Grandmothers and the Evolution of Human Sociality

KRISTEN HAWKES and JAMES E. COXWORTH

Abstract

We differ from the great apes in so many ways. Yet they all belong to our hominid family, and some are even more closely related to us than they are to each other. One distinctive human feature is our much great longevity, a difference that the Grandmother Hypothesis might explain. Grandmothering not only helps account for our long life spans but also changes childrearing in ways that may explain why distinctly human capacities for social engagement and mutual understanding evolved in our lineage. We review the background to this Grandmother Hypothesis and summarize it and related findings from evolutionary modeling and empirical measurements of both grandmother effects and social capacities of human infants. Then, we point to questions arising for social development, discriminating grandmothers, future mathematical modeling, and social strategies of men, as well as the physiology of human aging.

INTRODUCTION

Hominids are longest-lived of all the primates, and in humans and the other great apes, female fertility extends into the forties, not beyond. However, even in the high mortality regimes of hunting and gathering societies, people have average adult life spans twice those of other great apes who become decrepit during their fertile years and rarely survive them. In contrast, women usually remain healthy through and beyond the childbearing ages, so that human communities include substantial proportions of economically productive postmenopausal women. A Grandmother Hypothesis may explain why greater longevity evolved in our lineage without extending female fertility to older ages.

Grandmothering favors increased longevity as it changes relationships between mothers and children. The difference in childrearing between humans and other apes may explain distinctive features of human psychology that emerge in infancy as babies actively engage the commitment of caregivers who have other calls on their attention. These human interests

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and abilities to coordinate with others are continuing aspects of social relationships at all ages, supplying the foundation for the diversity of our cultural lives.

Deep antiquity of human longevity is often obscured by misunderstandings about life expectancy. National life expectancies only began to exceed 50 years in the twentieth century. This is because life expectancies at birth are low when fertility is high and many babies and children die. Hunter-gatherer populations have average life spans less than half those of Western nations, but of the hunter-gatherer girls that survive to adulthood, about three quarters live past 45. At any one time around a third of the adult women in these populations are beyond the childbearing ages.

However, Western life expectancies continue to lengthen with technological innovations that are increasingly effective at postponing death. Those technologies plus reports that improvements in life style and medical care can slow aging seem to shrink the relevance of evolution for understanding why we grow old. However, our evolutionary heritage of mid-life menopause and slower somatic aging remain. As women continue to delay first babies for sound economic reasons, and as we increasingly deploy technological assistance to hold off the inevitability of death, understanding those constraints should inform important public debates about workplace and health-care policies.

FOUNDATIONAL RESEARCH

The effects of evolution are easiest to see in cross-species comparisons. Mice may live a year or so, dogs and cats more than a decade; but the kittens and puppies we met as children grew old and frail before we reached adulthood. Although humans age more slowly than most other animals, the effects of aging are readily apparent in our grandparents and parents—and soon enough in ourselves, our siblings, and our children. Family reunions confirm that senescence is as much a part of our evolutionary legacy as handedness or blushing.

Evolutionary explanations for senescence assume that organisms trade off investment in current reproduction with repair and maintenance of their cells and physiological systems. Natural selection favors more investment in somatic maintenance only when it raises lifetime fitness. Two key contributions to develop this theory about living things in general also specifically mentioned humans, dwelling on the mid-life end of women's fertility as a crucial clue about human evolution.

In one of them, George Williams considered the relationship between the force of natural selection and senescence. Even in a hypothetical organism that did not become increasingly frail with age, some individuals would die in accidents or from illness or predation; groups of age-mates (or cohorts) necessarily shrink with time. This means that adult cohorts right at the age of first reproduction are largest and make the biggest genetic contribution to future generations. As a consequence, selection is stronger on traits expressed in young adults and weaker on traits expressed at older ages. How fast the force of selection declines across the life span depends on two things: what the chances are of surviving to older ages and what effects survivors can have on their own fitness.

As natural selection only spreads traits that produce more descendants, it will not favor a post-reproductive period in the normal life span of any species. What then, Williams asked, of menopause, which was assumed at the time 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 descendants, they affect the successful reproduction of their genes. Williams hypothesized that menopause evolved when other changes made late births riskier and infants more dependent. If older mothers were likely to die in childbirth leaving orphans unable to survive without them, selection would favor tendencies to put more investment into previously born offspring instead of risky new ones.

Now we know that menopause is not uniquely human. Menstrual cycling ends before death in other primate females as well—if they live long enough. In mammals generally, including primates, oocyte stocks continuously decline from early life, and cycling stops when stocks fall too low to support ovulation. It is possible for mammals to give birth at older ages than we do—elephants continue into their sixties and Antarctic fin whales into their eighties. However, similar ovarian aging rates in all living hominids make it improbable that humans had an ancestor with older ages at last birth that subsequently evolved to stop early. More likely what evolved in the human lineage is the distinctively slowed aging in other aspects of our physiology.

In the second paper, William Hamilton mathematically modeled George Williams' verbal arguments. Hamilton also addressed the human case, but he pointed to post-fertile survival of women as evidence of the ancestral importance of grandmothers. Like Williams, Hamilton also lacked information on the other great apes and on human populations not dependent on agriculture. Subsequent evidence from East African hunter-gatherers highlighted the special value of grandmothers in supplying foods that weaned juveniles cannot acquire for themselves.

This prompted a Grandmother Hypothesis about human evolution that links differences and similarities between human life histories and those of other living hominids to ecological pressures on childrearing. As climates dried in Africa around 2 million years ago, the spread of grasslands reduced the availability of fruits that youngsters could easily pick and meant that mothers who stayed in those environments had offspring that needed provisioning longer. If ancestral life histories were like those of the living great apes, most females would have died before their fertility ended. However, if the few that survived helped their dependent grandchildren, mothers of those youngsters could have next babies sooner without risking the survival of those previously born. Such a division of childcare between childbearers and older females would favor more investment in physiological maintenance and repair because more robust elders could help more. Helpful grandmothering would have favored increased longevity as longer-lived grandmothers left more descendants.

RECENT RESEARCH

The Grandmother Hypothesis takes advantage of Eric Charnov's formal models to explain systematic relationships among life history traits across the mammals. If adult mortality is high, selection favors maturing earlier because of the risk of dying before reproducing. Peter Kim used this framework in constructing a mathematical model of the Grandmother Hypothesis. Starting from an ape-like life history and assuming the end of female fertility remains fixed while increased longevity delays maturity and lengthens juvenile dependence, Kim's model shows that helpful grandmothering makes an ape-like longevity evolve into the human range. Grandmothering alone is enough to drive increased longevity with later maturity and longer juvenile dependence. The model suggests that grandmothering could have set the foundation for subsequent evolution of other distinctly human features including our predispositions for mutual understanding and its developmental timing, as well as language—a capacity serving that social preference—and, as briefly mentioned below, our distinctive habit of pair-bonding

The novel interdependencies entailed in a grandmothering life history have enormous consequences for human psychology. Sarah Hrdy focused attention on the new problems that cooperative childrearing would have 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 and keep more than one dependent offspring alive. This means that a mother's reproductive success depends on enlisting assistance and allocating her attention among multiple dependents (Hrdy 2009).

These new maternal 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 care and caregivers' attention have life and death consequences for infants. That implies a strong selective advantage for babies more successful at actively engaging their mothers and grandmothers. Hrdy's hypothesis 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. This set of abilities and motivations for joint attention and mutual understanding is the foundation for our distinctively human cultural lives.

Hrdy's hypothesis clarifies the evolutionary importance of the very early neurological development and social sensitivity of human babies, something obscured by longstanding characterizations of humans as "secondarily altricial," This label was first used to describe the immature state of birds that hatch naked, eyes closed and unable to stand. This helplessness contrasts with the precocial babies of other avian species that hatch more fully developed, nearly ready to leave the nest. Human babies *are* physically helpless, but this is also true of newborn apes. Human neonates smile and coordinate mutual gaze with caretakers, an initial interactivity that is also revealed in captive chimpanzees. Initial tracking of caretakers' attention in captive chimpanzee newborns hints that the tendency was likely present in our shared ancestors—a phenotype to be exaggerated by selection as rearing environments changed (Bard *et al.*, 2011; Hawkes 2014, and Tomonaga *et al.*, 2004).

While the drive for shared attention quickly fades in chimpanzees, it persists and expands in humans. Such elaboration of social sensitivities through the first months of life is consistent with Hrdy's hypothesis of strong selection on the social and emotional capacities of ancestral infants. Those more motivated to coordinate and more effective at doing so had increased survival in the novel circumstances of cooperative rearing. Recent techniques for probing the social sensitivities of very young human babies show them evaluating interactions and discriminating helpful from harmful actors in the first postnatal weeks.

KEY ISSUES FOR CONTINUING RESEARCH

Human language, cultural learning and cooperative activities depend on the distinctively prosocial motivations apparent in prelinguistic infants. Advantages of language and cultural cooperation are thus unlikely to 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. Hrdy's framework makes precocious social sensitivities as important a shift in our lineage as the retarded independence and maturity that have supported influential identification of neoteny—developmental delay—as *the* major determinant of human evolution.

Delayed independence and maturity combined with accelerated social cognition and weaning would all have been favored by ancestral grandmothering, which may have initially evolved in circumstances illustrated by modern East African hunter-gatherers where grandmothers contribute to descendants by digging deeply buried tubers that youngsters are not strong enough to dig for themselves. This ethnographic lesson links the evolution of helpful grandmothering to the ecological circumstances of our ancestral past. After evolving in ancient Africa, human life histories allowed our ancestors to inhabit most of the planet, with many leaving foraging for farming during the past 10,000 years. Researchers have found grandmother effects in human populations with diverse social organizations and subsistence regimes. Often measured by the gold standard of grandchild survival, these grandmother effects might be underestimated where grandmothers can direct their help where it matters most as Hadza grandmothers do. Free to leave dependents that can do better without them, and go to those that need them most, Hadza grandmothers obscure the magnitude of their effects.

Measured effects sometimes vary depending on whether grandmothers are paternal or maternal. With sons' children there is the issue of paternity assurance, and mother-daughter relationships differ from those between mothers and daughters-in-law. Surprisingly, effects sometimes also differ depending on the grandchild's sex. Grandmothers share an X chromosome with their sons' daughters, none with their sons' sons, and chances are 50% that they share an X with their daughters' children. Molly Fox analyzed this variation across several populations and 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.

Michael Cant and Rufus Johnstone have shown that mating and dispersal patterns have large consequences for the fitness benefits that elders gain by helping younger kin. Attention to this reproductive competition can help explain the harmful paternal grandmothers that Beverly Strassmann and others have detected in several societies with localized patrilineal descent groups whose senior members control access to basic resources.

More modeling of the longevity consequences of grandmothering is certainly in order. Peter Kim's simulations take the age that childbearing ends as given; future modeling may help explain why age-specific fertility still falls toward zero by 45 years even after longevity increased in our lineage. As mentioned earlier, we expect grandmother effects to be stronger through help to daughters' children—not only because of the assurance of shared genes with the grandchild, but also because a main effect is shortened birth intervals of the childbearer whose offspring are subsidized. Yet Kim's model shows that increased longevity evolves even when grandmothers help any dependent juvenile old enough to survive without its mother. 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.

In Peter Kim's simulations, adult life spans favored by female trade-offs alone were shorter than those favored when males were included. Helpful grandmothering evolved greater longevity for females, and the inclusion of males pushed longevity even higher. Model populations evolved adult life spans that are a compromise between the two sexes. This model did not allow male strategies to shift with increasing longevity. However, addressing that question is important. On the one hand, grandmothers' subsidies shorten birth intervals, increasing the rate of paternity opportunities per childbearer in humans. On the other hand, males continue to compete for paternities to much older ages, while childbearing ages do not increase. Our grandmothering life history expands the ages as well as the relative number of men in competition for paternities. A man's competitors and potential allies include old men who are always ahead of younger ones in establishing their social position. Consequences of the age structure changes for mate guarding and other male strategies invite modeling.

Shared intentionality also has important consequences for relationships among men. When joint activities are a preoccupation, in part because of their jointness, occasions for evaluating others multiply and expand opportunities for competition over relative social standing. That competition and its profound consequences can be obscured when men are characterized as primarily husbands and fathers with nuclear families highlighted as *the* distinctive social and economic units of human social structure. While pair bonds distinguish us from the other apes, fathers' contributions to childrearing vary widely both within and between societies. Private nuclear households, often distant from other kin, are a recent Western novelty that puts unusual weight on a few family relationships. In contrast, children and adults of all ages are in regular intimate contact in hunter-gatherer communities and traditional societies generally. Men's conjugal bonds depend on the respect of others; domestic concerns are in tension with the relationships men have with other men. Competition for social standing absorbs much of men's time allocation and effort allocated to developing and maintaining male alliances organizes much of public life.

Finally, the hypothesis that grandmothering slowed somatic aging in our lineage draws attention to physiological puzzles. How do we do it? That question has special relevance when focused on women because estrogen plays a key role in the maintenance of many physiological systems in both sexes. Men produce gonadal steroids throughout life that are converted to estrogen in peripheral tissues. However, women produce ovarian estrogen mostly during cycling and levels drop below detection after menopause. Nevertheless, post-menopausal women maintain competence in most physiological systems aside from fertility. To underscore the puzzle, other great ape females become decrepit and usually die while they are still cycling. The lack of correspondence between somatic aging and ovarian estrogen production converges with recent findings from studies of women's health that adrenal steroids and not ovarian estrogen are mostly responsible for somatic maintenance. Comparisons among the living hominids are the obvious way to identify mechanisms of human longevity. A great deal continues to be learned about aging from studies of model systems such as worms and rodents. However, it is comparisons between humans and our closet living relatives that can best guide hypotheses about what changed in the evolution of our own lineage.

REFERENCES

Bard, K. A., Brent, L., Lester, B., Worobey, J., & Suomi, S. J. (2011). Neurobehavioural integrity of chimpanzee newborns: Comparisons across groups and across species reveal gene–environment interaction effects. *Infant and Child Development*, *20*, 47–93.

Hawkes, K. (2014). Primate sociality to human cooperation, why us and not them? *Human Nature*, *25*(1), 28–48.

Hrdy, S. B. (2009). *Mothers and others: The evolutionary origins of mutual understanding*. Belknap Press of Harvard University Press: Cambridge, MA.

Tomonaga, M., Tanaka, M., Matsuzawa, T., Myowa-Yamakoshi, M., Kosugi, D., Mizuno, Y., . . . , Bard, K. A. (2004). Development of social cognition in infant chimpanzees (Pan troglodytes): Face recognition, smiling, gaze, and the lack of triadic interactions. *Japanese Psychological Research 46*, 227–235.

FURTHER READING

Blevins, J. K., Coxworth, J. E., Herndon, J. G., & Hawkes, K. (2013). Adrenal androgens and aging: Female chimpanzees (*Pan troglodytes*) compared with women. *American Journal of Physical Anthropology*, *151*(4), 643–648.

Fox, M., Sear, R., Beise, J., Ragsdale, G., Voland, E., & Knapp, L. A. (2009). Grandma plays favorites: X-chromosome relatedness and sex-specific childhood mortality. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 567.

Gopnik, A. (2009). *The philosophical baby*. New York, NY: (Picador) Farrar, Straus & Giroux.

Gurven, M., & Kaplan, H. (2007). Hunter-gatherer longevity: Cross-cultural perspectives. *Population and Development Review*, *33*, 321–365.

Hamilton, W. D. (1966). The molding of senescence by natural selection. *Journal of Theoretical Biology*, *12*, 12–45.

Hamlin, K. J., Wynn, K., Bloom, P., & Mahajan, N. (2011). How infants and toddlers react to antisocial others. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(50), 19931–19936.

Hawkes, K., & Coxworth, J. E. (2013). Grandmothers and the evolution of human longevity: A Review of findings and future directions. *Evolutionary Anthropology*, *22*(6), 294–302.

Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., Alvarez, H. P., & Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(3), 1336–1339.

Hawkes, K., & Paine, R. R. (Eds.) (2006). *The evolution of human life history*. Sante Fe, NM: SAR Press.

Johnstone, R., & Cant, M. (2010). The evolution of menopause in cetaceans and humans: The role of demography. *Proceedings of the Royal Society B*, *277*(1701), 3765–3771.

Kim, P. S., Coxworth, J. E., & Hawkes, K. (2012). Increased longevity evolves from grandmothering. *Proceedings of the Royal Society B*, *279*, 4880–4884.

Kim, P. S., McQueen, J. S., Coxworth, J. E., & Hawkes, K. (2014). Grandmothering drives the evolution of longevity in a probabilistic model. *Journal of Theoretical Biology*, *353*, 84–94.

O'Connell, J. F., Hawkes, K., & Blurton Jones, N. G. (1999). Grandmothering and the evolution of *Homo erectus*. *Journal of Human Evolution*, *36*, 461–485.

Sear, R., & Mace, R. (2008). Who keeps children alive? A review of the effects of kin on child survival. *Evolution and Human Behavior*, *29*, 1–18.

Sear, R., & Coall, D. (2011). How much does family matter? Cooperative breeding and the demographic transition. *Population and Development Review*, *37*, 81–112.

Strassmann, B. I., & Garrard, W. M. (2011). Alternatives to the grandmother hypothesis: A meta-analysis of the association between grandparental and grandchild survival in patrilineal populations. *Human Nature*, *22*(1–2), 201–22.

Tomasello, M. (2008). *Origins of human communication*. Cambridge, MA: MIT Press.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Science*, *28*, 675–735.

Voland, E., Chasiotis, A., & Schiefenhövel, W. (Eds.) (2005). *Grandmotherhood: The evolutionary significance of the second half of female life*. New Brunswick, NJ: Rutgers.

Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, *11*, 398–411.

Wynn, K. (2008). Some innate foundations of social and moral cognition. In P. Carruthers, S. Laurence & S. Stich (Eds.), *The innate mind*. Foundations and the future (Volume 3). Oxford, England: Oxford University Press.

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Kristen Hawkes is Distinguished Professor of Anthropology at the University of Utah. Her ethnographic projects with hunter-gatherers have investigated sex and age differences in foraging strategies to improve hypotheses about human evolution. The importance of grandmothers' help for youngsters when their mothers have newborns focused her attention on the evolution of human longevity, and prompted her continuing comparisons of human and chimpanzee life histories. She is a member of the National Academy of Sciences, The American Academy of Arts and Sciences, and the Scientific Executive Committee of the Leakey Foundation.

JAMES E. COXWORTH SHORT BIOGRAPHY

James E. Coxworth just completed his PhD in Anthropology at the University of Utah. He continues to contribute his statistical and modeling skills to an array of projects investigating the evolution of human life history. Coxworth's central interest is the application of evolutionary tools to describe and explain male competitive strategies, with particular emphasis on human evolution. He continues to visit Northwest Australia where his dissertation fieldwork focused on men's strategies of social competition among the Bardi.

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