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Female Reproductive Aging

The Proceedings of the 10th Reinier de Graaf Symposium, Zeist, The Netherlands, 9–11 September 1999

EDITED BY E. R. TE VELDE, P. L. PEARSON AND F. J. BROEKMANS

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Why do women have a mid-life menopause? Grandmothering and the evolution of human longevity

K. Hawkes, J.F. O'Connell and N.G. Blurton Jones

INTRODUCTION

In healthy women, fecundity is statistically zero by age 50, whereas other body processes continue for decades longer at a large fraction of maximum capacity. Among other species in the primate order, the timing and rate of development and ageing vary widely. In all of them, however, the rare females who reach menopause show age-related failure in other physiological processes at the same time. The fact that women experience menopause at mid-life, the ovaries senescing completely, well before the rest of the body, distinguishes humans from other primates and almost all other mammals.

The key to this distinctive mid-life menopause may also be the key to some of the other things that distinguish us and our evolutionary lineage from ancestral and collateral hominids. Our goal here is to explain that assertion, first reviewing evidence against the widely held view that postmenopausal longevity is a recent novelty.

HUMAN LONGEVITY

Historical demography

If demographic statistics are considered for many contemporary human populations, some are surely novel in human experience. Two of the authors live in the state of Utah, where today average life expectancy for a newborn girl is more than 80 years. This pattern is typical of most of the USA, Europe and the rest of the industrial world (Figure 1)[1]. Its consequence is an increasingly 'rectangular' population pyramid, with the fraction of people in the 'golden years' large and growing. This unprecedented pattern is causing enormous changes in the familial, political, commercial and medical dimensions of social life. However, the importance of those changes should not hide the

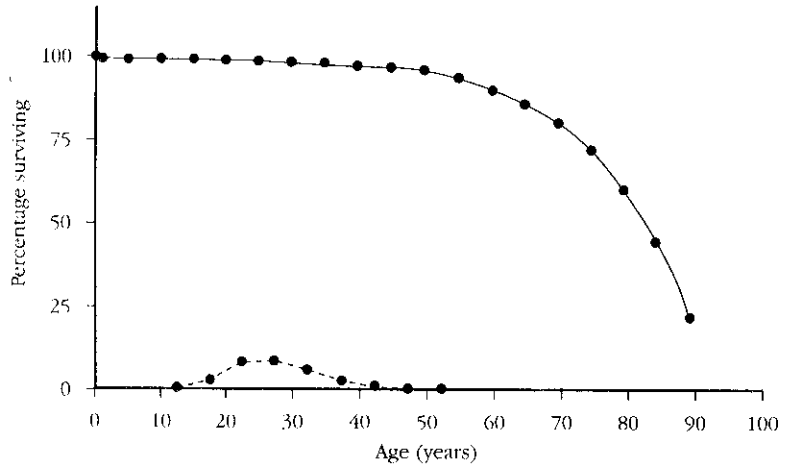

Figure 1 Utah 1990 age-specific fertility (---●---) and survival (—●—). Probability of survival, or annual fecundity (in daughters) indicated on the *y* axis. Data from reference 1

Table 1 Historical demography in France. From references 2 and 3

Year	e_x0	*At maturity, probability of living past 45*	e_x45
1985	79	0.96	36
1950	69	0.92	30
1926	57	0.84	27
1900	48	0.75	25
1850	39	0.72	24

e_x0, life expectancy at birth; e_x45, life expectancy at 45 years

much older pattern of postmenopausal longevity that appears to predate the evolution of *Homo sapiens*.

The older pattern can be obscured when life expectancy, an average, is misinterpreted as something like maximum lifespan. French historical demography illustrates this (Table 1)[2,3]. Life expectancy at birth (e_x0), near 80 in the last few years, was less than half that in 1850. The main determinant of the variation in life expectancy at birth across this time period is infant and juvenile mortality. In the early 19th century those who did not die as children had a good chance of long life ahead. Of those who reached adulthood, 72% lived past the end of their fertility, and those averaged another quarter century of survival (e_x45). The age-specific rates are shown in Figure 2.

Hunter-gatherers

People in 19th-century France were living in an agrarian and just industrializing society, depending on subsistence and economic systems that are

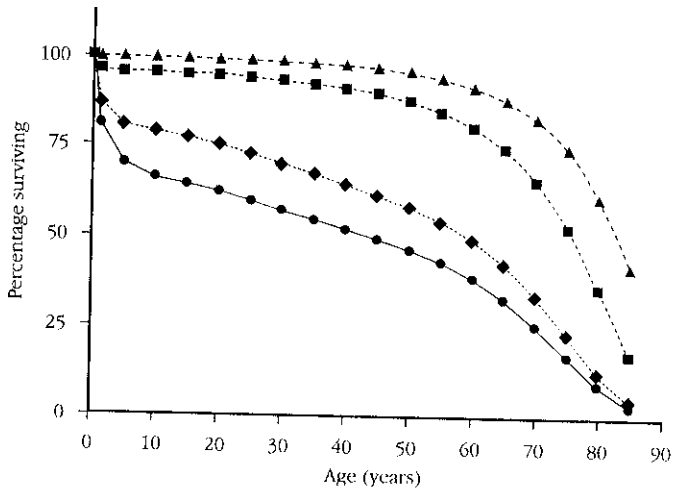

Figure 2 French historical demography. Age-specific probability of survival for 1985 (---▲---), 1950 (---■---), 1900 (---◆---) and 1850 (—●—) indicated on the *y* axis. Data from references 2 and 3

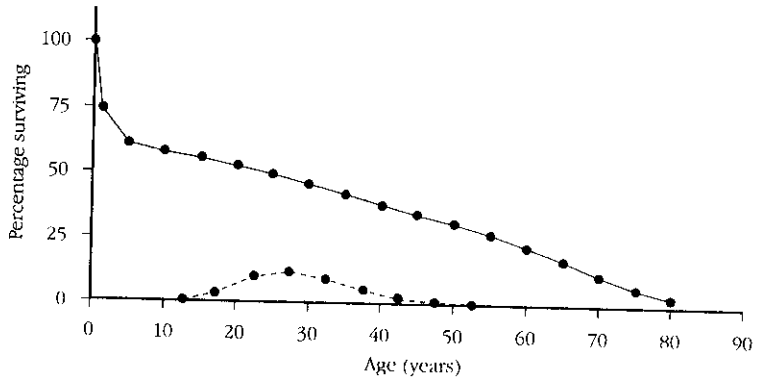

Figure 3 !Kung age-specific fertility (in daughters) (---●---) and survival (—●—). Data from reference 4

quite recent from the perspective of human evolution. Farming and herding are no older than about 10 000 years. However, we can begin to factor out some demographic effects of agriculture by looking at populations in which people live by hunting and gathering, and are largely independent of modern medicine and domesticated foods. Demographic data have now been compiled on a few such populations. We discuss three of the best described cases. They are populations with quite different recent genetic histories, spanning a wide range of ecological circumstances – from South American forests to the arid African tropics. Figure 3 shows age-specific

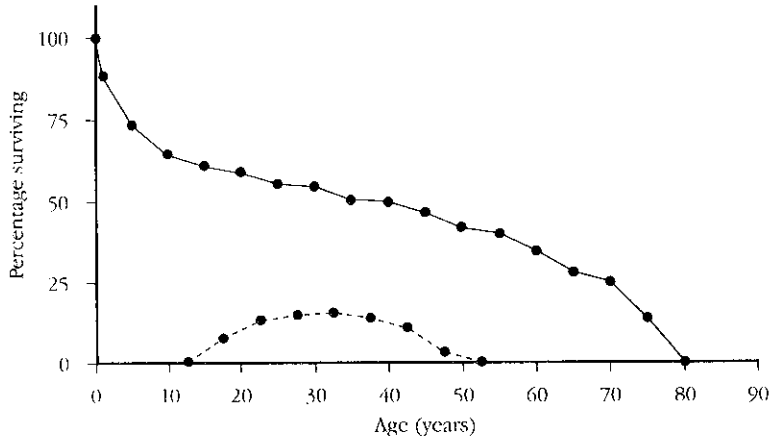

Figure 4 Aché age-specific fertility (in daughters) (---●---) and survival (—●—). Data from reference 5

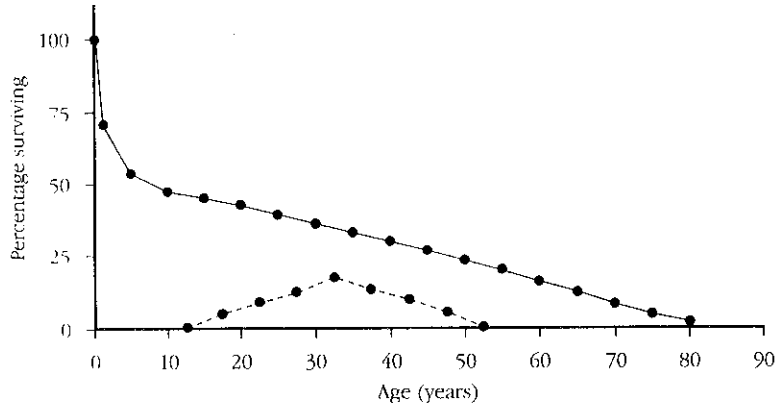

Figure 5 Hadza age-specific fertility (in daughters) (---●---) and survival (—●—). Data from reference 6

fertility (in daughters/year) and survival for the !Kung of Botswana and Namibia in the 1960s, reported by Howell[4]. Figure 4 shows the Aché of Eastern Paraguay before settlement in the 1970s, reported by Hill and Hurtado[5]. Figure 5 shows the Hadza of Northern Tanzania estimated by Blurton Jones and colleagues[6].

In all these populations life expectancy at birth was in the 30s, but anyone who reached adulthood was likely to live past menopause (66–78% did) and those alive at the end of their fertility had an average of two more

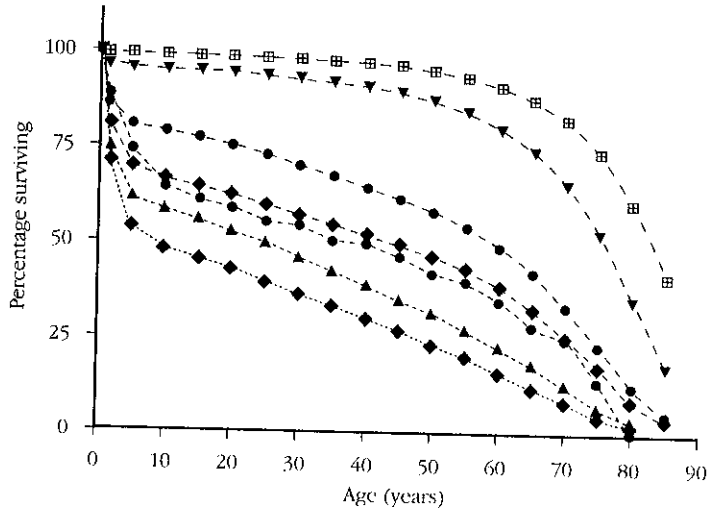

Figure 6 French historical and hunter-gatherer demography. ···◆···, Hadza; ---●---, Aché; ---▲---, !Kung; ---◆---, France 1850; —●—, France 1900; —▼—, France 1950; —⊞—, France 1985. Data reproduced from references 2–6

decades of survival. In these cases, as with other subsistence systems, menopause is not rare, it is the usual human thing (Figure 6).

OTHER SPECIES

The distinctiveness of this human pattern is clear when compared to age-specific fertility and survival in other mammalian species. Chimpanzees (Figure 7) are our nearest living relatives. Data have also been published on baboons (Figure 8)[8] and lions (Figure 9)[8]. It is very rare in all three species for an adult female to live past the end of her fertility.

LIFE HISTORY EVOLUTION

Aging

The aging patterns of other primates are consistent with some general expectations about the evolution of life histories. All aspects of physiology suffer similar age-related declines in performance at about the same time. Evolutionary explanations of aging turn on the proposition that the force of selection weakens with age because, even if the risk of death were constant, cohorts inevitably get smaller over time. Positive age-specific effects are worth

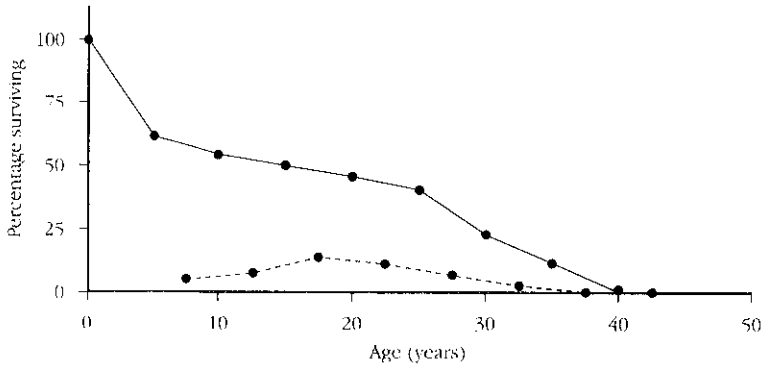

Figure 7 Gombe chimpanzee age-specific fertility (in daughters) (---●---) and survival (—●—). Data from reference 7

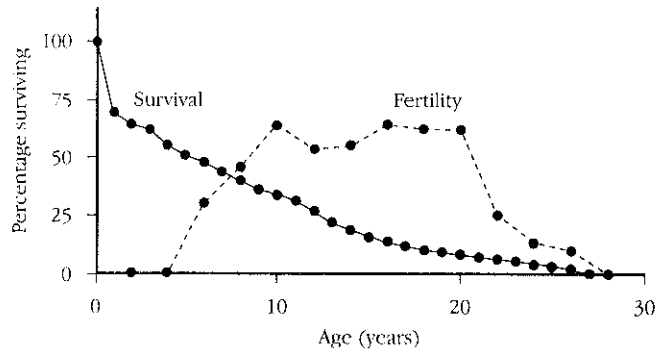

Figure 8 Gombe baboon age-specific fertility (---●---) (in daughters) and survival (—●—). Data from reference 8

more earlier in life, and negative effects less damaging later[9,10]. Moreover, performance declines in all systems at once; for example, longer-lasting kidneys are worthless if everything else fails, but very valuable if other systems are still in working order. This results in selection chipping away at outliers, maintaining general coincidence in the senescence of all aspects of an organism.

Stopping early

What then of mid-life menopause? In a 1957 paper that laid out many of the key ideas in modern life history theory, Williams[9] examined it. He suggested that, in species where maternal care was crucial to offspring survival, mothers who stopped reproducing early might end up with more surviving children. If babies were unlikely to survive their mother's death, and if pregnancy and parturition were more debilitating with age, then older mothers would do better

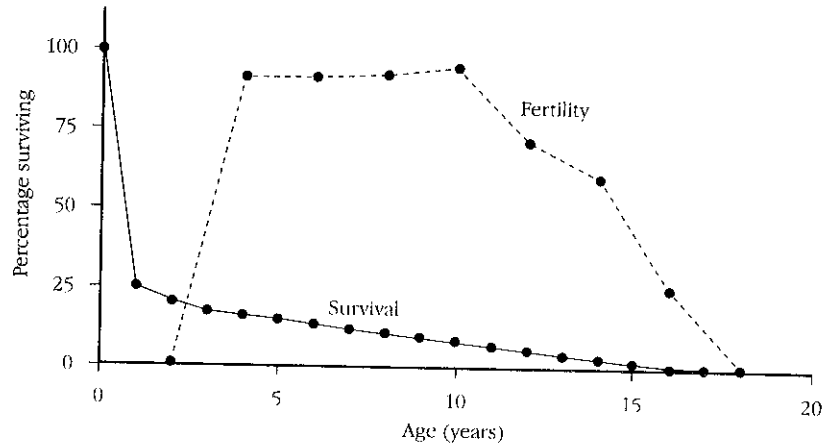

Figure 9 Serengeti lion age-specific fertility (---●---) (in daughters) and survival (—●—). Data from reference 8

to stop giving birth. They would leave more descendants if they allocated their late maternal efforts to increasing the welfare of children already born.

Williams' 'stopping early' hypothesis seems persuasive, and has often been reinvented. However, there are some compelling reasons to reject it and to look at mid-life menopause another way[11–13]. First, primates generally require substantial maternal care for offspring survival. In chimpanzees there is the famous case of Flo, whose life Jane Goodall chronicled at Gombe[14]. Flo was relatively fragile with age when her last baby was born. She died shortly thereafter, and so did the baby. Her previously born son, bereft of his mother, also died soon after. Goodall has since reported other examples of late-born babies dying with their mothers, and sometimes with an older sibling[15]. The examples illustrate the low survival chances of late babies and the cost they impose on a mother's reproductive success. They also show that chimpanzees continue to have them anyway.

A second, and related, reason for skepticism about the 'stopping early' hypothesis is the relatively *short* postnatal period during which human children are directly dependent on their mothers. Hill and Hurtado[5] have shown that, among Aché foragers in eastern Paraguay, a mother's death has no statistically significant effect on the survival of offspring who are over 5 years of age. Nevertheless, among human foragers, women at the age of last birth average about 20 years of additional survival. Moreover, human mothers have the next baby sooner than chimpanzee mothers do, a strong indication that there is more involved than extended maternal care.

A third line of evidence against the 'stopping early' hypothesis is entirely phylogenetic. Compared to our nearest living relatives, the other great apes, humans do not 'stop early'[5]. From a comparative perspective, our fertile spans reflect an ancestral condition that is conserved among all large-bodied

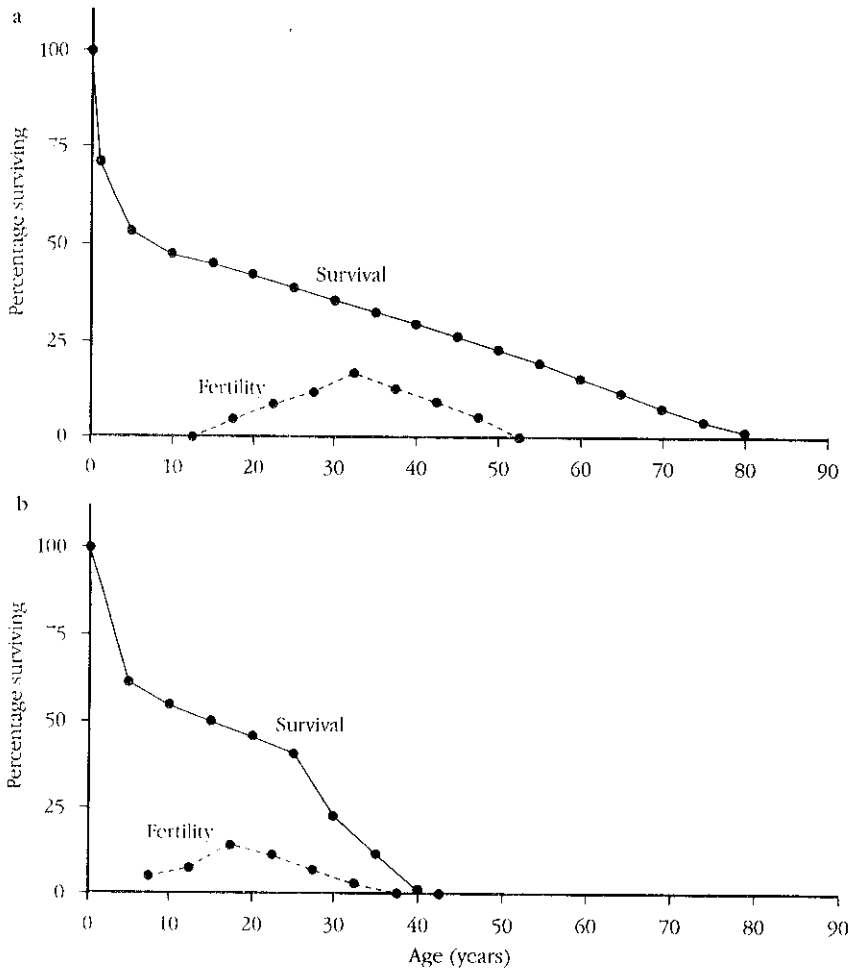

Figure 10 Human (Hadza) (a) and chimpanzee (Gombe) (b) age-specific fertility (---●---) (in daughters) and survival (—●—) on the same age scale. Data from reference 7

apes. Schultz compared life history features across the primate order and drew attention to this 30 years ago[16]. He depicted chimpanzees and humans with childbearing careers of similar duration, but very different postmenopausal lifespans. When the age-specific fertility and survival (under high mortality conditions) of humans[6] and chimpanzees[7] are compared directly (Figure 10), it is the adult survival curves that differ most. The *derived* human feature is this remarkable postmenopausal longevity[11–13].

Living longer

What selection pressures could have slowed senescence in other aspects of physiology without much change in the rate and timing of ovarian senescence? Lessons from hunter-gatherer ethnography provide a promising hypothesis.

Lessons from the Hadza

Among Hadza hunter-gatherers in Northern Tanzania[6,17] men define themselves as hunters and specialize in taking large ungulates[18]. However, successes are very unpredictable and when a hunter *is* successful the meat is widely shared, only a small fraction going to his own family. This makes hunting a poor strategy for supporting the household. People, especially children, need to eat every day. Women attend to the day-to-day business of feeding the children (and themselves) by gathering plant foods. Among the Hadza young children are energetic foragers: in some seasons those as young as 5 years old get half of their nutrient requirements by their own efforts[19]. Mothers take advantage of their children's foraging capacities, choosing to focus on foods the children can handle efficiently when those items are in season[20]. Postmenopausal women are active foragers, spending even more time gathering food than do women of childbearing age[21]. The extra time is largely devoted to digging deeply buried tubers, the year-round diet staple. Digging them requires strength and skill beyond the capacities of young children, but the long-experienced senior women earn rates equivalent to those of younger adults.

The grandmother hypothesis

The seasonal and age-related variation in Hadza foraging highlights some likely causes and consequences of human economic interdependence that have large evolutionary implications. In humans, weaned offspring depend on others to supply a substantial component of their nutrition. A chimpanzee just after weaning gets its own food. In one sense this seems to make human children a greater burden on their mothers. Children require more help with some foods than others. But if human children had to depend on their own foraging, they and their mothers – like chimpanzees – would be tied to foods that the young children could manage themselves. Food sharing allows adults accompanied by young juveniles to exploit resources and invade habitats that they otherwise could not.

Mother–child food sharing also provides a novel opportunity for senior females to have large effects on their own fitness. When a child is not able to feed itself at weaning, a mother who continues to provision it can allocate less effort to preparing for the next baby. This is an opportunity for grandmothers, one that has no parallel in other primates. An ageing female whose

fertility is declining can have a large effect on her own fitness by provisioning a just-weaned grandchild, so that her daughter can produce the next grandchild more quickly. More vigorous perimenopausal females can have larger effects on the fertility of younger kin. This would strengthen selection against senescence in older females, lower adult mortality and increase average adult lifespans.

The Hadza again

Interrelationships predicted by this scenario are evident among the Hadza[11]. The foraging effort of a mother who is not nursing has a measurable effect on the nutritional welfare of her weaned children. At the birth of a newborn her foraging effort declines (at the same time, her own nutritional needs go up with lactation) and the link between her work and the nutritional welfare of her weaned children disappears. Now the weight gains of those children depend on the foraging effort of their grandmother.

The evolution of grandmothers

Here is the scenario: imagine ancestral 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 give 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. Older females whose own fertility is declining are less likely to have weanlings of their own needing help. If they feed their just-weaned grandchildren, their daughters can have shorter interbirth intervals without reductions in offspring survivorship. The more vigorous elders will thus leave more descendants. In this scenario there is no pressure to lengthen fertile spans. Older females who continued to have babies themselves could not contribute to the increased fertility of young adults, which would erase the selective advantage for vigorous adaptive performance late in life – collapsing life histories back towards the chimpanzee-like pattern.

LIFE HISTORY INVARIANTS

This verbal argument about grandmothering is generally consistent with evolutionary theories of senescence, and some initial population genetic modelling supports it[22]. Combining it with recent life history theory developed by Charnov and colleagues[23–26] allows some actual tests. The tests in turn reveal previously unappreciated relationships among human life history traits, displaying them as systematic adjustments to a basic primate pattern.

Mortality and maturity

Charnov's assembly rules for mammalian life histories highlight relationships between variables that remain constant over transformations in the values of the individual variables. They provide a framework predicting life history consequences that would follow the evolution of grandmothering. His theory begins with a simple growth model. From weaning to maturity, growth is an allometric function of juvenile size. At maturity females redirect this production from their own growth into babies. Selection sets the age at maturity to maximize lifetime reproduction, given that growing longer means getting larger and so having more productive effort to put into babies, but waiting also means running the risk of dying before reproducing at all. If mortality rates around this age are high and lifespans are short, then the optimal age at maturity will be relatively early. If mortality rates are low and lifespans are long, then growing longer before maturing will be worthwhile. There will be time for the gains to pay off.

Among mammals generally (including primates), the relationship between average adult lifespans (the inverse of the instantaneous adult mortality rate (M) and age at maturity (α) is positive. The product αM is approximately invariant (Figure 11)[23].

If, as postulated in the grandmother hypothesis, the postmenopausal component of human lifespans is spent contributing to reproduction, then survival after menopause adds to the time over which the gains of growing longer will pay off. Grandmothering should therefore favor delaying maturity. Our long lifespans (low adult mortality rate (M)) should be associated with a late age at maturity (high α). We are in fact very late maturers, another aspect of human life histories that Schultz depicted in his classic treatment[16]. He picked out both late maturity and long postmenopausal survival as distinctively human.

If longer human adult lifespans are paying off in reproduction, and the tradeoffs captured in Charnov's model apply, then as M goes down, α goes up. Their product remains more or less invariant. Our αM should be about the same as that of other hominoids, and it is (Table 2)[27]. Our late maturity and long childhoods are as predicted by a combination of the grandmother hypothesis and Charnov's assembly rules.

Maturity and fertility

There is another systematic effect that can be expected if the grandmother hypothesis is correct and these assembly rules capture basic tradeoffs that apply to all mammals. At maturity, longer lived mothers have more to gain from future reproduction and so allocate relatively more to their own maintenence and less to current fertility. Charnov's theory deals with the *inverse* relationship between age at maturity and annual fecundity – the average number of babies produced each year (b) – through the growth allometry.

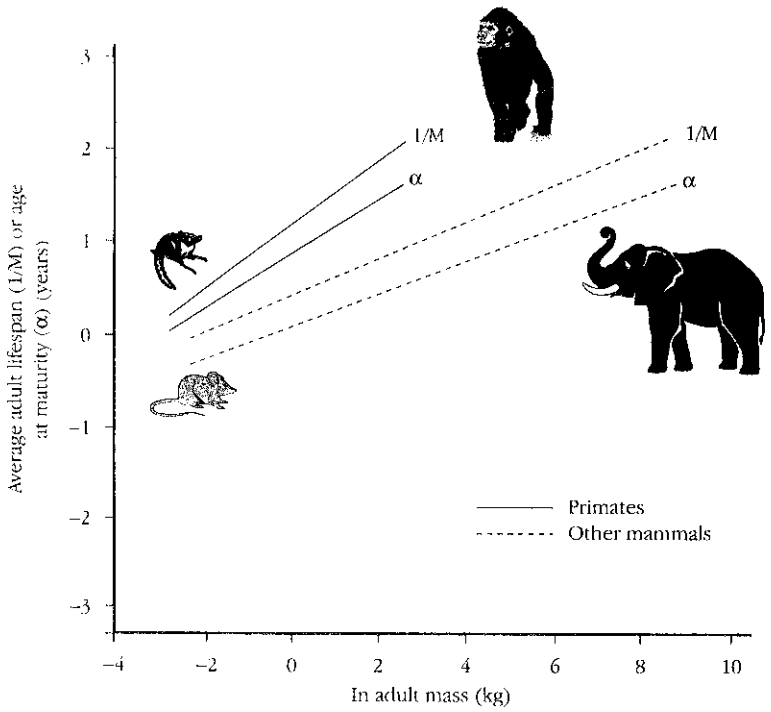

Figure 11 Age at maturity and average adult lifespan in primates and other mammals. Figure reproduced from reference 26 with permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc

Table 2 Average adult lifespan (1/M) and period from weaning to maturity (α) for four modern hominoids. From reference 27, using data from references 4–6 and 28–31

	Average adult lifespan (1/M)	*Weaning to maturity (α)*	*αM*
Orangutans	17.9	8.3	0.46
Gorillas	13.9	6.3	0.45
Chimpanzees	17.9	8.2	0.46
Humans	32.9	14.5	0.44

Later maturity means a longer growing period, so larger mothers. While larger mothers have more production to put into babies, they also make babies that are larger. So they make them at a slower rate (Figure 12)[26]. Consequently the product of α and b is another invariant.

If human longevity evolved because of grandmothering, then the fertility of childbearing-aged women should reflect the grandmothers' help. Human fertilities should be substantially higher than the fertilities of a grandmotherless primate, because the baby production of a whole lifespan is concentrated in the premenopausal years. Table 3[26] shows this to be the case – one thing Schultz was wrong about. He assumed a general lengthening of

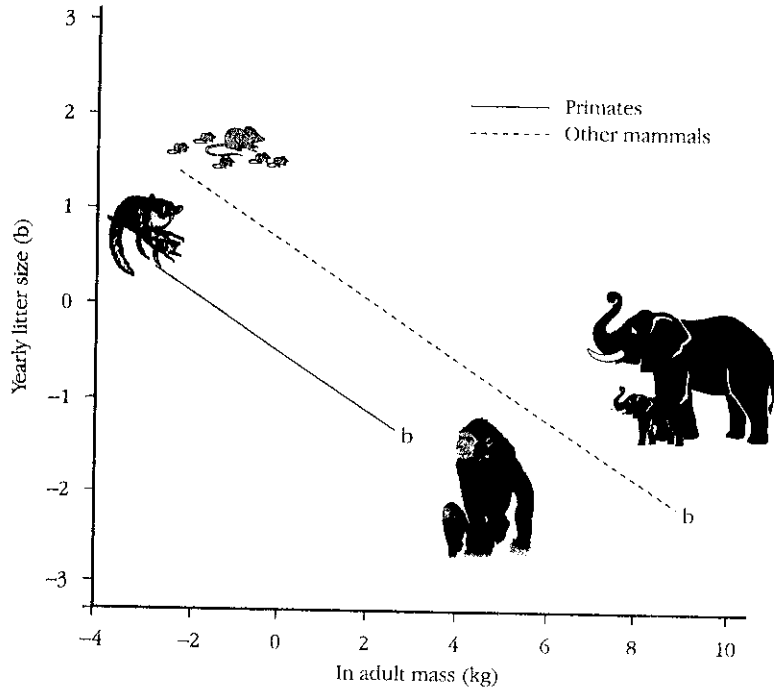

Figure 12 Annual fertility in daughters (b) and adult body size in primates and other mammals. Figure reproduced from reference 26 with permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc

Table 3 Period from weaning to maturity and annual fertility in daughters for four modern hominoids. From reference 27, using data from references 4–6 and 28–31

	Weaning to maturity (α)	*Daughters per year (b)*	*αb*
Orangutans	8.3	0.063	0.52
Gorillas	6.3	0.126	0.79
Chimpanzees	8.2	0.087	0.71
Humans	14.5	0.142	2.05

all growth stages, so depicted our weaning ages as higher than those of chimpanzees, but they are not. Instead we have interbirth intervals that are quite short, and so fertilities that are extremely high for our age at maturity (Table 3), exactly the results predicted of grandmothers.

PALEOANTHROPOLOGY

These comparative lines of evidence show that distinctively human life history features are consistent with predictions of the grandmother hypothesis. The hypothesis also makes predictions about the ecological circumstances, timing and sequence of specific evolutionary transitions in our

ancestral past. Only the partial record of paleoanthropology preserves direct evidence of those transitions. Now there are fossil specimens from more than a dozen other species of hominid in three or four genera over the past 5 million years. Initial exploration of this fragmentary but increasingly richer record finds paleontological, paleoecological and archeological evidence generally consistent with the hypothesis that grandmothering was the key adaptation distinguishing the first widely successful member of our genus from ancestral and collateral hominids[32]. This hypothesis is a radical departure from the popular view that hunting and paternal provisioning are the foundations of human evolution. One of the things it explains is our mid-life menopause. A wide array of corollary hypotheses await testing.

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