

Grandmothers and the Evolution of Human Longevity: A Review of Findings and Future Directions

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Women and female great apes both continue giving birth into their forties, but not beyond. However humans live much longer than other apes do.¹ Even in hunting and gathering societies, where the mortality rate is high, adult life spans average twice those of chimpanzees, which become decrepit during their fertile years and rarely survive them.^{2,3} Since women usually remain healthy through and beyond childbearing age, human communities include substantial proportions of economically productive postmenopausal women.^{4–7} A grandmother hypothesis^{8–12} may explain why greater longevity evolved in our lineage while female fertility still ends at ancestral ages. This hypothesis has implications for the evolution of a wide array of human features. Here we review some history of the hypothesis, recent findings, and questions for ongoing research.

THEORETICAL FOUNDATIONS

Aging rates vary widely among living things. Evolutionary explanations for varying senescence rates assume that organisms trade off investment in current reproduction against repair and maintenance of their cells

and physiological systems.¹³ Natural selection favors more investment in somatic maintenance only when it raises lifetime inclusive fitness. Two key theoretical contributions to the evolutionary study of senescence specifically mentioned humans, dwelling on the midlife end of women's fertility as a crucial clue about our evolution. Their inferences represent two different ways of posing the evolutionary riddle of mismatch between rates of ovarian and somatic senescence in women.

Stopping Early

George Williams¹⁴ elaborated on the consequences of the declining force of natural selection across adulthood. Even in populations of a hypothetical organism that did not become increasingly frail with age, some individuals would die in accidents or from illness or predation, so sets of age-mates necessarily shrink with time.¹⁵ Adult cohorts are largest at the beginning, the age of first reproduction. Thus, features expressed at early adult ages make

the biggest genetic contribution to future generations. That makes selection stronger on traits expressed in young adults and weaker on traits expressed at older ages. How fast the force of selection declines across adulthood depends on two things: the chances of surviving to older ages and what those survivors to older ages can do for their own inclusive fitness.

Since natural selection spreads only traits that increase their own reproduction, it should not favor a postreproductive period in the normal life span of any organism. What then, Williams¹⁴ asked, of menopause, which was then assumed to be a uniquely human trait? His answer began with the important point that the end of fertility is not the end of reproduction. As long as postmenopausal women contribute to the welfare of their kin, they affect the successful reproduction of their genes. Williams hypothesized that menopause evolved when other changes in our lineage made late births riskier and infants more dependent. Older mothers would be more likely to die in childbirth, leaving orphans unable to survive without them. He surmised that these circumstances would favor tendencies to stop fertility early and for mothers to invest more in previously born offspring than in risky new ones.

Subsequent work showed that menopause is not uniquely human.¹⁶ Menstrual cycling ends before death in other primate females as well, if they live long enough.^{7,17} In all

Kristen Hawkes's hunter-gatherer ethnography drew her attention to unexpected sex and age differences in foraging strategies, including the crucial productivity of grandmothers, which prompted further comparisons of human and chimpanzee life histories. James E. Coxworth's central interest is the application of evolutionary tools to describe and explain male competitive strategies, with particular emphasis on human evolution. This interest has led to statistical and modeling contributions and to projects investigating human life-history evolution.

Key words: life history evolution; senescence; cooperative child rearing; infant psychology; male-male competition

mammals, including primates, a finite stock of oocytes develops around or before birth and then is continuously depleted, mostly by cell death¹⁸; cycling stops when stocks fall too low to support ovulation. Follicle stock sizes and rates of atresia vary across mammals,¹⁹ with some species still ovulating and giving birth at older ages than humans do. For example, elephants continue to give birth into their sixties²⁰ and Antarctic fin whales into their eighties.²¹ Yet there are clear similarities in the oldest ages of parturition among all living hominids and in rates of decline in follicle stocks from birth to the late forties in humans and chimpanzees.²² These commonalities among members of the hominid radiation are inconsistent with the proposition that humans had an ancestor with older ages at last birth. It is likely that ancestral ovarian aging remained the same while increased longevity evolved in our lineage.²³

Williams^{14:407} also surmised that women's notably long postfertile survival was an "artifact of civilization." In this, he was misled by the incorrect inference that skeletal assemblages demonstrate the rarity of surviving elders in ancient human populations. While debate continues,^{24–26} paleodemographers have shown that the age structure of past populations cannot be retrieved by estimating ages of specimens in skeletal assemblages. Biases are imposed by comparative collections; preservation varies with age at death; and standard measures widely misestimate adult ages. Even if taphonomic and age estimation biases could be controlled, skeletal assemblages are not random samples of the deaths that occurred in different sexes at different ages.²⁷

The deep antiquity of human longevity is also obscured by widespread assumptions that because national life expectancies began to exceed 50 years only in the twentieth century,²⁸ our postfertile life stage is an artifact of recent history. Life-span averages are misleading guides to adult survivorship because high infant and juvenile mortalities have strong effects on them.²⁷ Hunter-gatherer life expectancies are less than half those of Western nations,

but, of the hunter-gatherer girls who survive to adulthood, about three-quarters live past the age of 45.²⁹ At any one time, a third or more of the adult females in human populations are beyond the childbearing ages.^{7,27}

Increased Longevity As a Consequence of Grandmother Effects

William Hamilton's³⁰ attention was drawn to grandmother effects when he used demographic data from a human population with mortality even higher than that typical of hunter-gatherers to evaluate the fit of his mathematical model of the evolution of senescence. Evidence of

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the substantial fraction of women who survived the childbearing years led him to point toward their role in the evolution of increased longevity. An earlier version of the idea that selection could favor increased longevity through grandmother effects was mentioned by Peter Medawar in a footnote to his 1951 lecture, "An Unsolved Problem in Biology," published in 1952.¹⁵ In that paper Medawar documented and began to solve the puzzle of the evolution of senescence by showing why the force of

selection must weaken as adult cohorts age, providing the foundation for Williams'¹⁴ arguments. Medawar also anticipated both Hamilton's 1964³¹ explanation of the importance of inclusive fitness and Hamilton's 1966³⁰ suggestions about grandmother effects by saying, "Grandparents, though no longer fertile, may yet promote (or impede) the welfare of their grandchildren, and so influence the mode of propagation of their genes."¹⁵

Hamilton³⁰ mathematically modeled Williams' verbal arguments about the evolution of senescence. Then, considering humans, he pointed out that the high rate of women's postfertile survival "inevitably suggests the special value of the old woman ... during a long ancestral period."³¹ Like Williams, Hamilton lacked information on the other great apes or human populations that were not dependent on agriculture. Subsequent evidence from the Hadza, a group of East African hunter-gatherers, highlighted a particular value of old women: They acquire and process foods that youngsters cannot handle for themselves.³²

A GRANDMOTHER HYPOTHESIS

Those Hadza observations, combined with Eric Charnov's formal models of life-history evolution in female mammals,³³ prompted a grandmother hypothesis to explain the evolution of human life histories. In Charnov's models, adult mortality determines an optimal age at maturity. When mortality is high and adult life spans are short, selection favors early maturation because those who wait are more likely to die before reproducing. When mortality is low, the cost of waiting goes down; net advantage goes to delaying maturity to reach a larger adult size. Larger mothers can allocate more to offspring [see Hawkes³⁴ for more discussion of the modeling assumptions]. Rates of growth are governed by trade-offs the models do not address, but they vary among mammalian orders. Primate growth rates are notably slower than those of most nonprimate mammals.³⁵

Looking just at primates, Charnov,³³ Fig. 5.6 illustrated the wide variation in age at maturity (first parturition) and average adult life span with a dataset that included humans. While age at first birth and average adult life spans are notably higher and longer in humans, Charnov's plot showed that the relationship between these traits is the same for us as for other primates. Yet, unlike other primates, human adults have life spans that include a postfertile stage. If postfertile grandmothers subsidize the childrearing of their daughters, who then produce more surviving offspring, the postfertile females, in consequence, have more descendants. Helpful grandmothing could therefore explain the shorter birth intervals of humans than the other great apes, the evolution of our exceptional longevity with its postfertile stage, and the evolution of our later age at first birth.³⁴ The grandmother hypothesis can explain why we mature so late by explaining why adult life spans increased in our lineage.^{8-12,36}

The Ecological Scenario

As climates dried in Plio-Pleistocene Africa, the spread of grasslands restricted the availability of foods that nonhuman apes depend on. Observation of Hadza foragers exploiting a modern analog of those environments found young children to be surprisingly active foragers and, like other juvenile apes, to be competent at picking soft fruits and berries.³⁷ But youngsters are too small to be effective at digging and processing the deeply buried tubers that are Hadza staples.^{32, 37} Geophytes like those relied on by the Hadza became more abundant as ancient grasslands spread,⁹ presenting valuable resource opportunities to those able to extract and process them. Young ancestral juveniles, like Hadza children, would not have been able to do it.

Ancestral mothers who relied on those foods would have had to subsidize their weaned offspring. That would have opened a novel fitness window for the few elder females whose declining fertility meant they had no newborns of their own. If

those elders subsidized their dependent grandchildren, the grandchildren's mothers could have their next babies sooner. Hadza foraging pointed directly toward links among ecology, size and strength constraints on youngsters' foraging, grandmothers' subsidies, and birth spacing. This is because Hadza grandmothers' tuber digging and processing supports the continuing growth of Hadza children when their mothers are occupied with newborns.³²

These connections between ecology and juvenile foraging competence suggested how ancestral grandmothing would have favored shifts in mechanisms of cell and molecular maintenance.

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nance that slowed aging and lengthened survival. Ape-like aging, previously maintained by stabilizing selection, would now be subject to directional selection. Where increased somatic maintenance had been selected against because it meant less allocation to current reproduction and reduced offspring survival, greater maintenance was now favored. Because grandmothers subsidized juveniles, mothers who shifted more resources to their own physiological maintenance, leaving less for current reproduction, did not suffer higher offspring loss. The more robust the elders, the more they could help. These inter-

dependencies point to pathways whereby selection would increase longevity as longer-lived grandmothers left more descendants.^{9, 11}

Mathematical Formalizations

Formal models of grandmothing depend on general principles, such as those investigated by Ronald Lee.³⁸ His one-sex model showed that intergenerational transfers of support maintain a human-like age structure. This extended his earlier model,³⁹ which demonstrated that when intergenerational transfers are crucial for successful reproduction, it is age-specific productivity, not fertility, that sets the strength of selection against senescence. Hillard Kaplan and Arthur Robson⁴⁰ formalized a different model for the evolution of longevity, highlighting increased investment in brains and skill learning, especially for hunting. Their one-sex model ignored questions about the postfertile longevity of females. But subsequently, Kaplan and coworkers⁴¹ drew on it and ethnographic data to show that households could not meet consumption requirements without the productivity of postfertile elders.

It was Frederike Kachel and colleagues⁴² who first built a two-sex model of the grandmother hypothesis. They concluded, from simulations of their agent-based model, that even when grandmother effects were so strong that they guaranteed the survival of grandchildren, those effects had little impact on longevity. To understand why, we investigated their model and found that simulations, either with or without grandmothing, never reached an equilibrium, because of their assumptions about males.⁴³ Longer lives had no cost for males, so the perpetual advantages they gained from increased longevity obscured the selection consequences of grandmother effects.⁴³

Building on lessons from Kachel's work and taking advantage of the life-history relationships assumed in Charnov's formal models,^{33,35} Peter Kim constructed an agent-based model and used deterministic difference equations to simulate the verbal grandmother hypothesis.¹² Starting

with an ape-like life history and assuming that the end of female fertility remained fixed, while increased longevity delayed maturity and lengthened juvenile dependence, Kim's simulations showed that very weak grandmothering was enough to drive the ape-like equilibrium to a human-like one. The ancestral ape-like condition included very few females who were eligible to grandmother, but in 60,000 years or less, postfertile grandmothers expanded to a proportion of the population similar to that observed among hunter-gatherers. In this model, trade-offs for increased longevity differ between the sexes, although grandmothering makes increased longevity advantageous through both males and females. The model includes no skill learning, no brain expansion, no hunting, and no paternal provisioning. It demonstrates that, at least in principle, grandmothering alone could have been the foundation for subsequent evolution of other distinctly human features.

Kim³⁶ then used the agent-based model to build probabilistic simulations. Adding stochasticity slowed the transition to a human-like life history by about an order of magnitude. It even, in some cases, prevented escape from the ancestral condition. But multiple simulations confirmed that our assumptions lead to two life-history equilibria, a great-ape-like one and a human-like one. Once the advantages of grandmothering begin to spread, selection moves inexorably to the human equilibrium. The absence of intermediates is consistent with the possibility that the evolution of this distinctively human feature, helpful grandmothering, is the foundation for genus *Homo*, long antedating the appearance of our species.⁹

BEHAVIORAL FINDINGS

The grandmother hypothesis is specifically directed at the evolution of human life history.^{8,9} When researchers look at contemporary and historical human populations with diverse social organizations and subsistence regimes, they always find characteristically human age structures, but vari-

ation in the sources of childrearing help is as wide as the variation in other aspects of socioecology.⁴⁴ Researchers looking for grandmother effects usually find them,^{45,46} although exceptions have been noted.⁴⁷ Often measured by the gold standard of grandchild survival, grandmother effects might be underestimated where women can choose where to direct their help. If they allocate it to those that need it most, as Hadza grandmothers do,⁴⁸ they reduce differences between those with and without grandmothers' help.

We assume that selection propelled by grandmother effects was stronger through help to daughters' children, not only because of the assurance of shared genes with the grandchild, but

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also because a main effect is shortened birth intervals for the childbearer whose offspring are subsidized. Yet, in our small initial Hadza sample, helpers were not always maternal grandmothers. Peter Kim's simulations^{12,36} include no restriction to helping daughters' children. Even though model grandmothers help any dependent juvenile old enough to survive without its mother, increased longevity evolves nevertheless. More investigation of this unexpected outcome and more modeling to evaluate the consequences of different family grouping patterns on the evolution of longevity are obvious next steps.

Variation in Grandmother Effects

Ethnographically and historically measured effects sometimes vary depending on whether grandmothers

are paternal or maternal.⁴⁹ Harmful paternal grandmothers^{50,51} and tensions between mothers and daughters-in-law are not uncommon, but this varies with details of socioecology.^{52,53} As Rebecca Sear⁵⁴ has shown, maternal grandmothers can also be harmful, as can mothers,⁵⁵ when scarce resources must be carefully allocated.

Surprisingly, measured effects also sometimes differ depending on a grandchild's sex. Grandmothers share one X chromosome with their sons' daughters and none with their sons' sons; there is a 50% chance that they share an X chromosome with their daughters' children. Molly Fox and colleagues,⁵⁶ analyzing this variation across several populations, found correlations between the strength and direction of grandmother effects and the likelihood of a shared X chromosome. Further investigation of these intriguing differences must continue.

Ethnographic and historical variation in the strength and direction of grandmother effects reveals the complexities of reproductive competition. Michael Cant and Rufus Johnstone⁵⁷ showed that if females disperse and then mate locally, fitness benefits from helping coresident kin change with age. They modeled an ancestral population in which fertility in females continued to late ages. Reproductive conflict over care of dependents led to an equilibrium in which elder females stopped childbearing early. This stopping-early scenario could, Cant and Johnstone suggested, explain the evolution of human menopause. However, in addition to the problems with stopping-early scenarios noted earlier, the assumption of ancestral female dispersal is disputable.⁵⁸ That assumption had been influentially justified by male philopatry in the genus *Pan* and longstanding characterizations of hunter-gatherer bands as patrilocal.⁵⁹ However, such characterizations of hunter-gatherer residence patterns have now been repeatedly falsified by evidence indicating high mobility and regularly changing group composition.⁶⁰⁻⁶²

PHYSIOLOGICAL FINDINGS

The hypothesis that grandmothering slowed somatic aging in our

lineage draws attention to physiological puzzles. How do we do it? Estrogen plays a key role in the maintenance of many physiological systems in both sexes, but that question has special force when it is focused on women. Although men produce gonadal steroids that, throughout life, can be converted to estrogen in peripheral tissues, ovaries secrete estrogen mostly during cycling; circulating levels drop below detection after menopause.⁶³ Nevertheless, postmenopausal women maintain competence in most physiological systems aside from fertility. The maintenance puzzle is underscored by comparison with other great ape females, which usually die while they are still cycling. Evidence of geriatric morbidities in these years is best documented in chimpanzees.^{2,17,64}

Adrenal Androgens

The lack of correspondence between somatic maintenance and ovarian estrogen production in hominids is reason to suspect that peripheral estrogen must have nonovarian sources. Consistent with that, studies of women's health report that adrenal steroids account for most of women's peripheral estrogen, even during their cycling years.⁶⁵ That evidence, combined with nomination of the adrenal steroid dehydroepiandrosterone sulfate (DHEAS) as a biomarker of aging in primates,⁶⁶ led us to expect higher DHEAS levels in women than in female chimpanzees. If that steroid plays an important role in somatic maintenance, then higher levels in women could help explain the persistent physiological health of women well beyond menopause.

The biomarker of aging hypothesis predicts that DHEAS levels decline twice as fast in chimpanzees as they do in women.⁶⁷ To find out, we requested that blood be drawn from captive female chimpanzees when they were anesthetized for reasons unrelated to our project. Hormonal assays showed that circulating DHEAS declines are slower, not faster in chimpanzees. But young adult DHEAS levels are three times as high in women as in chimpanzee females. Only as women reach their

late sixties do levels fall to the chimpanzee maximum.⁶⁸ Consistent with the proposition that increased production of DHEAS is one mechanism that slowed aging in our lineage, circulating DHEAS levels are even lower in the other great apes.⁶⁹ Adding to this notable and surprising variation among the hominids, correlations found between adrenal steroid levels and menopausal status in individual women⁷⁰ pose questions, as yet unexplored, about the roles of other adrenal androgens in hominid physiological maintenance.

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Telomeres

Another mechanism to retard somatic aging in humans might be slowed telomere attrition. Telomeres are the noncoding DNA repeats at the ends of chromosomes; they maintain chromosome integrity at each cell replication. Telomeres lose sequence repeats at each replication, arresting the cell cycle when they become too short. This attrition decreases an aging organism's capacity to regenerate tissues. While telomeres can be rebuilt by telomerase, one advantage of suppressing telomerase expression in replicating somatic tissues is that shortened telomeres block the growth of malignant cells. Thus, telomere shortening may protect against cancer.⁷¹

Telomere length in replicating tissues varies with age, and shortening rates correlate with rates of aging both within and between species.⁷² On these grounds, we expected the greater longevity of humans to be associated with slower telomere shortening rates and hypothesized that attrition rates would be twice as fast in chimpanzees as humans. To find out, Justin Tackney⁷³ extracted DNA from our chimpanzee blood samples and, using the same protocol, assayed telomere repeats in the chimpanzee sample and an age-matched sample of women. Instead of faster shortening rates in chimpanzees, results showed similar rates of attrition in the two species. Even more surprising, telomeres in humans are about half as long as those in chimpanzees.⁷³

Gomes and colleagues⁷⁴ have provided the phylogenetic framework for interpreting these initially astonishing results. Examining cell lines cultured from more than 60 mammal species, they found telomere lengths to be negatively correlated with life span. Their analysis indicated that ancestral mammals had relatively short telomeres. This, they hypothesized, was a response to the higher mutation load that accompanied the evolution of homeothermy and made the protective advantage of short telomeres and telomerase suppression outweigh the costs of replicative aging. Subsequently, telomerase expression and longer telomeres evolved in many smaller, shorter-lived species.

Comparative primate data are sparse, but human telomeres appear to be the shortest in the order.⁷³ Our very short telomeres may have evolved as greater longevity raised cancer dangers, increasing the advantages of protection against them. Our comparison of chimpanzee and human telomeres implicates the evolution of less sensitivity to cell death, increased DNA repair, decreased cell division rates, and/or other mechanisms to maintain function with shorter telomeres in the human lineage. This surprising finding underlines the indispensable role of great ape comparisons for understanding human aging.⁷³

FURTHER IMPLICATIONS OF THE GRANDMOTHER HYPOTHESIS

The grandmother hypothesis addresses the evolution of human life history. A distinctive postfertile life stage^{7,75} is a characteristic of our species. The grandmother hypothesis proposes that grandmothers drove the evolution of our genus *Homo*. The first expansion of our genus out of Africa implies a life history that allowed mothers to colonize habitats in which just-weaned juveniles could not feed independently. Grandmothers' subsidies can explain how our genus spread so quickly through much of the previously unoccupied temperate and tropical Old World. This scenario implicates cooking in the evolution of our genus; it entails shifts in maternal trade-offs that impose novel selection pressure on infant sociality; and those social capacities, as well as the substantial shift in operational sex ratio, have large consequences for competition among men.

Grandmothers' Cooking

Ethnographic lessons from the modern Hadza link the evolution of helpful grandmothers to the ecological circumstances of the African savannah and the likely importance of cooking in the evolution of genus *Homo*.⁹ Richard Wrangham^{76, 77} and collaborators⁷⁸ have marshaled and elaborated compelling morphological and physiological evidence of the dependence of our genus on cooked food. They have also recognized that cooking increases the vulnerability of resources to expropriation.⁷⁹ Cooks gain notable economies of scale as items are accumulated, fuel gathered, and the nutritional utility of the meal increased with processing. These steps concentrate feeding into long handling stages followed by bursts of highly efficient consumption.⁸⁰ The size and nutritional richness of meals make them attractive opportunities for potential consumers other than the processor.^{77, 79} Youngsters are especially likely appropriators. Some food sharing between mothers and offspring is widespread among primates and more likely with foods that are diffi-

cult for infants and juveniles to handle on their own.⁸¹ The processing steps of cooking vastly expand opportunities for resource pooling.^{82,83} Wrangham's enumeration of the anatomical characteristics of *Homo erectus* that indicate dependence on cooked food^{76,77} identifies evidence of reliance on processing that young juveniles cannot manage. This directly implicates helpful grandmothers in the evolution of our genus.⁹

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Selection on Infants and Distinctively Human Prosociality

Novel interdependencies entailed in a grandmothers' life history have enormous consequences for human psychology. Sarah Hrdy^{55,84} has focused attention on the new problems that cooperative childrearing posed for both ancestral mothers and infants. Unlike other ape mothers, who rear offspring one at a time, help allows human mothers to have next babies sooner without necessarily reducing the chances for survival of their previous child. Mothers' reproductive success then depends on enlisting assistance and allocating their attention among multiple dependents.

These trade-offs set up challenges for human babies not faced by other ape babies. Unlike other apes, human babies cannot count on their mothers' undivided commitment even though attention from their caregivers has life and death consequences for them. Thus, infants who are more successful at actively engaging their mothers and grandmothers have a strong selective

advantage. Hrdy⁸⁴ explicitly links our cooperative childrearing patterns and the selection pressures they impose on infants to the evolution of social and emotional capacities that Michael Tomasello and collaborators characterize as shared intentionality.^{85,86} Hrdy⁸⁷ highlights evidence of the ingratiating sensibilities of human infants who are especially prone to detect and repeat what appeals to caregivers. These abilities and the motivation to please others and establish joint attention and mutual understanding are the foundation for our distinctively human cultural lives.

Hrdy's hypothesis draws attention to the evolutionary importance of the very early neurological development and social sensitivity of human babies,⁸⁸ which has been obscured by longstanding characterizations of humans as "secondarily altricial." Babies are physically helpless, but this is also true of newborn nonhuman apes. Human neonates smile and coordinate mutual gaze with caretakers, an initial interactivity not evident in wild chimpanzees,⁸⁹ but seen in captivity.⁹⁰ The attention of multiple caretakers in captivity evokes these responses from chimpanzees under circumstances similar to those of the first ancestral infants arriving in a world where grandmothers was displacing independent mothering.⁸⁷ Such responses hint that this tendency was also present in our shared ancestors. It appears to be a trait that was exaggerated by social selection as a consequence of the change in rearing environments.⁸⁴ The drive for shared attention quickly fades in chimpanzee babies,⁹⁰ but persists and expands in humans. This is consistent with Hrdy's hypothesis of a history of strong selection on the social and emotional capacities of human infants. With cooperative rearing, engaging caretakers' commitment became a matter of life and death, leading to greater survival for ancestral infants more motivated to coordinate with others and more effective at doing so. Thus, "emotionally modern hominins," to use Hrdy's label, evolved well before the appearance of *Homo sapiens*.

Human language, cultural learning, and cooperative activities depend on the distinctively prosocial

motivations apparent in prelinguistic infants. Recent techniques for probing the social sensitivities of very young human babies show them evaluating interactions and discriminating between helpful and harmful actors during the first postnatal weeks.⁸⁸ If the advantages of language and cultural cooperation are subsequent to prosocial capacities, those subsequent advantages cannot explain why our unique psychology evolved in the first place. Hrdy's child rearing hypothesis might. Continuing work to assess the social motivations and abilities of infants in all the hominids will help clarify these early differences. Postnatal brain imaging and gene expression studies are also promising lines of comparative evidence about the developmental timing of interactive capacities.⁸⁸ Hrdy's framework makes precocious social sensitivities a crucial shift in our lineage, a shift as important as the delay in other aspects of development that has made neoteny seem to be the major determinant of human evolution.⁹¹ Accelerated social cognition, as well as delayed independence and delayed maturity, would all have been favored as longevity increased with ancestral grandmothering.⁸⁸

Men's Strategies

Our grandmothering life history alters the constraints and opportunities for men compared to other ape males. Morton and colleagues⁹² recently modeled the effects of men's preference for young mates in a population having human longevity but female fertility that continues to older ages. As noted, the similarity in latest ages of parturition in all living hominids make such an ancestor unlikely. Moreover, Morton and coworkers' assumptions about reproduction invite skepticism. In their model, a birth occurred only after a death, with potential mothers then competing for the maternity. With those assumptions, men's preference for young mates could explain the evolution of early termination of fertility. Men's preference for young mates does seem to be established,⁹³

and it notably contrasts with the opposite preference in other primates, especially well documented in chimpanzee males, which prefer old females.⁹⁴ But the human reversal might well be a consequence, not a cause, of our midlife menopause. With the evolution of human longevity and its postfertile stage, many healthy and competent females are not fertile. Under these circumstances, males that favored mates with markers of youth might have left more descendants.

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In Peter Kim's simulations,^{12,36} adult life spans favored by female trade-offs alone are shorter than those favored when males are included. The simulations do not allow male strategies to shift with increasing longevity, however. Exploring these potential shifts could contribute to explanations for the evolution of pair bonding. Other ape males compete for paternities within a narrower range of adult ages. With human longevity, a man's competitors and potential allies include old men who are always ahead of younger ones in establishing their social position. On one hand, grandmothers' subsidies shorten birth intervals, increasing the rate of paternity opportunities in humans; on the other, men continue to compete for paternities to much older ages, while child-bearing ages do not increase. As a consequence, our grandmothering life

history expands both the ages and the relative number of men in competition for paternities.⁹⁵ The consequences of these age-structure changes for mate guarding and other male strategies are overdue for attention. Notably, comparison of four hunter-gatherer societies with wide variation in pair-bond stability⁹⁶ showed that father effects cannot explain the variation. Pair-bond stability depends instead on variation in the operational sex ratio. When there are fewer fertile females relative to the number of competing males, pair bonds last longer.⁹⁶

Grandmothering contributes to the evolution of shared intentionality⁸⁵ through its effects on infants whose mothers have overlapping dependents. Resulting capacities and motivations for mutual engagement have important consequences for all of social life, including relationships among men.⁹⁷ When joint activities are a preoccupation, in part due to their jointness, occasions for evaluating others multiply, expanding opportunities for competition over relative social standing.⁹⁷ That competition and its profound consequences can be obscured when men are characterized as primarily husbands and fathers, with nuclear families highlighted as the basic social and economic units of human societies. The grandmother hypothesis underscores the importance of relationships beyond nuclear families. Pair bonds likely evolved in our lineage as additions to other social relationships.^{58, 98} Preferences for shared intentionality would have affected all of those relationships, expanding both the opportunities for coordination and the range of occasions to identify and impress potential allies and competitors.

CONCLUDING REMARKS

Hypotheses about what happened in human evolution are necessarily constrained by the ancestors we assume. Frans de Waal's continuing documentation of emotions and empathy in other primates^{99,100} enriches Darwin's case that these mechanisms for social behavior also characterized our ancestors.¹⁰¹ From an already smart, empathic, social ancestor, social sensitivities evolved to develop earlier and extend further in humans;⁸⁸ appetites

for mutual attention distinguish us from other apes.^{85,86} The most promising hypothesis to explain those features is our distinctive habit of cooperative childrearing,⁸⁴ a pattern that, as we have argued here, likely began with helpful grandmothering. Human appetites for shared attention, as well as the relatively male-biased operational sex ratio that evolved with our life history, have consequences for men's social strategies that we are only beginning to explore.

The grandmother hypothesis focuses attention on singular features of human life history, including our exceptional longevity, a postfertile life stage in women, and both our very short birth intervals and very late ages of first parturition as compared to those of the other great apes. This hypothesis makes comparisons with the other living hominids a central line of inquiry. The similarity in oldest ages of pregnancy among humans and other hominids¹ and similar rates of decline in ovarian follicle stocks in humans and chimpanzees²² point to similar ages of fertility decline in our ancestors. The differences in longevity between humans and other living hominids^{1,3,11,27,29} suggest that our common ancestor had aging rates more like theirs. Unexpected differences in aging physiology between humans and chimpanzees highlight the importance of further comparisons with great apes if we are to understand the evolution of human somatic aging. The grandmother hypothesis continues to stimulate new comparative questions about youngsters as well as adults of both sexes. Further, it continues to stimulate more careful appraisal of the behavior and effects of those Hadza grandmothers¹⁰² who supplied initial reasons for inquiry into the distinctive postmenopausal longevity that evolved only in our lineage of the hominid radiation.

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