

GRANDMOTHERHOOD

The Evolutionary Significance of the Second Half of Female Life

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Human Age Structures, Paleodemography, and the Grandmother Hypothesis

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Evolutionary life-history theory and demography provide strong reasons to suppose that long human life spans are not a recent novelty. Here we focus on one robust model of mammalian life history evolution, and a grandmother hypothesis about our own lineage that is based upon it. This hypothesis takes long adult life spans to be an ancient human trait. Claims that few adults survived to old age until the last century are a serious challenge to it. Such claims are generally based on the inference that when life expectancy is less than forty, most adults die before they grow old. We use demographic evidence to show that inference is wrong. Findings in paleodemography also show that ancient skeletal assemblages do not reflect the age structure of past populations. By contrasting human and chimpanzee age structures, we further underline that point. The comparison with chimpanzees also serves to highlight the likely importance of ancestral grandmothers in human evolution.

Life History Evolution

Initial work in life-history evolution recognized that the strength of selection on genes with age-specific expression must depend on mortality schedules since juvenile and adult mortality rates have quite different effects on the lifetime reproductive success of the individuals carrying those genes (Fisher 1930; Williams 1957; Hamilton 1966; Gadgil and Bossert 1970; Charnov and Schaffer 1973). Scaling regularities, of interest in their own right, offer especially important clues for students of mammalian life-history evolution as rates of adult mortality, maturation, and fecundity scale with adult body size (Harvey and Clutton-Brock 1985). Consequently, the rate and timing variables correlate with each other, and mammal life histories fall along a fast-slow continuum even when body size is statistically controlled (Harvey, Read, and Promislow 1989).

Eric Charnov (1991, 1993) built a model that reproduces this variation from a few basic trade-offs underlying mammalian life histories. In this most successful theory to explain the empirical patterns (see discussion in Harvey and Purvis 1999; Purvis et al. 2003), stationary populations are assumed

and adult mortality rates determine other life-history variables. When adult mortality rates decline (adult life spans lengthen), the risk of waiting to reproduce goes down, so selection favors longer duration of growth to reach larger adult size. Average adult life span thus determines the optimal age at maturity, which in turn sets the adult size.

Charnov's simple model has the particularly important property that it identifies the (approximately) invariant relationships among species' average life-history traits (Charnov 1993). Values of the traits themselves change across the fast-slow continuum--some mammals mature in months, others take two decades. But the relationship between the age at maturity and average adult life span does not change. The model shows that this results from trade-offs between the costs and benefits of delaying maturity in the face of adult mortality risk.

Charnov (1993) displayed the approximately invariant relationship between these features in primates by plotting average age at maturity and average adult life span across fifteen subfamilies, drawing data from Harvey and Clutton-Brock (1985). Our subfamily fell just as predicted by the mammalian invariant. While unnoted at the time, this showed that our late age at maturity is the expected consequence for a primate with our long adult life spans. Yet for humans, unlike other primates, a substantial component of adulthood is postmenopausal (Pavelka and Fedigan 1991). In wild non-human primates, very few of the adult females are past the age of terminal fertility (Hawkes, O'Connell, and Blurton Jones 2003). Not so in humans. Even though fertility declines at similar ages in humans and chimpanzees (Gage 1998; Nishida et al. 2003; Hawkes 2003), we usually live much longer. From the perspective of the life-history model, those longer life spans are the reason for our late maturity. And, as previously expected on other grounds (Williams 1957), the whole adult life span must be reproductive. Moreover, the evolution of that longer (and substantially postmenopausal) life span becomes the key to explaining other aspects of our life histories (Hawkes et al. 1998).

A Grandmother Hypothesis

The modern Hadza (Blurton Jones et al. 1992) provide clues toward a likely explanation for the evolution of our longevity. Hunting and gathering in the arid tropics of the East African Rift, these modern people display a connection between the foraging patterns of children and their mothers and grandmothers that suggests a scenario for our ancestral past that includes a reproductive role for senior females and a consequent shift in rates of aging (Hawkes 2003). Young Hadza children are energetic foragers (Blurton Jones 1993; Blurton Jones, Hawkes, and O'Connell 1989). Mothers take

advantage of this, 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 to collect effectively. Senior Hadza women, long-experienced gatherers, spend even more time acquiring these foods than do women of childbearing age (Hawkes, O'Connell, and Blurton Jones 1989). With acquisition rates similar to those of younger adults (Hawkes, O'Connell, and Blurton Jones 1989; Blurton Jones and Marlowe 2002), their overall harvest of these resources is greater, making a substantial contribution to the nutritional needs that youngsters cannot fulfill for themselves. Weaned Hadza children usually depend on the foraging effort of their mothers. But when their mothers have a newborn, the weaned juveniles' nutritional welfare depends on the effort of their grandmothers instead (Hawkes, O'Connell, and Blurton Jones 1997).

The economic productivity of these older women and the feeding dependence of weaned children combined with current paleoanthropology suggest the following evolutionary scenario (O'Connell, Hawkes, and Blurton Jones 1999, 2002; Hawkes, O'Connell, and Blurton Jones 2003). Australopithecines are assumed to be ancestral to genus *Homo* (Klein 1999; Wood and Collard 1999). On grounds of body size, brain size, and maturation rates, australopithecines are often characterized as "bipedal apes," estimated to have life histories similar to those of modern chimpanzees (Smith and Tompkins 1995). At weaning, juveniles probably fed themselves. But the increasing aridity and seasonality of late Pliocene east and southern Africa would have constricted the forests and likely reduced the availability of fruits that young juveniles could handle (deMenocal 1995). The same ecological changes would favor plants that cope well with dry seasons by, for example, holding nutrients in underground storage organs. Such resources can give high return rates to those with the strength to extract and process them. Young juveniles cannot do it. To rely on these resources and succeed in these changing environments, mothers would have to provision offspring who are still too small to extract and process the tubers for themselves.

Increased food-sharing would allow mothers and the youngsters accompanying them to remain in habitats they otherwise could not and to colonize new, previously unexploited habitats. But the feeding dependence of those juveniles would delay a mother's next child. Maternal provisioning would create a novel opportunity for older females whose declining fertility made them less likely to have a newborn of their own: feeding their just-weaned grandchildren would allow childbearing-aged daughters to have shorter interbirth intervals without reductions in offspring survivorship.

Assuming these populations initially had aging rates and adult age structures like modern chimpanzees, the ecological change would alter the fitness benefits for slight variation in rates of senescence. The more vigorous elders would raise the fertility of their daughters and nieces more, resulting in more grandchildren endowed with their qualities and lengthening adult life spans (see Hawkes 2003 for further discussion of trade-offs and the evolution of rates of senescence).

The longer average adult life spans would in turn adjust the trade-offs captured in Charnov's mammal model, favoring delayed maturity and growth to larger maternal size. This hypothesis makes distinctive features of human life histories a consequence of the productivity of ancestral grandmothers (Alvarez 2000; Hawkes et al. 1998). The later maturation, increased body size, and rapid spread into previously unoccupied habitats by the first widely successful members of genus *Homo* are consistent with this scenario (O'Connell, Hawkes, and Blurton Jones 1999, 2002; Hawkes, O'Connell, and Blurton Jones 2003; Hawkes 2003).

This grandmother hypothesis claims central importance for the distinctive adult age structure of human populations. The evolutionary scenario proposes that ancestral populations with substantial fractions of elders actually antedate our species. According to it, our life histories evolved and have been maintained by low adult mortalities, implying that old age structures usually characterize human populations. But do they? Serious contrary assertions abound (Washburn 1981; Weiss 1981; Trinkaus 1995; Olshansky, Carnes, and Grahn 1998; Kennedy 2003; Crews and Gerber 2003). High levels of mortality in the past are widely assumed to have sharply limited numbers of surviving elders.

That assumption is fueled by confusion about the information contained in the widely used demographic statistic, life expectancy at birth (e_0). Since life expectancy has been steadily increasing in industrialized countries (Oeppen and Vaupel 2002) with ever increasing fractions of seniors, it is easy to mistakenly infer that lower life expectancy in the past means few survived to old age. However, within the range of variation of human age structures, the fraction of elders--very sensitive to variation in fertility level--is remarkably insensitive to variation in life expectancy at birth. We use Ansley Coale and Paul Demeny's (1966) *Regional Model Life Tables and Stable Populations* to illustrate this point.

The Coale and Demeny Model Life Tables

Coale and Demeny used the same stable population theory used in evolutionary life-history theory to model the age distributions implied by 326 observed human life tables. Populations converge on a stable (unchanging)

age distribution when age-specific fertility and mortality rates remain constant for a few generations. That stable age distribution is represented by a mortality schedule that can be characterized by shape (mortality changes with age) by level (life expectancy at birth), and by fertility.

Shape, level, and fertility specify a growth rate, but the dimensions can vary separately. Schedules with similar shapes can differ in level. The overall height of the survival curve shifts, so the area under it (life expectancy at birth) varies. Schedules can have the same level (the area under the survival curve) although they have different shapes; and different schedules can share the same level of mortality and fertility, but differ in shape. Coale and Demeny found that their empirical life tables generated four stable population shapes, and they constructed four regional families of models, West, North, East, and South, labeled for the regions of Europe supplying most of life tables associated with each shape. Each regional family of models consists of a series of male and female stable age distributions that vary by mortality level and fertility level while sharing a characteristic shape.

The models do not include variation in the shape of age-specific fertilities, although this variation has been analyzed and characterized by demographers (for example, Coale and Trussell 1974). The neglect is justified by "an empirical property of the age schedules of human fertility. . . . In all populations where reliable records have been kept, Fertility is zero until about age 15, rises smoothly to a single peak, and falls smoothly to zero by age 45-50. The mean age of the fertility schedule is usually between 26 and 33 years" (Coale and Demeny 1983, 27).

Limited variability in the shape of human fertility schedules is represented by the use of the gross reproductive rate (GRR) to characterize fertility level. GRR is the average number of daughters born to a woman who survives the fertile years. Each regional family is a series of stable population models with varying levels of fertility and mortality.

Figure 6.1 builds on Coale and Demeny's (1983) table 13 to show how various parameters of their West female series vary in relationship to each other (Hawkes 2004). Three mortality levels are included here, their level 1 (life expectancy of twenty years), level 9 (life expectancy of forty years), and level 17 (life expectancy of sixty years). Their models assume that the mean age of women giving birth is twenty-nine. The combination of a GRR and a mean maternal age is "sufficient to estimate r [the population growth rate] with a very small margin of error" (1983, 27). The population growth rate is represented as the annual rate of increase per 1000 females. When $r = 0$, the population is non-growing (stationary). When $r = 20$, the population is growing at 2 percent per year.

Figure 6.1 reveals the broad pattern of variation in age structures familiar to demographers from stable population models (for example, Coale

1956). Coale and Demeny used their table 13 to draw attention to "the small effect of mortality and the large effect of fertility on the mean age of the population" (1983, 31). Panels A, B, and C show that at the same fertility level (GRR), the age structures are similar across varying mortality levels. Consider panel A: when fertility is held constant (each cluster of three bars), the mean age of the population varies less than four years over three-fold differences in life expectancy. Conversely, at the same mortality level, mean age decreases by about ten years at each doubling of fertility (compare all the white bars, all the hatched bars, all the black bars).

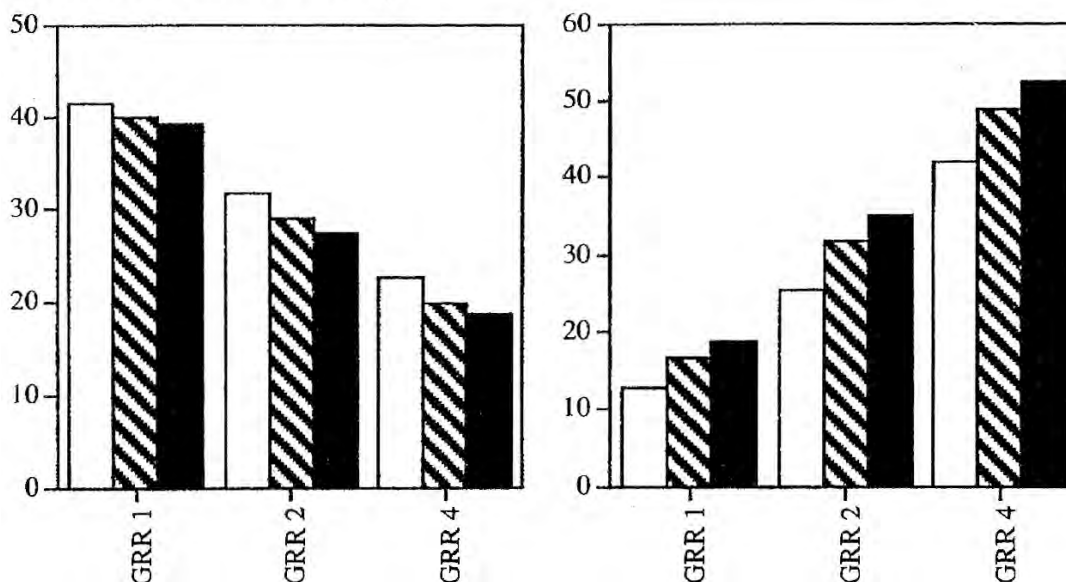
Panel B shows that the fraction of the population under fifteen years old varies less across different mortality levels with the same fertility (each cluster of three bars), than with differing fertility at the same mortality (compare all the white bars, all the hatched bars, all the black bars). The fraction of adults over forty-five is shown in panel C, similar across mortality levels with the same fertility but decreasing with increases in fertility. Note that, perhaps contrary to initial intuition, at a given fertility (the three bar clusters), populations with higher mortality levels have older mean ages, fewer children, and more women past childbearing age.

Panel D of figure 6.1 shows the population growth rate that results from particular combinations of fertility and mortality. A GRR of 1 (very low fertility) makes populations decline at all mortality levels, but the decline is steeper when overall mortality is high. Conversely, a GRR of 4 (high fertility, an average of four daughters per woman who lived to forty-five) results in a growing population at all mortality levels with growth higher when mortality is lower. Specific population growth rates imply particular combinations of these variables. Where growth rates are highest, the fraction of juveniles is highest and of adults over forty-five is lowest.

This variation in human populations occurs within limits: the fraction of women past their childbearing years drops below 20 percent only when fertility is (unsustainably) high. Population growth reduces the fraction of elders because each succeeding cohort is larger than the last. Noting the ecological unsustainability of continuing growth, Coale (1959) made this point about age structure with special force by pointing out that the fraction of elders would always decrease with increasing population growth *even if no one ever died*.

Following Coale and Demeny's table 13, we used the West series. Drawn from the largest amount of data and the most cosmopolitan group of countries, this category is least tied to European regions. The North, East, and South families show the same patterns. While the shapes differ enough to distinguish for population planning, they are nearly identical on the dimensions highlighted here. The proportion of living seniors found in all models indicates a tendency for women to remain healthy past the end of

Figure 6.1 Age structure variation in Coale and Demeny's (1983) West series with varying levels of mortality and fertility.

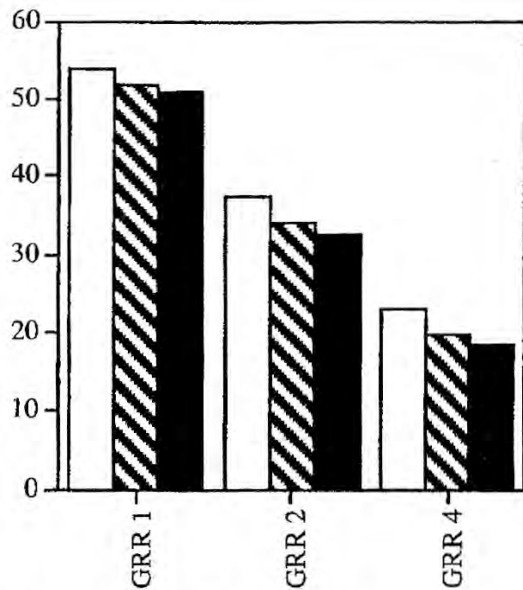


A. Variation in mean population age across different life expectancies and fertilities. Fertility on the x-axis. GRR, gross reproductive rate, is the average number of daughters produced by a woman who survives the fertile years. Mean age of the population is on the y-axis. The open bars show West 1 (life expectancy of 20 years), hatched bars West 9 (life expectancy of 40), and black bars West 17 (life expectancy of 60).

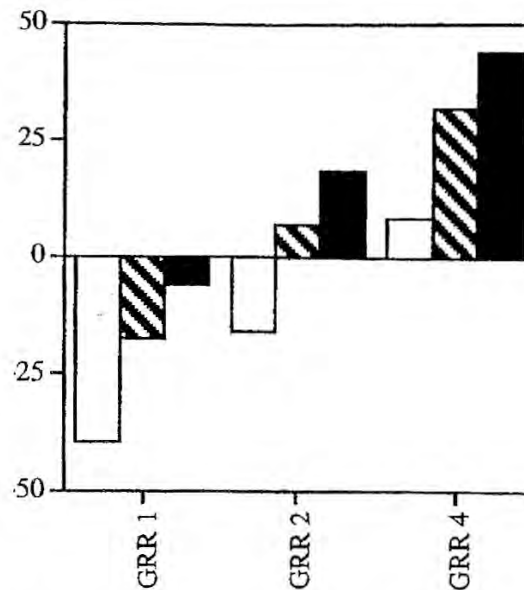
B. Variation in the percent of the population under 15 years of age with different life expectancies and fertilities. Fertility on the x-axis. GRR, gross reproductive rate, is the average number of daughters produced by a woman who survives the fertile years. Percent of the population under fifteen on the y-axis. The open bars show West 1 (life expectancy of 20 years), hatched bars West 9 (life expectancy of 40), and black bars West 17 (life expectancy of 60).

fertility. This is explicitly recognized in another demographic convention, the "dependency ratio," the number of females assumed to be too young or too old to be productive, relative to the number in the "productive" ages. Those under fifteen and over sixty (sometimes over sixty-five) are considered dependent. Those between the ages of fifteen and fifty-nine (or fifteen and sixty-four) are classified as producers. Each of the Coale and Demeny stable age models specifies a dependency ratio. Just as the use of the birth-woman ratio recognizes that there is limited variation in the shape of human age-specific schedules, this dependency ratio recognizes that women continue to be productive adults well into their grandmothering years.

The Coale and Demeny models illustrate general features of human age-specific mortality and fertility and the effects of changing mortality and fertility levels on age structure. But the sample of life tables they used to construct their models included only those based on good national vital sta-



C. Variation in the percent of adults (those over 15) that are over 45 with different life expectancies and fertilities. Fertility on the x-axis. GRR, gross reproductive rate, is the average number of daughters produced by a woman who survives the fertile years. Percent of the adults (those over 15) who are over 45 on the y-axis. The open bars show West 1 (life expectancy of 20 years), hatched bars West 9 (life expectancy of 40), and black bars West 17 (life expectancy of 60).



D. Variation in population growth rate with different life expectancies and fertilities. Fertility on the x-axis. GRR, gross reproductive rate, is the average number of daughters produced by a woman who survives the fertile years. Population growth rate r (annual change per 1000) on the y-axis. The open bars show West 1 (life expectancy of 20 years), hatched bars West 9 (life expectancy of 40), and black bars West 17 (life expectancy of 60).

tistics. So they came largely from European populations. They explicitly recognized an "unresolvable" problem: "[T]here is no strong reason for supposing that the age patterns of mortality exhibited in these four families covers anything like the full range of variability in age patterns in populations under different circumstances. . . . The question of what is the pattern of mortality in a population of an underdeveloped area is essentially unresolvable, because there exists no way to determine the exact age of an illiterate person who does not know it himself" (1983, 25).

That pessimistic view assumes that mortality schedules can only be constructed from data on large populations collected by demographers' standard census methods, ruling out the appraisal of mortality experience in small nonliterate populations, the setting for most of human history and all of prehistory. "Unresolvable" with demographers' census methods, this is the central inquiry of anthropological demographers.

Anthropological Demography

Seeking to broaden the range of reference models for ethnographers and paleodemographers, Kenneth Weiss (1973) constructed an alternative set of stable models meant to represent the populations often studied by anthropologists. He used data from fifty populations to build his model life tables. Fourteen data sets came from ethnographic censuses. Thirty-six of them were derived from archaeological assemblages.

Weiss concluded his analysis with the question "why are there no old folks?" (1973, 78). But inspection of Weiss's own data and analysis does not show the finding this question implies. Most of his source cases (Weiss 1973, appendix A) and most of his model populations *do* contain old people. His archaeological cases average more than one-fifth of adults past their mid-forties. In the ethnographic censuses, almost one-third of the adults are past their mid-forties. The difference between the archaeological and ethnographic samples is statistically significant, but neither of the averages justifies Weiss's surmise. Old folks are not absent. Weiss concluded that no "evolutionary/adaptive reason for the post-reproductive survival of human beings" is needed because "survival to old age is rare among 'primitive' peoples" (Weiss 1981, 41). But the data he assembled himself do not bear out that claim. We will return to the difference between ethnographic and archaeological cases below.

Ethnographic demography has been especially influential in highlighting the "old" age structure of human populations even when overall mortality levels are relatively high. Nancy Howell (1979) faced exactly the problem noted by Coale and Demeny when she applied demographic tools to !Kung hunter-gatherers in the Dobe area of western Botswana. Her subjects did not know their ages, so she had to develop methods for estimating them. Through interviews she ranked individuals by age and then used historically known events to anchor points in this array with Gregorian years. To smooth the final age estimates of adults, she chose a stable model from the Coale and Demeny series, West 5. Checks for internal consistency, especially the age differences between mothers and children, showed that she could not be far off in her age assignments.

A central question of Howell's study was whether the age pattern of mortality experience for the !Kung conformed to the Coale and Demeny models.

The models, after all, have been constructed by summarizing the experience of well-studied populations of agricultural and industrialized societies, people who live under different conditions than those of hunter-gatherers. . . . If the !Kung experience fits the model life tables, we can tentatively conclude that the general of the model life tables express general features of human

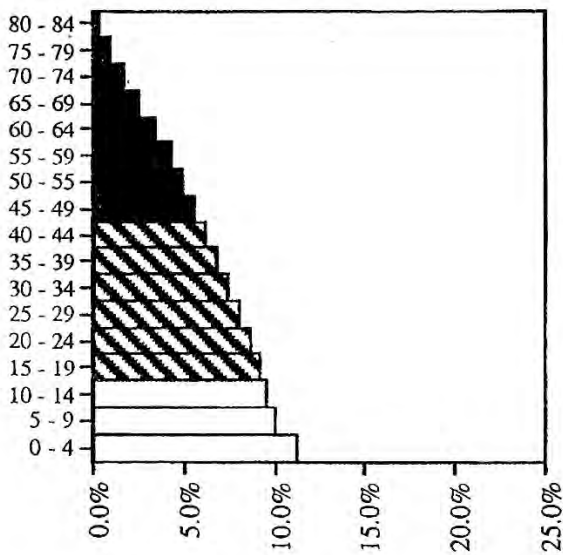
biological processes that are sensitive to environmental fluctuations in level but not in age patterns of mortality (Howell 1979, 79-80).

Several estimation procedures and a series of simulations led her to conclude that, indeed, the observed characteristics of this population did not differ from the age patterns of the models. Elsewhere she explicitly characterized the "uniformitarian assumption" that her analyses supported this way: "the human animal has not basically changed in its direct biological response to the environment in processes of ovulation, spermatogenesis, length of pregnancy, degree of helplessness of the young and rates of maturation and senility over time" (Howell 1976, 25).

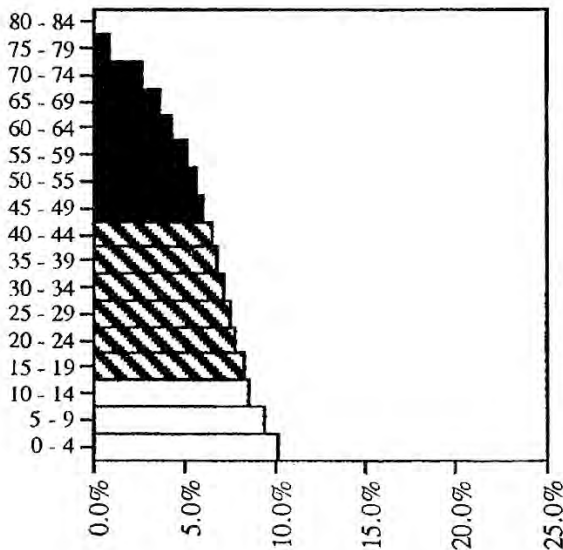
The population of hunter-gatherers she analyzed did not suffer age-specific mortality rates that leave no elders. The West 5 model she chose as best representing the !Kung population has life expectancy at birth of thirty years. Yet with this high level of mortality, a third of the women (those over fifteen) are over the age of forty-five. This age structure is displayed in figure 6.2, panel A. Howell also constructed another schedule, based on observed !Kung deaths between 1964 and 1973 (both sexes combined). That mortality schedule gives a life expectancy at birth of fifty, and an age structure with 46 percent of the adults past the age of forty-five.

Other anthropological demographers worried that the use of Coale and Demeny's models to estimate ages might obscure differences between the mortality schedules in small populations and those in the (European) regional models. Timothy Gage argued that "the uniformitarian view is overly simplistic and clearly incorrect at some level of specificity" (1998, 198-99). He noted that in the European cases used by Coale and Demeny, high mortality "is associated with high-density urban areas in the early 1800s. . . . [M]ortality in low-density populations may not follow this pattern" (1998, 205). As noted above, life tables built from archaeological data have different age structures. The age structures are younger, containing significantly fewer elders. If the Coale and Demeny mortality shapes are restricted to high-density populations, as Gage suggests, the small fraction of living elders estimated from skeletal series might accurately represent human mortality experience in other socioecological contexts. Howell's !Kung demography stands against this, but it is one case, and a case in which the Coale and Demeny models were used in the age estimations.

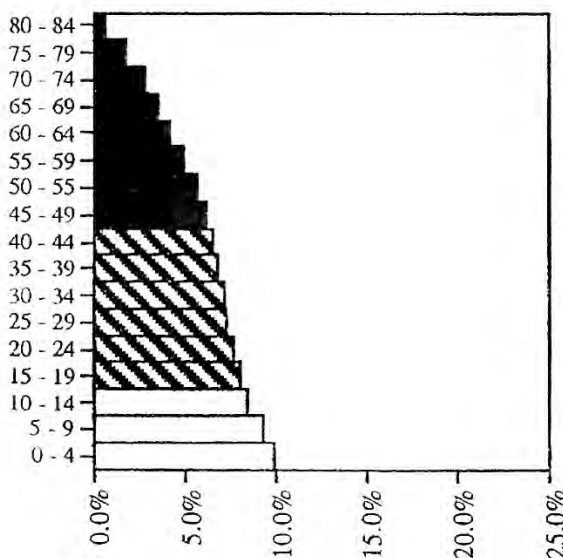
Three other demographic projects, undertaken with less reliance on the Coale and Demeny series, add to the burden of evidence in favor of Howell's depiction of old age structures in small-scale, low-density, non-European populations. Renee Pennington and Henry Harpending (1993) studied the demography of the Ngamiland Herero, the Bantu pastoralists who moved into the Dobe area occupied by the !Kung mostly after 1950.

Figure 6.2 Population Age Structures

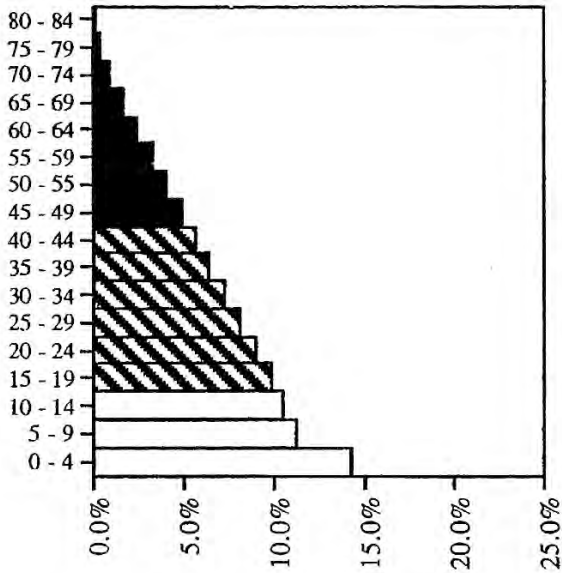
A. Female age structure (West 5) chosen by Howell (1979) for Dobe !Kung. X-axis represents the percentage of the female population in each five-year age class. Five-year age classes on the y-axis. Open bars are girls under 15; hatched bars are childbearing-aged women 15–45; black bars are seniors past childbearing age. In this West 5 model selected by Howell (1979) to represent the Dobe !Kung population, life expectancy (e_0) is 30 years, and 33.5% of the adults are over 45.



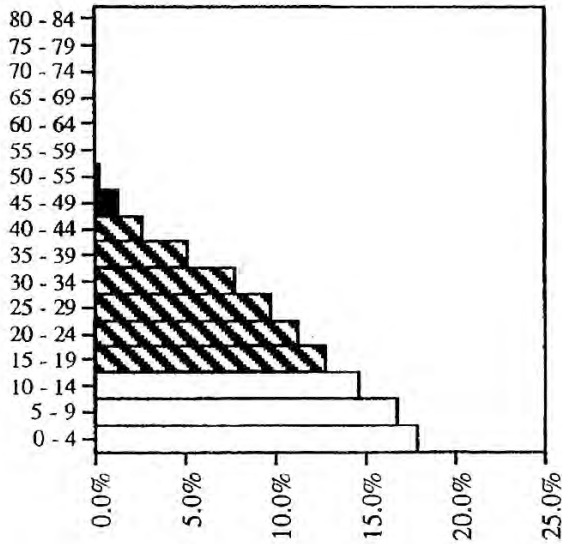
B. Female age structure from the forest period Ache life table constructed by Hill and Hurtado (1996). X-axis represents the percentage of the female population in each five-year age class. Five-year age classes on the y-axis. Open bars are girls under 15; hatched bars are childbearing-aged women 15–45; black bars are seniors past childbearing age. This model represents the life table constructed by Hill and Hurtado (1996) for the Ache during the forest period. Life expectancy (e_0) is 37 years, and 39% of the adults are over 45.



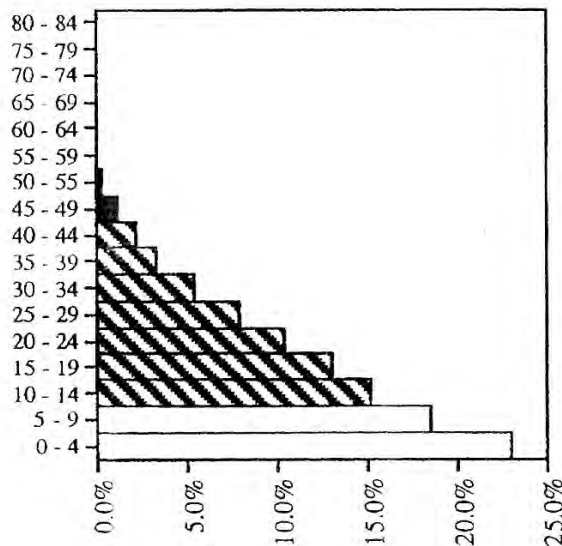
C. Female age structure from the Hadza life table constructed by Blurton Jones et al. (2002). X-axis represents the percentage of the female population in each five-year age class. Five-year age classes on the y-axis. Open bars are girls under 15; hatched bars are childbearing-aged women 15–45; black bars are seniors past childbearing age. In this model constructed by Blurton Jones et al. (1992) for the Hadza, life expectancy (e_0) is 33 years, and 40.4% of the adults are over 45.



D. Female age structure for Coale and Demeny (1983) West Model 1. X-axis represents the percentage of the female population in each five-year age class. Five-year age classes on the y-axis. Open bars are girls under 15; hatched bars are childbearing-aged women 15–45; black bars are seniors past childbearing age. In this West 1 model, life expectancy (e_0) is 20 years, and 27.4% of the adults are over 45.



E. Female age structure from the Libben life table constructed by Lovejoy et al. (1977). X-axis represents the percentage of the female population in each five-year age class. Five-year age classes on the y-axis. Open bars are girls under 15; hatched bars are childbearing-aged women 15–45; black bars are seniors past childbearing age. In this model, life expectancy (e_0) is 20 years, and 2.9% of the adults are over 45.



F. Age structure for synthetic life table for wild chimpanzees constructed by Hill et al. (2001) using data from five sites. X-axis represents the percentage of the female population in each five-year age class. Five-year age classes on the y-axis. Open bars are juveniles (under 10); hatched bars are childbearing-aged females 10–45; black bars are seniors past childbearing age. In this model, life expectancy (e_0) is 15 years, and 2.2% of the adults are over 45.

While Pennington and Harpending disagreed with aspects of Howell's analysis of the Dobe !Kung population, they noted strong similarity between their Herero survival curve and the survival curve Howell had constructed from observed !Kung deaths. Howell had speculated that these observed deaths underestimated actual, long run !Kung mortality, but Pennington and Harpending concluded that, on the contrary, "her estimates of !Kung survivorship are quite reasonable" (1993,221). In their Herero life table for the period before 1966, life expectancy is about 50, and 49.5 percent of the women (those over fifteen) are over forty-five.

Kim Hill and Magdalena Hurtado's (1996) Ache demography describes a hunter-gatherer population with a very different history than the !Kung, occupying a very different habitat. The !Kung (and Herero) live in arid southern Africa; the foraging Ache are Native Americans who live just outside the Amazon Basin in the forests of eastern Paraguay. Hill and Hurtado constructed a population register for the Ache back to the early 1900s. Their survival schedule for forest-living Ache females--without any reliance on the Coale and Demeny models--gives a life expectancy at birth of thirty-seven, and an adult age distribution in which 39 percent of the women (those fifteen years and older) are past their fertility (that is, forty-five and older). This second hunter-gatherer age structure is shown in figure 6.2, panel B.

Additional evidence of old age structure in low-density populations comes from a third hunter-gatherer demography (Blurton Jones et al. 1992; Blurton Jones, Hawkes, and O'Connell 2002), the Hadza discussed above in summarizing the grandmother hypothesis. Like the !Kung, Hadza foragers inhabit the arid African tropics, but they live in northern Tanzania just south of the equator in the East African Rift. From census data collected by James Woodburn in 1966-67, the population was initially analyzed by Tim Dyson (1977), who selected the Coale and Demeny model North 6 to represent it. Blurton Jones and Lars Smith conducted another census in 1985. Using the two censuses and an initial set of age estimates, Blurton Jones corroborated Dyson's analysis (Blurton Jones et al. 1992). Subsequent censuses and reproductive interviews allowed Blurton Jones to further correct the population age ranking, tie births and deaths to datable events, and construct a mortality schedule independent of the Coale and Demeny models (Blurton Jones, Hawkes, and O'Connell 2002). This schedule represents a stable age distribution in which 40.7 percent of the adults (those fifteen and over) are forty-five or older, shown in figure 6.2, panel C.

The Archaeological Assemblages

Skeletal remains are often said to tell a different story. Weiss (1973) recognized that mortuary assemblages might not reflect the mortality experience

of populations. Still, he used mostly archaeological cases to build his models. As noted above, the adult age structures estimated from those skeletal assemblages are significantly different from the ethnographic life tables. (Recall that, nevertheless, on average more than 20 percent of the adults in the life tables of Weiss's archaeological cases are past the ages of terminal female fertility.)

Subsequent to Weiss's monograph, paleodemographers began to explicitly examine sources of bias in archaeological skeletal samples. Jean-Pierre Bocquet-Appel and Claude Masset showed how much the age structure of reference samples could bias the aging of skeletal material and drew the devastating conclusion that "early mortality of adults, overmortality of women, lack of old people in those populations, whether prehistoric or medieval: all these hackneyed notions were born from the misinterpretation of data. As they are in no way vindicated, we must get rid of them" (1982, 329).

Phillip Walker and colleagues (1988) found dramatic evidence of bias arising from differential preservation of the bones of older individuals in their study of the remains from the California mission cemetery at La Purisima. Mission records showed that 53 percent of the adults buried at the cemetery were over forty-five, but only 7 percent of the recovered adult skeletons were over forty-five. That cemetery is less than 200 years old. The investigators conclude that, other things equal, the magnitude of the age-related bias should be "roughly proportional to the length of time a group of burials has been in the ground" (Walker, Johnson, and Lambert 1988, 188). Implications for Paleolithic samples are severe.

Age estimation techniques have been the center of paleodemographic attention since Bocquet-Appel and Masset's "Farewell to Paleodemography" (1982). Age misestimation of skeletal material can be corrected by more sophisticated modeling techniques (Hoppa and Vaupel 2003) and perhaps preservation bias can also be estimated. But, even with these marked improvements in dealing with skeletal series, the age structure of a mortuary assemblage is unlikely to reflect the mortality experience of the population that left it. Deceased members of different ages and sexes are not equally likely to be interred in the same deposits. As Lyle Konigsberg and Susan Frankenberg caution, skeletal assemblages "cannot be considered as random samples of all members of a population who died within a certain period" (1994, 92).

Despite this recognition within paleodemography, a cemetery accumulated between 800 and 1100 AD at the Libben site in northern Ohio (Lovejoy et al. 1977) continues to be cited as empirical evidence that there were few old people in the past (Washburn 1981; Trinkhaus 1995; Austad 1997; Kennedy 2003). C. Owen Lovejoy and colleagues (1977) argued that because the preservation was excellent, the excavation careful, the assemblage large, and the aging techniques good, the life table they constructed from the

Libben skeletons was not subject to the usual archaeological biases. Their life table showed the "typical low infant mortality and high adult mortality of many skeletal series and thus contrasts inversely with most extant 'anthropological populations'. . . This general discrepancy between skeletal and ethnographic censuses is usually attributed to underenumeration of infants and errors of age estimation among adults from skeletal series" (Lovejoy et al. 1977, 291). But they claimed instead that the age profile was a reflection of the actual age structure of a population unexposed to the battery of novel pathogens with European arrivals in America.

Howell (1982) elaborated the implications of such a possibility by drawing out the social and economic consequences of the life table proposed for Libben. She compared the age structure for this life table to a Coale and Demeny model with the same level of mortality. The comparison under-lined both how little life expectancy says about adult age structure and also how the family relationships and economic interdependencies known for human populations would be absent in the Libben reconstruction.

The female age structure of the West 1 model from Coale and Demeny that has the same life expectancy, $(e_0)=20$, as the Libben model is shown in figure 6.2, panel D. It is not so different from the three hunter-gatherer populations, panels A, B, and C. The very different age structure of the Libben life table is shown in panel E. Only about half the Libben population is adult (over fifteen) and only 2.9 percent of those are past their child-bearing years, that is, there are almost no grandmothers. In contrast, 65 percent of the West 1 population, panel D, is adult (over fifteen), and 27.4 percent of them are past their childbearing years. Howell (1982) pointed out that the dependency ratio of the Libben population implies improbably heavy loads on relatively few young adults. In West 1, there are many adults, and those in their grandmothering years could help younger adults with the children.

Human vs. Chimpanzee Age Structures and Grandmothers Again

Because chimpanzees are our closest living relatives, many (but not all, cf. Gage 1998; Crews and Gerber 2003) look to similarities and differences between humans and chimps to specify questions about the evolution of human life histories. Our genetic similarities and the paleoanthropological reasons to see chimpanzees as models for australopithecine life histories make these comparisons particularly important (Hawkes 2003).

Figure 6.2, panel F shows the age structure implied by a life table for wild

chimpanzees (Hill et al. 2001). The chimpanzee population is just slightly younger than the Libben model and has a higher mortality level, but the adult age structures are very similar. With their shorter adult life spans, chimpanzees mature earlier than humans. Classifying all those over ten as adults (from the age-specific fertility schedule of Nishida et al. 2003) is parallel to classifying all over fifteen as adults in human populations. That makes 58.5 percent of the chimpanzee population adult (compared to 50.7 percent for Libben). Females past childbearing age are all but absent in both models: less than 3 percent of the adults are past forty-five.

Consistent with aging rates implied by this demographic picture of chimpanzees, observers describe chimpanzees as frail with age by their mid-thirties (Goodall 1986; Nishida et al. 2003). In humans, strength measures of foraging women show no marked decline through the forties, fifties, and well into the sixties (Blurton Jones and Marlowe 2002; Walker and Hill 2002). Chimpanzees have an age structure similar to the one suggested for Libben. Humans do not. As noted initially, life-history variation across the mammals is correlated with variation in adult age structures. Life-history differences between chimpanzees and humans add to Howell's reasons to surmise that the Libben cemetery assemblage does not represent the mortality experience of the human population that left the remains.

The difference in adult age structure between chimpanzees and humans is associated with a difference in subsistence dependence of juveniles. When chimpanzee infants are weaned, they become nutritionally independent and forage for themselves. By contrast, although human children can be surprisingly eager and successful foragers at very young ages (Blurton Jones, Hawkes, and O'Connell 1989; D. W. Bird and R. B. Bird 2002; R. B. Bird and D. W. Bird 2002), they continue to depend on others to supply substantial fractions of food after their mothers are investing in a subsequent baby. The subsistence dependence of human juveniles increases with reliance on foods that are difficult for youngsters to exploit efficiently enough to completely feed themselves (for example, Hawkes, O'Connell, and Blurton Jones 1995). In the case of the Hadza, the foraging effort of postmenopausal women affects the nutritional welfare of their grandchildren when the mothers of those children are nursing new babies (Hawkes, O'Connell and Blurton Jones 1997). The grandmother hypothesis links our age structure and our unusual pattern of bearing the next baby before the previous one is independent. Ancestral human mothers could overlap dependents because they had help.

Sarah Hrdy (1999, 2001) has characterized humans as cooperative breeders. She notes that mothers' commitment to their infants may be conditional on social support. Because we overlap dependent offspring, help

can be crucial, and mothers may face large trade-offs between investment in a newborn and other offspring. That need for support (our relatively short interbirth intervals, Hawkes et al. 1998) would only evolve if help was likely. Short-term variation in the availability of help would make it advantageous for mothers to strategically adjust their commitment to a new baby. Uncertain maternal commitment, combined with the importance of allo-maternal help, would also have favored features in infants and toddlers that enhanced their likelihood of attracting investors (Hrdy 1999). By this life-history argument, both the range of helpers and the maternal and infant strategies to assess and to extract help depend on the human age structure. If so, our special form of cooperative breeding is a legacy of the importance of ancestral grandmothers.

Only recently have investigators begun to look at grandmothers' help (Hill and Hurtado 1991, 1996; Rogers 1993; Shanley and Kirkwood 2001; Sear, Mace, and McGregor 2000; Voland and Beise 2002; Leonetti et al. this volume, Jamison et al. 2002; Hames and Draper in press; Lahdenpera et al. 2004). There are important difficulties. For example, senior women distributing their help to maximize its marginal effect might supply most to those kin most in need. Then comparisons between the welfare of juveniles with grandmothers and those without would necessarily underestimate the magnitude of grandmother effects (Blurton Jones, Hawkes, and O'Connell this volume). Assessing the fitness benefits (and costs) that flow through characteristic human age structures is challenging.

Conclusion

Adult age structure and other life-history characteristics are interrelated across the mammals. The most successful evolutionary models currently available to explain that systematic variation make adult life span the determinant of other life-history variables. If theory that applies to primates in general also applies to us, then our late maturity and slow aging imply that old adult age structures have generally been characteristic of humans. Counterarguments that life expectancies of forty or less imply few elders in past populations are in error. Human populations that experience such high mortality levels nevertheless include large fractions of women past child-bearing age.

Claims of discrepant evidence from paleodemography depend on unwarranted inferences from mortuary assemblages about the mortality experience of past populations. Other aspects of the fossil and archaeological evidence are consistent with the hypothesis that old age structures are a feature of our lineage that antedate *Homo sapiens* (O'Connell et al. 1999, 2002;

Hawkes, O'Connell, and Blurton Jones 2003). An especially important clue to our evolutionary history is the persistence of a chimpanzee-like age-specific fertility decline to menopause accompanied by much slower aging in other aspects of our physiology (Hawkes 2003).

Ronald Lee (2003) has developed an evolutionary model of aging in which subsistence contributions to kin (transfer effects), not remaining fertility, can favor lower age-specific mortality rates. We construe this as a formal treatment of elements of the verbal grandmother hypothesis, showing how slowed senescence would have been favored in our lineage under socioecological circumstances that prompted the economic productivity of elders. With increased reliance on foods difficult for young juveniles to handle, elder females unencumbered by their own infants could use their productivity to help provision grandchildren, consequently shifting the age structure and the social organizational possibilities of genus *Homo*.

Summary

A grandmother hypothesis in combination with Charnov's model of mammalian life-history evolution can explain the long potential life spans, short interbirth intervals, late age at maturity, and midlife menopause that distinguish humans from our closest living relatives. We summarize the model and hypothesis that assume that low adult mortality is a general characteristic of human populations. Then we examine the implications of large variation in human life expectancies over time, something widely seen as evidence against the hypothesis. Shorter expectations of life in the past are misread to imply that few adults survived to old age. We use model life tables and anthropological demography to show this error. Then we turn to paleodemography. Life tables that depict past human age structures unlike any known for living populations have already drawn skepticism from demographers. Models that highlight patterns of life-history variation across species supply additional reasons for doubt. We conclude that claims of younger age structures in the human past are not well warranted. Current evidence is consistent with the hypothesis of an ancient shift to characteristically human age structures when ancestral grandmothers helped to provision younger kin.

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