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Why Menopause?

By Craig Packer

Shenzi (left) a 17 yr old lion and Cauliflower a 20-something baboon. Both have lived beyond their reproductive years.

As more and more baby boomers reach middle age, advances in assisted fertility make headlines almost every day, and infertile couples can now employ a variety of techniques to conceive a child. So far, however, technology has failed to alter a basic biological limit: the end of a woman's reproductive life span. From about the age of forty, ovaries become less responsive to estrogen, fertilized eggs give rise to embryos with more chromosomal abnormalities, and menstrual cycles become increasingly irregular, ceasing by an average age of fifty-one. Why is this process so relentless? And why does reproductive cessation occur when women are still so vigorous, while a man can become a father at any age?

Since many women today live well into their seventies, menopause seems a frustrating, old-fashioned constraint. Indeed, evolutionary biologists have long viewed menopause as a reflection of life-history patterns adapted to a pretechnological era. Biologists have not agreed, however, on just why and how menopause evolved. Some consider it a natural part of the aging process; others see it as some sort of adaptation, a milestone like puberty, marking a new phase in life.

The evolutionary theory of aging predicts a programmed senescence in any species that suffers "extrinsic mortality," that is, death from external causes. The world is a dangerous place, filled with predators and disease. Consequently, although everyone gets to be young, old age is a rarity for most species. Genetic traits that inflict damage only in old age can thus persist in the general population because they do not interfere with successful reproduction - the ultimate test of "fitness" (which is usually defined as the total number of surviving offspring produced over a lifetime). Most individuals who carry the genes for Alzheimer's disease, for example, will die long before these genes have a chance to do any harm. If, in the distant past, few women lived long enough to experience menopause, then reproductive cessation might be just the inevitable outcome of an overall pattern of senescence.

But human menopause happens so early in life compared with other physiological declines (like heart failure or senility) that many biologists have been dissatisfied with the "reproductive senescence" hypothesis and have proposed instead that menopause might be an evolutionary adaptation. The "risky childbirth" hypothesis points out that pregnancy becomes more hazardous with increasing age and that when a woman dies in childbirth, any young children still dependent on her are also at risk. Thus, the hypothesis goes, middle-aged women might do better to forego the risks of reproduction and enhance their genetic legacy by concentrating their energies on their surviving children and grandchildren. A variant of this theory is that since newborn infants are so demanding, a mother who already has a large brood and gives birth to additional babies will inevitably neglect her earlier offspring. ("There was an old woman who lived in a shoe; she had so many children she didn't know what to do.") Both of these hypotheses view menopause as a gateway to a purposeful new phase in life.

A woman's reproductive life stops while she is still vigorous. A man can become a father at any age. Why?

Like the reproductive senescence hypothesis, however, the various adaptive hypotheses have shortcomings. First, the risk of dying during childbirth is actually quite low. Even in undeveloped nations, middle-aged women suffer an average risk of only 3 percent, which - although sobering for the individual mother-to-be - is far too low for natural selection to favor reproductive cessation. Second, in order to have a chance of becoming a grandmother, a woman must have postpubescent children. High infant survival rates are largely restricted to the developed nations of the twentieth century. Throughout our evolutionary history, most women would have been lucky to raise any surviving offspring at all, so why should they be hard-wired to forego further reproduction during middle age? Surely, it would be more plausible for women to have evolved a birth-spacing mechanism that was sensitive to their levels of nutrition and/or stress, and thus to have prevented further pregnancies only when they were overwhelmed by the demands of their older children.

So is menopause a harbinger of senescence or an adaptive transformation? The reproductive senescence hypothesis is difficult to evaluate in humans. Only a few hominid skeletons have been discovered, and whether these specimens provide an accurate picture of ancestral life spans is unknown. In defense of the adaptive hypotheses, anthropologists Kristen Hawkes and Nick Blurton Jones have noted that the presence of grandmothers in traditional hunter-gatherer societies improves the survival of grandchildren.

However, older women can potentially leave more descendants by continuing to have their own babies than by looking after their grandchildren. Further, even if postmenopausal women's help does enhance their grandchildren's survival, this would not necessarily account for the origins of menopause, which could have evolved as a side effect of senescence, leaving postmenopausal women with nothing better to do than help care for grandchildren.

One way to test these alternative hypotheses is to study other mammals. I have been involved in long-term studies of two species that are often viewed as useful models of hominid evolution: the olive baboon and the African lion. Lions and baboons both live in complex social groups that revolve around the relationships of female kin. The lion pride centers on a core of female relatives who hunt together, defend a joint territory, and raise cubs communally-even to the point of nursing one another's young. Lion grannies sometimes "babysit" and join their daughters in defending territory. The baboons form family-based, hierarchical social groups, with daughters ranking just below their mothers. Elderly females frequently groom their grandchildren and help their daughters maintain their social status by defending them against other females. In addition, baboons, as higher primates, have a reproductive physiology that is essentially the same as that of humans.

I first encountered baboons in 1972, when I went to Tanzania's Gombe National Park with fellow biologist Anthony Collins. (Jane Goodall is most famous for her studies of chimpanzees, but she has also overseen a continuous project on olive baboons at Gombe since 1967. Collins has headed the project for the last sixteen years and supervises a team of Tanzanian field assistants who census the troops every day.) Gombe provides a relatively mild habitat for baboons: the park contains no lions or hyenas and only a few leopards, and the forests are so rich that each troop travels only a few hundred yards a day in search of food. Most Gombe females survive into their twenties, and troops always have a few elderly females, some of whom are so frail they can no longer climb into the troop's sleeping trees at night. None, however, has reached her twenty-eighth birthday.

After several years in Gombe, I moved to northern Tanzania to continue the long-term study of Serengeti lions initiated by George Schaller in 1966. Lions are seldom attacked by other species, so they often survive into their dotage. One of the first lionesses I saw was named Shenzi (Swahili for "shabby"). At the age of fifteen, she had very few teeth, a battered snout, and shredded ears. Again, after gathering data for decades, we know how long lions live: no lioness here has reached eighteen.

Years of fieldwork have taught us much about the reproductive lives of lions and baboons. Baboons are especially gratifying to study because much of their love life is so, well, obvious. Females have a conspicuous "sex skin" that swells as the menstrual cycle progresses, reaching maximal size about the time of ovulation, which occurs every thirty-eight days. Shortly after conception, the skin turns scarlet. Gestation is 185 days, so if a pregnant female's sex skin begins to swell before that much time has elapsed, we can tell that she has miscarried. Tracking fertility in the field this way has enabled us to determine that the overall maternity rate in these baboons remains constant from age six (when puberty begins) to age twenty-one, after which the miscarriage rate soars. Two years later, menstrual cycles become irregular and fertility declines; in four more years, when a baboon reaches twenty-seven, cycling has ceased altogether.

Pregnancies and sexual cycling are harder to detect in lions, but our observations revealed that reproduction also remains constant over most of a lion's life, starting at the age of three and continuing until thirteen. But when lionesses hit their fourteenth year, the average number of cubs in a litter drops sharply, from 2.5 to 1, and the number of litters per year appears to decline. By the time a lioness is seventeen, her reproductive days are over.

Thus, in both species, reproductive performance is constant for many years, followed by decline and eventual cessation - a pattern that is reminiscent of reproduction in the human female. What, then, do these species tell us about the possible adaptiveness of reproductive cessation? Do granny baboons catch a second wind by stopping breeding and devoting themselves to their grandchildren? Do aging lions become the *grandes dames* of their prides and boost their daughters' reproductive rates?

Female mammals – whether lion, baboon, or human – may not be adapted to live much past the years crucial for rearing the final offspring

I asked Marc Tatar, an evolutionary biologist at Brown University, to help address these questions with a detailed demographic analysis of our data. Together, we tested for evidence of an adaptive menopause by comparing the survival rates of animals that had living grandmothers with those that didn't. Unfortunately for the adaptive hypothesis, we could find no evidence of a "granny effect" in either baboons or lions. Grandchildren survived just as well when their grandmother was dead as when she was alive and postmenopausal. Our one significant finding even ran counter to the adaptive "granny hypothesis": a grandmother lioness enhanced the survival of her grandchildren only when she continued to bear young herself. Since a lioness nurses her daughter's cubs only when she has a litter of her own, reproductive cessation *reduces* her ability to look after her grandchildren.

In the end, the reproductive senescence hypothesis provides a more powerful explanation of why lions and baboons stop giving birth. In both species, only a few females survive long enough to experience a declining reproductive rate, at which point they have short life expectancies.

The advantage of maintaining reproduction at these advanced ages is therefore very small. Tatar calculated the lifetime genetic contribution of a hypothetical female that continues breeding to the end of her life: A continuous breeder would leave only 0.24 percent more offspring than the "typical" female; a lioness, only 0.15 percent more.

No one yet knows the precise genetic basis for programmed senescence. Aging may result from mutations that remain harmless until the carrier reaches old age or may be a consequence of traits that enhance survival and reproduction during youth but have a ravaging effect in old age. Either way, Tatar's estimated "costs" of reproductive senescence, are low enough to be consistent with general models of aging.

Still, the question remains, why don't females all drop dead at menopause? Women today regularly live well past menopause. Occasionally, a woman may live nearly as long after menopause as before it: Jeanne Calment of France, for example, went through menopause sometime in the 1920s and died in 1997 at the age of 122, showing no signs of mental impairment. Again, our analysis of baboons and lions provides some clues.

All mammals are characterized by prolonged maternal investment. Mammalian infants are so dependent on their mothers that they may be doomed by her frailty or death. Thus, past a certain age, a female will gain no advantage from further reproduction. She needs the rest of her bodily functions, however, long enough to rear her final "survivable" offspring. It makes sense, therefore, for female reproductive organs to deteriorate before other parts of the body. In most mammals, males, in comparison, do not contribute as much parental care, so retaining their reproductive function could allow them to father surviving offspring at any age.

In baboons, maternal care has a profound effect on infant survival: at Gombe, infants are much more likely to die if they are orphaned prior to their second birthday. At the age of twenty-one (when reproductive senescence first becomes apparent), a typical female has a life expectancy of another five years and thus has a good chance of rearing any infant born in her twentieth year; any infant born after that is increasingly likely to be orphaned too young to survive. In the lions, maternal survival is only important during the first year of a cub's life, and when a lioness reaches the age of fourteen (at which time her litter size drops dramatically), she can expect to live another 1.8 years - long enough to raise the last cub born. Using these data as a rough guideline, and assuming that human infants need their mothers until they are ten years old, we would guess most "ancestral" menopausal women lived to anywhere between fifty-eight to sixty-five.

Like reproductive cessation in lions and baboons, menopause in humans may indeed be a milestone, but its message is one of impending bodily decline. A woman's body might only have been adapted to survive the crucial years necessary to raise her final offspring. Now that we have eliminated so many sources of mortality, women survive long enough to endure long-term consequences of menopause that were outside the experience of our ancestors. Menopausal women today have the option of hormonal replacement therapy to alleviate or prevent some of these long-term consequences, although the appropriate therapy, as well as possible adverse effects of the therapy itself, remain a matter of debate. In the meantime, studies like ours suggest that menopause is not only a universal feature of mammalian life history but also an inevitable legacy of the very feature that defines mammals: the remarkable care that we receive from our mothers.

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