Living longer: Information revolution, population expansion, and modern human origins

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The dramatic increase in life expectancy and the rising numbers of old people so clearly visible in the 19th and 20th centuries are the result of medical and lifestyle changes that have important social and economic ramifications. Anthropologists have suspected for some time that these recent demographic changes build on a long-term trend that was continuous throughout human evolution. In this issue of PNAS, Drs. Rachel Caspari and Sang-Hee Lee (1) provide powerful evidence to demonstrate the antiquity of this trend toward increasing numbers of older people in society. Furthermore, they show evidence that a dramatic acceleration of this process occurred relatively recently (in evolutionary terms), along with the advent of modern human behavior in the Upper Paleolithic, beginning ≈30,000 years ago.

Caspari and Lee base their conclusions on an analysis of a large sample of fossils representing the last 3 million years of human evolution. The trend for more people to live to older age throughout that time period accelerated sharply in the last part of the human evolutionary record, the Upper Paleolithic, when there was a 4-fold increase in the number of adults old enough to be grandparents. There are at least two significant consequences of having more older adults in a population: greater overlap between generations and higher fertility. Caspari and Lee argue that this life-history change had a major impact on human social and cultural life in enhancing the transfer of information between generations as grandparents helped to educate and enculturate the younger generation and contribute to extended families. It also means that adults lived longer in their reproductive years, increasing potential fertility and increasing the opportunity for passing on cultural knowledge. This demographic transformation was associated with major cultural changes (the "creative explosion") and fueled a dramatic population increase and geographic range expansion of humans that culminated in the colonization of most of the world by 15,000 years ago.

Aging Fossils from Teeth

Caspari and Lee's work is based on relative tooth wear and involves the largest sample analyzed yet of Paleolithic demographic data. They examine the question of when more people started living longer in human evolution in an elegant and innovative way that sidesteps the previous problems limiting our ability to address questions about changes in the adult portion of the human life cycle. They argue that from an evolutionary point of view, the critical measure of longevity is the proportion of a population that lives to an "advanced" age. Following the observation that among primates third molar eruption and sexual maturation are closely correlated, they divide adults into two categories: (*i*) young adults, old enough to be parents, whose third molars have erupted but who have limited dental wear, and (*ii*) older adults, old enough to be grandparents, whose tooth wear indicates an age more than twice the age of third molar eruption. These two groups are the basis of their "OY ratio" (the ratio of older-to-younger adults). Regardless of the exact chronological age of reproductive maturation and the rate of dental wear for early hominids, Caspari and Lee's results are internally consistent across species because they are looking at relative age categories.

Two consequences of having older adults in a population are greater overlap between generations and higher fertility.

Caspari and Lee's novel research design circumvents a range of pitfalls that have limited progress in paleodemography, the study of evolutionary changes in the human life history pattern. The restriction of their analysis to adults avoids the problem of bias imposed by differential preservation of fragile juvenile skeletons. Their use of low-resolution age groups (older and younger adults) allows their age assessments to be categorical rather than numerical. This approach frees these assessments from the ongoing debates about earlier human maturation rates. Their definition of longevity as how many live to be older instead of how long people live allows focus on the aspect of aging that has evolutionary consequences for populations. They checked for bias that might be imposed by differential burial treatment of certain segments of the population and determined that the dramatic increase in the OY ratio in the Upper Paleolithic did not reflect differential mortuary treatment of old people. Finally, their resampling approach avoids the simplistic assumptions required of parametric models and allows them to apply robust statistical tests to the OY ratio, providing a way to determine what differences are truly unexpected, and therefore significant.

Information Revolution and Population Expansion

What is most intriguing about this study is the possibility it raises for the long-standing debate on modern human origins and the creative revolution or origin of modern human behavior (2, 3). This revolution included many changes in behavior reflected in the archaeological record, including the proliferation of symbolic behavior such as that seen in the famous cave art from France and Spain. Whether or not this revolution was associated with significant population replacement, Caspari and Lee's results suggest that the behavioral changes that produced what we call modernity flow from the dramatic demographic changes they have documented. Such increases in numbers of older people whose memories functioned as living repositories of information useful to a successful human adaptation may have constituted a kind of early version of the recent information revolution. The consequences of this revolution may be seen in the increased complexity of Upper Paleolithic society, the explosion of symbolism, including art, the long-distance extension of population movement and trade, the colonization of new ecological niches, the invention and spread of hunting, gathering, and stor-

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age technology, the elaboration of burial rituals, the presence of items of personal adornment and markers of ethnic differences; in a word, the preserved reflections of modernity itself. Similarly, the rapid population growth fueled the geographic expansion and range of social interactions symbolized by rituals and ethnic markers (4). These consequences of the change in life history could in turn also operate by a feedback process as the growing cultural complexity enhanced the potential for survival of older individuals. The mechanism for the higher survival of older individuals is in fact not clear and to what extent the increased cultural complexity caused the changes or was a consequence of them remains an interesting area for further research.

Another theory that has been used to account for how humans became different from their australopithecine ancestors (the earliest of the four groups Caspari and Lee examined) may be adapted to account for how longevity and cultural complexity may be related much later in human evolution. This theory is the Grandmother Hypothesis, which states that longevity evolved in early *Homo* (the second of Caspari and Lee's samples) and promoted reproductive success of grandmothers who invested time and energy in their daughters' children (5, 6). A second hypothesis proposes the coevolution of brain size and intelligence with longevity, suggesting that the long human lifespan was correlated with other changes in the life cycle as a result of a shift to a diet focusing on high-quality, but difficult to obtain foods that require intelligence and skill to acquire (7, 8). This hypothesis also predicts that longevity evolved in early *Homo* and argues that transgenerational communication promoted the accurate continuation of complex traditions. Caspari and Lee show that the increase in the number of people who live to be older in the early *Homo* sample is significant, but small, and may be explained by evolving brain size and behavioral complexity. Much the same could be said for the continued, but small, increase of longevity in Neandertals, the first humans with modern human-sized brains. But the paleodemographic data that cry out for these explanations are in the Upper Paleolithic, long after brain expansion reached modern human size. The 4-fold increase of older individuals that Caspari and Lee demonstrate occurred in this period. Their results suggest that grandmothers (and grandfathers, too) first came to play an evolutionarily significant role at this time; at the very least, significant numbers of grandparents first survived to play such a role during the Upper Paleolithic creative revolution. That revolution may, in fact, be partially a dramatic consequence of the demographic change.

Significant numbers of grandparents first survived to play an evolutionarily significant role in the Upper Paleolithic.

What next? The Grandmother Hypothesis was primarily developed to address why humans began to live well past the age when women can reproduce. According to this theory, the extension of the human lifespan beyond menopause evolved along with the other unique aspects of human life history such as late maturity of children and reduced birth spacing through early weaning of the older offspring. Caspari and Lee's work does not directly address the question of menopause or senescence because they do not attempt to determine specific ages for older adult individuals. However, this work may have implications for understanding menopause, senescence, and their associated problems. For instance, recent research in genetics has shown that many of the differences in cognitive abilities between humans and other primates are associated with increased levels of gene expression rather than the occurrence of new genes (9). However, age-related changes in levels of expression of some of these genes within individual lifetimes may be responsible for some of the degenerative changes in brain function, such as Alzheimer's disease, seen in aging humans (10). This insight suggests that changing gene expression over the human lifetime rather than wear and tear on the body is a direct factor in at least some of these age-related problems. Thus, Caspari and Lee's demonstration of a recent date for a shift in the extension of the human life cycle may be of significance for understanding the evolutionary basis of the cognitive deterioration that often afflicts aged members of our society.

Certainly, we can now surmise that the differences between human and ape life cycles, including the human characteristics of reduced birth spacing, helplessness of newborns, extension of the juvenile period, prolonged adolescence, menopause, and an increase in life expectancy, evolved in a complex mosaic fashion rather than as part of a single evolutionary or demographic shift.

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