis	42	–72–156	51	33	1.54	B
Au. afarensis s. s.	38	31–45	45	29	1.55	B
K. platyops	?	?	?	?		
Au. bahrelghazali	?	?	?	?		
Au. africanus	34	30–38	41	30	1.36	B
Au. garhi	?	?	?	?		
P. aethiopicus	38	?	38	?		C
P. boisei s. s.	41	–52–134	49	34	1.44	B
P. robustus	36	27–45	40	32	1.25	B
H. habilis s. s.	33	25–41	37	32	1.16	B
H. rudolfensis	55	46–64	60	51	1.18	B
H. ergaster	64	53–76	68	54	1.26	F
H. erectus s. s.	58	50–65	59	57	1.04	D,C,F
H. antecessor	?	?	?	?		
H. heidelbergensis	71	62–80	84	78	1.08	F
H. neanderthalensis	72	69–76	76	65	1.17	F
H. sapiens s. s.	64	63–66	68	57	1.19	F
(C) Lumping taxonomy						
Ar. ramidus s. l.	40	?	?	?		G
Au. afarensis s. l.	39	32–45	46	30	1.53	G
Au. africanus	34	30–38	41	30	1.36	G
P. boisei s. l.	40	21–59	43	34	1.26	G
P. robustus	36	27–45	40	32	1.25	G
H. habilis s. l.	46	34–57	52	41	1.27	G
H. erectus s. l.	61	55–66	65	57	1.14	G
H. sapiens s. l.	66	6–67	70	59	1.19	G

*See Appendix I for the fossil specimens used to estimate body mass for each taxon.

†The 95% confidence intervals are calculated using a quantile from Student's *t* distribution, instead of a quantile of 1.96 from the normal distribution. This gives a more realistic estimate of the confidence interval for a mean derived from a small sample size (e.g. *P. boisei s. s.*).

‡Body-mass sexual dimorphism calculated as the ratio of the estimated male mean and the estimated female mean body mass.

§Method key: A = sex-specific body mass reported for wild (Plavcan & van Schaik, 1997) or ethnographic (Jenike, 2001) populations, B = based on a modern human regression of hindlimb joint size, C = based on a hominiod-derived regression of orbital area, D = based on a hominoid-derived regression of orbital height, E = a comparative estimate of upper limb joint size of *Ar. ramidus* and AL 288-1 (*Au. afarensis*), F = based on regressions of femoral head diameter and/or stature and bi-iliac breadth (see Ruff et al. 1997), and G = body mass estimates for the more inclusive taxa, calculated as the mean value of all specimens from appropriate individual taxa listed in the splitting hominin taxonomy.

taxa that have more inclusive and less inclusive interpretations (for example, *H. habilis sensu lato* and *H. habilis sensu stricto*). However, whether one uses the lumping or the splitting taxonomy, there is apparently a substantial increase in the mean body mass of some hominin taxa with FADs around 2 Ma (Figs 4, 5). Prior to 2 Ma the estimated body mass of each hominin taxon did not appear to differ markedly from each other or from the average body mass of extant chimpanzees (c. 35–45 kg; Table 6A). Exceptions to this pattern are the estimated body masses of *H. rudolfensis* and *H. habilis s. l.* (Taxon F in Fig. 4 and D in Fig. 5), which at 2.4 Ma have estimates of mean body mass

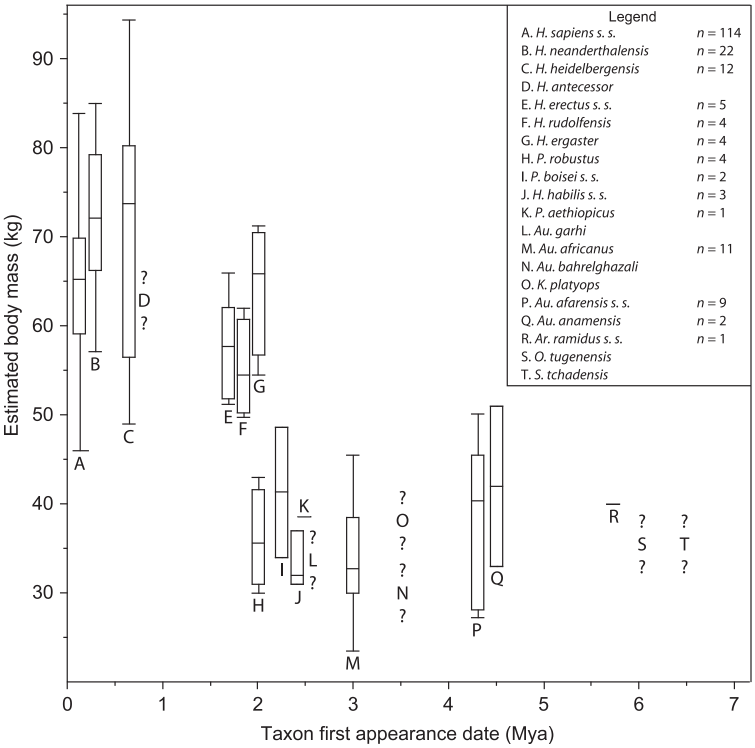

Fig. 4 Estimated body mass plotted against first appearance date for the fossil hominin taxa recognized in the splitting taxonomy. Box and whisker plots show the median, upper, and lower quartiles (box) and the maximum and minimum values (whiskers). The number of individual estimates (n) used for each variable in this comparison is listed in the legend. Taxa represented by a single horizontal line have only a single estimate for this variable. Taxa with no data for this variable appear between question marks; their position along the vertical axis is determined by their informal group membership.

of 55 kg and 46 kg, respectively. It is important to note that in both cases the specimens from which body mass is actually being estimated and which give a reasonably large body mass estimate for *H. rudolfensis* and *H. habilis s. l.*, respectively, date to ~1.8 Ma and not to 2.4 Ma, the first appearance datum for this taxon. This apparent difference in the pattern and timing of body size evolution within hominins is an example of the influence of differing taxonomic hypotheses on the interpretation of life history evolution.

The body mass of a species can increase during hominin evolution because both males and females within a taxon are larger, or because there is a selective increase in female body mass and thus a reduction in body mass sexual dimorphism. Female body mass has long been considered a critical life history-related variable as we noted above, so it is of particular interest to see when in hominin evolution there is evidence of any significant reduction in the relatively high levels of sexual dimorphism seen in Miocene higher primates and in at least some archaic hominin taxa, such as *Australopithecus afarensis* and *P. boisei* (Lockwood et al. 1996; Silverman et al. 2001 – but see Reno et al. 2003 for a different interpretation of the extent of sexual dimorphism in the former).

We calculated sexual dimorphism as the ratio of male to female estimated body mass. In the speciose hominin taxonomy (Table 6B) body mass sexual dimorphism appears to be greater than or equal to that of chimpanzees (~ 1.3, Table 6A) until the appearance of early *Homo*. The less speciose hominin taxonomy (Table 6C) presents a similar pattern, with early archaic hominin taxa (e.g. *Au. afarensis s. l.* and *Australopithecus africanus*) exhibiting higher levels of body mass sexual dimorphism than chimpanzees. *Paranthropus* taxa and *Homo habilis s. l.* exhibit levels of sexual dimorphism that are similar to those of chimpanzees and sexual dimorphism decreases to modern human levels with the appearance of *Homo erectus s. l.* (but see the arguments in Spoor et al. 2007 and Lockwood et al. 2007 for more substantial sexual dimorphism in *H. erectus s. l.* and *Paranthropus robustus*, respectively). Thus, working back from extant *H. sapiens* the pattern of moderate levels of body mass sexual dimorphism seems to be consistent back to, and including, *H. heidelbergensis*, with greater body mass differences between presumed males and presumed females now thought to be more likely in *Homo erectus s. l.* and almost certainly the case in archaic hominins. The larger mean body mass of *H. ergaster,* which is temporally the earliest taxon included in *H. erectus s. l.,* may be because there are no small individuals in the sample that was used to generate that estimate.

Brain mass/endocranial volume

Though measures of brain growth and development do not correspond with the timing of life history events in the

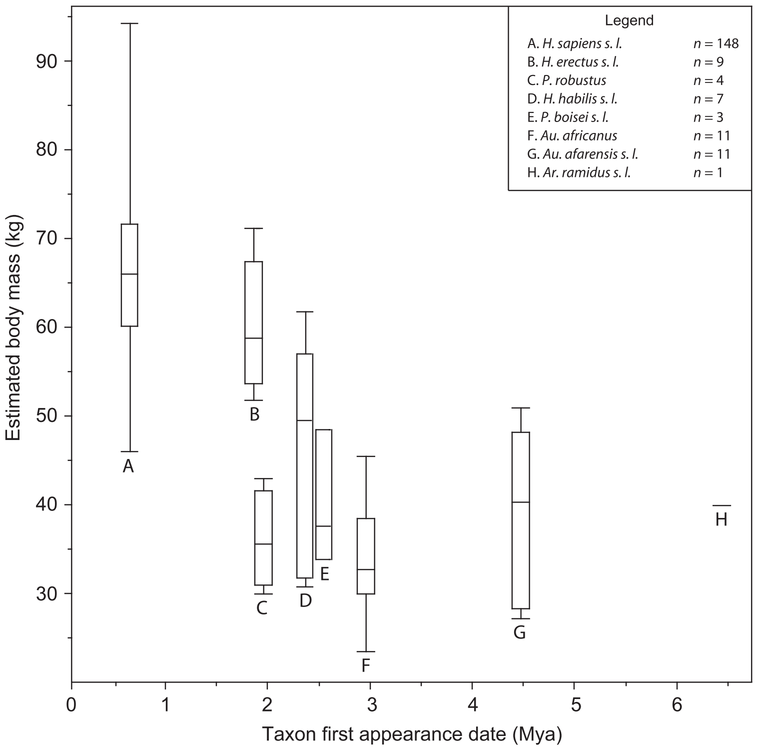

Fig. 5 Estimated body mass plotted against first appearance date for the fossil hominin taxa recognized in the lumping taxonomy. Box and whisker plots show the median, upper, and lower quartiles (box) and the maximum and minimum values (whiskers). The number of individual estimates (n) used for each variable in this comparison is listed in the legend. Taxa represented by a single horizontal line have only a single estimate for this variable. Taxa with no data for this variable appear between question marks; their position along the vertical axis is determined by their informal group membership.

extant great apes, adult brain size has been shown to be strongly correlated with many life history variables (Sacher, 1975; Harvey & Clutton-Brock, 1985; Deaner et al. 2003; and see above). While it is not possible to make direct measurements of brain size using fossil evidence, it is possible, with varying degrees of precision, to measure the volume of the cranial cavity, otherwise known as endocranial volume. Brain mass can be derived from brain volume, and brain volume can be derived from endocranial volume if allowance is made for the space occupied by endocranial vasculature and the intracranial extracerebral cerebrospinal fluid. Few fossil hominin crania are well enough preserved to be able to measure endocranial volume with the precision and accuracy one can achieve using museum specimens of extant taxa. Holloway (1983a) attempted to classify endocranial volumes recorded from fossil hominin crania according to what he considered was the likelihood that the estimated volumes were an accurate reflection of the actual volume, but most published endocranial volumes of fossil hominins lack any assessment of the precision or accuracy of the estimated volumes.

Parameters for the cranial capacity (i.e. endocranial volume) of hominin taxa in the splitting and lumping taxonomies are listed in Table 7 and illustrated in Figs 6 and 7. The confidence intervals (CIs) provided in Table 7 reflect interindividual variation within each taxon, but they take no account of the precision and accuracy of each individual endocranial volume measurement. All archaic hominins have brain sizes that do not differ significantly from *P. troglodytes* (~400 cm^3). The brain sizes of *H. habilis s. s.*, *H. rudolfensis*, *H. habilis s. l.*, *H. ergaster* and *H. erectus s. s.* are intermediate between the values for *P. troglodytes* and *H. sapiens* (Table 7B). The value for *H. erectus s. s.* is the only one in this group that is closer to that for *H. sapiens* than it is to that of *P. troglodytes*. Only *Homo neanderthalensis* and *Homo heidelbergensis* have brain sizes that are indistinguishable from those of *H. sapiens* (Table 7B). Thus, there appears to be a discontinuity between two LHRVs (body mass and brain size) in the timing of the appearance of the modern human expression of those variables.

Dental LHRVs

Crown and root formation times: extinct species

For fossil teeth (which are not naturally fractured or from which thin-sections cannot be made) determining crown formation time involves summing the estimated duration of appositional enamel growth (that is, enamel covering the cusp of a tooth whose long period lines do not reach the surface of the crown) and the duration of imbricational enamel growth (that is, the product of the number of perikymata, defined as striae of Retzius that reach the surface of the enamel in the form of steps that resemble

Table 7 Cranial capacity estimates for the hominin taxa recognized in the splitting and lumping hominin taxonomies*

	Mean cranial capacity (cm^3)	95% CI†	Sample size
(A) Splitting			
S. tchadensis	365	?	1
O. tugenensis	?	?	
Ar. ramidus s. s.†	?	?	
Au. anamensis	?	?	
Au. afarensis s. s.	458	335–580	4
K. platyops	?	?	
Au. bahrelghazali	?	?	
Au. africanus	464	426–502	8
Au. garhi	450	?	1
P. aethiopicus	410	?	1
P. boisei s. s.	481	454–507	10
P. robustus	563	–542–1668	2
H. habilis s. s.	609	544–674	6
H. rudolfensis	726	501–950	3
H. ergaster	764	640–888	6
H. erectus s. s.	1003	956–1051	36
H. antecessor	1000	?	1
H. heidelbergensis	1204	1130–1278	17
H. neanderthalensis	1426	1351–1501	23
H. sapiens s. s.	1478	1444–1512	66
(B) Lumping‡			
Ar. ramidus s. l.	365	?	1
Au. afarensis s. l.	458	335–580	6
Au. africanus	464	426–502	8
P. boisei s. l.	472	447–498	12
P. robustus	563	–542–1668	2
H. habilis s. l.	648	579–716	9
H. erectus s. l.	969	919–1019	42
H. sapiens s. l.	1418	1384–1452	108

*See Appendix I for fossil specimens included in the estimation of cranial capacity for each taxon.

†The 95% confidence intervals are calculated using a quantile from Student's t distribution, instead of a quantile of 1.96 from the normal distribution. This gives a more realistic estimate of the confidence interval for a mean derived from very small sample sizes (for example, *P. robustus*).

‡Cranial capacity estimates for these more inclusive taxa are calculated as the mean value of all specimens from appropriate individual taxa listed in the splitting hominin taxonomy above.

those of a tiled roof, and an estimated long period duration of 6–9 days).

In a recent analysis of enamel formation times in the incisors and canines of early hominins, Dean et al. (2001) counted long-period cross-striations, then used an empirically derived modal periodicity of 9 days to calculate enamel formation times, and plotted these against enamel thickness. These analyses show that archaic hominins take on average 100 days less than modern humans to reach an enamel thickness of 1000 μm. The authors conclude that 'none of the trajectories of enamel growth in apes, australopiths or fossils attributed to *H. habilis*, *H. rudolfensis* or *H. erectus* falls within that of the sample from modern humans' (Dean et al. 2001, p. 629). Similarly, in his analysis of root formation time in OH 16 (a specimen assigned to *H. habilis s. s.*) Dean (1995b) identified a pattern unlike modern humans.

Generally, crown formation times of anterior teeth are related to crown height (the taller the tooth, the longer it takes to form) and those of postcanine teeth are related to overall crown size (Macho & Wood, 1995b). Within fossil hominin taxa the major exception to these generalizations is that the premolar and molar crowns of *P. boisei* take the same time, or less, to form than in modern humans and chimpanzees, despite having crowns that are approximately twice the overall size of those of modern humans. This is due to a combination of more enamel secretion per day by ameloblasts, and a faster rate of ameloblast activation (Beynon & Wood, 1987). But we need more information before we can determine whether these differences are due to selection operating on life history, or diet, or on a combination of the two. In her analysis of crown formation times and life history evolution Macho (2001) suggests that the rapid crown formation times of *P. boisei* are due to a disjunction between body mass and brain mass. However, she uses an estimated body mass for *P. boisei* that is little different from modern humans. In fact the available evidence suggests that neither *P. boisei s. s.* nor *P. boisei s. l.* is likely to have been significantly heavier than other archaic hominin taxa (Table 6). Thus, in this respect at least, there is no evidence for a unique life history pattern for *P. boisei*.

Dean et al. (2001) concluded, albeit based on analysis of a single specimen, that *H. neanderthalensis* shared similar enamel growth rates with modern humans. Using perikymata packing patterns on the anterior dentition as a proxy for crown formation times (that is, closely spaced perikymata reflect decreased rates of maturation of enamel-forming ameloblasts and thus longer crown formation times) Ramirez-Rozzi & Bermúdez de Castro (2004) countered Dean et al., concluding that *Homo antecessor* and *H. heidelbergensis* had shorter periods of dental growth than *H. sapiens* (both modern and Upper Paleolithic-Mesolithic) and that *H. neanderthalensis* had decreased crown formation times that were derived with respect to *H. antecessor* and *H. heidelbergensis*, suggesting a shorter period of somatic growth in this taxon.

Guatelli-Steinberg et al. (2005, 2007) also analyzed Neanderthal enamel formation times by counting perikymata-packing rates, but their sample was not the same as that used by Ramirez-Rozzi & Bermúdez de Castro (2004), and *contra* the latter authors, Guatelli-Steinberg and colleagues report growth rates within the range of modern human variation. Guatelli-Steinberg et al. (2007) suggest that 'the most important question of all is the degree to which variation in lateral-enamel formation time of anterior teeth reflects life-history differences

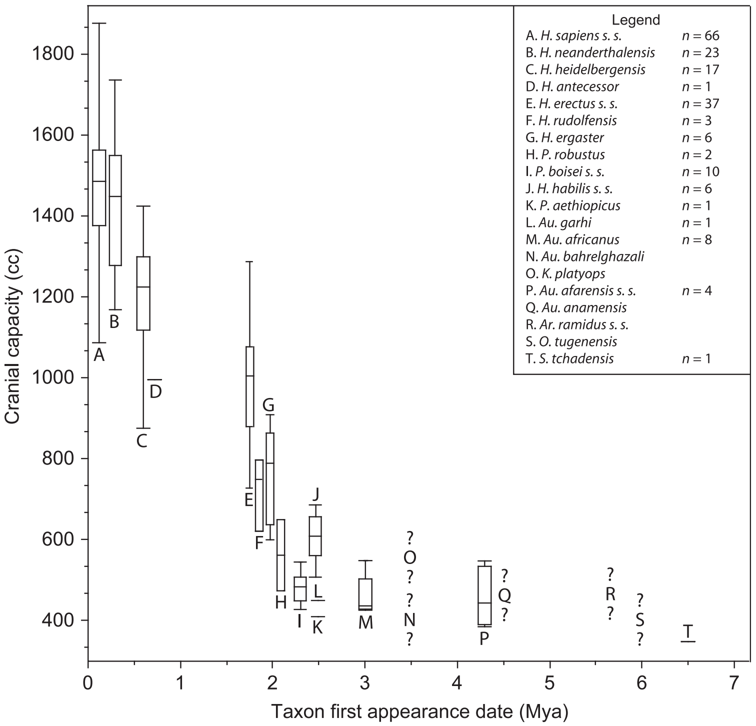

Fig. 6 Estimated endocranial volume plotted against first appearance date for the fossil hominin taxa recognized in the splitting taxonomy. Box and whisker plots show the median, upper, and lower quartiles (box) and the maximum and minimum values (whiskers). The number of individual estimates (n) used for each variable in this comparison is listed in the legend. Taxa represented by a single horizontal line have only a single estimate for this variable. Taxa with no data for this variable appear between question marks; their position along the vertical axis is determined by their informal group membership.

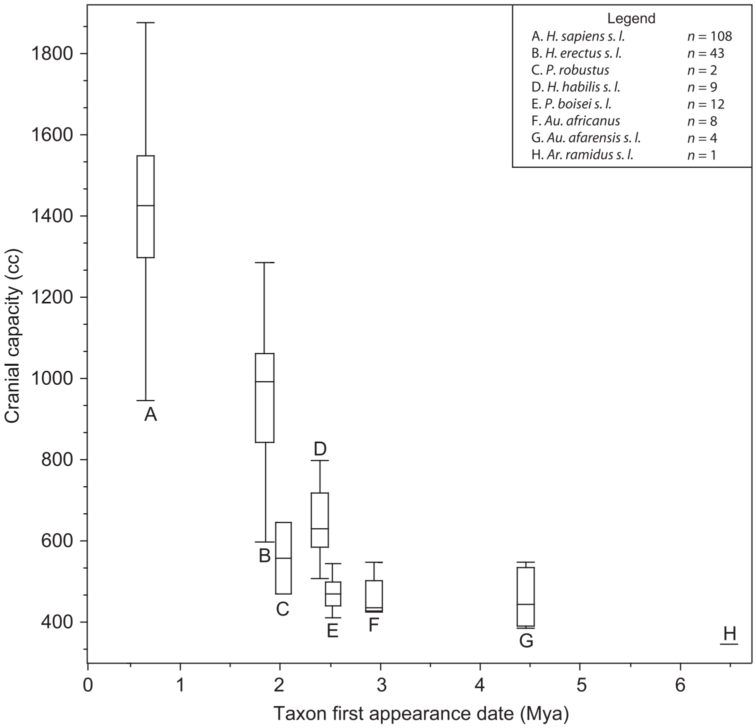

Fig. 7 Estimated endocranial volume plotted against first appearance date for the fossil hominin taxa recognized in the lumping taxonomy. Box and whisker plots show the median, upper, and lower quartiles (box) and the maximum and minimum values (whiskers). The number of individual estimates (n) used for each variable in this comparison is listed in the legend. Taxa represented by a single horizontal line have only a single estimate for this variable.

among and within species' (*ibid*, p. 117). The high variation in anterior tooth growth rates within modern humans (Reid & Dean, 2006) and between modern humans and other great ape populations (Dean & Reid, 2001) suggests these rates are not reliable predictors of life history (Smith et al. 2007d).

Tooth eruption is considered the best predictor of life history (Smith, 1991; Smith et al. 1994) and two recent studies (Macchiarelli et al. 2006; Smith et al. 2007d) have conducted the first preliminary attempts to associate enamel formation rates with age of tooth eruption in Neanderthals based on internal molar microstructure visible using high-resolution microcomputed tomography, but with conflicting conclusions. Macchiarelli et al. (2006), based on a single permanent Neanderthal M1 (from La Chaise-de-Vouthon, Charente, France), show enamel formation times and root completion times comparable to modern humans. They conclude that these data 'firmly place Neanderthal life history variables within those known for modern humans' (p. 748). Smith et al. (2007d) conducted similar analyses on the entire dentition of juvenile Neanderthal (from Scladina, Belgium) and determined the opposite, that formation times were shorter and eruption times earlier than in modern humans. Smith et al. conclude that 'a prolonged childhood and slow life history are unique to *Homo sapiens*' (p. 20220). While the majority of available evidence suggests Neanderthals, and perhaps earlier *Homo* species, share a similar pattern of dental growth and development with extant modern humans (Dean 2007), the scant evidence is equivocal and conclusions about similarities or differences in the pattern of dental growth and development modern humans and Neanderthals must wait until further data are accumulated.

Timing of tooth formation and eruption

The extent of root development in the teeth of living taxa can be assessed relatively crudely by radiography, and more precisely if the teeth are available for sectioning and histological analysis (Anemone, 2002). Unfortunately, all these methods are more difficult to apply to fossil hominin jaws. The mineralized bone of most fossils is resistant to conventional radiographic techniques, but images can be obtained by using computerized tomography (e.g. Conroy & Vannier, 1987). Developments in hardware and software are leading to expanded datasets for those fossil hominin taxa with large hypodigms, but even so the data for most extinct hominin taxa are still not sufficient to form definite conclusions. As noted more than a decade ago by Conroy & Vannier (1991b), just because the eruption sequence differs between modern humans and living chimpanzees it does not follow that fossil hominin taxa, whose eruption sequence is the same as that as modern humans, will have modern human rates of dental development.

Figure 8 emphasizes the complexity of the interactions between several aspects of the development of lower incisors and molars in modern humans, living chimpanzees and *Paranthropus* taxa. Despite similarities in gross dental ontogeny between *Pan* and *Paranthropus* (that is, eruption of M1 at ~3 years of age), different incisor crown formation times in *Pan* and *Paranthropus* result in different eruption sequences. However, despite modern humans and *Paranthropus* having similar eruption sequences there are marked differences in their rates of crown and root formation. Even though similar eruption sequences can mask differences in other aspects of dental development, it is nonetheless a truism that eruption sequences are bound to differ among hominin taxa unless all aspects of

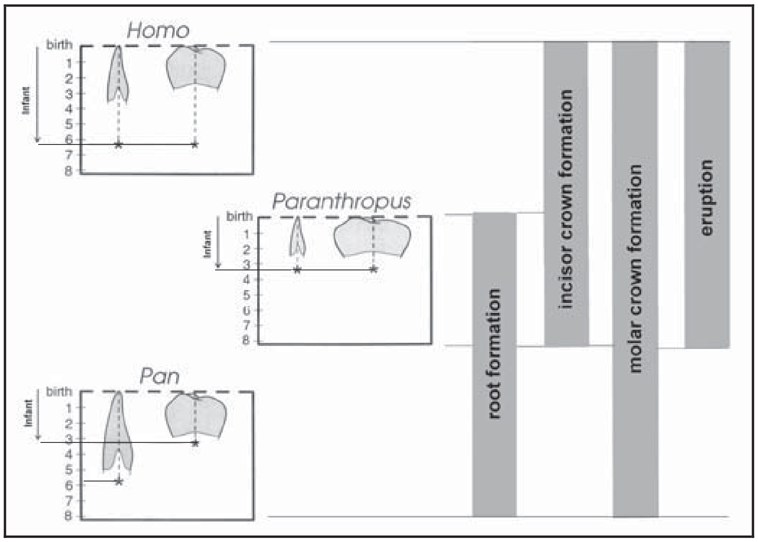

Fig. 8 The relationship between crown formation and eruption sequence in modern humans, *Pan*, and *P. boisei*. The vertical dashed line represents the time from the onset of crown formation to eruption. The height of the crown represents the approximate time taken for crown formation; the balance of the period to eruption represents the time taken for the root to form. The tooth crowns are approximately to scale. Infancy is taken to cease at the time of M1 eruption (*). The vertical gray bars indicate rates and patterns in common among the taxa. All three genera share similar molar crown formation times, but *Pan* differs from the other two in eruption schedules and *Homo* in root formation times. Adapted from Macho & Wood (1995b).

dental ontogeny change their rates proportionally (Macho & Wood, 1995a).

Bermúdez de Castro et al. (2003) compared the relative timing of tooth formation in a variety of hominin specimens, and in samples of modern humans and the non-human great apes, and found similarities between the non-human great apes and archaic hominins on the one hand, and *H. antecessor*, *H. erectus s. s.*, *H. heidelbergensis*, and modern humans on the other, with *H. ergaster* (or early *H. erectus s. l.*, depending on your taxonomic hypothesis) specimens appearing to be intermediate between these two groups.

In appropriate juvenile fossil hominin specimens it is possible to use aspects of dental microstructure, assessments of dental attrition and the sequence of eruption of the dentition to determine the age-at-death and thus compare dental development among extant great apes, modern humans and fossil hominin specimens of the same chronological age. Bromage & Dean (1985) pioneered this approach by using counts of perikymata on the central incisor crown, together with assumptions about the time it takes to begin calcification of the tooth and the time it takes to begin root formation, to more accurately age fossil specimens and thus enable comparisons with modern human dental specimens at a comparable stage of development. They did this for several fossil hominin mandibles, LH 2 (*Au. afarensis*), Sts 24 (*Au. africanus*), SK 63 (*P. robustus*), and KNM-ER 820 (*H. ergaster*) and concluded that the timing and duration of the dental development of these specimens was much closer to that of extant chimpanzees than to modern humans. However, although perikymata counts made up c. 90% of the age estimates for LH 2 and Sts 24, for KNM-ER 820 the majority of the elapsed time was based on assumptions, not observations, about ontogeny.

Subsequent studies have achieved greater accuracy and precision by sectioning whole teeth to recover information about the cellular events involved in tooth development (e.g. Dean et al. 1993; Moggi-Cecchi et al. 1998). Age at death estimates for other early *Homo* specimens (e.g. KNM-ER 1590 and KNM-WT 15000) assigned to *H. rudolfensis* and *H. ergaster* (or *H. erectus s. l.*), respectively, also suggest that the timing of dental development of these taxa was not modern human-like (Smith, 1991). However, any inferences drawn from these results must be tentative until we better understand the extent of variation of dental development within regional samples of *H. sapiens* (Liversidge, 2003; Reid & Dean, 2006).

Within the context of dental LHRVs such as crown and root formation time and the relative timing of tooth formation and eruption, *H. neanderthalensis* and Upper Paleolithic *H. sapiens* exhibit a modern-human like pattern, whereas the available evidence suggests that archaic and transitional hominins were more chimpanzee-like. Dental development in later *H. erectus s. s.*, *H. antecessor*, and *H. heidelbergensis* is more derived in the modern direction than that of the archaic and transitional hominins, but the pattern is still not like that of anatomically modern humans. This would suggest that these pre-modern *Homo* taxa have life histories that are unlike those of either archaic hominins or modern humans.

Phylogenetic trends in fossil hominin life history-related variables

If the application of cladistic methods to the hominin fossil record was known to generate robust hypotheses about the structure of the hominin clade, then in theory we should be able to predict the primitive condition of LHRVs for each of the hominin subclades, look for any evidence of homoplasy in life history, and determine at what stage in hominin evolution the distinctive aspects of modern human life history make their appearance. However, there is disagreement about the reliability of the results of cladistic analyses of the hominin fossil record that are based on traditional metrical or non-metrical data. Some researchers (e.g. Strait & Grine, 2001, 2004) are more willing than we are to accept as reliable the results of hominin cladistic analyses. Other researchers (e.g. Corruccini, 1994), especially those who have tried to test the validity of these methods by applying them to living higher taxa for which we have independent molecular evidence about taxonomic relationships (e.g. Collard & Wood, 2000), are more skeptical about the reliability of cladistic analyses of early hominins that are based on conventional (i.e. non 3D) metric and non-metrical data.

Just as a well-supported hypothesis about evolutionary relationships among the living higher primates (see above) is essential for predicting the primitive condition for life history in the *Pan-Homo* and hominin clades, a robust hypothesis about evolutionary relationships among extinct hominin taxa is required to enable us to explore the evolution of life history within the hominin clade. There have been many attempts to determine phylogenetic relationships within the hominin clade. Most differ in their detailed conclusions, but nearly all (e.g. Chamberlain & Wood, 1987; Skelton & McHenry, 1992; Strait et al. 1997, 2007) share the conclusion that around 2.5 Ma the hominin clade split into two major subclades. One is the subclade that contains the megadont archaic hominins assigned to the genus *Paranthropus*; the other subclade includes taxa assigned to *Homo* (i.e. *H. erectus s. l.*, *H. heidelbergensis*, and *H. neanderthalensis*, and the only living hominin, *H. sapiens*).

If we accept that a genus should be both a clade and a grade (see Wood & Collard, 1999a, 2001 and Wood & Lonergan, this volume for a discussion) then it would be natural to want to know whether all the taxa included in *Paranthropus*, on the one hand, and *Homo*, on the other, have the same life history. With respect to the *Paranthropus*

Table 8 The presence of modern human-like LHRVs within the taxa recognized in a splitting hominin taxonomy (Y = present; N = not present; ? = not known)

Informal Group	Splitting taxonomy	Body Size	Brain Mass	Dental crown and root formation	Timing of tooth formation and eruption
Basal hominins	*S. tchadensis*	?	N	?	?
	O. tugenensis	?	?	?	?
	Ar. ramidus s. s.	N	?	?	?
Archaic hominins	*Au. anamensis*	N	?	?	?
	Au. afarensis s. s.	N	N	N	?
	K. platyops	?	?	?	?
	Au. bahrelghazali	?	?	?	?
	Au. africanus	N	N	N	N
Megadont archaic hominins	*Au. garhi*	?	N	?	?
	P. aethiopicus	N	N	?	?
	P. boisei s. s.	N	N	N	N*
	P. robustus	N	N	N	N*
Transitional hominins	*H. habilus s. s.*	N	N	N	N
	H. rudolfensis	Y	N	?	?
Pre-modern *Homo*	*H. ergaster*	Y	N	N	N
	H. erectus s. s.	Y	N	N	N
	H. antecessor	?	N	N	Y
	H. heidelbergensis	Y	Y	N	Y
	H. neanderthalensis	Y	Y	Y	Y
Anatomically-modern humans	*H. sapiens s. s.*	Y	Y	Y	Y

*Sequence but not timing.

clade, the data gathered for this review suggest that there is little evidence for any significant increase in body mass (but see Lockwood et al. 2007). There is, however, evidence for a slight increase in endocranial volume compared to modern chimpanzees (Elton et al. 2001). However, enamel and dentin formation are faster in *Paranthropus* taxa (see above) than they are for any other member of the *Pan-Homo* clade for which data are available. This suggests that if the pattern of *Paranthropus* life history mirrors its dental growth and development, then it was most likely distinct from that of modern humans, on the one hand, and from chimpanzees and bonobos, on the other (Kuykendall, 2003).

With regard to the *Homo* clade, there is disagreement about the criteria used to determine whether a taxon should be included within *Homo*, and thus where we should place the boundary between *Homo* and non-*Homo* hominin taxa (Wood & Collard, 1999a,b). As seen below in a summary of LHRVs present in *Homo* taxa (which is just one of the several categories of evidence that could be used to determine the boundaries of a genus), there is little evidence to support a grade distinction that applies to all the taxa presently included in the genus *Homo*.

Implications of fossil hominin life history-related data for hypotheses about the evolution of modern human life history

There are a substantial number of differences between the life history of modern humans and the life history of our closest living relatives within the genus *Pan*. A summary table outlining the presence of modern human-like LHRVs within a speciose hominin taxonomy is presented in Table 8. Prior to the transitional hominins, there is no evidence of any hominin taxon possessing a body size, brain size or aspects of dental development that differed significantly from what we assume (but remember that this is an untested assumption) to be the primitive life history pattern for the *Pan-Homo* clade.

Within the transitional hominin grade, that is *H. habilis s. s.* and *H. rudolfensis* (or *H. habilis s. l.* for those unconvinced that this hypodigm subsumes more than one taxon), what can be inferred about LHRVs is consistent. No LHRVs (with the possible exception of *H. rudolfensis* body mass) are consistent with the type of prolonged ontogeny seen in modern humans. The situation is only slightly different for *H. ergaster*, the mean body mass estimates for which are similar to those of modern humans. Neither its adult brain size, nor its crown and root formation times, nor the timing and sequence of its dental eruption are consistent with a modern human pattern. Middle Pleistocene *H. erectus s. s.* may be more modern human-like in its dental development, although the evidence is conflicting (for example, Sangiran 4 being more modern human-like and Sangiran 7 less so). Non-craniodental evidence for fossil hominin growth and development in *H. ergaster*/*H. erectus s. s.* is sparse and conflicting. Whereas some workers interpret the pattern of growth and development of the postcranial skeleton in these taxa as compatible with that of modern humans (Clegg & Aiello, 1999; Smith, 2004), others point to subtle but significant differences (Tardieu, 1998) from the ontogeny of modern humans.

The fossil material attributed to *H. antecessor* does not provide a good estimate of body mass, and it indicates an adult brain size similar to that of *Homo erectus s. s.* The crown formation times of *H. antecessor* are not yet modern, but there is some evidence for modern human-like timing of tooth formation and eruption. The body and brain sizes of *H. heidelbergensis* and *H. neanderthalensis* are consistent with a modern human life history. However, although both of these taxa appear to possess a modern human-like pattern of dental development, the crown formation times of the former are similar to *H. antecessor* and those of the latter appear to be autapomorphically rapid. Thus, depending upon the weight one wants to give to these LHRVs, and it is possible that a modern human pattern of life history was present in *H. heidelbergensis* and *H. neanderthalensis*.

Summary

Using the hominin fossil record, the second part of this contribution attempted to answer the following questions:
1) Did the unique features of modern human life history (or LHRVs) appear piecemeal, or did they appear suddenly as an integrated package?
2) If they did appear as an integrated package, did that package appear when large-bodied hominins with modern human skeletal proportions emerged?
3) Were modern human and modern chimpanzee life histories the only ways that life history has been configured within the *Pan-Homo* clade?

The clear contrasts between the life history of modern humans and the life history of our closest living relatives, the chimpanzees, perhaps promoted the expectation that there would be a point in evolutionary history when all these variables switched simultaneously from their primitive non-modern human condition to the modern human condition. The reality seems to be more complicated. Some LHRVs (for example, body mass) shift to the modern human condition earlier while others, for example, some aspects of dental development, do not appear until the Middle/Late Pleistocene with *H. neanderthalensis* and *Homo sapiens*.

Initial attempts to describe the dental ontogeny of fossil hominins were mostly confined to statements about whether it was ‘modern human-like’ or ‘ape-like’. Additional data and more sophisticated ways of displaying those data resulted in the realization that the dental ontogeny of many early hominins was distinctive, and was not an amalgam of some modern human-like characteristics and some ape-like ones (Bromage, 1987; Kuykendall, 2003). As we come to know more of the life histories of early, and most likely also later, hominins we are also discovering that they can have distinctive life histories that do not conform to any living model (see Kelley, 2002, 2004 for insightful reviews of life history evolution within living and extinct higher primates). At least one extinct hominin subclade, *Paranthropus*, has a pattern of dental LHRVs that most likely set it apart from the life histories of both modern humans and chimpanzees.

Conclusion

Life history is an important component of the shared adaptive mix that justifies grouping taxa into genera. The tantalizing glimpses existing data and methods have provided into the life history of taxa included in *Homo*, suggest that this genus, as traditionally defined, subsumes at least two different patterns of life history. If LHRVs are used to reconstruct life history, then the life histories of transitional hominins and pre-modern *Homo* appear to differ from each other as well as from the life history of anatomically modern *Homo*. How these differences relate to hominin ecology and patterns of social and cultural evolution within the hominin clade are pressing research problems. The evolution of modern human life history, as well as the evolution of life history in other parts of the hominin clade, are clearly complex though there have been some attempts to reconstruct evolutionary scenarios (Hawkes et al. 1998; O’Connell et al. 1999; Kaplan et al. 2000). The task of using the hominin fossil record to document and help understand these complexities has barely begun.

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Appendix I

Notes for body mass and brain size data as used in Tables 3–4.

Table 6. Body mass estimates

Splitting taxonomy

Ar. ramidus s. s. Wood & Richmond (2000). Estimate based on the observation that shoulder joint size of *Ar. ramidus* is 30% larger than that of AL 288-1 (30 kg).

Au. anamensis Male estimate from Leakey et al. (1995), and female estimate from McHenry & Coffing (2000) (calculated from the ratio of male to female in *Au. afarensis*).

Au. afarensis s. s. Adapted from McHenry (1992). Based on A.L. 333-3, 333-4, 333-7, 333w-56 and 333x-26 for male, and 129-1a, 129-1b, 288-1, 333-6 for female.

Au. africanus Adapted from McHenry (1992). Based on Sts 34, Stw 99, 311, 389 for male, and Sts 14, Stw 25, 102, 347, 358, 392, and TM 1512 for female.

Paranthropus aethiopicus Taken from Kappelman (1996). Based on KNM-WT 17000 for male.

P. boisei s. s. Adapted from McHenry (1992). Based on KNM-ER 1464 for male, and KNM-ER 1500 for female [but see Wood & Constantino (2004) for a discussion of whether KNM-ER 1500 can be confidently assigned to *P. boisei*].

P. robustus Adapted from McHenry (1992). Based on SK 82 and 97 for male, and SK 3155 and TM 1517 for female.

H. habilis s. s. Adapted from McHenry (1992). Based on KNM-ER 3735 (1503) for male, and OH 8 and 35 for female.

H. rudolfensis Adapted from McHenry (1992). Based on KNM-ER 1481 and 3228 for male, and KNM-ER 813 and 1472 for female. It is possible that some or all of these specimens belong to *H. ergaster* and not *H. rudolfensis*.

H. ergaster Adapted from Ruff et al. (1997). Based on KNM-ER 736, 1808 and KNM-WT 15000 for male and KNM-ER 737 for female.

H. erectus s. s. Taken from Aiello & Wood (1994) (Sangiran 17 = male), Kappelman (1996) (Zhoukoudian XI = female) and adapted from Ruff et al. (1997) (OH 28 and OH 34 = female; Zhoukoudian FeIV = no sex determination).

H. heidelbergensis Adapted from Ruff et al. (1997), Rosenberg et al. (1999) (Jinniushan) and Arsuaga et al. (1999) (Atapuerca-SH-1). Species estimate based on Atapuerca (SH) Pelvis 1 (m), Broken Hill 689, Broken Hill 690, Broken Hill 691, Broken Hill 719 (m), Broken Hill 907, Boxgrove 1 (m), Jinniushan (f), Arago 44 (m), Gesher-Benot-Ya'acov, KNM-BK 66, Ain Maarouf 1. Male (*n* = 4) and female (*n* = 1) estimates based on sex determinations taken from references and denoted by (m) and (f), respectively.

H. neanderthalensis Adapted from Ruff et al. (1997). Species estimate based on Amud 1 (m), La Chapelle-aux-Saints (m), La Ferrassie 1 (m), La Ferrassie 2 (f), Kebara 2 (m), Neanderthal 1 (m), La Quina 5, Regourdou 1, Saint-Cesaire 1 (m), Spy 1 (f), Spy 2 (m), Shanidar 1 (m), Shanidar 3 (m), Shanidar 5 (m), Krapina 207 (m), Krapina 208 (f), Krapina 209 (f), Krapina 213 (m), Krapina 214 (f), Shanidar 2 (m), Shanidar 4 (m), Shanidar 6 (f), Tabun C1 (f). Male (*n* = 14) and female (*n* = 7) estimates based on sex determinations taken from Ruff et al. (1997) and denoted by (m) and (f), respectively.

H. sapiens s. s. Adapted from Ruff et al. (1997). Species estimate based on Qafzeh 3 (f), Qafzeh 7 (m), Qafzeh 8 (m), Qafzeh 9 (f), Skhul 4 (m), Skhul 5 (m), Skhul 6 (m), Skhul 7 (m), Skhul 7a (f), Skhul 9 (m) and 104 specimens (49 male, 31 female and 24 unsexed) dated to between 10 ky and 35 ky BP. Male (*n* = 56) and female (*n* = 36) estimates based on sex determinations from Ruff et al. (1997) and denoted by (m) and (f), respectively.

Lumping taxonomy

Au. afarensis s. l. Includes specimens attributed to *Au. afarensis s. s.* and *Au. anamensis*. Sample sizes: species estimate (*n* = 11); male (*n* = 6), female (*n* = 5).

P. boisei s. l. Includes specimens attributed to *P. boisei s. s.* and *P. aethiopicus*. Sample sizes: species estimate (*n* = 3); male (*n* = 2), female (*n* = 1).

H. habilis s. l. Includes specimens attributed to *H. habilis s. s.* and *H. rudolfensis*. Sample sizes: species estimate (*n* = 7); male (*n* = 3), female (*n* = 4). It is possible that some or all of the specimens attributed to *H. rudolfensis* in this calculation actually belong to *H. ergaster*.

H. erectus s. l. Includes specimens attributed to *H. erectus s. s.* and *H. ergaster*. Sample sizes: species estimate (*n* = 9); male (*n* = 4), female (*n* = 4).

H. sapiens s. l. Includes specimens attributed to *H. sapiens s. s.*, *H. neanderthalensis*, and *H. heidelbergensis*. Sample sizes: species estimate (*n* = 148); male (*n* = 74), female (*n* = 42).

Table 7. Cranial capacity estimates

Splitting taxonomy

Sahelanthropus tchadensis Based on TM 266-01-060-1 (Zollikofer et al. 2005)

Au. afarensis s. s. Based on AL 162-28, 333-45 (Delson et al. 2000), 333-105 – adult est. (Holloway, 1983b), 444-2 (Kimbel et al. 2004).

Au. africanus Based on MLD 1, 37/38; Sts 19/58, 5, 60, 71; Taung – adult est. (Delson et al. 2000), Stw 505 (550 cc. Holloway pers. comm. 2003).

Australopithecus garhi Based on BOU-VP-12/130 (Asfaw et al. 1999).

P. aethiopicus Based on KNM-WT 17000 (Walker et al. 1986)

P. boisei s. s. Based on KGA 10-125 (Suwa et al. 1997), KNM-ER 406, 13750; Omo L338y-6 (Delson et al. 2000), KNM-ER 407, 732; OH 5 (Falk et al. 2000), KNM-ER 23000; Omo 323-1976-896, KNM-WT 17400 (Brown et al. 1993); and (Holloway, 1988).

P. robustus Based on SK 1585 (Falk et al. 2000), TM 1517 (Broom & Robinson, 1948).

H. habilis s. s. Based on KNM-ER 1805, 1813; OH 7, 13, 24 (Delson et al. 2000), OH 16 – adult est. (Tobias, 1971).

H. rudolfensis Based on KNM-ER 1470, 1590, 3732 (Delson et al. 2000).

H. ergaster Based on D2280, 2282 (Gabunia et al. 2000), 2700 (Vekua et al. 2002); KNM-ER 3733, 3883 (Delson et al. 2000); KNM-WT 15000 (Begun & Walker, 1993). Note that the inclusion of the recently discovered KNM-ER 42700 does not change the average cranial capacity of *H. ergaster* by more than 10 cm^3 if the actual capacity is close to 720 as tentatively reported (Leakey et al. 2003).

H. erectus s. s. Based on BOU-VP-2/66 (Asfaw et al. 2002); Ceprano (Ascenzi et al. 2000); Gongwangling 1/Lantian (Woo, 1966); Hexian/PA 830 (Wu & Dong, 1982); Narmada/Hathnora [mean of 1155 and 1421cc in Wolpoff (1999)]; Ngandong 1, 5, 6, 10, 11; Sambungmacan 1; Sangiran 4/Pith IV (Delson et al. 2000), Ngandong 7, 12; Sangiran 2/Pith II, 10/Pith VI, 17/Pith VIII; Trinil 2/Pith I; Zhoukoudian II/D, X/L1, XI/L2, XII/L3 (Grimaud-Herve, 1997); Ngandong 9; Zhoukoudian III/E1, Zhoukoudian VI (Weidenreich, 1943); Ngawi [Wolpoff cited in Antón (2002)]; OH 9, 12 (Holloway, 1983b); Perning 1/Mojokerto – adult est. (Antón, 1997); PL-1/Poyolo (Mowbray et al. 2000); Sambungmacan 3 (Márquez et al. 2001), 4 (Baba et al. 2003); Nanjing 1 (Liu, Zhang and Wu, in press); Sangiran 12/Pith VII (Holloway, 1981a), Sangiran IX (Anton and Swisher III pers. comm. 2003); Zhoukoudian V/H3 (Chiu et al. 1973).

H. antecessor Based on ATD-15 (Bermúdez de Castro et al. 1997).

H. heidelbergensis Based on Arago 21; Broken Hill-1/Kabwe; Petralona 1; Reilingen; Swanscombe 1; Vertesszollos II (Delson et al. 2000); Atapuerca 4, 5 (Arsuaga et al. 1997), 6 (Ruff et al. 1997); Bodo (Conroy et al. 2000); Dali 1 (Wu, 1981); Florisbad [Beaumont et al. cited in Aiello & Dean (1990)]; Jinniushan (Wolpoff, 1999); Ndutu (Brauer, 1984); Saldanha/Hopefield/Elandsfontein [Drennan cited in Brauer (1984)]; Sale (Holloway, 1981b); Steinheim (Ruff et al. 1997).

H. neanderthalensis Based on Amud 1; Biache-Saint Vaast; Ganovce 1; Krapina 2/B, 3/C, 4/D; La Quina 5; Monte Circeo I/Guattari 1; Neanderthal; Saccopastore I, II; Tabun C1 (Delson et al. 2000); Ehringsdorf 9; Gibraltar 1; La Chapelle-aux-Saints; La Ferrassie 1; Le Moustier 1; Teshik-Tash 1 (Grimaud-Herve, 1997); La Quina 18-adult est.; Shanidar 5 (Ruff, et al. 1997), Shanidar 1 [Stewart cited in Day (1986)]; Spy 1, 2 (Holloway, 1983b).

H. sapiens s. s. Arene Candide 1, 1-IP, 2, 4, 5; Barma Grande 2; Bruniquel 2; Cap Blanc 1; Dolni Vestonice III; Grotte des Enfants 4, 5, 6; Minatogawa 1, 2, 4; Mladec 1; Nazlet Khater 1; Oberkassel 2; Paderbourne; Pataud 1; Qafzeh 11; San Teodoro 1, 2, 3, 5; St. Germain-la-Riviere 1; Veryier 1; Zhoukoudian Up. Cave 1, 2, 3 (Ruff et al. 1997); Asselar (Tobias, 1971); Border Cave 1 (de Villiers, 1973); BOU-VP-16/1 (White et al. 2003); Brno II, III; Dolni Vestonice XIII, XIV, XV, XVI; Pavlov 1 [Vlcek cited in Schwartz & Tattersall (2002)]; Combe-Cappelle; Predmosti 3, 9 (Grimaud-Herve, 1997); Cro-Magnon 3; Mladec 2, 5 (Wolpoff, 1999); Eyasi 1 [Protsch cited in Brauer (1984)]; Jebel Irhoud 1 (Holloway, 1981b) Jebel Irhoud 2 [Ennouchi cited in Brauer (1984)]; Kanjera 1 [Coon cited in Brauer (1984)]; LH 18/Ngaloba (Brauer, 1984); Omo-Kibish 1 Omo-Kibish 2 [Day cited in Brauer (1984)]; Qafzeh 6 (Vallois & Vandermeersch, 1972) Qafzeh 9 [Genet-Varcin cited in Brauer (1984)]; Singa 1 [Wells cited in Stringer (1979)]; Skhul 4 [McCown and Keith cited in Brauer (1984)]; Brno I; Chancelade 1; Cro-Magnon 1; Oberkassel 1; Predmosti 4, 10, Skhul 5, 9; Yinkou (Delson et al. 2000).

Lumping taxonomy

P. boisei s. l. Includes specimens attributed to *P. boisei s. s.* and *P. aethiopicus*.

H. habilis s. l. Includes specimens attributed to *H. habilis s. s.* and *H. rudolfensis*.

H. erectus s. l. Includes specimens attributed to *H. erectus s. s.* and *H. ergaster*.

H. sapiens s. l. Includes specimens attributed to *H. sapiens s. s.*, *H. neanderthalensis*, *H. heidelbergensis*, *H. antecessor*, and Fontechevade (Delson et al. 2000).

CHAPTER 3

AGE AT FIRST BIRTH IN HUMANS: EVALUATION OF A DEMOGRAPHIC VARIABLE WITHIN THE CONTEXT OF LIFE HISTORY

Abstract

Age at first birth is a central variable in demographic life history models because it identifies the beginning of fertility. For most mammals, age at first birth is closely aligned with the timing of physiological maturity. Humans, however, live in varying ecologies that influence maturation rates and have marriage institutions that can constrain sexual access to fecund females. Using data from the published literature I examine human ages at menarche, ages at first birth, and ages at marriage to characterize relationships among them. I identify the observed variation in each of these variables and review the proximate mechanisms that influence their timing. These data show that, with few exceptions, the floor of the range of human age at first birth is remarkably consistent at about 17-18 years old across space and time. Women who bore their first births before this age suffer maternal and infant costs. I investigate the effect of age at marriage on age at first birth and find that, although there is broad variation in age at marriage across cultures, there is a strong tendency for marriage age to just precede female sexual maturity. I propose that, in general, female sexual maturity determines marital age rather than the reverse. Comparisons with other great ape species confirm relatively late ages for all aspects of human sexual maturity, a pattern consistent with our slow life history. Finally, I consider the contribution of demographic heterogeneity to secular shifts documented in reproductive timing of women.

Introduction

Life history encompasses the timing of vital life events and primates have been described as living „life in the slow lane‟ (Harvey and Clutton-Brock 1985; Stearns 1992; Charnov and Berrigan 1993). In comparison with other mammals, primates exhibit slow growth rates, long juvenile periods, low fertility and mortality rates, large neonates and longer lifespans than predicted for their body size (Ross 1998; Robson et al. 2006; Robson and Wood 2008; Bernstein 2010). Life history theory postulates that age at maturation in determinant growers is set by the tradeoff between the advantages of early sexual maturation for producing more offspring before dying (Kaplan et al. 2000; Hawkes 2006) and the advantages of waiting longer to achieve larger body size (Stearns 1992; Purvis and Harvey 1995). Special attention has been paid to the relatively long juvenile period and slow growth process in primates (Blurton Jones 2006; Mumby and Vinicius 2008).

In Charnov‟s invariant life history model (1993) for female mammals, the production a female can put into offspring is a function of her size, which generally increases the longer she continues to grow before maturity. Time available to use the gains of larger size depends on the adult life span, which can be represented by its inverse, M, the instantaneous adult mortality rate. As that rate falls and average adult lifespan increases, selection favors delayed maturity to reap the benefits of larger size (Charnov 1993; Charnov and Berrigan 1993). Age at maturity and expected adult lifespan vary widely but the product of age at maturity and the inverse of average adult lifespan is approximately invariant (Charnov 1993).

When organisms experience high levels of extrinsic adult mortality, they tend to evolve faster life history strategies (Charlesworth 1980; Promislow and Harvey 1990). In this context, selection favors a shorter period of growth and earlier maturation and reproduction (Harvey and Zammuto 1985). For primates, with slow life histories, greater longevity strongly correlates with later ages at first reproduction both across and within primate clades (Alvarez 2000; Walker et al. 2006a; Migliano et al. 2007; Mumby and Vinicius 2008).

Partridge and Harvey (1988) define life histories as “the probabilities of survival and the rates of reproduction at each age in the life-span” highlighting the demographic framework of life history models. As such, most life history studies focus on females, because female fertility and mortality determine population growth and age structure (Hawkes 2010). Age at first birth is a key life history variable in models of life history evolution because it represents the onset of female fertility. Age at first birth in humans, however, is complicated by the effects of vastly differing ecologies on the timing of physiological reproductive maturity. Unlike other female mammals, human age at first birth is also potentially constrained by marriage institutions that often restrict sexual access of males to fecund females.

The goal of this paper is to summarize what we know about the mechanistic pathways through which age at menarche and age at first birth may be adjusted in humans, and to situate this information in a broader adaptive context. I begin by reviewing the variation in age at menarche and age at first birth, key components in the onset of female fertility, for populations across ecologies. I compare and discuss environmental influences that adjust them, including the effects of both adolescent subfecundity and marital fertility. I compare these human parameters with those of great apes and evaluate recent studies that test the invariant components of Charnov"s model. Finally, I propose that heterogeneity may play an important role in adjusting the population averages of these variables and make suggestions for future study.

Variation in human age at menarche

The biological capacity for a young woman to conceive and deliver offspring is mediated by the pace of pubertal development, age at menarche and the duration of subfecundity before consistent ovulation. Wide variation in age at menarche, or first menstruation, has been well documented for different human populations (Worthman 1999; Parent et al. 2003; Ellis et al. 2009). In a sample of 19 small-scale forager, horticultural, and agricultural populations, the average age at menarche is 14.8 years old, ranging from 12.5 among the Yanamama to 18.5 among the Gainj of Paupa New Guinea (see Figure 3.1 and Table 3.1). Figure 3.2 compares menarche of these small scale populations with 67 contemporary countries of varying affluence. The mean (or median) age at menarche for large-scale populations is 13.5 years, ranging from 12-16.2 years old. Although the small-scale populations have a later average age at menarche than contemporary populations both groups have 4-6 years of overlap in these ranges. This variability has been shown to result from ecological, socioecological and epigenetic factors that influence the critical timing of pubertal development.

Age at menarche has been a topic of great interest for anthropologists beginning with evaluation of the critical-weight hypothesis by Frisch and Revelle (1970). It is now evident that menarche is strongly associated with skeletal maturity and occurs after girls have accomplished the majority of their stature (Ellison 1981; Moerman 1982; Lancaster 1986; Ellison 2001). The pace and timing of pubertal development and menarche vary widely at both among individuals and between populations, and depend on the influence of local ecology and energy availability (Parent et al. 2003; Ellis 2004). Differences in the timing of sexual maturity are strongly associated with nutritional condition during adolescence (Ellison 1990; Rosetta 1990; Cumming et al. 1994; Ulijaszek 1995; Strassman 1996; Bentley 1999; Ellison 2001; Gillett Netting et al. 2004). This is clearly demonstrated by the dramatic differences in age at menarche between impoverished girls adopted into affluence, compared with their peers who are not adopted (Mul et al. 2002; Teilmann et al. 2006). Enhancements in health and nutrition can also account for the worldwide secular trend toward earlier puberty and median menarchal ages over the past century (Eveleth and Tanner 1990; Tanner 1990; Ellis et al. 2009). Since the secular trend toward earlier age at menarche was first recognized, earlier maturity has been shown to be associated with good and improved childhood nutrition and health, while slow and delayed maturity is linked with poor childhood conditions (Foster et al. 1986; Garn 1987; Eveleth and Tanner 1990; Riley et al. 1993; Ellis 2004).

Several studies indicate that girls who reach menarche early have a proportionally shorter duration of subfecundity and time to establishment of adult ovarian function. A comparison of Kikuyu (east African horticulturalists) and urban British girls found that earlier maturing girls progress more quickly through the pubertal sequence (Worthman 1987, 1993). Apter and Vihko (1983) find that girls who reach menarche at age 12.0–12.9 achieve 50% ovulatory cycles 3.0 years after menarche. In contrast, girls who are 13.0 and older at first menses, achieve the same level of ovulatory function 4.5 years after menarche (but see Foster et al. 1986). However, an earlier onset of menarche does always result in a swifter pace through the pubertal sequence (Kramer and McMillan 1998, 1999, 2006). Disruptions in energy balance and energy flux, can delay female fecundity (Ellison 2001, 2003; Jasienska and Ellison 2004) and aspects of growth (Steinberg et al. 2008).

Social experiences have been brought to the fore as additional causal factors that shape pubertal timing (Belsky et al. 1991; Kim et al. 1997; Ellis et al. 2003; Ellis 2004). Evidence suggests that psychosocial stressors have both inhibiting and accelerating effects on developmental pace (Boyce and Ellis 2005). Several studies propose that an extended period of juvenility and delayed maturity are adaptive in high-quality social environments, whereas emotionally stressful childhoods and family dysfunction tend to predict earlier menarche (Hulanicka et al. 2001; Coall and Chisholm 2003; Chisholm et al. 2005). Father absence in particular has been identified as a stressor associated with early menarche, earlier ages of sexual activity and adolescent pregnancy (Ellis et al. 2003; Quinlan 2003; Bogaert 2005).

Potential intergenerational mechanisms have recently emerged as an important connection between environmental cues and pubertal timing. Prenatal conditions, birthweight and early childhood environment have all been tied to reproductive development (Adair 2001; Karlberg 2002; Koziel and Jankowska 2002; Lienhardt et al. 2002). Other studies have found that daughters born to teen mothers are significantly more likely to become teen mothers themselves (Meade et al. 2008). New research also points to epigenetic effects on juvenile growth rates (Kuzawa 2005, 2007; Kuzawa and Sweet 2009). Ecological and nutritional information are transferred prenatally so that growth rates are established, not only on short-term ecological fluctuations that may occur during gestation, but also based on inputs averaged over the last few generations in the maternal line.

Together these many thoroughly documented lines of inquiry about female pubertal development show that body size, growth rates, age at menarche and establishment of adult fecundity are related in complex and highly variable ways. This suggests that phenotypic plasticity in these traits are a response to the range of ecological and social settings in which humans grow up and begin to reproduce (Kramer and Lancaster 2010). Flexibility is advantageous in giving girls the best chance of success under variable energetic, epidemiological, mortality and social conditions (Gluckman and Hanson 2006).

Human adolescent subfecundity and the consequences of early teen pregnancy

Female fertility does not begin at menarche. Instead, puberty is a step in a series of hormonal feedback loops that slowly activate consistent ovulatory cycles and peak ovarian function is not ordinarily achieved until the late teens or early twenties (Moerman 1982; Ellison 1990). A transitional period between menarche and peak ovarian function has long been recognized in the published literature. Once known as "adolescent sterility" (Montagu 1946), it is now recognized as "adolescent subfecundity” (Ellison 1990). During the first years after menarche, menstrual cycles are characterized by a high frequency of ovulatory failure and luteal phase defects (Vihko and Apter 1984; Venturoli et al. 1987). Significant suppression of ovarian function is still observable in women aged 18 to 22 years relative to women 23 to 35 years, after controlling the potentially confounding factors of exercise and energetic balance (Ellison, Lager, and Calfee 1987). Research into the relationship between age at menarche and the length of adolescent subfecundity is not exact. Some studies show a positive correlation (late age at menarche implies a long period of subfecundity). Other studies show the opposite (Wood 1994).

Stature only marginally increases during this period whereas biiliac breadth reaches adult dimensions and the pelvic basin and birth canal are remodeled (Ellison 1982). Once full adult height and pelvic size is achieved, fat deposition accrues and girls transition from partial to full adult ovarian function (Ellison 2001). Therefore, the period of subfecundity following menarche serves as an important buffer, preventing women from conceiving until the completion of physical maturity.

Measuring the period of adolescent subfecundity from demographic data is often problematic as age at menarche was rarely collected prior to the mid-20th century (Foster et al. 1986). Table 3.1 reports values for age at menarche, age at first birth, and the period between them for 19 small-scale forager, horticultural, and agricultural populations. The average period between these two life history events is 4.3 years, ranging from 2.7 among the Pume“ to 7.9 among the Hiwi, both foraging populations of Venezuela. These data show that menarche and first conception are not simultaneous events. In fact, very early maturers and girls who do conceive within 2 years after menarche suffer significant negative reproductive outcomes (Wyshak 1983; Lancaster and Hamburg 1986; Scholl et al. 1989; Forrest 1993; Satin et al. 1994; Fraser et al. 1995; Olausson et al. 1999; Stevens-Simon et al. 2002), possibly reflecting the combined effects of maternal physiological immaturity and nutritional competition between a still growing mother and her fetus.

Given a tradeoff between growth and current reproduction, postmenarchal but still growing mothers have a smaller pool of energetic resources to devote to production of offspring (Ellis et al. 2009). As such these mothers are smaller and have smaller infants than do adult mothers (Garn et al. 1986; Wallace et al. 2004). Young teen mothers also experience higher rates of gestational complications and mortality, and their babies are at an increased risk of reduced fetal growth, stillbirths, congenital abnormalities, prematurity, low birthweight, and retardation (Black and DeBlassie 1985; Furstenberg et al. 1989; Luster and Mittelstaedt 1993; but see Frisancho 1981; Naeye 1981; Scholl et al. 1990; Scholl et al. 1994; Smith and Pell 2001; King 2003). Rates of infant mortality, very low birth weight and preterm delivery are significantly greater among mothers 15 and younger compared to older teens and experience increased risk of ectopic pregnancy (Sandler et al. 1984), intrauterine fetal growth retardation (Scholl et al. 1989) and miscarriage (Martin et al. 1983).

Variation in human age at first birth

Age at first birth is easier to measure than age at menarche, as date of birth and parentage are commonly collected vital records. Among 20 small-scale societies age at first birth is about 18.97 years, ranging from 15.5 among the Pume of Venezuela to over 25 years among the Gainj of Paupa New Guinea (see Figure 3.1 and Table 3.1). When these small-scale populations are compared with 56 contemporary nations (Figure 3.3), the range for the contemporary nations is narrower, between 17.8 to 23.5 years old. This approximately 8-10 year distribution in average ages at first birth has been reported elsewhere (Walker 2006; Low et al. 2008; Kramer and Lancaster 2010; Nettle 2011) and shows that there is surprisingly little variation in the floor of the age at first birth population averages in humans across temporal and ecological settings. Even under affluent 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 1999; Westoff 2003).

Data from preindustrial and natural fertility (i.e., precontraception) industrial populations (Table 3.2) reveal a later average age at first birth for these populations, in the early to mid-20s. Historic populations, such as the 17th and 18th century French Canadians (LeBourg et al. 1993), demonstrate remarkably high total fertility rates despite their late average age of fertility onset at 23 years old. Over 50% of this population achieved at least 8 children in a lifetime. This runs counter to generalizations that earlier age at first birth implies higher lifetime reproductive success.

Together, these ages at first birth data underscore how late humans tend to have their firstborns compared to age at menarche among the other great apes. While variation is evident, aside from the extremely early age of the Pume“ (15.5 years old), age at first birth in human populations is rarely earlier than 17-18 years old. The upper limit, however, can be much later especially when contraception is a factor. The demographic transition, characterized by later ages at initial reproduction, control of interbirth intervals and the total number of offspring, and substantial declines in total lifetime fertility, results from shifting female strategies in the face of changing market competition and increasing costs of children (Borgerhoff Mulder 1998; Low 2005). Long right-side tails in age at first birth can shift population averages later but do not alter the initial timing of menarche or sexual maturity.

There is a strong, well documented negative association between female age at first birth and education, with the youngest teen mothers concentrated among the least educated segment of the population (Westoff 2003). Postindustrial populations now reflect a bimodal pattern of age at first birth, a peak at around 18 and a second peak around 30 years old (Sullivan 2005). Over the past few decades, nonmarital cohabitation and nonmarital childbearing have increased substantially, and while marriage age and the portion never marrying has increased and age at reproductive onset has been delayed (Bumpass and Raley 1995; Morgan and Rindfuss 1999), the initial potential age at first birth has not.

Marital fertility

Women can bear children only between sexual maturity and menopause, if they are sexually active. Beginning in the 1970s and 1980s demographers began to consider whether cultural marriage norms play an important role in the timing of age at first birth, a constraint referred to as marital fertility (Coale 1971; Coale and Trussell 1974). Marriage - an event that can occur at any time, be entered into at varying ages, can be undone, and may include more than two participants - was incorporated into demographic models as a factor influencing the timing and pace of childbearing (Bumpass et al. 1978; Trussell and Menken 1978). It was proposed that the definition of a woman"s first-birth interbirth interval be revised to include the period between marriage and first parturition, introducing female marital status as a characteristic of firth birth (Marini and Hodsdon 1981; Teachman and Heckert 1985).

Since the mid-1800s developed European countries experienced a postponement of marriage that had a significant effect on reproductive rates (Hajnal 1965). Rural Ireland demonstrated the highest percentage of unwed, reproductive aged individuals with 74% of males and 55% of females between 25-35 years old remaining single in 1936 (Strassmann and Clarke 1998). During each decade between 1871 and 1966 the number of out of wedlock births in this population was less than 4%, indicating a direct link between marriage and fertility (Strassmann and Clarke 1998). By contrast, Coale (1965) selected the Hutterites as the standard for his estimate for total potential fertility of marital fertility, as nearly all women in this population marry at a median age of 22 (Robinson 1986). Coale‟s (1971) models of marital fertility rates for natural fertility populations indicate that changes in the proportion married in a population do not seem to affect the age-specific pattern of fertility within marriage (Coale and Trussell 1974). Those who do marry begin reproduction. Coital frequency may play a significant role in declining fertility with age and marriage length but seems to have little influence on the age at reproductive onset within marriage (Glasser and Lachenbruch 1968).

As Figure 3.4 illustrates there is a 4-6 year lag between age at menarche and age at first birth. Adolescent subfecundity accounts for a large portion of this temporal gap, but first birth is also mediated by sexual exposure necessary for conception. There is some evidence that age at marriage plays a role in the timing of a woman‟s first birth (Kramer & Lancaster 2010). Several cross-cultural studies report that girls who reach menarche early tend to marry and have their first born at a younger age (Urdy and Cliquet 1982; Sandler et al. 1984; Borgerhoff Mulder 1989; Wood 1994; Ellis et al. 2003). But the influence of age at menarche on age at marriage and first birth is not clear. In a sample taken from the United States Tremin Trust dataset, once secular trends in both age at marriage and age at menarche were taken into account, there was no evidence that age at menarche affects either age at marriage or the timing of first births in this population (Riley et al. 2001). In natural fertility populations, the lapse between menarche and exposure to conception is highly variable, and may last from as little as one to 2 years up to over a decade (Schlegel 1995; Whiting et al. 1986), primarily due to differences in ages at marriage. There is broad cultural variation in the frequency and „normative rules‟ about sexual access to young women and premarital sex. While some of the variation between age at menarche and first birth (Figure 3.1) can be attributed to differences in timing of sexual activity characteristic of marriage, it is more likely that age at sexual maturity and first birth dictates the age at which females are likely to be married.

Figure 3.5 illustrates the median age at first marriage and age at first birth for women aged 25-49 in 56 developing countries (Westoff 2003), which shows the strong temporal association between these events. Age at first birth for these populations occurs between 18-24 years old, within the same range as those of small-scale and historic natural fertility populations (Figures 3.1 and 3.3, Table 3.2). While restricting sexual activity by delaying age at marriage can extend the age when women begin to reproduce, marriage does not seem to be timed as a hindrance to female reproduction. The floor of age at first birth for populations represented in these figures is 18 regardless of marriage or other cultural practices across different geographies. There does appear to be a relationship between age at marriage and age at first birth, though it is more likely that the cultural practice of marriage is timed to anticipate female sexual maturity rather than the reverse. Marriage can thus be seen as a life history related event (Robson and Wood 2008).

Great ape comparison

It is possible to compare human age at menarche with other great ape species because all catharrhine primates (old world monkeys and apes, including humans) experience menses. Menstruation is unique to a minority of mammals and occurs when death of some of the endometrial tissue leads to sloughing a part of the uterine lining with some blood flow from the vagina (Strassmann 1996). Detection of menstrual flow makes menarche an observable event, although the amount of overt bleeding is much greater in chimpanzees, bonobos and humans than gorillas and orangutans (Strassmann 1996). In addition to menstruation, reproductive cycling in female chimpanzees and bonobos is also detectable via sexual swellings, a specifically derived feature in the Pan lineage within the great ape taxonomy. Sexual skin swellings are estrogen induced, characterized by edema and pinkness around the genital area. Swelling size and coloration is greatest during puberty with an initial period of „blister swellings" occurring during adolescence that diminish in size with successive menstrual cycles over a period of years (Dixson 1998). During this time, adolescent females experience a period of subfecundity and display heightened proceptive behavior compared to adults (Goodall 1986).

Using the detectable events of menstruation and sexual swellings, researchers have recorded the ages at menarche and at first birth for our great ape relatives. Figure 3.6 shows that age at menarche and first birth are much later for humans than for other great apes, with our closest cousins, the chimpanzees and bonobos showing averages around 8-10 for menarche and 13-14 for first birth, 4-5 years, earlier than the mean age for small-scale societies (see also Figure 3.1 and Table 3.1 for human data). Humans, as life history theory predicts, have much later ages at menarche and first birth than the other great ape species. As for human females, a period of adolescent sterility characterized by irregular, anovulatory cycles preceding fertile cycles commonly occurs in monkeys and apes (Hartman 1931; Young and Yerkes 1943).

There is less known about how social factors might influence the timing of menarche, age at first birth, or the duration of adolescent subfecundity in nonhuman primates. The daughters of dominant females have been found to produce their offspring at an earlier age in several macaque species (Harcourt 1987). Social conditions have a similarly important impact on resource acquisition and growth rates in savanna baboons (Altmann and Alberts 2005). However, stressful social conditions have no influence on age at first conception in rhesus macaques (Maestripieri 2005). Affluence of captivity impacts chimpanzees as affluence does in humans; captives tend to reach menarche earlier, have a shorter duration of adolescent sterility than their counterparts in the wild (Tutin 1980) and earlier ages at first birth (Tutin 1994). A similar finding has been shown for bonobos (de Lathouwers and Van Elsacker 2005). Gorilla age at first birth, however, did not differ under these two conditions (Tutin 1994). Provisioned free-ranging orangutans have earlier ages at first birth than their wild counterparts (Kuze et al 2008). It is clear that young macaque primapare have smaller infants (Bowman and Lee 1995), higher rates of reproductive failure (Berkovitch et al. 1998), stillbirths and failed pregnancies (Altmann et al. 1988), suggesting that still immature pregnant nonhuman primates suffer the same poor outcomes as seen in young human teens.

Central tendencies for age at first birth persist for all great ape species in spite of differences in environment and ecology among populations in the wild (Robson et al. 2006; Robson and Wood 2008). 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. Aside from gorillas, 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 2006). Larger mothers have greater resources for offspring production, and great ape mothers translate this energy into absolutely and relatively larger and more expensive babies (Hawkes 2006; Robson et al. 2006; Stearns 1992). Gorillas grow much faster than the other great apes, a difference that could be due to a largely folivorous diet. Leigh (1994) found that folivorous anthropoids tend to exhibit faster growth rates than comparably sized nonfolivorous ones. Mumby and Vinicius (2009) examined the variation in the pace of growth and correlations with age at first reproduction, maximum longevity and duration of the juvenile period for 36 primate species and their results found a strong decreasing rate of growth with later age at first reproduction.

Evaluating Charnov's life history model

Charnov‟s invariant model predicts that early sexual maturity is achieved by completing growth at a younger age and smaller body size when faced with high extrinsic adult mortality risks and there is compelling evidence supporting a strong relationship between mortality rates, growth rates, body size, and timing of reproductive development and fertility, as predicted. It is generally true that when life expectancy is low, reproductive maturity is early (Chisholm 1999; Hill and Kaplan 1999; Lancaster et al.

2000; Walker et al. 2006b). Across diverse ecologies - Chicago neighborhoods (Wilson and Daly 1997), modern nation-states (Low et al. 2008; Nettle 2011), and small-scale natural fertility societies (Walker et al. 2006a; Migliano et al. 2007; Walker and Hamiton 2008) - higher adult mortality rates are strongly associated with earlier ages at first birth (Ellis et al. 2009).

The association between high morbidity and mortality, and early reproduction has been observed in developed populations (Geronimus 1992, 2003; Wilson and Daly 1997). In studies of interurban US black women, Geronimus demonstrates that under conditions where older women are more likely to be physically disadvantaged, in poor health or not survive, teen motherhood gives children the best chance of having multigenerational caretakers (Kramer and Lancaster 2010). Low et al. (2008) found that for 170 nations, variation in life expectancy at birth accounted for 74% of the variation in age at first birth, with shorter life expectancy and impoverished conditions predicting earlier age at first birth. A similar pattern was found in small-scale human societies (Walker et al. 2006a).

Delaying first reproduction allows individuals to reach larger sizes. Most life history models use body weight to compare quadrapedal species, but in our species generally, using the weights of ethnographic hunter-gatherers may under-represent body size due to decreases in body size during the last 10,000 years (Ruff, Trinkhaus and Holliday 1997). This, and the large inter- and intravariation in human body weight have prompted studies to utilize height for comparisons in bipedal humans. Using data from seven populations, Migliano (Walker et al. 2006a; Migliano et al. 2007) tested whether small pygmy stature was the result of a “fast” life history strategy (Charnov 1993) in which early start of reproduction and growth termination are adaptive responses to high external mortality rates. Walker et al. (2006a) expanded Migliano‟s dataset with 15 additional populations, and these analyses confirm the proposed fast-slow continuum across humans (Migliano et al. 2010).

Across human societies, small stature and early fertility peaks are associated with high overall mortality rates, independent of nutritional factors (Migliano et al. 2007). A notable exception to this pattern is the Pumé population, of Venezuela. Though also documented to experience an early age at first birth and having high adult mortality profiles (Kramer and Greaves 2007), the Pumé are not unusually shorter in adult stature compared to other native South Americans (Kramer et al. 2009). Several studies have shown that taller mothers have better infant survivorship. Using a broad range of maternal height across developing countries, Monden and Smits (2010) found that maternal height is significantly and negatively related with under-five child mortality. Each additional centimeter of maternal height decreases the risk of child mortality, a pattern also found by Walker et al. (2006a).

Discussion

There is clear evidence that high adult mortality and morbidity risk sets the norms of reaction for human fertility. Long-term, prospective studies that follow individual women through adolescence and natural fertility into old age are needed to understand the longitudinal relationships that probably determine aspects of growth and maintenance, morbidity, and fecundity (Ellison 1990).

Although age at marriage can extend the age when women first reproduce, the floor of age at first birth rarely extends below 17-18 regardless of marriage or other cultural practices across different geographies. There appears to be a relationship between age at marriage and age at first birth, probably due to fecundability where marriage nearly always precedes first birth. Marriage can thus be seen as a life history related event (Robson and Wood 2008).

Genetic research has documented substantial genetic influences on a wide range of human life history traits including age at menarche, age at first birth, interbirth interval, fecundity, age at last reproduction, and adult longevity (Kirk et al. 2001; Rodgers et al. 2001; Rowe 2002; Pettay et al. 2005). Strong genetic correlations are also known for macaques (Bloomquist 2009, 2011). Additional studies on these nonrandom genetic associations as well as the long-term epigenetic effects are clearly warranted.

Hawkes (2010) and Hawkes et al. (2009) have described how heterogeneity complicates comparisons of mortality and fertility schedules across populations and across species. Models of life history assume that finite resources require tradeoffs with fitness payoffs assessed over lifetimes. But, the tradeoffs assumed in the models are often difficult to measure directly because individuals differ in the amount of resource they have to allocate (Service 2000; Cam et al. 2002; Zens and Peart 2003; Nussey et al. 2008). Age at sexual maturity is set by extrinsic mortality risk and is earlier if the chance of dying before reproducing is higher. If individual vulnerabilities vary, and developmental schedules are adjusted to those vulnerabilities, then when background mortality decreases, allowing more frail individuals survive, their earlier ages of menarche of would reduce the average age. A similar pattern is seen in comparison of human demographic aging rates (Hawkes et al. 2009), when background mortality is higher, fewer frail individuals survive to older ages. Consequently the mortality rates of older age classes are determined by those who were at lower risk all along. In addition to the ecological effects such as nutrition, the late ages at menarche in small-scale populations compared to large-scale populations (see Figure 3.5) could be due to severe culling at earlier ages. The selective removal of frail individuals who die earlier under severe conditions increases the average age of menarche, reflecting only those more robust individuals who survive to adulthood. Such simple culling of these vulnerable individuals changes the average risk to the survivors and contributes to population averages in the opposite direction. In modern conditions, medical care and affluence allow for the survival of frail individuals who fall within the faster end of the norm of reaction. These individuals move the population average earlier.

Overwhelming evidence suggests that 5-year demographic age class grouping is an inappropriate category for 15 to 20 year old females because young teens, those under 15 years old, are at a substantially higher risk of poor reproductive outcomes than older teens and this pattern cross-cuts diverse human populations (Kramer and Lancaster 2010). Studies that do distinguish outcomes between early versus later adolescents find that adverse outcomes are far more pronounced for very young mothers (Lancaster and Hamburg 1986; Forrest 1993; Satin et al. 1994; Fraser et al. 1995; Olausson et al. 1999) and very early maturers (Scholl et al. 1989). Risks for older teens more closely resemble those of adults (Phipps et al. 2002; Phipps and Sowers 2002). Very young maternal age (girls under the age of 14) is rare. These stark distinctions at specific ages are obscured when all teens are combined into one age class.

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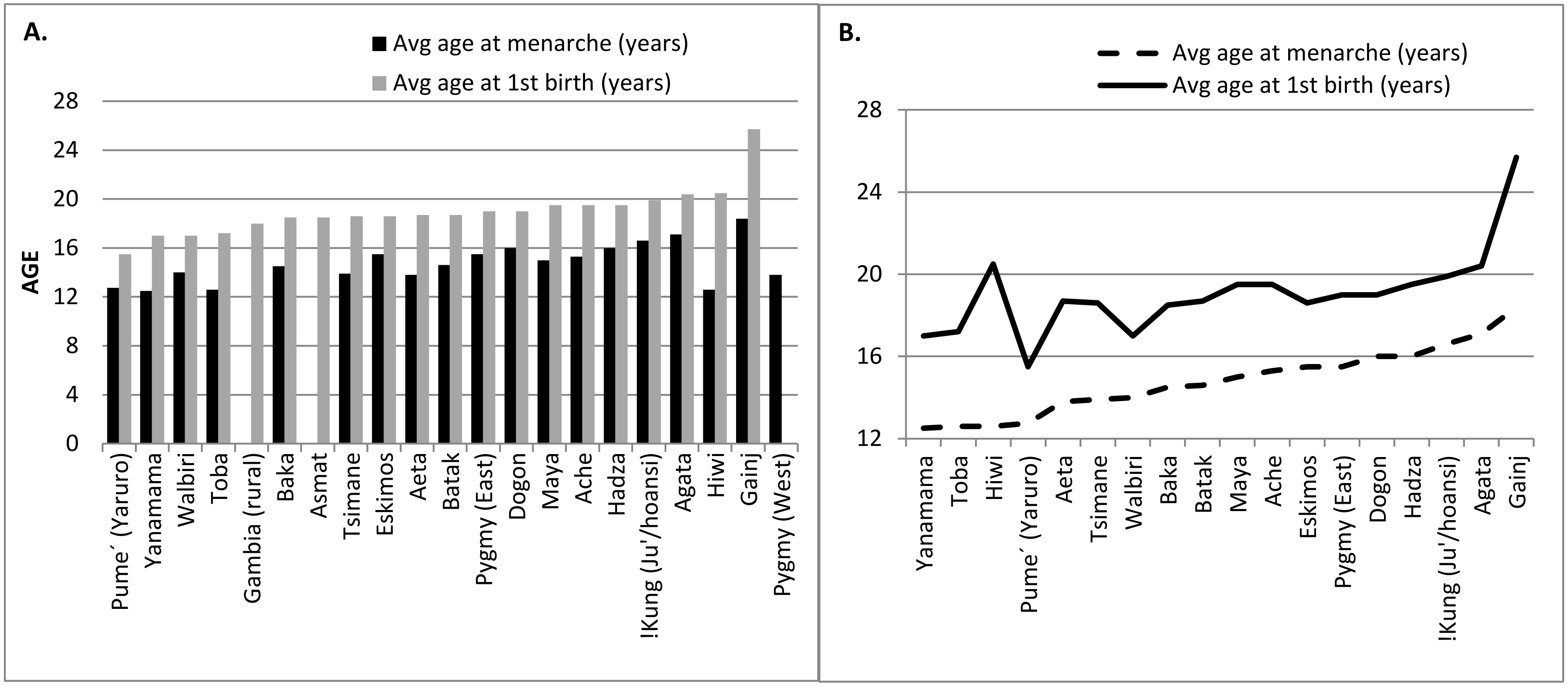

Figure 3.1. Average ages at menarche and first birth for natural fertility foragers, horticulturalists, and agriculturalists. Panel A as plotted by Kramer and Lancaster 2010. Panel B includes only those populations with paired values for each variable. See Table 3.1 for source references.

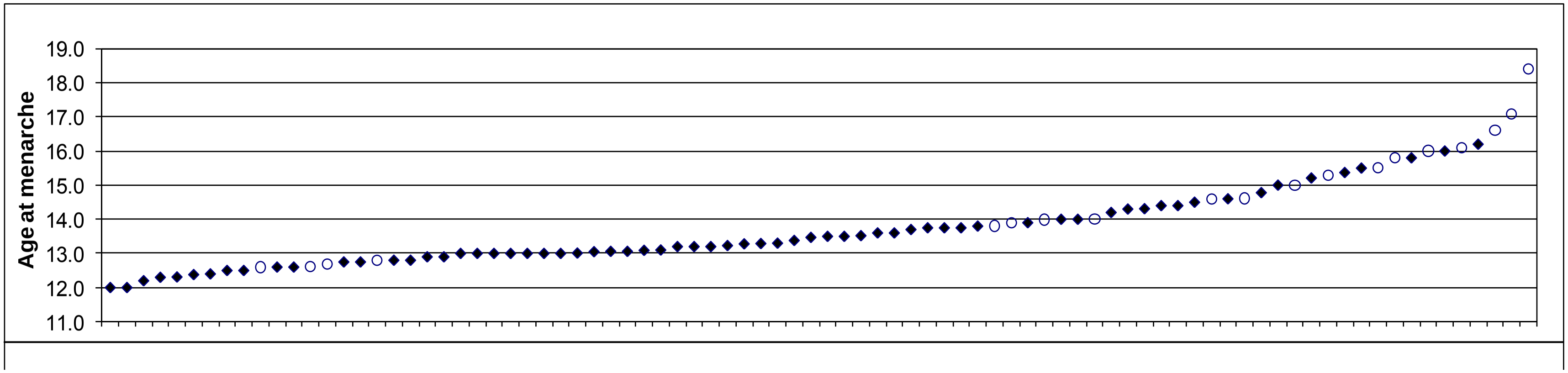

Figure 3.2. Modern mean (or median) age at menarche for 67 contemporary countries worldwide (filled diamonds) and 17 small-scale societies (open circles). Sources: Modern populations from Thomas et al. 2001, small-scale societies see Table 3.1.

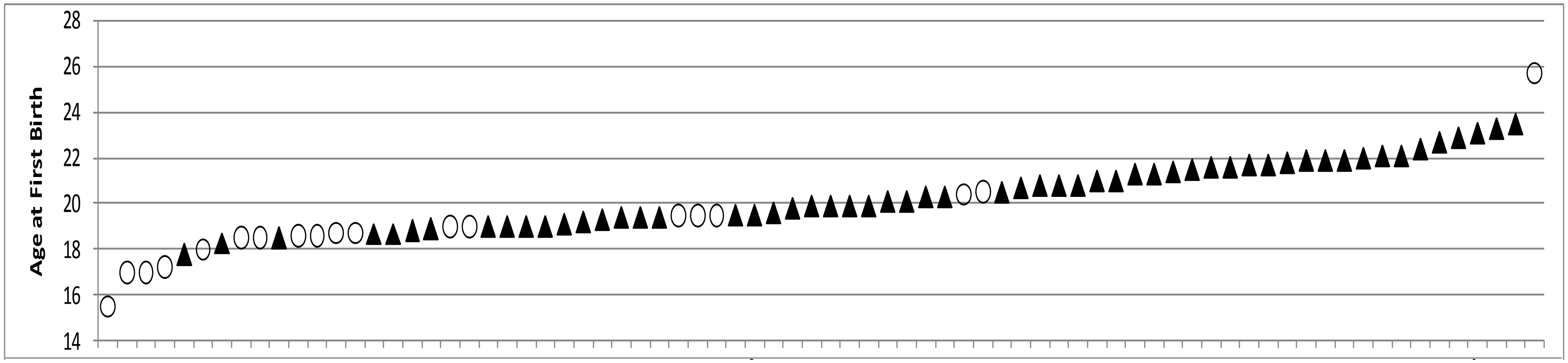

Figure 3.3. Modern mean (or median) age at first birth for 56 developing countries worldwide (filled triangles) and 17 small-scale natural fertility societies (open circles). Sources: Modern values from Westoff 2003, DHS Surveys 1990-2002, small-scale natural fertility societies see Table 3.1.

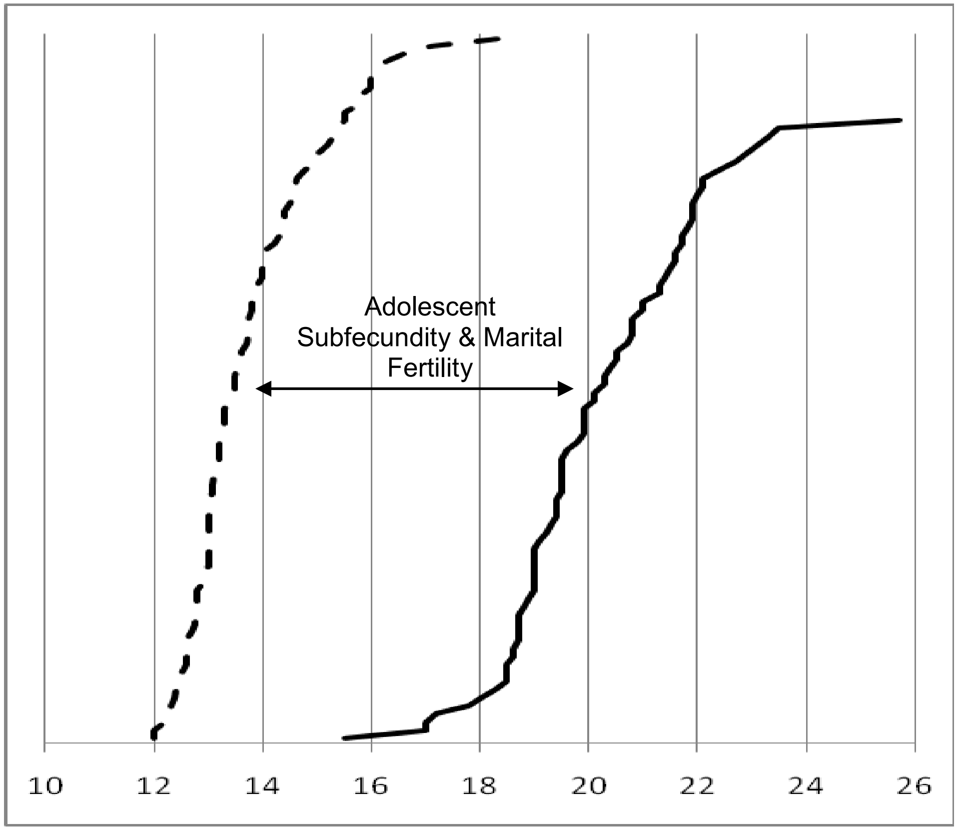

Figure 3.4. The period between human age at menarche and age at first birth (unpaired populations; data from Figures 3.2 & 3.3 transformed vertically), results from adolescent subfecundity and marital fertility.

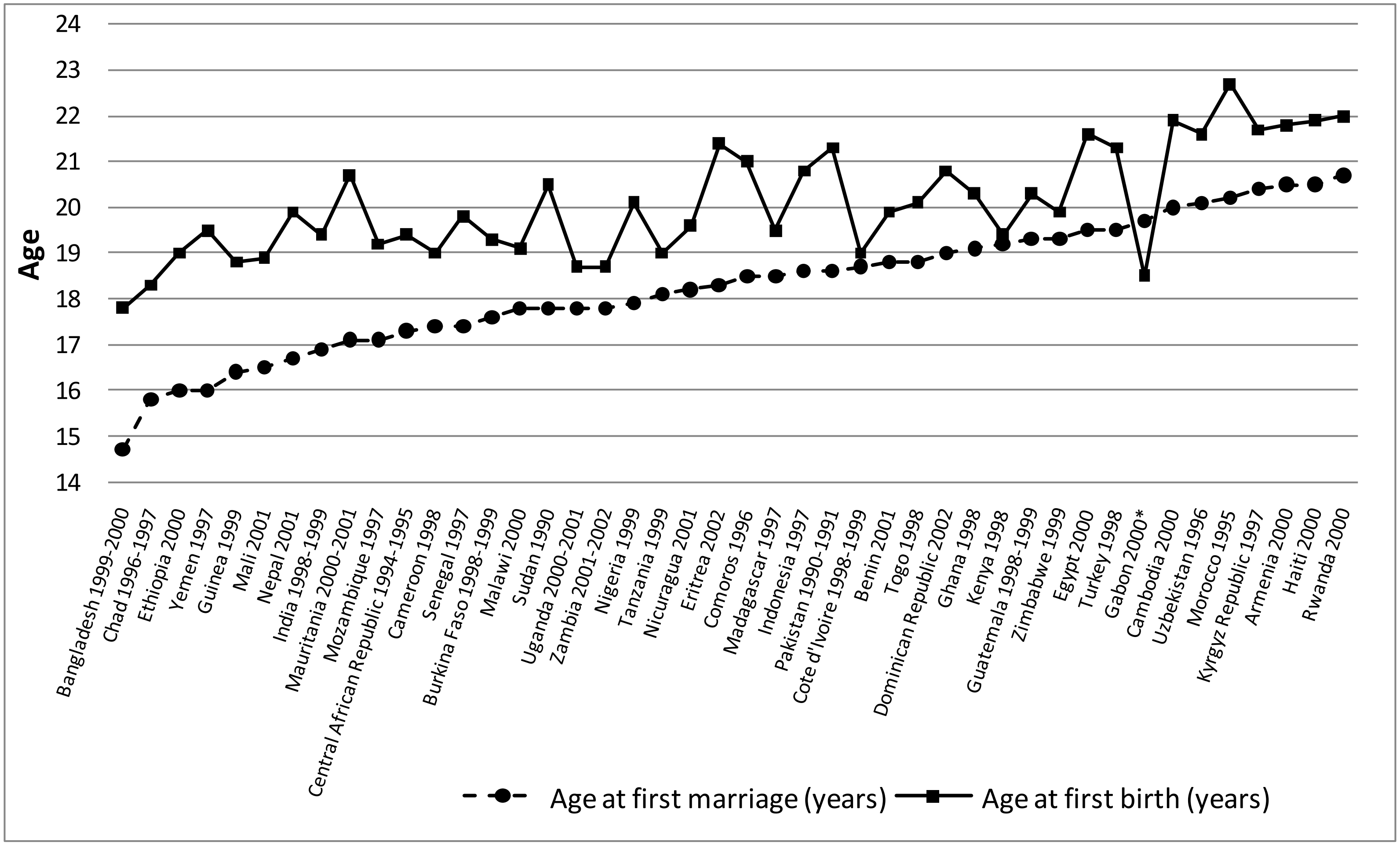

Figure 3.5. Median age at first marriage and at first birth among women aged 25-49 in fifty-six developing countries. Gabon (starred) is the only population in this sample where average age at first birth precedes average age at marriage. Source: Westoff 2003, DHS Surveys 1990-2002.

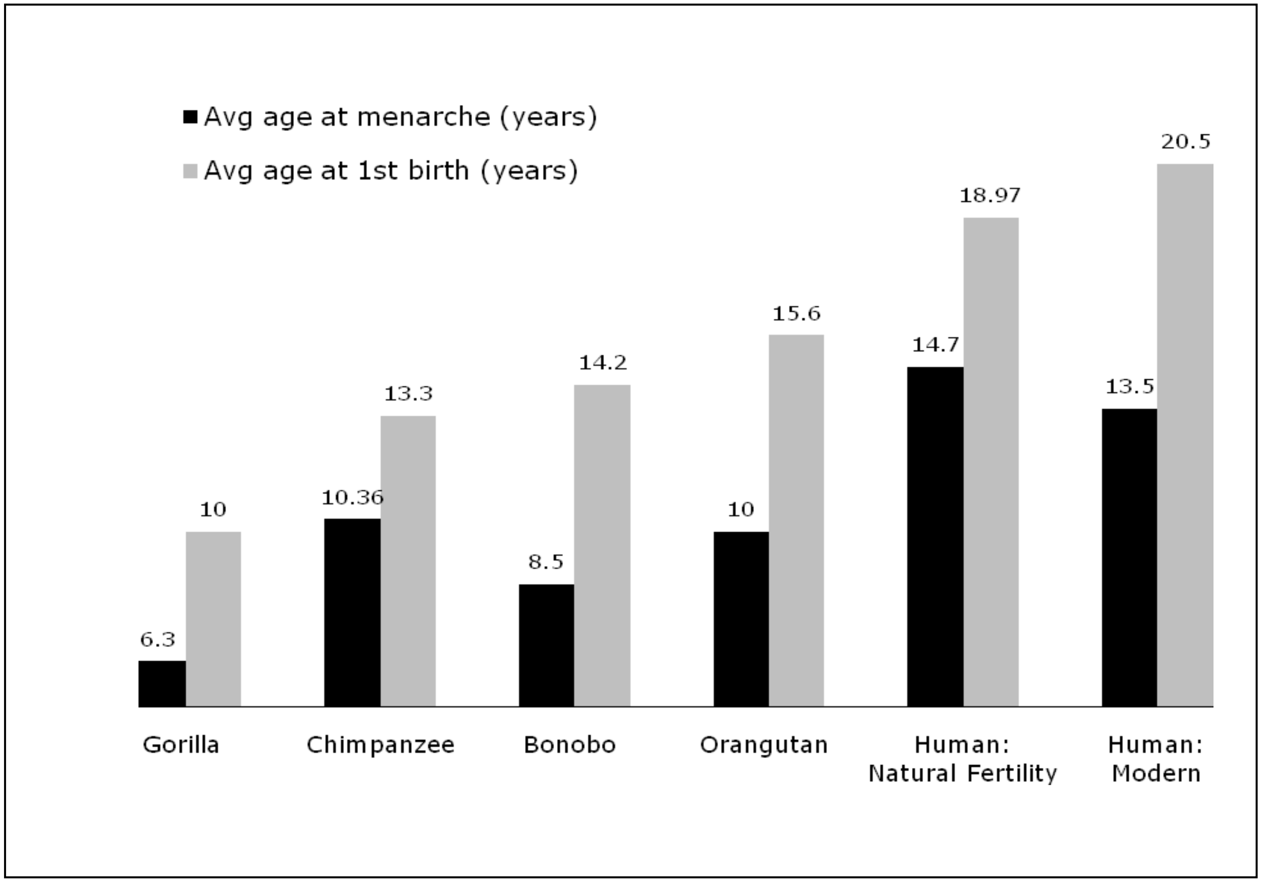

Figure 3.6. Comparison of age at menarche and age at first birth for the great apes. Sources: Orangutan, gorilla, bonobo menarche averages from Knott 2001 and chimpanzee averages from Atsalis and Videan 2009. Age at first birth for these species from Robson and Wood 2008. Small-scale society human averages from sources in Table 1, contemporary human menarche from Thomas et al. 2001, contemporary human ages at first birth from Westoff 2003, DHS Surveys 1990-2002.

Table 3.1. Reproductive and general information for natural fertility foragers, horticulturalists, and agriculturalists.

Study population	Country	Avg age at menarche (years)	Avg age at 1st birth (years)	Sub-fecundity (years)	Data collection period	Source
Pume´ (Yaruro)	Venezuela	12.75	15.5	2.75	1990–93 & 2000-5	Kramer 2008
Yanamama	Venezuela	12.5	17	4.5	1986	Early and Peters 1990
Walbiri	Australia	14	17	3	1950's	Walker et al. 2006a
Toba	Argentina	12.6	17.2	4.6	2003	Lanza, Burke & Valeggia 2008
Gambia (rural)	Gambia		18		1950-74	Allal et al. 2004
Baka	Cameroon	14.5	18.5	4	1996	Walker et al. 2006a
Asmat	Irian Jaya		18.5		.	van Arsdale 1978
Tsimane	Bolivia	13.9	18.6	4.7	2002-03	Walker et al. 2006a
Eskimos	Alaska, USA	15.5	18.6	3.1		Eaton et al 1994, Oswalt 1963
Aeta	Philippines	13.8	18.7	4.9	2002-03	Migliano et al. 2007
Batak	Philippines	14.6	18.7	4.1	1980 & 2003	Eder 1987, 1996
Pygmy (East)	D. R. of Congo	15.5	19	3.5	1980's-90's	Walker et al. 2006a
Dogon	Mali	16	19	3	1988-98	Strassman & Dunbar 1999
Maya	Mexico	15	19.5	4.5	1992-93	Kramer 2005
Ache	Paraguay	15.3	19.5	4.2	1984	Hill & Hurtado 1996
Hadza	Tanzania	16	19.5	3.5	1980's	Blurton Jones et al. 1992
!Kung (Ju'/hoansi)	Botswana/Namibia	16.6	19.9	3.3	1967-69	Howell 1979, 2000
Agata	Philippines	17.1	20.4	3.3	1950-93	Early & Headland 1998
Hiwi	Venezuela	12.6	20.5	7.9	1985-88	Hurtado & Hill 1987, Kaplan et al. 2000
Gainj	New Guinnea	18.4	25.7	7.3	1960s-70s	Wood 1992
Pygmy (West)	Cameroon/Congo	13.8			1975-77	Walker et al. 2006a
		14.76	**18.97**	**4.23**		

Table 3.2. Reproductive and general information for historic populations (1940 or earlier, before widespread availability of contraception).

Study population	Avg age at 1^{st} birth (years)	Historic time period	Source
England/Wales	25.73	1911-1940	Grundy & Tomassini 2005
Maya	20	1900's	Beyene 1989
Greeks	24.5	1900's	Beyene 1989
Rural Finland	25.5	1870-1949	Kopelainen 2003
Utah Mormons	21.73	1800-1900	Smith et al. 2003
Sweden	27.5	1766-1895	Dribe 2003
Amish (old order)	23.75	1749-1912	McArdle et al 2006
European Aristocrats	22.8	1700-1899	Korpelainen 2000; Westendorp & Kirkwood 1998
Rural Germany	26.3	1700-1899	Knodel 1987
French-Canadians	22.4	1608-1765	LeBourg et al. 1993
Britian (NSHD study)	23	1946	Kiernan & Diamond 1983
United States	22	1940	Frejka & Sardon 2004
Bulgaria	22.01	1940	Frejka & Sardon 2004
Slovak Republic	22.33	1940	Frejka & Sardon 2004
Czech Republic	22.48	1940	Frejka & Sardon 2004
Former GDR	22.76	1940	Frejka & Sardon 2004
Hungary	22.77	1940	Frejka & Sardon 2004
Serbia & Montenegro	22.91	1940	Frejka & Sardon 2004
Bosnia & Herzegovina	23.13	1940	Frejka & Sardon 2004
Croatia	23.29	1940	Frejka & Sardon 2004
Macedonia	23.3	1940	Frejka & Sardon 2004
England and Wales	23.89	1940	Frejka & Sardon 2004
Slovenia	23.96	1940	Frejka & Sardon 2004
Netherlands	24.98	1940	Frejka & Sardon 2004
Italy	25.35	1940	Frejka & Sardon 2004
	23.53		

CHAPTER 4

TWINNING IN HUMANS: MATERNAL HETEROGENEITY IN REPRODUCTION AND SURVIVAL

by
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Twinning in humans: maternal heterogeneity in reproduction and survival

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While humans usually give birth to singletons, dizygotic twinning occurs at low rates in all populations worldwide. We evaluate two hypotheses that have differing expectations about the effects of bearing twins on maternal lifetime reproduction and survival. The maternal depletion hypothesis argues that mothers of twins will suffer negative outcomes owing to the higher physiological costs associated with bearing multiples. Alternatively, twinning, while costly, may indicate mothers with a greater capacity to bear that cost. Drawing from the vast natural fertility data in the Utah Population Database, we compared the reproductive and survival events of 4603 mothers who bore twins and 54 183 who had not. These mothers were born between 1807 and 1899, lived at least to the age of 50 years and married once to men who were alive when their wives were 50. Results from proportional hazards and regression analyses are consistent with the second hypothesis. Mothers of twins exhibit lower postmenopausal mortality, shorter average inter-birth intervals, later ages at last birth and higher lifetime fertility than their singleton-only bearing counterparts. From the largest historical sample of twinning mothers yet published, we conclude that bearing twins is more likely for those with a robust phenotype and is a useful index of maternal heterogeneity.

Keywords: twinning; heterogeneity; maternal depletion; reproduction; life history

1. INTRODUCTION

Though rare, twinning is not uncommon among humans, universally occurring at persistently low rates worldwide [1]. Rates of spontaneous twinning range from about 6 per thousand (‰) livebirths in Asia, 10–20‰ in Europe and the United States, to about 40‰ in Africa [2] The overall twinning rate is primarily owing to differences in dizygotic twinning [2], the gestation of two separately fertilized ova. Monozygotic twinning, the split of one fertilized egg into two identical zygotes, is random and non-heritable, occurring at a fairly stable rate of 3.5–4.0‰ across populations sampled [3]. Dizygotic twinning results from polyovulation, which varies by population and clusters in families [4]. While dizygotic twinning may have a heritable component [2], many studies have shown that it is more environmentally facultative than genetic [5–9].

Twinning and increased litter size have high maternal and offspring mortality risks, reducing offspring quality and often cancelling out any fitness advantages of bearing multiples [10–12]. These mortality risks combined with the low rates of twinning in humans and other catarrhine primates [13,14] suggest that these primate species are all adapted to bear only one offspring per gestation [12]. Anderson [15] argues that twinning is not itself adaptive, but rather may be a by-product of 'insurance ovulation' designed to hedge the risks of early embryo loss and increase the survival of at least one viable zygote. It is well documented that many more twins are conceived than born, an event known as the 'vanishing twin phenomenon' [16]. This suggests that there is individual variation in both the frequency of polyovulation and the efficiency of embryo rejection [17]. As such, bearing twins may be a 'cost-intensive error in an adaptive brood reduction system' [10, p. 700]. The insurance ovulation hypothesis predicts that bearing twins exacts fitness costs that outweigh any fitness benefits gained from increased offspring quantity. Successful twin pregnancies are more costly than singletons and mothers of twins are expected to suffer maternal depletion effects [18].

Yet, evidence for a maternal depletion effect is equivocal [19]. Hurt *et al.* [20] found that in some selected cases, mortality actually declined with increasing births among 12 historical cohorts (populations unable to benefit from better healthcare available in modern societies), though results were inconsistent and not always significant.

In opposition to the maternal depletion hypothesis, mothers who are able to sustain the cost of twin pregnancies may gain a fitness advantage by doing so. Sear *et al.* [21] found that mothers in rural Gambia who had given birth to twins had higher overall fertility than mothers who bore only singletons. Twinning may be an indicator of higher maternal capacity and may identify those women whose enhanced phenotypic quality allows them to bear these elevated reproductive costs. Under this hypothesis, women who twin should outperform mothers of singletons on other life-history measures as well.

This heterogeneity hypothesis is consistent with observations that women with higher fertility rates and later ages at last birth (ALB) also have higher subsequent survival rates [22–24]. While these correlations appear to challenge the allocation trade-offs between somatic maintenance and reproduction predicted by most evolutionary models [25], the paradox of unmeasured heterogeneity obscures the trade-offs [26–28]. When subjects differ in their inherent quality, those with fewer resources are prone to fail at earlier ages while more robust individuals survive and thrive in measurable ways. Accordingly, twinning mothers should exhibit additional features of a robust

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phenotype, including shorter average inter-birth intervals, later ALB and longer reproductive spans resulting in higher parities, and longer postmenopausal lifespans.

To evaluate these alternative hypotheses, we measured correlations between twinning and maternal reproductive and life-history measures using a large sample of parous women from a vast historical database documenting a natural fertility population in Utah where fertility was high. We first compare survival past the age of 50 between twinning and singleton-only mothers. Then we compare several key reproductive traits: lifetime parity, average inter-birth interval, ALB and reproductive span length.

2. DEMOGRAPHIC DATA AND METHODS

We examined whether mothers of twins were more robust by comparing the reproductive and survival events of mothers who bore at least one set of twins with those women who did not in the Utah Population Database (UPDB). The UPDB is one of the world's most comprehensive computerized genealogies collating the vital records of migrants to Utah and their Utah descendants for more than 1.6 million individuals born from the early 1800s to the mid-1970s (see http://www.huntsmancancer.org/groups/ppr/). Because these records include basic demographic information on parents and their children, fertility and mortality data are extensive with coverage up to the present [29]. Previous studies by Wyshak [4,30–35] investigated the inheritance, demographics and characteristics of human twinning using the UPDB. However, there are many limitations of these early studies that precede digitization, including a lack of non-twin control for comparison, very restrictive time periods (1850 and earlier) and data quality concerns (fallibility of hand sorting and linkage). A subsequent investigation on twinning in the UPDB by Carmelli *et al.* [36] describes the demographics and kinship survey of twins finding a variable twinning rate of 11.5–14.0‰ births between 1820 and 1910, with a steady decline in both fertility and twinning thereafter.

The large size of the UPDB allowed us to restrict our sample to parous women who were born between 1807 and 1899 and lived at least to the age of 50 years, thereby including only those women who experienced their entire reproductive span and complete fertility. To avoid confounding reproductive variables by widowhood, we limited the sample to those women who were married just once to men who were still alive when their wives were 50. We also excluded women in polygamous marriages, which constituted a small per cent of the data. Even with these restrictions, we captured a sizable number of women who bore twins in a natural fertility population. The final restricted sample had records for 58 786 women, 4603 of those were mothers of twins (7.84%) and 54 183 had singleton-only births. To examine social and cultural impacts of the demographic transition, we divided our sample into those women whose birth date was before or after 1870 to distinguish the natural fertility era from the early stages of fertility planning. We trimmed the pre-1870 birth cohort to those who were married after 1850. Those marrying prior to 1850 were generally a select set who often were married outside of Utah. Table 1 summarizes the descriptive statistics for all of the model variables for both cohorts.

We conducted several analyses to determine whether females in our sample who bore twins differed significantly

Table 1. Descriptive statistics of the Utah Population Database sample. (The sample is divided into two cohorts by birth year (before and after 1870) to examine any effects of the demographic transition in the younger cohort. AFB, age at first birth; ALB, age at last birth; LDS, Latter-day Saints.)

	mother's birth year before 1870						mother's birth year 1870–1900					
variable	*n*	mean	median	s.d.	min	max	*n*	mean	median	s.d.	min	max
postmenopausal longevity (after 50 years)	21 150	75.09	76	11.0374	50	108	37 636	78.33	80	11.7900	50	112
birth year	21 150	1853.73	1857	11.7308	1807	1869	37 636	1885.77	1886	8.5298	1870	1899
ever mother of twins	21 150	0.098	0	0.2969	0	1	37 636	0.07	0	0.2507	0	1
number of children (lifetime)	21 150	8.39	9	3.0757	1	21	37 636	5.72	5	3.1124	1	20
AFB	21 150	22.01	21	3.9095	15	35	37 636	23.30	23	3.8254	15	35
ALB	21 150	39.73	41	4.9855	16	50	37 636	36.21	37	6.1279	15	50
number of children died before 18 years	21 150	1.50	1	1.5410	0	17	37 636	0.07	0	1.0287	0	13
husband age at death	21 150	72.64	74	12.6278	23	105	37 636	73.57	75	13.2614	20	108
LDS religion (yes/no)	21 150	0.68	1	0.4667	0	1	37 636	0.64	1	0.4806	0	1
number of spouses (limit 1)	21 150	1	1	0	1	1	37 636	1	1	0	1	1
polygamous (yes = excluded)	21 150	0	0	0	0	0	37 636	0	0	0	0	0
average inter-birth interval	20 789	2.62	2.4	1.0249	0.82	25	34 834	3.24	2.8	1.7166	0.83	27
marriage year	21 150	1874.48	1876	11.6505	1850	1910	37 636	1907.32	1908	9.2161	1883	1937
reproductive span (ALB–AFB)	20 814	18.00	19	5.8368	1	33	34 881	14.04	14	6.3093	1	34

Table 2. Mortality hazard ratios for women living past age 50. (The interaction term twin-parity is introduced to the model and parity is centred at the cohort average to account for collinearity. HRR, hazard rate ratio; AFB, age at first birth; ALB, age at last birth; LDS, Latter-day Saints.)

	dependent variable: postmenopausal longevity							
	likelihood ratio = 116.3047, $p > \chi^2 \le 0.0001$				likelihood ratio = 1227.8321, $p > \chi^2 \le 0.0001$			
	mother's birth year before 1870, $n = 21\,150$				mother's birth year after 1870–1900, $n = 37\,636$			
		95% confidence limits				95% confidence limits		
variable	HRR	lower CI	upper CI	$p > \chi^2$	HRR	lower CI	upper CI	$p > \chi^2$
birth year	0.996	0.995	0.998	<0.0001	0.982	0.981	0.983	<.0001
ever mother of twins	0.924	0.872	0.98	0.0081	0.967	0.927	1.008	0.1137
parity_centred	1.013	1.004	1.002	0.0058	1.018	1.011	1.025	<0.0001
twin-parity: interaction	1.031	1.014	1.049	0.0004	0.988	0.975	1.002	0.0894
AFB	0.996	0.991	1.001	0.1578	0.995	0.992	0.999	0.0122
ALB	0.987	0.983	0.992	<0.0001	0.990	0.987	0.993	<0.0001
children died before 18	1.002	0.992	1.013	0.6299	1.032	1.020	1.044	<.0001
husband lifespan	1.001	1.000	1.002	0.1883	0.998	0.997	0.998	<0.0001
LDS religion	0.977	0.949	1.006	0.1168	0.925	0.905	0.945	<0.0001

from singleton-only mothers on standard reproductive and life-history measures. First, we assessed whether twinning was associated with a woman's survival past menopause based on results from Cox proportional hazards regression analysis. Model covariates included year of mother's birth, age at first birth (AFB), ALB, age at death of husband, total number of children (lifetime parity), ever having twins and number of children who died before the age of 18 (a measure of child mortality). In this model, we introduce an interaction term (twin-parity) to control for increases in twinning at later maternal age. We also adjusted for religious affiliation (member or non-member of the Church of Jesus Christ of Latter-day Saints (LDS religion)). We then assessed whether mothers of twins had higher parity, shorter average inter-birth intervals, longer reproductive spans and later ALB than non-twinning mothers from regression analyses using SAS statistical software.

3. RESULTS

(a) *Postmenopausal survival*

Table 2 reports the results of Cox proportional hazards regression comparing the postmenopausal survival of women who did or did not have a twin set during her reproductive career. We centred parity to control for the effects of collinearity introduced by the interaction term (twin-parity). Model results (table 2) show that when evaluated at average parity (pre-1870 cohort = 8.39, post-1870 cohort = 5.72), mothers of twins have a survival advantage over singleton-only bearing mothers (pre-1870) hazard rate ratio (HRR) = 0.924, $p = 0.008$, post-1870 HRR = 0.967, $p = 0.1137$). Although this effect is only significant for the pre-1870 birth cohort, there was a survival benefit of being a mother of twins that persisted until very high parities. The benefit of bearing twins did not diminish until a parity of 12, which is extreme for this population, when both sets of mothers then share the same survival.

(b) *Parity*

We examined whether total lifetime parity differed between twin and non-twin mothers using regression analyses. The overall average number of children per mother in the pre-1870 cohort was 8.39 and for the post-1870 cohort was 5.72 (table 1). Table 3(*a*) shows that mothers of twins in both birth cohorts had a significantly higher lifetime parity (pre-1870, $p < 0.0001$; post-1870, $p < 0.0001$), averaging 1.9 and 2.3 more children, respectively, than non-twinning mothers controlling for the effects of age at marriage and AFB, survival of husband after the mother reached age 50 and LDS religious affiliation. In table 3(*b*), we examined whether higher parity results from child replacement owing to higher offspring mortality of twins by controlling for child mortality before the age of 18. The parity advantage of twinning mothers dropped slightly to 1.24 in the pre-1870 cohort and 1.56 more children in the post-1870 than singleton-only mothers, but remained significantly greater than non-twinning mothers (both cohorts, $p < 0.0001$). While a twin set itself increases a mother's parity by 1, the parities of twinning mothers in the UPDB exceed this advantage, showing that mothers of twins bear a higher number of singletons as well.

(c) *Average inter-birth interval*

Table 4 reports the results of a regression model showing that mothers of twins had shorter, albeit small, average inter-birth intervals than non-twinning mothers (pre-1870, $p = 0.1228$; post-1870, $p = 0.0013$), controlling for AFB and ALB, offspring mortality, survival of husband after the mother reached the age of 50 and LDS religious affiliation. The average inter-birth interval in the pre-1870 cohort was 2.62 years and for the post-1870 cohort was 3.24 years (table 1). As expected, the largest variable influencing the length of the average inter-birth interval is child mortality. The inter-birth intervals of twinning mothers were significantly shorter in the later era cohort even when average birth intervals were longer.

(d) *Reproductive span and ALB*

Tables 5(*a*) and 6(*a*) show that that mothers of twins had a significantly longer reproductive span (calculated as ALB minus AFB; pre-1870, $p < 0.0001$; post-1870, $p < 0.0001$) and later ages at last birth (pre-1870, $p < 0.0001$;

Table 3. Linear regression results for the effects of bearing twins on lifetime parity. (Panel (*b*) controls for offspring mortality. AFB, age at first birth; ALB, age at last birth; LDS, Latter-day Saints.)

	dependent variable: number of children (mother's parity)							
	mother's birth year before 1870, $n = 21\,150$				mother's birth year after 1870–1900, $n = 37\,636$			
		95% confidence limits				95% confidence limits		
variable	β	lower CI	upper CI	$p{>}\chi^2$	β	lower CI	upper CI	$p{>}\chi^2$
(*a*)	$p > F \leq 0.0001$, $r^2 = 0.3086$				$p > F \leq 0.0001$, $r^2 = 0.3088$			
intercept	74.4104	68.8272	79.9935	<0.0001	185.1639	179.4108	190.8571	<0.0001
ever mother of twins	1.9352	1.8190	2.0515	<0.0001	2.3286	2.2240	2.4331	<0.0001
marriage year	−0.0322	−0.0351	−0.0292	<0.0001	−0.0916	−0.0946	−0.0885	<0.0001
AFB	−0.3597	−0.3686	−0.3507	<0.0001	−0.2763	−0.2835	−0.2690	<0.0001
husband lifespan	0.0222	0.0195	0.0249	<0.0001	0.0126	0.0106	0.0146	<0.0001
LDS	0.5406	0.4661	0.6151	<0.0001	0.7923	0.7376	0.8471	<0.0001
(*b*)	$p > F \leq 0.0001$, $r^2 = 0.4290$				$p > F \leq 0.0001$, $r^2 = 0.4240$			
intercept	50.0987	44.9757	55.2217	<0.0001	140.1592	134.8633	145.4551	<0.0001
ever mother of twins	1.2446	1.1371	1.3521	<0.0001	1.5556	1.4586	1.6527	<0.0001
marriage year	−0.0201	−0.0229	−0.0174	<0.0001	−0.0688	−0.0716	−0.0660	<0.0001
AFB	−0.3136	−0.3218	0.3053	<0.0001	−0.2357	−0.2424	−0.2291	<0.0001
children died before 18	0.7258	0.7045	0.7471	<0.0001	1.0871	1.0625	1.1167	<0.0001
husband lifespan	0.0192	0.0167	0.0217	<0.0001	0.01168	0.0099	0.0135	<0.0001
LDS religion	0.4580	0.3902	0.5257	<0.0001	0.7170	0.6670	0.7670	<0.0001

Table 4. Linear regression results for the effects of bearing twins on average inter-birth intervals. (AFB, age at first birth; ALB, age at last birth; LDS, Latter-day Saints.)

	dependent variable: average inter-birth interval							
	$p > F \leq 0.0001$, $r^2 = 0.1086$				$p > F \leq 0.0001$, $r^2 = 0.0897$			
	mother's birth year before 1870, $n = 20\,350$				mother's birth year after 1870–1900, $n = 31\,909$			
		95% confidence limits				95% confidence limits		
variable	β	lower CI	upper CI	$p{>}\chi^2$	β	lower CI	upper CI	$p{>}\chi^2$
intercept	−8.1086	−9.4646	−6.7526	<0.0001	−18.4527	−20.5780	−16.3275	<0.0001
ever mother of twins	−0.0219	−0.0497	0.0059	0.1228	−0.0571	−0.0918	−0.0224	0.0013
birth year	0.0056	0.0049	0.0063	<0.0001	−0.0688	−0.0716	−0.0660	<0.0001
AFB	−0.0100	−0.0123	−0.0078	<0.0001	−0.0162	−0.0188	−0.0137	<0.0001
ALB	0.0149	0.0130	0.0167	<0.0001	0.0278	0.0260	0.0296	<0.0001
children died before 18	−0.1242	−0.1299	−0.1185	<0.0001	−0.2153	−0.2244	−0.2062	<0.0001
husband lifespan	0.0018	0.0011	0.0025	<0.0001	0.0025	0.0018	0.0032	<0.0001
LDS religion	−0.0965	−0.1144	−0.0787	<0.0001	−0.0332	−0.0525	−0.0139	0.0008

post-1870, $p < 0.0001$) than non-twinning mothers, controlling for AFB, offspring mortality, survival of husband after the mother reached the age of 50 and LDS religious affiliation. Both dependent variables remain significant for the pre- and post-1870 birth cohorts after controlling for age at marriage (tables 5(*b*) and 6(*b*)).

4. DISCUSSION

Our results from analyses using a large, historical, natural fertility population show that twinning mothers 'outperformed' their singleton-only counterparts by living longer past menopause, having higher overall parity, shorter average inter-birth intervals, longer reproductive spans and later ALB than non-twinning mothers. We restricted our sample to parous women who had survived to the age of 50, already a robust subset of the UPDB, making the comparison groups more similar, and yet our results still found significant differences between twinning and non-twinning mothers. If twinning mothers had 'underperformed' on these measures, this would have supported the maternal depletion hypothesis that twinning is costly and detrimental to female health and fertility. We found that mothers of twins in the UPDB sample exhibit a robust phenotype on several reproductive and life-history measures compared with their singleton-only bearing counterparts, suggesting that bearing twins marks a more robust maternal phenotype.

Lack of support for negative long-term consequences of twin childbearing is consistent with the heterogeneity hypothesis, which predicts that some women in a population bear reproductive costs more readily than others

Table 5. Linear regression results for the effects of bearing twins on total reproductive span. (The model in panel (*a*) controls for AFB while panel (*b*) includes marriage year. ALB, age at last birth; AFB, age at first birth; LDS, Latter-day Saints.)

	dependent variable: reproductive interval (ALB–AFB)							
	mother's birth year before 1870, $n = 21\,150$				mother's birth year 1870–1900, $n = 37\,636$			
		95% confidence limits				95% confidence limits		
variable	β	lower CI	upper CI	$p>\chi^2$	β	lower CI	upper CI	$p>\chi^2$
(*a*)	$p > F \leq 0.0001$, $r^2 = 0.4197$				$p > F \leq 0.0001$, $r^2 = 0.3101$			
intercept	30.5754	30.0542	31.0967	<0.0001	26.9117	26.4330	27.3904	<0.0001
ever mother of twins	0.3038	0.0979	0.5097	0.0038	0.8531	0.6365	1.0697	<0.0001
AFB	−0.8417	−0.8578	−0.8257	<0.0001	−0.7656	−0.7810	−0.7501	<0.0001
children died before 18	0.7628	0.7223	0.8034	<0.0001	1.4698	1.4156	1.5241	<0.0001
husband lifespan	0.0594	0.0546	0.0643	<0.0001	0.0366	0.0324	0.0408	<0.0001
LDS religion	0.5533	0.4224	0.6843	<0.0001	1.2696	1.1533	1.3858	<0.0001
(*b*)	$p > F \leq 0.0001$, $r^2 = 0.1327$				$p > F \leq 0.0001$, $r^2 = 0.2343$			
intercept	93.2099	81.1301	105.2896	<0.0001	456.9310	444.5654	469.2967	<0.0001
ever mother of twins	0.3118	0.0601	0.5636	0.0152	0.8684	0.6402	1.0966	<0.0001
marriage year	−0.0438	−0.0502	−0.0374	<0.0001	−0.2350	−0.2415	−0.2285	<0.0001
children died before 18	1.0731	1.0237	1.1226	<0.0001	1.4846	1.4270	1.5423	<0.0001
husband lifespan	0.0590	0.0531	0.0649	<0.0001	0.0464	0.0419	0.0509	<0.0001
LDS religion	1.3205	1.1615	1.4796	<0.0001	1.0615	0.9393	1.1838	<0.0001

Table 6. Linear regression results for the effects of bearing twins on age at last birth. (The model results in panel (*a*) control for AFB while panel (*b*) controls for marriage year. ALB, age at last birth; AFB, age at first birth, LDS, Latter-day Saints.)

	dependent variable: ALB							
	mother's birth year before 1870, $n = 21\,150$				mother's birth year after 1870–1900, $n = 37\,636$			
		95% confidence limits				95% confidence limits		
variable	β	lower CI	upper CI	$P>\chi^2$	β	lower CI	upper CI	$p>\chi^2$
(*a*)	$p > F \leq 0.0001$, $r^2 = 0.1075$				$p > F \leq 0.0001$, $r^2 = 0.1283$			
intercept	30.5965	30.0519	31.1411	<0.0001	27.0483	26.5560	27.5406	<0.0001
ever mother of twins	0.3893	0.1714	0.6072	0.0005	1.1633	0.9283	1.3982	<0.0001
AFB	0.1290	0.1124	0.1457	<0.0001	0.1604	0.1449	0.1759	<0.0001
children died before 18	0.8653	0.8225	0.9081	<0.0001	1.8084	1.7499	1.8669	<0.0001
husband lifespan	0.0621	0.0570	0.0671	<0.0001	0.0412	0.0368	0.0456	<0.0001
LDS religion	0.6553	0.5180	0.7926	<0.0001	1.6738	1.5572	1.7949	<0.0001
(*b*)	$p > F \leq 0.0001$, $r^2 = 0.0984$				$p > F \leq 0.0001$, $r^2 = 0.1524$			
intercept	53.7946	43.3852	64.2040	<0.0001	270.7687	258.6164	282.9809	<0.0001
ever mother of twins	0.3968	0.1778	0.6159	<0.0001	1.1064	0.8746	1.3381	<0.0001
marriage year	−0.0108	−0.0163	−0.0052	<0.0001	−0.1259	−0.1323	−0.1196	<0.0001
children died before 18	0.7931	0.7503	0.8359	<0.0001	1.4133	1.3552	1.4714	<0.0001
husband lifespan	0.0618	0.0567	0.0669	<0.0001	0.0461	0.0417	0.0504	<0.0001
LDS religion	0.5356	0.3985	0.6727	<0.0001	1.8445	1.7252	1.9638	<0.0001

[37]. More frail women have both longer inter-birth intervals and earlier ALB, resulting in lower fertility. The women who continue to bear offspring to older ages are a more robust subset who have higher fertilities and are more likely to successfully incur the cost of twins.

Several previous studies also have suggested that the ability to twin may reflect enhanced maternal phenotypic quality. Instead of twin deliveries, Helle *et al.* [38] used the expected productivity of a singleton delivery and found that 'twin mothers would have had higher fitness than singleton mothers independently of twinning... suggesting that twin mothers were generally of higher phenotypic quality' (p. 434). While 'there may be some qualities of twin mothers that allow them to bear the elevated costs of a twin pregnancy', [21, p. 441], 'mothers with twins usually had singletons too' [12, p. 576], suggesting that twinning is an opportunistic reproductive strategy of some women during favourable ecological circumstances or maternal condition. In addition, mothers of twins are generally in better physiological condition and are taller [6,9,21,39,40].

Among the studies of twin mothers in pre-industrial populations, Haukioja *et al.* [12] found that twinning did not increase lifetime reproduction in eighteenth and nineteenth century Finland owing to high maternal and offspring mortality. Gabler & Voland [10] report that that life expectancy of twinning mothers in the Krummhorn dataset of eighteenth to nineteenth century Germany was not statistically different from those only bearing singletons, therefore finding no maternal mortality costs as a result of twinning. They also report, as we do, that mothers of twins have shorter inter-birth intervals, longer reproductive spans, later ALB and a higher overall fecundity (though high parities in this population are not owing to twinning, but rather from a higher overall fertility rate of singletons). Skjaervo *et al.* [41] show that mothers of twins in 1700–1900 central Norway have higher fecundity, longer reproductive spans and later ALB.

Lummaa *et al.* [8] found no differences in inter-birth interval length between twinning and non-twinning mothers in historical data from northern Finland. Comparing two pre-industrial Finnish populations with differing food resource availability, Lummaa *et al.* [8,42] found that twins enhanced the reproductive success of mothers where food was abundant and reliable, but reduced lifetime fertility where crop failures and famines were more common. This suggests that twinning may be an opportunistic reproductive strategy, or its genetic frequency selected, during favourable environmental circumstances.

This pattern of reproductive robustness and enhanced survival among twinning mothers is also seen in a contemporary natural fertility population. Sear *et al.* [21] examined the reproductive histories of women in rural Gambia, Africa, and found that mothers of twins had shorter inter-birth intervals, higher age-specific fertility, more surviving offspring and higher anthropometric status during their teen years than mothers of singletons only. From these results, the authors suggest that 'twin mothers may be of higher phenotypic quality than women who only give birth to singletons' (p. 441).

Historical demographic data offer important value for testing evolutionary hypotheses in natural fertility populations that best approximate reproductive conditions during human evolutionary history [43,44]. The few studies that have investigated the reproductive and life-history effects of twinning in natural fertility populations have conducted analyses with very small sample sizes (largest ≈ 250) [10,12,21,38,41,42,45,46] often yielding equivocal results. Using the largest dataset of twin mothers yet published, at least 18 times larger than any previously analysed historical sample, we have shown that mothers of twins surpass their singleton-only bearing counterparts on several life-history and reproductive measures. Our results strongly support the hypothesis that twinning is an index of phenotypic quality associated with other dimensions of maternal heterogeneity.

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