9 Human Life Histories: Primate Trade-offs, Grandmothering Socioecology, and the Fossil Record

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Human life histories differ from those of other animals in several striking ways. Recently Smith and Tompkins (1995, p. 258) highlighted the combination of "slow" and "fast" features of human lives. Our period of juvenile dependency is unusually long, our age at first reproduction is late, and we have the maximum life span of the terrestrial animals. Yet we wean babies relatively early, and we space births closely. We also have (midlife) menopause. Smith and Tompkins predicted that the evolution of our life cycles would be explained by a combination of developments in life history theory with increasingly sophisticated techniques for extracting information from the fossil record. Their prudent guess was that "no new sunburst theory—in which all human characteristics are drawn from one adaptive shift—is likely" to emerge (1995, p. 274).

Here we use work since that review to confirm Smith and Tompkins's optimism about the explanatory gains of combining life history theory with paleoanthropology. We focus on the framework provided by Charnov's symmetry approach, combining Charnov's mammal model with a grandmother hypothesis about the socioecology of *Homo erectus (ergaster).* This combination links several otherwise contradictory features of human life histories, showing that our remarkable longevity, late maturity, and relatively high fertility could all be a systematic consequence of a single adaptive shift from an australopithecine life history like that of modern apes. If ancestral life spans were similar to those of modern chimpanzees, with few females surviving past the age of menopause, an ecological change that increased maternal provisioning of juveniles would alter the optimal allocation to somatic survival (Williams 1966; Schaffer 1974; Kirkwood 1977). If mothers shared more food with juvenile offspring, then help from aging females who were not nursing infants themselves would have a large, novel effect on their daughters' fertility. The increased fitness payoffs for adult survival would favor longer average adult life spans and, in turn, would alter the optimal age of first reproduction. This hypothesis is a partial "sunburst." It links some of our life history features to one another, but does not tie those features to the greatly expanded *Homo sapiens* brain or to increased meat eating and the contribution of males to subsistence—features long assumed to be foundations for our late maturation and longevity (e.g., Kaplan et al. 2000).

We conclude by consulting the paleoanthropological record for the ecological context and dates of life history changes, specifically to see how those changes are associated with the evolution of modern encephalization and with changes in the meat fraction of hominid diets. The evidence reviewed is consistent with the proposition that distinctive features of our life histories may have come before large brains and increased carnivory, and may have been responsible for the character and spread of the first widely successful and longest enduring members of our genus.

Life History Theory

A framework that links variation in different life history features is especially valuable for investigating human life history evolution for (at least) two reasons. First, all the other species in the hominid radiation(s) are known only from the fossil record. While paleoanthropologists can estimate some life history features from skeletal specimens, the difficulties of doing so are not trivial, and other features may never be indexed directly in the fossils. A framework that points from more easily measured features to features that are less easy to measure directly can help to extract more information from fossil data. It can leverage more from the paleoanthropological data—the only line of evidence we have for the timing, context, and order of appearance of the modern human patterns.

Second, a framework linking variation among life history features is valuable for investigating our own evolution because of the wide developmental and behavioral gulf between contemporary humans and our closest living primate relatives. There are so many differences between modern people and the (other) great apes that each feature of human life histories can be attributed to a wide array of possible causes. Yet some fundamental trade-offs that apply to other primates apply to us as well. A framework that can generate expected life histories for a model primate with our age-specific mortalities or fertilities will show how many of the human patterns could result from the same trade-offs that we share with other members of the order.

Is There a Framework?

The search for a general model of life history strategies has been fueled over the past few decades by some tantalizing regularities. MacArthur and Wilson (1967; Pianka 1970) proposed *r* and *K* selection to account for some of them. They hypothesized that *r*-selected species evolve in the face of repeated ecological disruptions, reasoning that population crashes with periodic opportunities for rapid population growth should favor life history tactics that give high maximal rates of population increase (*r*): early maturity at small size, with all effort expended in producing many small offspring, and thus early death. Species of the *K*-selected type were hypothesized to evolve in "saturated" environments. With population densities near carrying capacity (*K*), they hypothesized that selection would favor life histories that maximize competitive capacities: late maturity at large size and the production of a few large, well-developed offspring over long adult lives. This theory was especially influential because the logic was simple and compelling, and it gained wide use as a description of relative differences. But subsequent empirical and theoretical work showed that density-dependent mortality has different effects on optimal strategies depending on which age classes suffer the mortality (Gadgil and Bossert 1970; Charnov and Shaffer 1973; Stearns 1977), and that both *r* and *K* clusters of characters can evolve and persist in stable populations (see Stearns 1992 for review). Life history features do correlate generally with body size, but many features are even more strongly correlated with one another when the effects of body size are removed (Harvey and Read 1988; Harvey, Read, and Promislow 1989).

The value of a framework that explains links among life history features depends on whether the model's assumptions about fundamental trade-offs capture enough of the actual trade-offs in the empirical world to explain what really happens. The failure of *r* and *K* selection on that score has stimulated pessimism about the possibility of finding broad regularities. Stearns (1989b) enumerated a long list of trade-offs that can all be important, and, in the face of so many variables, addressed life history evolution one trait at a time in his (1992) text. In a recent discussion of life span variation, Finch (1997, p. 247) concluded that the range is so enormous (a millionfold in eukaryotes) that it "implies the absence of evolutionary limits in life-history schedules."

Yet, many relationships among life history variables are quite robust within particular taxonomic groups. Stearns labeled these relationships "lineage specific effects" (1992, chap. 5), and Finch (1997, p. 247) noted that limits are set by "the physiological architecture of the species." Within taxonomic groups, larger-bodied species do live "slower" lives, but some taxa are relatively slower, and others faster, at similar body sizes. During the last decade, Charnov, building on his own earlier work and that of many others (see Purvis et al., chap. 2, this volume, for additional review) has focused on only a very few trade-offs, elaborating a symmetry approach to explain both aspects of this interspecific variation (Charnov 1991; Charnov and Berrigan 1991). In his "dimensionless" model of mammalian life histories, he adopts the widely used assumption that adult mortality risk selects age at maturity, because growing longer increases maternal size (and consequent production capacity) but trades off against the risk of dying before reproducing. Age at maturity, in concert with taxon-specific growth (production) capacity, sets adult size. Trade-offs in offspring quantity versus quality determine optimal weanling size and combine with the growth assumptions to set fecundity. Elaborations and criticisms of Charnov's mammal model (Charnov 1993; Kozlowski and Weiner 1997; Harvey and Purvis 1999; Purvis and Harvey 1995, 1996; Purvis et al., chap. 2, this volume) do not undercut the main elements of this framework (see below). To the extent that something like Charnov's model is generally correct, it provides a powerful guide to developing and evaluating hypotheses about the evolution of human life histories.

Charnov's Model

Patterns of growth vary widely between and within species (e.g., Leigh 1996; Pereira and Leigh, chap. 7, this volume). Charnov's mammal model uses a simplified growth model based on the assumption that the energy a mammal can put into production (of itself or of offspring) is captured by a characteristic average rate for size. He divides growth into two parts. The first is conception to weaning, which is assumed to be fueled by production from the mother. The second is weaning to maturity, assumed to be under juvenile control. At maturity, production previously allocated to growth is redirected to offspring. Growth rates are an allometric function of body mass (W) and a characteristic production coefficient (A). Individual production rates take the form $dW/dt \sim AW^c$, where the exponent c is ~ 0.75 (Kleiber 1932; West, Brown, and Enquist 1997). Adult size at maturity (W_α) and production available for offspring both vary directly with A, which is characteristically low in primates compared with other mammals (Charnov and Berrigan 1993). In a recent elaboration of the model, Charnov (2001) makes within-species growth sigmoid rather than a power function and includes a cellular maintenance rate that is adjusted by selection.

Charnov captures key features of mortality schedules with another simplification. He assumes an early burst of mortality that incorporates any density-dependent effects. Mortality then drops to a constant level before the age of first reproduction. Given that constant mortality risk, selection sets α (the period from weaning to maturity) according to the trade-off between the benefits of continued growth (and so larger adult size) versus reproducing sooner. Since adult production is a function of maternal size, it increases with age at maturity. The probability of dying before reproducing depends on the instantaneous mortality rate (M), which is unaffected by size. As that rate falls (average adult life span increases), selection favors delaying maturity to reap the benefits of larger size. Thus α and M vary widely, but inversely. Their product (αM) is approximately invariant.

Another set of trade-offs affects fecundity in this model. Weaning releases the mother to allocate production to the next offspring, so weanling size determines the rate of offspring production. But what determines weanling size? Charnov (1993, pp. 107–108) notes that a version of the offspring size-number trade-off (Smith and Fretwell 1974) easily leads to an optimum ESS. For a sample of mammals (cf. Purvis and Harvey 1995, 1996), *and for primates separately,* the ratio of size at weaning to adult size ($W_o/W_\alpha = \delta$) is approximately constant (Lee, Majluf, and Gordon 1991; Ross and Jones 1999). That means that the (ESS) weanling size in these taxa scales isometrically with adult size. Since production scales allometrically with size (the exponent in the initial growth model is about 0.75, modified to include the cost of cell maintenance in the sigmoid model), the ESS size of weanlings goes up faster with maternal size than does the production the mother can put into them. Consequently, the number of daughters produced per year (b) goes down as age at maturity (α) goes up. Larger mothers produce larger but fewer babies, making αb another approximate invariant.

Kozlowski and Weiner (1997) and Harvey and Purvis (1999) suggest that Charnov's model may be crucially flawed because later maturity means both a greater risk of dying before reproducing and lower fecundity, so that there can be no optimal α. But the model treats these as independent adjustments, one to an ESS α in which weanling size is assumed fixed (the same assumption used by Kozlowski and Weiner 1997), and one to an ESS weanling size, which takes W_α as fixed (since the ESS W_α is independent of W_0: Harvey and Nee 1991).

These assembly rules for mammalian life histories identify links that could account for an array of observed covariates. Other variables, other trade-offs, clearly play important roles as well (Stearns 1989b, 1992; Pereira and Leigh, chap. 7, this volume), but the general fit of empirical patterns to the model predictions (confirmed since Charnov 1993 on other, larger data sets: Purvis and Harvey 1995, 1996) suggests that the trade-offs in the model are close to the real trade-offs shaping the broad variation in mammalian life histories.

Charnov's Model and Primate Life Histories

Charnov's model captures similarities between primate and nonprimate mammals in the relationships among life history features as well as some distinctive features of the primate order (Charnov 1993; Charnov and Berrigan 1993). The "mouse lemur to gorilla" curve looks like the "mouse to elephant" curve. In both cases, larger bodies are associated with longer adult lifetimes, later ages at maturity, and lower fecundity. Not only are these features correlated within each group, but the relationships among adult life spans, age at maturity, and fecundity remain the same across transformations of body size. Primates and other mammals share the same αM invariant. But primates, growing more slowly, are smaller at a given α. The "production factor" (A) accounts for both lower growth rates (and thus smaller sizes for a given age at maturity) and lower fecundities for size in primates. This variable (A), approximately 1 in mammals, is generally less than half that in primates (Ross and Jones 1999). (It is even lower in modern humans [Hill 1993] than in the average primate—about the same for us as it is for chimpanzees.) Within each taxonomic group, smaller maternal size is associated with relatively higher fecundity (b). The lower primate b for a given size offsets the higher α for a given size, so that primates and other mammals share the same αb invariant.

Charnov (1993, p. 104) plotted the relationship between age at maturity (α) and average adult life span (M^{-1}, i.e., the inverse of the instantaneous rate of adult mortality) for fifteen primate subfamilies using data from Harvey and Clutton-Brock (1985). In this scatter, one point holds a much higher value on both variables than any other, but is not an outlier. It falls almost exactly on the best-fit regression line (correlation coefficient = 0.95, intercept not different from zero). That point represents the Hominidae, and there is, of course, only one species in the sample: modern *Homo sapiens.*

The fact that modern humans show the primate relationship between adult life span and age at maturity highlighted by Charnov's framework is initially astonishing. Unlike that of other primates (and most other mammals), the average adult life span of women includes a substantial postmenopausal component, a part of the life span often characterized as "postreproductive." If the symmetry captured in the αM invariant really depends on selection setting α according to the trade-off between the risks and the benefits of delaying maturity, and if the total expected benefits depend on the duration of time over which the gains for waiting will accumulate (Charnov 1997), then the human case should fit only if the whole life span is spent putting "production" into making descendants.

Postmenopausal Longevity as a Species Characteristic

This deduction points directly to questions about postmenopausal survival. Is it really typical of humans, and if so, why did it evolve? These are classic evolutionary puzzles. Williams (1957), noting that selection cannot maintain "post-reproductive" function, suggested that human midlife menopause might have evolved with increasing offspring dependence on maternal care. As the probability of seeing the next baby through to independence declined, and pregnancies became increasingly dangerous to aging mothers, those who "stopped early" and allocated late reproductive effort to the welfare of children already born would leave more surviving descendants. This hypothesis takes long human life spans as given and assumes that selection favored "premature reproductive senescence." It continues to stimulate useful work (Hill and Hurtado 1991, 1996, 1999; Rogers 1993; Peccei 1995; Shanley and Kirkwood 2001). But age at last birth is quite similar in humans and chimpanzees, suggesting that we may share our age at menopause with all descendants of our common ancestor. The derived feature that distinguishes us from our nearest living relatives is not our age at menopause, but our extreme longevity (Hawkes, O'Connell, and Blurton Jones 1997, 2000; Hawkes et al. 1998; Kaplan 1997; Kaplan et al. 2000).

The claim that extended longevity—relatively slowed senescence—is a general human characteristic is not without challenge (e.g., Austad 1997a; Olshansky, Carnes, and Grahn 1998). The extremely high life expectancies of many (but not all) contemporary human populations are clearly a very recent novelty. In most of the United States, Europe, and Japan, newborns can now expect to live about eighty years, while historical demography and population profiles in high-mortality settings show life expectancies of less than four decades. But life expectancies at birth are averages and are strongly affected by rates of infant and juvenile mortality (so that a life expectancy of thirty years does not mean that few adults live to forty) (e.g., Bailey 1987; D. W. E. Smith 1993; Lee 1997). French historical demography provides an instructive set of comparisons (table 9.1). Life expectancy at birth was only 39 in 1850, compared with double that in 1985. The largest source of difference between these two time periods is the rate of death in the juvenile age classes. Even in 1850, anyone who lived to adulthood had the prospect of a long life ahead. As table 9.1 shows, most women lived past the age at last

Table 9.1 French historical demography

	At birth: Average life expectancy (e_x0)	At maturity: Probability of living past age of last birth (45)	At age of last birth: Average additional life expectancy (e_x45)
France 1985	79	.96	36
France 1950	69	.92	30
France 1926	57	.84	27
France 1900	48	.75	25
France 1850	39	.72	24

Source: Keyfitz and Flieger 1968, 1990.

birth, and the average number of years remaining for anyone who reached that age was more than two additional decades.

Nineteenth-century France had an agrarian economy, something relatively recent in human experience. Where people depend only on wild foods, however, survival curves are very similar. In all four of the best-studied cases of modern hunter-gatherers, the !Kung (Howell 1979), the Ache (Hill and Hurtado 1996), the Hadza (Blurton Jones et al. 1992), and the Agta (Early and Headland 1998), representing populations in different environments with distinct recent genetic histories, age-specific survival is very like that recorded in nineteenth-century France (table 9.2). Although life expectancies at birth are less than four decades, this does not mean that people live only into their thirties. Most women live past the age of last birth, and those who do have an *average* of more than twenty years of life still ahead.

The inference from history and ethnography that substantial post-menopausal longevity is a usual characteristic of human populations has

Table 9.2 Contemporary hunter-gatherers

	At birth: Average life expectancy (e_x0)	At maturity[a]: Probability of living past age of last birth	At age of last birth: Further life expectancy (e_x45)	Women past age of last birth (%)	Source
!Kung	31	.66	20	31	Howell 1979
Ache	38	.79	22	36	Hill and Hurtado 1996
Hadza	33	.71	21	29	Estimated from Blurton Jones et al. 1992
Agta	24	.59		36	Early and Headland 1998

[a] If maturity is at 20, and last birth at 45 (40 for the Agta).

been challenged by age distributions observed in archaeological skeletal assemblages (Weiss 1973). Remains from individuals estimated to be over sixty at death are rare, supporting skepticism about the generality of the demographic patterns found among living populations (Austad 1997a; Trinkhaus 1995). But new sources of error are introduced in constructing population profiles from archaeological assemblages. Where historical records have provided independent evidence of the ages of individuals interred, two especially important sources of bias have come to light. The bones of the old and the young are disproportionately unlikely to sustain long preservation, and the ages of adults are systematically underestimated (Walker, Johnson, and Lambert 1988; Paine 1997). Standard aging techniques applied to samples of known ages illustrate the pervasiveness of this problem (Bocquet-Appel and Masset 1982; Key, Aiello, and Molleson 1994). Attempts to model sustainable populations using parameters estimated from cemetery profiles have repeatedly shown that the usual estimates are quite unrealistic (e.g., Howell 1982; Bermudez de Castro and Nicolas 1997).

Biases in the other direction, novel features of the modern world that might extend longevities in ethnographically known foraging populations, can also be explored. Living people are now everywhere affected to some degree by global networks of interaction (e.g., Wolf 1982; Schrire 1994; Blurton Jones, Hawkes, and O'Connell 1996 discusses interactions with the Hadza and the !Kung). We have tried to assess the effects that some access to Western medical care and interaction with neighboring farmers and herders might have on Hadza demography (Blurton Jones, Hawkes, and O'Connell 2002). Even the most generous estimates of regional medical services and the investigators' own possible effects make only negligible differences in the population parameters initially reported (Blurton Jones et al. 1992).

Comparisons with other mammals clearly show the unusual longevity of humans (Pavelka and Fedigan 1991). Table 9.3 lists the percentage of females who, having reached maturity, live past the age of last birth in three other primate species for whom vital rates have been monitored outside captivity. In macaque and baboon populations (Pavelka and Fedigan 1999; Packer, Tatar, and Collins 1998), reaching the age of last birth is the luck of only a very few individuals (whereas it is the norm among humans even under high-mortality conditions; see table 9.2). The living primates most closely related to us, the chimpanzees, have slower life histories than smaller-bodied macaques and baboons, and a few more females may live past childbearing age (table 9.3; Caro et al. 1995). But in all three of these nonhuman species, only a very small fraction of the adult females in a living

Table 9.3 Nonhuman primates

	At maturity: Probability of living past age of last birth	Adult females past age of last birth (%)
Macaques[a]	<.05	<2
Baboons[b]	.04	<1
Chimpanzees[c]	.17	<6

[a] *M. fuscata*, Texas (Pavelka and Fedigan 1999).
[b] Gombe (Packer, Tatar and Collins 1998).
[c] Composite of five study sites (Hill et al. 2001).

population are past the age of last birth. Even in high-mortality human populations (e.g., the hunter-gatherer examples in table 9.2), about a third of the adult females are beyond childbearing age.

None of these findings should obscure the novelty of the increasingly larger proportions of adults in senior age ranks in many contemporary human populations. This large fraction of oldsters presents economic, medical, and social challenges that can hardly be overestimated. But neither should the novelty and importance of those challenges obscure the strength of the evidence that long adult lives are normal for humans. Based on the arguments summarized below, they may be a feature of our lineage much older than *Homo sapiens.*

Lessons from the Hadza

In high-mortality circumstances, there is a characteristic human pattern of age-specific survival and fertility. Most women live long past the age of last birth. The additional years of life are several multiples of average birth intervals, which mark the time mothers devote to one offspring before turning to the next. Yet humans mature unusually late, as expected for our unusually long adult life span; thus, human life histories preserve the αM invariance. This fit to the broad primate (and more generally mammalian) pattern would be expected if women actually continued to produce descendants during those postmenopausal years. There are good reasons to think that they do.

The Hadza, hunter-gatherers in the arid Tropics of northern Tanzania (Woodburn 1968; Blurton Jones et al. 1992), provide an instructive lesson. Here, postmenopausal females have clear effects on the production of descendants, and the basis for those effects points to aspects of socioecology that could be key to an adaptive shift in ancestral life histories.

Young Hadza children are energetic foragers. Those between the ages of five and ten years supply half their own nutrient requirements in some seasons (Blurton Jones, Hawkes, and O'Connell 1989). Mothers take advantage of their children's foraging capacities, choosing to focus on foods the children can handle efficiently when those resources are in season (Hawkes, O'Connell, and Blurton Jones 1995). But the year-round staple in this habitat is deeply buried tubers, which young children are not strong enough or skilled enough to handle effectively. Senior Hadza women, long-experienced gatherers, spend even more time acquiring food than do women of childbearing age (Hawkes, O'Connell, and Blurton Jones 1989). The extra time is largely devoted to digging those deeply buried tubers, which they acquire at rates equivalent to those of younger adults (Hawkes, O'Connell, and Blurton Jones 1989).

The seasonal and age-related variation in Hadza foraging highlights some likely causes and consequences of human economic interdependence that could have large evolutionary implications. Other primate juveniles must be successful enough at feeding themselves to support their own survival (Altmann 1998). In humans, unlike other primates, weaned offspring depend on other individuals to supply a substantial component of their nutrition (Bogin and Smith 1996; Bogin 1999; Kaplan 1997; Kaplan et al. 2000). In one sense, this dependence seems to make human children a greater burden on their mothers. Yet, if human children depended on their own foraging, their mothers, like mothers in other primate species whose weanlings remain in their close company for other reasons, would face increased offspring mortality from extended foraging in habitats where the youngsters could not feed themselves. Food sharing allows adults accompanied by young offspring to invade habitats and exploit foods they otherwise could not.

Some mother-offspring food sharing occurs in many primate species (Feistner and McGrew 1989), but shared food accounts for at most a small component of juvenile diets in all living primates but one. When mothers supply a substantial fraction of their weanlings' nutrition, this sharing opens a novel opportunity for senior females to have large effects on their own fitness. An aging female, unencumbered by nurslings of her own, can provision a just-weaned grandchild so that its mother can allocate less effort to that child and can produce the next child more quickly. In this way, more vigorous perimenopausal females can have larger effects on the fertility of younger kin. These effects would strengthen selection against senescence in elder females, lowering adult mortality and increasing average adult life spans.

The interrelationships described in this scenario are evident among the Hadza (Hawkes, O'Connell, and Blurton Jones 1997). The foraging effort of a mother who is not encumbered with a nursing infant has a measurable effect on the nutritional welfare of her children. At the birth of a newborn, its mother's foraging effort declines. The link between a mother's effort and the nutritional welfare of her weaned children disappears. Now the weight gains of those children depend on the foraging effort of their grandmother (Hawkes, O'Connell, and Blurton Jones 1997).

An Evolutionary Scenario

Imagine ancestral australopithecine populations with a chimpanzee-like life history. Ecological changes constrict the forests and the availability of fruits that young juveniles can handle. Increasing aridity and seasonality favor plants that cope well with dry seasons—for example, by holding starches in underground storage organs. Such resources can yield high return rates, but only to those with the strength and skill to extract and process them. Young juveniles cannot do it. To rely on these resources and succeed in these environments, mothers must provision offspring who are still too young to extract and process the tubers for themselves. If older females whose own fertility is declining feed their just-weaned grandchildren, the mothers of those weanlings can have shorter interbirth intervals without reductions in offspring survivorship. The more vigorous elders will thus raise their daughters' fertility. Under this scenario, normalizing selection would maintain menopause at about the age at which it usually occurred in the ancestral population. The fraction of females living beyond menopause would increase, but any who continued to have babies at later ages themselves (as a consequence of increased initial oocyte stocks or slowed rates of follicle loss) would thereby reduce their contribution to the fertility of their daughters. Continued childbearing would interfere with grandmothering, erasing the selective advantage of vigorous adaptive performance late in life and collapsing life histories back toward the chimpanzee-like pattern.

Grandmothering and the Human αM

The novel effects that aging females could have on their own fitness in the socioecological circumstances sketched above would strengthen selection against age-related declines in somatic performance. Senescence is an important source of mortality in any large-bodied primate (Ricklefs 1998). Enhanced selection for continued adult vigor would reduce this mortality, increasing average adult life spans. (Effects on most physiological systems—e.g., cardiovascular, renal, gastrointestinal, pulmonary—would likely be correlated across sex: longer-lived mothers would have longer-lived sons as well as longer-lived daughters.) Lower adult mortality rates and greater longev-

Table 9.4 αM for living hominoids

	Average adult life span (years) M^{-1}	Weaning to maturity (years) α	αM
Orangutans	17.9	8.3	.46
Gorillas	13.9	6.3	.45
Chimpanzees	17.9	8.2	.46
Humans	32.9	14.5	.45

Note: See Hawkes et al. 1998 for sources; Alvarez 2000 for discussion of alternative calculations of α and statistical evaluation.

ity would, in turn, favor delaying maturity. The risk of dying before reproducing would decline, and the greater productive capacity of larger adults could be exercised over a longer period. So, according to Charnov's symmetry arguments (1993, 1997, 2001), the lower M (the inverse of the average adult life span) would favor higher α, a longer juvenile period, and continued growth to a larger size before maturing. In fact, the αM products of four living hominoids are strikingly similar (table 9.4). Alvarez (2000) shows that the human αM falls well within the confidence interval for sixteen primate species.

A grandmothering socioecology, combined with the interrelated life history trade-offs expected for any large-bodied female primate, could account for our unusual longevity—with midlife menopause—as well as our late maturity. This framework can explain why humans take about "twice as long to reach adulthood, and live about twice as long as great apes" (Smith and Tompkins 1995, p. 260).

Grandmothering and the Human αb

This scenario also has implications for the duration of lactation, and thus for interbirth intervals. As with age at maturity and average adult life span, discussed above, the "mouse lemur to gorilla" curve is like the "mouse to elephant" curve for variation in annual fecundity (b) (Charnov 1993; Charnov and Berrigan 1993). Whereas age at maturity and adult life span rise with increases in adult body size across the mammals, fecundity declines. In general, the (ESS) weanling size is larger for larger mothers ($W_0/W_\alpha = \delta$, approximately a constant: Lee, Majluf, and Gordon 1991). In Charnov's mammal models, the trade-off between offspring size and number changes as the ESS α rises. The optimum for larger mothers is more investment per offspring; in other words, larger babies at longer intervals.

Table 9.5 ab for living hominoids

	Weaning to maturity (years) α	Offspring per year (daughters) b	ab
Orangutans	8.3	.063	0.52
Gorillas	6.3	.126	0.79
Chimpanzees	8.2	.087	0.70
Humans	14.5	.142	2.05

Note: See Hawkes et al. 1998 for sources; Alvarez 2000 for discussion of calculations and statistical evaluation.

Grandmothering, however, is allocation of production by senior females to the offspring of younger kin. Females nearing the end of their own fertility gain fitness by changing the size-number trade-off faced by their daughters. The annual baby production (b) of childbearers in a grandmothering species incorporates production by both mother and grandmother, so it should be higher during the childbearing years than expected for a grandmotherless species with the same age at maturity (α). Table 9.5 shows the αb products for four living hominoid species. Human interbirth intervals are slightly shorter than those of chimpanzees and similar to those of gorillas. The instructive comparison is the expected b given our α. Human fertilities are more than twice that expected for a grandmotherless primate with our late maturity. Alvarez (2000) has extended the comparison to include sixteen primate species, showing human fertilities to be well outside the confidence interval of grandmotherless primates.

A general expectation from life history theory is that organisms must trade off current and future reproduction, so that lower fertility is the price of greater longevity (Williams 1966; Kirkwood 1977; Rose 1991). Primates generally spend less energy on lactation than do other mammals (Oftedal 1984). Some measures suggest that human mothers, who are likely to be grandmothers and have long lives ahead, put even less energy into current reproduction than do other primates (Prentice and Whitehead 1987). The grandmother hypothesis assumes that effort in producing children comes not only from mothers, but from postmenopausal helpers as well, so that even with less allocation to current reproduction, human fecundity is high relative to that expected for such a late-maturing primate.

This hypothesis accounts for the surprising combination of late maturity with a short nursing period and short interbirth intervals. Bogin and Smith (1996, p. 703) phrased the puzzling combination of human life history features this way: The problem is to explain "how humans successfully combined a vastly extended period of offspring dependency and delayed reproduction with helpless newborns, a short duration of breast-feeding, an adolescent growth spurt, and menopause." A grandmothering socioecology, combined with Charnov's symmetry framework, explains almost all the items in the list.

Grandmothering and *Homo erectus*

The grandmother hypothesis and Charnov's framework link an array of distinctive features of human life histories as systematic adjustments of a general primate pattern. If these features are the result of a single adaptive shift that actually took place in an ancestral population, then the paleoanthropological record should be consistent with that scenario. Evidence linking this shift to the appearance of the first widely successful member of our genus, *Homo erectus (sensu latu),* can be found in the paleoecological record of the early Pleistocene in Africa, the geographic distribution of this taxon, and morphological and developmental characteristics indicated in the skeletal evidence (O'Connell, Hawkes, and Blurton Jones 1999).

Data from a wide range of sources (e.g., deep marine sediments, soil chemistry, pollen, fossil faunas) consistently indicate that the 1.9–1.7 mya time period bracketing the first appearance of African *H. erectus (ergaster)* was marked by ecological changes likely to alter foraging opportunities for a large-bodied primate. Africa saw an unusually pronounced shift toward cooler, drier, more seasonal conditions and a related trend toward open, less wooded plant communities (e.g., Cerling 1992; deMenocal 1995; Reed 1997; Spencer 1997). Extinctions among frugivorous primates in various East African localities after 1.8 mya may all be related to the restriction of closed forest habitats (e.g., Reed 1997).

These circumstances could have favored the exploitation of previously unused or little-used resources that provide predictable returns to an adult forager, although they are difficult for young juveniles to handle. Many resources meet these criteria, notably certain varieties of small game, shellfish, nuts, seeds, and the underground storage organs of plants. Though none of these foods are especially well represented in the archaeology of early *H. erectus,* this may reflect problems of preservation, the absence of attention to their recovery by archaeologists, or both.

The best (though not the only) prospective candidates for increased exploitation under these circumstances may be underground plant storage organs ("USOs" or, loosely, "tubers") (see also Hatley and Kappelman 1980;

Wrangham et al. 1999). They are encountered in many forms across a wide array of habitats, sometimes occurring at densities greater than one metric ton per hectare (Raunkiaer 1934; Vincent 1985; Thoms 1989). Data from African, Australian, and North American settings indicate returns to modern human foragers of 1,000–6000 calories per hour, which commonly translates to about 8,000–12,000 calories per forager-day, all with very low day-to-day variance—easily enough to support at least two consumers (e.g., Blurton Jones, Hawkes, and O'Connell 1999; Couture, Ricks, and Housley 1986; Hawkes, O'Connell, and Blurton Jones 1995; O'Connell, Latz, and Barnett 1983; Thoms 1989; see Schoeninger et al. 2001 for a contrary estimate of nutrient value and discussion of this estimate in Hawkes, O'Connell, and Blurton Jones 2001b).

These dependable return rates make USOs attractive food resources, but mechanical and chemical defenses limit consumer access (Coursey 1973; Thoms 1989; Wandsnider 1997). Children's primary acquisition of USOs among modern human foragers is limited to forms found close to the surface that require little or no processing (e.g., Blurton Jones, Hawkes, and O'Connell 1989; Hawkes, O'Connell, and Blurton Jones 1995). Tuber use among other primates is probably limited by the same factors: chimpanzees rarely take them; baboons do so only in highly arid environments, and even then target only forms that juveniles can handle on their own (McGrew 1992; Whiten et al. 1992; Altmann 1998).

Archaeological evidence of tuber exploitation is often limited and indirect because the activity itself leaves ephemeral traces. Still, several lines of evidence are consistent with increased use of USOs beginning with the appearance of *H. erectus.* Efficient exploitation of deeply buried USOs requires, at minimum, a digging tool. The earliest known examples of such tools date to about 1.7 mya (Brain 1988). Cooking is essential to the use of chemically defended tubers and important for the conversion of the complex carbohydrates they commonly contain to simpler, more readily digestible forms. Though controversial, the earliest dates for humanly controlled fires, suitable for tuber processing, fall in the range 1.4–1.6 mya (Bellomo 1994; Rowlett 1999).

The geographic range of *Homo erectus* indicates the capacity of this taxon to exploit a far broader range of habitats than any previous hominid. While earlier hominids are restricted to Africa, early *H. erectus* is found as far east as Java and as far north as 50° latitude (Dennell and Roebroeks 1996; Gabunia and Vekua 1995; Gabunia et al. 2000). This sharp change in distribution strongly implies access to new food sources. Tubers are a staple among ethnographically known hunters in continental habitats extending to approximately 50° N (Thoms 1989), and so may also have been important in the first expansion of the genus *Homo.*

Aspects of *H. erectus* morphology also indicate a shift in resource exploitation. Reductions in chewing architecture clearly point to increased use of resources that require less postconsumption processing (Aiello and Wheeler 1995; Klein 2000; Wood and Collard 1999a,b; Suwa, White, and Howell 1996), implying either a narrower range of foods exploited or increased investment in preconsumption processing. Tuber cooking is a good example of such processing.

Skeletal criteria also clearly identify early African *H. erectus* as the first hominid with a nonpongid life history (D. W. E. Smith 1993; Wood and Collard 1999a,b). Australopithecines have been characterized as "bipedal apes" (D. W. E. Smith 1993; Smith and Tompkins 1995; Klein 2000). With *H. erectus,* there is a substantial increase in body size (McHenry 1994; Kappelman 1996; Ruff, Trinkhaus, and Holliday 1997), an expected consequence of delayed maturity. In addition to adult size, other maturation measures (e.g., Smith 1991b; Tardieu 1998; Clegg and Aiello 1999) suggest that age at maturity may have been within the range of modern humans (but see Dean et al. 2001). Since age at maturity plays a central theoretical and empirical role in the life history ideas discussed here, this aspect of the fossil evidence is of primary importance.

Delayed maturity implies a change in mortality rates. But, given the character of the fossil record (including the age biases in archaeological assemblages discussed above), it is not possible to directly test the expectation that *H. erectus* life spans were substantially longer than those of australopithecines. Recent work on aging skeletal specimens has focused on characterizing the biases in standard methods (Paine 1997). Clearer appreciation of these biases is spurring the development of new techniques for aging adult skeletons. It may also eventually be possible to identify osteological traces of postmenopausal physiology (Ruff 1991; Bogin and Smith 1996). At present, all that can be said is that claims of *short* adult lifetimes in premodern (and early modern) human populations are not empirically warranted.

Another direct test of the proposed adaptive shift in *H. erectus* should be feasible. A grandmothering primate should have higher fertility during the childbearing years than expected for a grandmotherless primate with the same age at maturity because that higher fertility in young adults is the benefit that drives selection against senescence. The specific prediction is that if grandmothering *is* the adaptive shift of *Homo erectus,* weaning ages will be lower (implying higher annual fecundity during the childbearing years) than expected for a grandmotherless ape with the age at maturity estimated for this taxon. It may be possible to monitor age at weaning by reference to changes in trace element composition (especially ^{18}O and ^{13}C) in teeth formed across the weaning period (e.g., Wright and Schwarz 1998).

What About Brains?

This hypothesis about the evolution of human life histories gives no instrumental role to changes in brain size. But brains are central in many influential scenarios of human evolution. Finding maximum life span more strongly correlated with brain size than with body size in his analysis of variation across mammals, Sacher (1959) hypothesized that increases in brain size improved physiological regulation and consequently slowed rates of aging. Others (notably Allman 1999) have continued to pursue work along these lines. Many analysts have linked the provisioning of human juveniles to a delay in maturity, which they propose to be a consequence of selection for larger brains (e.g., Washburn and Lancaster 1968; Bogin 1999; Kaplan et al. 2000).

Above, we reviewed evidence suggesting that modern human life histories may begin with *Homo erectus.* If so, then brain size in this taxon is relevant to any hypothesized causal role for brains. Differential preservation of cranial remains should make brain size a much easier feature to estimate for fossil taxa than many life history variables (e.g., Leigh 1992a). But because larger mammals have larger brains, measures that remove effects directly attributable to body size alone are required (Jerison 1973; Eisenberg 1981; Armstrong 1985a; Martin 1983). A dimensionless index, EQ (encephalization quotient), which compares observed brain size to that expected for a reference animal of the same body size, solves this problem. But the brain size expected due to changes in body size alone depends on the scaling relationship assumed. Observed scaling relationships between body size and brain size vary among orders and with taxonomic level (Martin and Harvey 1985).

The lower the taxonomic level, the smaller the observed change in brain size for each change in body size—in other words, the flatter the slope of the regression (Martin and Harvey 1985). One hypothesis to explain this taxon-level effect proposes that evolutionary changes in body size can be more rapid than evolutionary changes in brain size. A direct test of this lag hypothesis using pairwise contrasts in living primate species found no support for it (Deaner and Nunn 1999). Body size data are inherently extremely noisy. Much of the taxon-level effect could be a systematic consequence of measurement error (Pagel and Harvey 1988b, 1989).

Difficulties in estimating body sizes for living species are compounded in fossil taxa. Calculating EQ requires not only a choice of allometry, but a body size to go with each brain size. Even with a full skeleton, body mass estimates are not straightforward (e.g., Smith 1996), and they are even less so when fossils represent immatures and when elements cannot be clearly assigned to single individuals. Moreover, the very small number of specimens associated with some fossil taxa and with some time periods makes estimates of within-species variability, and thus between-species differences, difficult to assess.

The work to date is especially impressive in light of these difficulties. Brain size in *Homo erectus* is about double that found in australopithecines and modern chimpanzees. McHenry (1994) estimated female body size to be about 60% larger in *H. erectus* than in australopithecines and so calculated encephalization as only slightly higher—much lower than his EQ for modern humans. Using a cranial measure to estimate body size, Kappelman (1996) found that EQ increased in *H. erectus* over australopithecines, then remained stable in the genus *Homo* throughout the lower and middle Pleistocene, increasing again only within the upper Pleistocene. Ruff, Trinkhaus, and Holliday (1997) applied other indices of body size and also found no increases in relative brain size over time in *H. erectus sensu latu,* but "archaic" *H. sapiens,* appearing in the late middle Pleistocene, was more encephalized.

Most recently, Wood and Collard have reconsidered the definition of genus *Homo.* Linking several morphological features to adaptive strategies (body size and form, locomotion, maturation rate, and chewing architecture), they sorted fossil hominids into two broad categories, australopithecines on one hand and members of genus *Homo* on the other. This sorting reassigns *H. habilis* and *H. rudolfensis* to *Australopithecus* spp. *H. erectus (ergaster)* aligns with modern humans on these criteria, although "relative brain size does not group the fossil hominins in the same way" (Wood and Collard 1999b, p. 203). As they say elsewhere, "Although there are twofold differences in the mean absolute brain size of early hominids, these differences are almost certainly not significant when body mass is taken into account. A notable effect of body-mass correction is that the absolutely larger brain of *H. ergaster* is 'cancelled out' by its substantial estimated body mass" (Collard and Wood 1999, p. 324).

New fossils, of course, as well as increasing attention to the bases for estimates of relative brain size (including within-taxon variation), will clarify the picture. While the timing and extent of changes in encephalization across hominid phylogeny continue to be disputed, there *is* clear consensus that the extremely high EQs of contemporary human populations are quite recent, no older than the late middle Pleistocene. *Homo erectus* emerged and spread 1.5 million years before that. If essentially modern human life histories did evolve with that taxon, then the grandmothering adaptive shift is distinct from, *and much older than,* the adaptive shift that gave us our very big brains.

The Evidence for Meat Eating

The appearance of *Homo erectus (ergaster)* at the beginning of the Pleistocene coincides with the dates of the best-known Plio-Pleistocene archaeological sites (Isaac 1997; Leakey 1971), all of which fall in the 1.5–1.9 mya range (Feibel, Brown, and McDougal 1989; White 1995). Sites of this age often contain the bones of large ungulates in close association with stone tools. Though opinions differ on whether these animals were hunted or scavenged, cut marks show that early humans certainly took meat from them (Bunn 1981; Potts and Shipman 1981). Following Isaac (1978), many argue that these sites were "central places," similar to the base camps occupied by modern hunters—spots to which meat and marrow were routinely transported, probably by hominid males, for distribution to mates and offspring (e.g., Rose and Marshall 1996; Oliver 1994). Paternal provisioning and increased meat eating are central elements of most versions of this argument (e.g., Kaplan et al. 2000). Even those who disagree with certain aspects of this hypothesis usually assume that meat was a significant part of early human diets and was crucial to the emergence and subsequent evolutionary success of *H. erectus* (e.g., Blumenschine 1991; Rogers, Feibel, and Harris 1994). Increased carnivory is linked to the invasion of more seasonal habitats (Shipman and Walker 1989). Furthermore, the nutritional quality of meat and, especially, provisioning by males (Lovejoy 1981) are assumed to allow mothers to produce more offspring that are more dependent on provisioning through a longer childhood (Kaplan et al. 2000).

This scenario has been supported by appeals to the importance of meat and paternal provisioning among modern hunter-gatherers. But quantitative data on modern human foragers show that big game hunting and scavenging are often highly unreliable food acquisition strategies, and are not aimed toward family provisioning, even in tropical Africa, where both practices are thought to have evolved. Among the Hadza, for example, whose foraging practices provide a stimulus to the grandmothering argument, men specialize in taking big ungulates. These excellent hunters operate in a game-rich savanna woodland habitat. Even with bows and arrows (modern projectile weapons that appear archaeologically only in the late upper Pleistocene), they succeed in acquiring large animal prey at an annual average of only one every thirty hunter-days (O'Connell, Hawkes, and Blurton Jones 1988; Hawkes, O'Connell, and Blurton Jones 1991). The animals are very large, and a success draws the interest of many. Ninety percent *or more* of the meat goes to claimants outside the hunter's own household (Hawkes, O'Connell, and Blurton Jones 2001a). Marked variation in hunters' success rates has no effect on the number or size of shares their household gets from the kills of other men. This wide sharing, with no evidence of "risk reduction reciprocity," makes big game hunting clearly inferior to many alternative strategies for provisioning families (Hawkes, O'Connell, and Blurton Jones 2001b). Annual average meat consumption is high, but weeks may pass with no meat in camp, even in camps with several active hunters. Everyday support for children must come from elsewhere.

Archaeological data are sometimes said to indicate higher rates of meat acquisition in the past. Bunn (1982; Bunn and Kroll 1986), for example, claims that the well-known assemblage from the Olduvai site named FLK Zinjanthropus, containing the remains of at least forty-eight large ungulates, accumulated in less than two years, implying a minimum carcass acquisition rate of more than twenty-five animals per year at this site alone. Assuming that early humans were primarily responsible for these remains, that most of the carcasses represented were taken in complete or nearly complete condition, and that this was only one of many large faunal assemblages created by the local hominid group involved, then a meat consumption rate much higher than reported for the modern Hadza is implied. As many have observed, however, the basis for Bunn's estimated carcass deposition rate is weak: other, more plausible interpretations imply a much longer period of accumulation, possibly up to several centuries (e.g., Kroll 1994; Lyman and Fox 1989; Potts 1988). If most of the carcasses represented at FLK Zinj and other sites from that time period had also been heavily ravaged by other predators by the time hominids took control (Blumenschine and Marean 1993; Marean et al. 1992), then a lower, even more sporadic large animal tissue intake than enjoyed by the modern Hadza is indicated—far too low to support effective offspring provisioning.

Another aspect of the emerging paleoanthropological record is inconsistent with the argument that dependence on meat is the key to the evolution of *H. erectus*. Whatever the pattern of carcass acquisition represented at Plio-Pleistocene Olduvai and East Turkana, it may have a much greater antiquity than previously suspected. Reports from Kanjera in southern

Kenya indicate that a hominid-created large faunal assemblage comparable to the one at FLK Zinj was deposited there as early as 2.2 mya (Plummer et al. 1999); similar assemblages in Ethiopia may have been deposited by 2.6 mya (Asfaw et al. 1999; Heinzelin et al. 1999; Semaw et al. 1997). If these early assemblages do indeed prove to have been deposited by the same hominid-related processes, at about the same rates, as those at the later sites, then either *H. erectus* appeared 400,000–800,000 years earlier than currently supposed, or australopithecines are the hominids implicated. If the archaeology *is* associated with australopithecines (Heinzelin et al. 1999), then it cannot represent a distinctive adaptation of genus *Homo.*

Summary and Conclusions

A combination of Charnov's model of the trade-offs that underlie the variation in mammalian life histories and a specific hypothesis about ancestral socioecology can explain why "humans live on a vastly extended time scale compared to most other mammals" (Smith and Tompkins 1995, p. 258). It can also explain why the extreme slowness of some aspects of our life history is combined with producing offspring faster than they can become independent foragers. Grandmothering is not just a hypothesis about the fitness payoffs of postmenopausal survival; rather, it is part of a framework that links several life history features to one another as aspects of a single adaptive shift.

This theory is only a partial "sunburst" (Smith and Tompkins 1995). Changes in brain size or paternal provisioning, which Smith and Tompkins also list among the features that distinguish us from other primates, are not included in it. The paleoecology, the geographic spread of *Homo erectus (sensu latu),* and an array of characteristics inferred directly from the fossils themselves are generally consistent with a scenario in which a systematic cascade of life history changes occurs in this taxon. But, as we have noted above, the fossil record does not show marked encephalization in younger taxa. Nor does the archaeology show any clear indication of increased meat eating with the appearance of this first long-enduring and widely successful member of our genus. Results of stable carbon isotope analysis on one set of fossils shows no more meat in *H. ergaster* diets than in the diets of contemporary australopithecines (Lee-Thorp, Thackery, and van der Merwe 2000). A combination of the life history framework and the paleoanthropology data points toward the possibility that for *most* of the history of genus *Homo* (the first million and a half years of the Pleistocene), the successful way to be human included life histories similar to ours. Our very large brains, however, are much more recent, and the increased consumption of meat that characterizes some modern human foragers may have no greater antiquity. Instead, grandmothers may have been the distinctive addition to the human story during the Pleistocene.

This hypothesis has implications for each of a series of distinctive features of human life history:

1. **Our extended juvenile dependency.** An ecological shift in tropical Africa at the beginning of the Pleistocene reduced the availability of foods young juveniles could handle for themselves and increased the prevalence of foods that gave high return rates to an essentially frugivorous, large-bodied primate old (large) enough to overcome the mechanical or chemical defenses of those foods. Young children had to depend on their mothers for these resources.

2. **Our long life span.** Maternal provisioning allowed older females whose own fertility was declining to have a large effect on the fertility of their younger kin. Without infants and weanlings of their own, older females could provision the weanlings of their daughters. These fitness benefits strengthened selection against senescence, altering the apelike equilibrium allocation to somatic maintenance and repair and so lowering rates of adult mortality and lengthening adult life spans.

3. **Our unusual midlife menopause.** Longer life spans allow the production of more descendants through higher fertility in young adults. With senescence delayed, the fraction of postmenopausal females increased. But any tendency to delay menopause would not be favored because older females who were occupied with their own weanlings could not help younger females, removing the advantage for increased somatic maintenance and repair in those lineages. Higher fertility at young ages in the grandmothering lineages would continue to select against delaying menopause beyond midlife.

4. **Our late maturity.** Longer average adult life spans would alter the optimal age at maturity. As the risk of dying before reproducing declined, selection would favor continuing to grow for a longer period, and so to a larger size, before maturing. Gains from the added productive capacity due to an extended period of growth would be enhanced as they accumulated over the longer duration of adulthood.

5. **Our early weaning and short birth spacing.** The assistance of grandmothers would lower the offspring survival costs of earlier weaning. This would alter

the optimal size (age) at weaning otherwise expected for a primate of our size (age) at first reproduction.

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