ABSTRACT Long postmenopausal lifespans distinguish humans from all other primates. This pattern may have evolved with mother–child food sharing, a practice that allowed aging females to enhance their daughters' fertility, thereby increasing selection against senescence. Combined with Charnov's dimensionless assembly rules for mammalian life histories, this hypothesis also accounts for our late maturity, small size at weaning, and high fertility. It has implications for past human habitat choice and social organization and for ideas about the importance of extended learning and paternal provisioning in human evolution.

Mother–child food sharing occurs among many primates (1), but only human mothers provide a substantial fraction of their weaned children's diets. This allows mothers to use resources that they themselves can gather at high rates but that their children cannot. Among some hunter–gatherers, for example, deeply buried tubers are year-round staples (2, 3). Young children cannot extract them efficiently (4, 5), but their mothers do so well enough to earn a surplus that can support more than one child. Postmenopausal women earn the same high rates (2). With no young children of their own, they help feed their daughters' and nieces' offspring. This help is especially important for the nutritional welfare of weaned children when their mothers forage less at the arrival of a newborn (3).

This division of labor suggests a solution to the riddle of menopause in humans. Other apes live no longer than ≈50 years (6). That is, they become frail with age so that all physiological systems, including fertility, fail in tandem. This threshold defines maximum lifespan, a parameter that can be used to estimate other life history averages (7, 8) (see note 1 to Table 1). In humans, maximum lifespan is nearly 100 years, but fertility in women universally ends in approximately half that time, well in advance of other aspects of physiological frailty (9). The question is how natural selection came to favor this distinctly human "postreproductive" component of life history.

Many have assumed that the answer lies in Williams' (10) suggestion that early termination of fertility would likely evolve when extended maternal care became crucial to offspring survival. Aging mothers who stopped being fertile and devoted their reproductive effort to insuring the survival of children already born would leave more descendants than those who continued risky pregnancies with babies unlikely to survive the mother's death.

The "stopping early" hypothesis continues to stimulate useful work (11–15), but there are good reasons to be skeptical of it. Other primates among whom extended maternal care is vital fail to show the predicted early end to fertility. In chimpanzees, for example, available data indicate low survival

probabilities for late-borns (16–17), yet a substantial fraction of aging females still continue to produce them (18). In fact, human reproduction does not end early in comparison with other apes. Our reproductive spans are at least as long as those of chimpanzees. The striking difference between us and the other great apes lies in the low adult mortalities that give us long average lifespans after menopause. This characteristic is not restricted to populations in which age-specific mortalities have declined recently with scientific medical advances. Age structure among hunter–gatherers with no access to Western pharmaceuticals shows distinctively low adult mortalities compared with other apes (12, 19). Schultz's (20) often reprinted figure makes the point (Fig. 1) (see also ref. 11). Postmenopausal longevity, not early termination of fertility, appears to be the derived characteristic of our species.

There are two evolutionary explanations for aging: mutation–selection balance and inter-temporal tradeoffs in reproductive effort (reviewed in ref. 21). Because the risks of mortality accumulate over time, there are fewer individuals in older cohorts for selection to affect. So the force of selection declines with age (22). Mutation–selection balance is reached when the force of selection is no greater than the mutation rate. Deleterious effects on adaptive performance thus accumulate at later ages. Inter-temporal tradeoffs lead to senescence because genes have multiple effects. The same genes can affect fitness in different ways at different stages in an individual's life history. Genes that have positive effects at younger ages may be favored even though they have negative effects later in life. Those that have positive effects late in life will be disfavored if they have negative early effects. Senescence results from this antagonistic pleiotropy (10).

Grandmothering could slow aging by either means. It would strengthen selection against late-acting deleterious mutations by increasing the contribution to descendant gene pools of longer-lived females through the increased reproductive success of their daughters. It would also change the tradeoffs between opposing effects expressed at different ages. Slower senescence generally comes at the cost of reduced fertility at younger ages (23). If ape adult mortalities are in equilibrium on this tradeoff, then apes age early by human standards because mutations that would increase adaptive performance at later ages are continually removed by the reductions those mutations impose on fertility earlier in life. Regular mother–child food sharing could perturb that equilibrium by increasing the payoffs for late somatic performance as vigorous senior women earned more descendants by feeding grandchildren. Increased "somatic effort" that slowed aging would come at the cost of lower "reproductive effort" at younger ages. But the contributions of senior females would increase the reproductive success of childbearers more than enough to offset the reduced expenditure of the childbearers themselves. Continued childbearing, on the other hand, which would conflict with grandmothering, would be no more favored than in other ape

Table 1. Average values for selected life history variables

1	Average adult lifespan, $1/M$*	Age at maturity†	Age at weaning‡	α§	αM	Ratio of weaning weight to adult weight,¶ δ	Daughters per year,‖ b	αb
Orangutans	17.9	14.3	6.0	8.3	0.46	0.28	0.063	0.52
Gorillas	13.9	9.3	3.0	6.3	0.45	0.21	0.126	0.79
Chimpanzees	17.9	13.0	4.8	8.2	0.46	0.27	0.087	0.70
Humans	32.9	17.3	2.8	14.5	0.44	0.21	0.142	2.05

*If mortality is Gompertz, maximum lifespan increases with the double logrithm of sample size, making it nearly independent of sample size for samples on the order of 10^3 or more (8). Maximum lifespan (T_{max}) can then be used to estimate average adult mortality (M), the inverse of which is average adult life span, by the method described in Charnov (see legend to figure 5.6, ref. 24) that we follow here: $1/M = 0.4T_{max} - 0.1$. Values for orangutans: Leighton *et al.* (29); gorillas: Stewart *et al.* (30); chimpanzees: Nishida *et al.* (31). The human value is estimated from Howell's (19) oldest observed !Kung individual, age 88, and Hill and Hurtado's (12) oldest observed (forest-living) Ache individual, age 77.

†Age at first birth minus gestation. Orangutans: Leighton *et al.* (29); gorillas: Stewart *et al.* (30); chimpanzees: the mean of the means from Wallis (32) for Gombe, Nishida *et al.* (31) for Mahale, and Sugiyama (33) for Bossou; humans: the mean of the mode for !Kung in Howell (19) and Ache in Hill and Hurtado (12).

‡Orangutans: Galdikas and Wood (34); gorillas: Stewart *et al.* (30); chimpanzees: the mean of the estimate from Goodall (16) for Gombe and from Nishida *et al.* (31) for Mahale; humans: the mean of the median for !Kung in Howell (19) and Ache in Hill and Hurtado (12).

§Defined as the period of independent growth, from weaning to maturity.

¶Data from Lee *et al.* (35) for the great apes. Maternal size for orangutans is estimated to be 40 kg, for gorillas 93 kg, and for chimpanzees 40 kg. In that data set, δ for humans is 0.16 with maternal size at 55 kg (the upper end of the range for modern foragers who are generally smaller than either contemporary nonforagers or pre-Mesolithic moderns). We use the mean of the !Kung (19) (who are at the lower end of the size range for modern foragers) and the Ache (12) (who are at the upper end) to represent humans.

‖Great ape data from Galdikas and Wood (34), who reappraise birth spacing in all species in the same way. We use medians calculated therein (for closed intervals) plus 2 months to approximate the mean interval, then divide by 2 to get the rate in daughters. Galdikas and Wood use the Gainj, a population of horticulturalists in highland Papua New Guinea, to represent humans for which $b = 0.132$. We use the mean of the !Kung (19) and the Ache (12).

species. Aging in all aspects of physiology, except fertility, would be slowed as a result.

Charnov's (7, 24, 25) dimensionless approach to life histories provides a framework for developing and testing this argument. His "assembly rules" for mammalian life histories seem quite robust. The general fit of empirical patterns to predictions [since confirmed on other, larger data sets (26)] suggests that Charnov's model (CM) identifies key tradeoffs that shape mammalian life histories. Several extensions of the basic model (24, 27) are discussed elsewhere but do not play a role in the comparisons made here.

In CM, growth is comprised of two periods: (*i*) conception to independence (weaning) and (*ii*) independence to maturity. At maturity, production previously allocated to growth is redirected to offspring. Growth rates are approximately an allometric function of body mass (W) and a characteristic "production coefficient" (A); individual production rates take the form $dW/dt = AW^c$, where the exponent c is ≈ 0.75. Adult size at maturity ($W\alpha$) and production available for offspring both vary directly with A, which is characteristically low in primates compared with other mammals (28) and even lower in humans (12).

CM assumes that, given adult mortalities, selection sets α (the period of independent growth) according to the tradeoff between the benefits of growing longer vs. reproducing sooner. Because production is a function of maternal size, it generally increases with age of maturity. Time available to use those gains depends on the instantaneous adult mortality rate (M). As that rate falls (and average adult lifespans increase), selection favors delayed maturity to reap the benefits of larger size. α and M thus vary widely but inversely. Their product (αM) is approximately invariant.

If human longevity has been extended by grandmothering, then age at maturity should be delayed accordingly. Humans reach maturity at a relatively late age compared with other large bodied primates (Table 1). CM extracts previously unappreciated information from the difference. αM for humans is similar to that of other apes, implying that α is adjusted to whole lifespan. The extreme delay in maturity for humans, another characteristic human feature evident in the Schultz diagram (Fig. 1), indicates that gains from growing longer before reproducing pay off throughout adulthood, including both childbearing and grandmothering years.

CM finds that, for a large sample of mammals (and for primates separately), the ratio of size at independence to adult size ($W_o/W\alpha = \delta$) is approximately constant (see figure 5.4 in
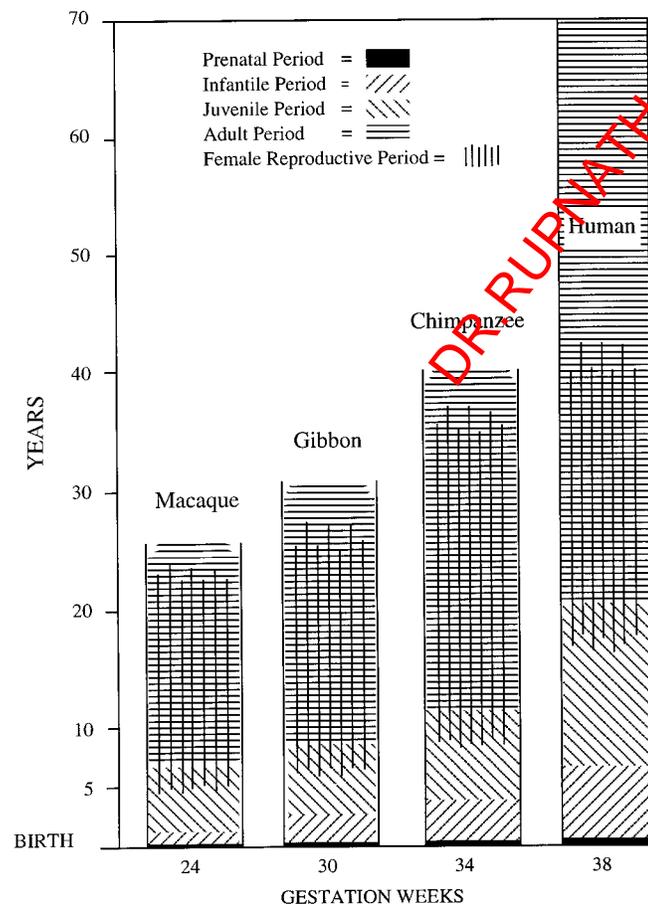

FIG. 1. Modified from A. H. Schultz (1969) *The Life of Primates* (20), page 149.

ref. 24). Weaning size scales approximately isometrically with adult size whereas the production allometry is less steep. Thus, the size of weanlings increases more rapidly with maternal size than does the production the mother can put into them. Consequently, annual fecundity (b) declines as age at maturity (α) increases. Larger mothers produce larger but fewer babies; αb is another approximate invariant.

If the grandmothering hypothesis is correct, childbearing women should produce babies faster than otherwise expected because of grandmothers' contribution to production. Grandmothers might affect the growth of infants in two ways: (*i*) by feeding nursing mothers and infants, thus accelerating the growth of infants, who then reach size of independence more quickly and (*ii*) by supplying food to weanlings, thus allowing infants to be weaned earlier. Here, we consider only the second alternative. If humans wean infants early, δ should be relatively low. Values in Table 1 show it to be as low as any of the great apes.

Grandmother's contribution must increase daughters' annual fecundity. Table 1 includes estimates of b for four modern hominoid species. As expected, interbirth intervals are shortest (b is highest) for humans. Because b scales inversely with α, the αb value is of special interest. αb for humans is at least double that of the other great apes. The grandmother hypothesis predicts just such a result. αb should be high because it incorporates the production of both mothers and grandmothers. The production of the whole lifespan is concentrated in the childbearing years.

Combined with CM, the grandmother hypothesis can account for long lifespans after menopause, late age at maturity, early weaning, and high fertility. Other hypotheses have been offered to account for each of these distinctive features of human life history individually (36, 37), but all could be systematic adjustments on the primate pattern that follow from grandmothering. Longstanding ideas about human evolution can be profitably reviewed in this light.

The notion that childhood has been extended to allow the development of larger brains and the learning required for competent human adults has long been a central tenet of paleoanthropology, even though a broad perspective on life history variation does not favor it (38). It is adult lifespans that predict age at maturity, not only in mammals but in other classes of vertebrates as well (24). Very late ages of maturity for body size occur in many species with small brains and limited learning. Among nonhuman primates juvenile periods are much longer than needed to learn the ecological skills of adulthood (39). Studies of modern hunter–gatherers indicate wide variation in the ages at which children begin to forage, even in broadly similar ecological circumstances (40). There is no indication that large differences in time spent "practicing" affect adult performance (41). If longer lifespans favor later maturity as the advantages for growing longer before reproducing outweigh the cost of delay, then that "waiting time" can be allocated in ways that enhance the child's fitness. Among primates like us, these could include substantial learning. This argument draws the causal arrow from long childhood to learning, not the other way around (39).

In emphasizing the provisioning role of women, the grandmother hypothesis also runs counter to the idea that long childhoods and relatively high fertility evolved as results of men's big game hunting (37, 42). Elsewhere we have challenged this argument on two grounds, one pointing to the relative unreliability of big game hunting as a means of supporting mates and offspring (43, 44), the other to the likelihood that men have more to gain from mating than from parenting effort (45, 46). The grandmother hypothesis not only avoids problematic assumptions about men's foraging goals but in addition shows several distinctive aspects of human life history to be systematic variations on the primate pattern.

Inferences about community organization among ancestral hominids also are challenged. Apparent similarities in local group composition between humans and the other African apes, especially chimpanzees, have supported arguments about likely patterns of natal dispersal among ancestral hominids. At maturity, other African ape females, unlike females in most monkey species, usually leave the social unit of their birth to join another (47). Among humans, postmarital residence is usually patrilocal (48). The bias toward female natal dispersal in living hominoids suggested that the pattern might characterize past members of the African ape clade as well, including all hominids (47, 49–51).

The grandmother hypothesis directs attention to likely ecological pressures for variation. The use of high return resources that young juveniles cannot handle favors mothers and daughters remaining together. As daughters grow, they acquire the strength and skill needed to help feed their younger siblings (5, 41). When daughters mature, the assistance of aging mothers continues to enhance the benefits of proximity (3).

Cross-cultural tabulations show that there is variation in the expected direction; patrilocality is less frequent among nonequestrian, nonfishing-dependent hunter–gatherers than in the *Ethnographic Atlas* sample as a whole (56% vs. 71%) (52, 53). Among hunter—gatherers, the tendency toward matrilocality increases with women's relative contribution to subsistence and (separately) with increased dependence on gathering (48).

Although modern humans might be expected to display more variation in social organization with local ecology than nonhuman primates, other apes also show variation both within and among populations. Chimpanzee females often migrate at maturity but not always (16, 54). In one community, paternity tests showed that more than half of the infants sampled were not fathered by resident males (55), revising estimates of inbreeding costs to any nondispersing females and also raising questions about the frequency of female dispersal in that population. Sometimes it is males that disperse (56). In captivity, male chimpanzees readily construct and manipulate alliances with unrelated strangers (57), suggesting an evolutionary history that favored those capacities.

Senior females could affect the fertility of their sons' mates through food sharing as well as that of their daughters. But the grandmother hypothesis, combined with the assembly rules of CM and the variation in ape life histories highlighted here, favors co-residence between older mothers and their daughters. Coincident foraging patterns between mother and maturing daughter, with increasing benefits to older daughters helping junior siblings, would guide this transition. Moreover, any effects on the production of descendants through a son's mate would be diluted by uncertain paternity.

The important question of male life histories is left unexplained here. Increased selection against senescence in women would surely have correlated effects on men, but selection pressures on male life histories would necessarily differ (an issue discussed further in ref. 3, pp. 573–574).

We expect routine mother–child provisioning to have been favored initially under ecological conditions that promoted access to resources yielding high return rates to adults but not to young juveniles. This pattern would allow expansion into previously unoccupied habitats and relax density-dependent effects on juvenile mortality (7, 12, 24), thereby stimulating sharp increases in local population densities. Both effects should be evident archaeologically. The life history changes initiated by grandmothering should be marked by evidence for later age at maturity and increased postmenopausal lifespan.

Available archaeological and paleontological data suggest at least three possible dates for the evolution of this distinctively human set of behavioral and life history traits. The initial appearance of *Homo erectus* (more narrowly *ergaster*) 1.8 million years ago (58) is associated with delayed maturity

relative to earlier hominids (59) and wide dispersal into previously unoccupied habitats outside Africa (60). Early archaic *sapiens* [≤600,000 years ago (61)] spread to higher latitudes (62) and may have been first to show the specific pattern of delayed maturity typical of modern humans (63). Alternatively, the modern pattern may not have appeared until ≈50,000 years ago, coincident with the dispersal of anatomically modern *sapiens*, who may have enjoyed unprecedented ecological and competitive success because they had what other, earlier hominids lacked (64): long postmenopausal lifespans and the associated population dynamics underwritten by grandmothers.

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