

## Grandmothers and Their Consequences

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Both what we share and don't share with our primate cousins make us human. Easy enough to start a list. At least since Darwin, most would rate moral sentiments as distinctively human. But our modern selves didn't emerge from ancestral apes in one step. When did populations along the way become human? Before our big modern brains, before language, and before pair bonds, our longer lives, later maturity, and earlier weaning could have evolved in an already smart and gregarious ancestor due to rearing help from grandmothers. Although cooperative hunting and lethal between-group aggression are often nominated as evolutionary foundations for human prosociality, neither distinguishes us from chimpanzees. Grandmothering does. Our grandmothering life history intensified selection on infant appetites and capacities for social engagement, the foundation of our moral faculties.

What could have led to these changes in hominin life history? Plio-Pleistocene climates posed great challenges as increased aridity and seasonality constricted the distribution of foods that ancestral ape youngsters could effectively handle. That left mothers two choices: follow the retreating foods and maintain the diets their weanlings could manage or subsidize them longer. Increased juvenile dependence would allow mothers to remain in habitats inhospitable to youngsters and move into new ones as well. Although extended juvenile neediness would seem to reduce a mother's reproductive success, it offered a novel fitness opportunity for older females with

declining fertility. This novel opportunity is central to the Grandmother Hypothesis: by provisioning grandchildren, elders would allow younger females to bear subsequent babies sooner without net losses in offspring survival. As more vigorous grandmothers left more descendants, rates of aging slowed. That raised longevity and the fraction of female years lived past the fertile ages. The reduction in adult mortality lowered the risk of dying before reproducing, favoring delayed maturity to net the benefits of further growth to larger adult size.

Our characteristic postmenopausal longevity has long been recognized as a major clue to the evolution of human life history. But when George Williams tackled it more than half a century ago, menopause was still thought to be uniquely human. He proposed that it evolved because other changes in our lineage made late births riskier and offspring more dependent. Subsequent evidence shows that women don't stop early. Female fertility ends at similar ages in humans and the other great apes. The human difference is not menopause, but our slower somatic aging. Other apes become frail during the fertile years and rarely outlive them. Not so humans. Among traditional hunter-gatherers, a girl lucky enough to survive childhood usually has more than a 70% chance of living beyond the childbearing years; and women are more economically productive after menopause than before it.

In these hunter-gatherer populations, the standing fraction of adult women beyond the childbearing ages is near a third, even though life expectancies at birth are less than 40 years. Life expectancies in that range contribute to another common mistake. The fact that the highest national life expectancy now almost doubles the global record of 1850 is widely cited as evidence that postmenopausal survival is an artifact of recent history. But life expectancies

at birth are not measures of longevity. Instead they are very sensitive to the short lives of dying babies and rise dramatically when infant and juvenile mortality decline.

Sarah Hrdy revealed a momentous implication of our grandmothering life history in developing her Cooperative Breeding Hypothesis. Hrdy does not privilege grandmothers as I do here, but her synthesis identifies far-reaching consequences of human mothers' reliance on others for successful childrearing. Great ape mothers focus on one infant at a time. But human mothers have overlapping dependents to juggle and must worry about the availability and disposition of helpers. As a result, human babies, unlike other ape infants, cannot count on their mother's full attention. Both mothers and grandmothers have investment alternatives; in high-mortality environments, their commitment can mean life or death. So grandmothering makes infant survival more subject to variation in infants' own abilities to engage caregivers. Human infants' sensitivity to that engagement leaves them (ironically?) more psychologically vulnerable to social approval.

The increased stakes for infants intensify the sociality that we share with other primates. Social bonds matter across the order, as demonstrated by long-term demographic and behavioral observations, experiments, and hormonal assays, both in the wild and captivity. Starting from ancestral ape sociality, grandmothering magnifies selection pressures for desires and capacities to engage mutual attention in earliest life. So the social virtues Darwin identified as distinctively human need not depend on the bigger brains and language that certainly distinguish us. Instead, our brains, language, and even pair bonds may depend on the prior evolution of strong appetites for shared intentions, with sensitivity to praise and blame selected in ancestral youngsters reared in environments with ancestral grandmothering.

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