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CHAPTER 1

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Why Menopause?

TO A HUMAN, it seems natural to stop reproducing in midlife. The very thought of becoming pregnant, giving birth, and caring for an infant through, say, age 70 is exhausting, even perverse. But this is what most other animals do. Only in rare circumstances does nature select for lifespans much longer than an organism's reproductive life; most female animals, that is, continue to reproduce in old age. Human menopause is one of science's profound puzzles, the hinge on which much discussion of our evolution turns: one of the most unique features of our species, it must be explained, or explained away.

Menopause is probably adaptive. That is, it's not a mistake or an artifact of modern life whereby women live past some natural test of usefulness. This conclusion has important consequences for how we should think about it and how we should research and treat it. But first, let's talk about the puzzle of menopause, before discussing in the next chapters some of its solutions.

The discipline with the potential to answer the question "Why menopause?" is evolutionary biology—a field that can seem more abstract and more speculative than other natural sciences. Its hypotheses can be hard to test. But only evolutionary biology can answer the big questions about how humans came to have their unique life course, defined by long childhoods, long lifespans, short intervals between births, and, for women, long post-reproductive lives. Most evolutionary biologists and anthropologists agree that all of these factors are related. I am going to describe different ideas about why menopause exists and how it arose—theories that do not always agree, but that are all compelling in their

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own way. I think that several of these theories, and not just one of them, are probably right, and I will try to convey how they might work together.

DOES MENOPAUSE OCCUR IN OTHER ANIMALS?

This question has proved surprisingly difficult to answer. Any study of life cycles of large mammals takes many years, and even then the results can be muddled. How long, for instance, do chimpanzees live? We can't determine whether they have a post-reproductive lifespan without knowing the answer to that question, but that task is not as simple as it seems. Chimpanzees live longer in captivity than in the wild, some groups of wild chimpanzees live longer than others, and some individuals in both groups live much longer than average.[1]

Because chimpanzees are humans' closest living relatives, evolutionary biologists often study similarities and differences between the two species to determine when, and whether, a trait might have evolved. If we share a trait with chimpanzees, it is possible (though not certain) that this trait evolved sometime in our common history. For example, many biologists believe that the tendency of both humans and chimpanzees (as well as other great apes) to exchange females among groups is a behavior that evolved before the divergence of the human and great ape lineages.[2] This "male-philopatric" (meaning "male-father-friendly") dispersal pattern is less common among most mammals than the practice of exchanging males. On the other hand, some scientists have argued that human male philopatry is a result of socioeconomic developments in the agricultural period and not typical of our Paleolithic ancestors.[3]

In a similar way, biologists have tried to determine whether chimpanzees experience an equivalent of human menopause and whether female chimpanzees commonly live past their reproductive lives. Depending on one's definitions, these may be two different questions. In humans, fertility ends some years before the ovaries stop ovulating and producing sex hormones. While human menopause as defined by most

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researchers—that is, as the last menstrual period—occurs around age 50 in most populations, historically only a small percentage of women have given birth after age 45. In a collection of data from 31 populations with "natural fertility," average ages at last birth cluster around 39 and 40.[4] Among the Hutterites, an Anabaptist sect in North America often studied by demographers because of their very high fertility rates, the average age at last birth in the mid-twentieth century was 41.[5] Some animal studies test their subjects' hormone levels or dissect their ovaries, but most wild animal studies rely on the observed ages of females at the birth of their last offspring. Because evolutionary fitness is measured in terms of reproduction, the end of fertility, rather than menopause per se, is usually the more relevant factor when thinking about evolution and natural selection.

The evidence suggests that humans' long post-reproductive lifespan emerged or evolved sometime after the divergence between humans and chimpanzees around 6 to 10 million years ago. But because menopause occurs in all known human populations, it probably emerged before our species divided into groups with little contact with one other; that is to say, probably before about 130,000 years ago.

The most spectacular documented example of an animal that undergoes menopause is the Japanese aphid *Quadrartus yoshinomiyai,* famous among insect researchers for its "glue-bomb" stage of life. Older adult aphids stop reproducing and instead secrete a sticky substance in their abdomens. When predators attack the colony, they selflessly fling themselves into the fray, sticking to the predators and defending the colony at the cost of their lives. These aphids reproduce parthenogenically—all females, they clone themselves in a series of "virgin births"—so the phenomenon called "kin selection" is an especially powerful force among them. A sacrifice by one aphid might save several with identical genes.[6]

What about animals more closely related to us? Do mammals, including our close relatives the chimpanzees, have post-reproductive lifespans? And what counts as a post-reproductive lifespan? Neither of these questions is easy to answer, but based on the research now available, it appears that humans share this trait with very few other mammals, and not with our closest relatives.

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In the past, an obstacle to understanding whether menopause is unique to humans has been the problem of how to measure post-reproductive lifespan. This challenge has been overcome recently by Daniel Levitis of the University of South Denmark and his colleagues, who introduced two measures in 2011 and 2013. First, a simple measure called "Post-Reproductive Viability" solves the problem of how to define a maximum reproductive lifespan and a maximum natural lifespan for a species; another, more complex calculation called "Post-Reproductive Representation" describes the proportion in a given population of adult years lived after fertility ends.[7] Both of these calculations require information that we don't always have: detailed statistics on fertility and a demographic life table, which tabulates mortality, survivorship, and life expectancy at different ages.

Post-Reproductive Viability is the age at which 95 percent of a cohort's years have been lived, minus the age at which 95 percent of its children have been born. (A "cohort" is a group within a population whose members are the same age.) For the women of the !Kung, a foraging population of the Kalahari Desert in southern Africa, this number is 25 years. It is possible for the number to be negative, in which case the animal has no Post-Reproductive Viability.

Post-Reproductive Representation is a little more complicated. Let's imagine a cohort of 1,000 women, all born in the same year (figure 2). Imagine that 5 percent of this group's babies are born by the time its members reach age 20—we can call this the age of adulthood for that group. At that age, 600 of the original cohort are still alive, and they have an average life expectancy of 40 more years—that is, the group at age 20 has a combined total of 24,000 years of adult life ahead. By the time the women are 40 years old, they have given birth to 95 percent of all the babies they will ever have. Four hundred are still alive, and they have an average remaining life expectancy of 25 years; as a group, they will live about 10,000 more years past the age at which they will produce very few more children. To find the *proportion* of adult years lived post-reproductively, we divide 10,000 by 24,000 to get about 0.42 (or 42 percent), which is close to the value that Levitis and his team calculated for !Kung foragers. In a "stationary" population that is neither growing nor

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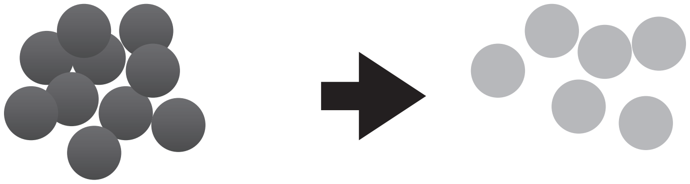

A cohort of 10 newborn girls at time X

The same women at age 15 (time X + 15 years). Four have died. Each survivor will live an average of 40 more years. 5% of their children have been born.

The same women at age 45. Each will live an average of 25 more years. 95% of their children have been born.

Among adult women in this population, about 4 in 10 are post-reproductive (age 45 or older). PrR is 0.42.

FIGURE 2. Calculating Post-Reproductive Representation in an Imaginary Population.

shrinking, this is also *the proportion of adult women in the population who are past reproductive age*.

Because of the way it is calculated, Post-Reproductive Representation, or PrR, is always a positive value between 0 and 1, so there are further complicated tests to determine whether it is significant (a huge value of 0.42 is obviously significant, however). Animals with significant PrR can be said to have a *post-reproductive life stage* that suggests some force of natural selection. Human populations have very large values for PrR that are hard to explain except as an adaptation of some kind.

Post-Reproductive Representation has become the gold standard in menopause research and is better than other methods of calculating post-reproductive lifespan—including Post-Reproductive Viability—because it considers the percentage of the population that lives to post-reproductive age. If some long-lived animals in a species have extended post-reproductive lives, but only a few individual animals live that long, then post-reproductive life has probably not been important in the evolutionary history of that animal. Many animals have some

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Post-Reproductive Viability, but very few can claim PrR comparable to that of humans.

Another problem in menopause research has already been noted: zoo and laboratory animals can have very different life histories than populations in the wild. A few chimpanzees in captivity have lived lives much longer than average without continuing to reproduce; for example, Fifi at the Taronga Park Zoo in Sydney, Australia, died in 2007 at age 60, 20 years after she had her last baby. But after all, some humans survive past the "normal" maximum lifespan of around 75–80 years, to reach age 100 or more.

Protected zoo populations are like humans living in industrialized countries with low mortality, for whom PrR is much higher than for foragers. In order to understand how animals have evolved, it is important to use data from wild animals living in the environments that shaped their natural histories; likewise, we must use data from traditional human societies without industrialization or modern medicine to understand how humans have evolved. Only in the last few decades have researchers begun publishing the results of labor-intensive, long-term studies of animal populations in the wild. For large, relatively long-lived animals, these "demographic" studies—inquiries into questions about population size, fertility, longevity, and mortality—take a long time; researchers must observe groups of animals over decades, in conditions in which even catching sight of them can be difficult.

Thankfully, several research teams have studied wild chimpanzees over the very long term, beginning with the famous work of Jane Goodall, who has studied the Kasakela chimpanzee community of Gombe National Park in Tanzania since 1960. Researchers have published demographic studies of other wild populations in Tanzania, Guinea, and the Ivory Coast, as well as analyses that combine all of this information.[8] The demography of captive chimpanzees has also been studied, based on the records kept by zoos and primate laboratories.[9]

Among most populations studied, the natural lifespan for a wild chimpanzee is around 40 years. Only 7 percent of wild chimpanzees live past this age, though a few individuals have lived to age 50, and this is more common in captivity. Chimpanzee fertility peaks around age

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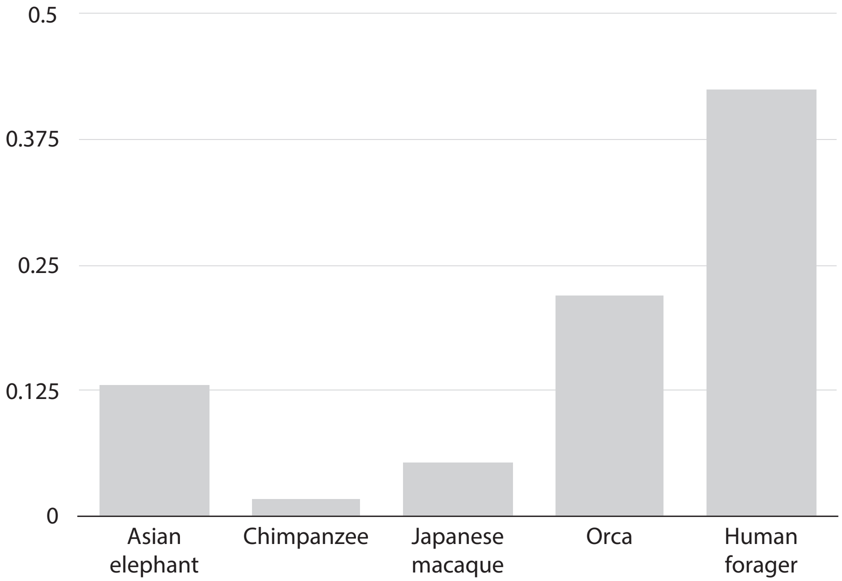

FIGURE 3. Post-Reproductive Representation in Some Mammals.

25–30 and declines after that. But about half of the small number of wild chimps who live past age 40 have at least one more baby. Chimpanzee fertility reaches zero around age 50, about the same age as in humans, but this is close to the normal limit of a chimpanzee's natural lifespan.[10] By the calculations of Levitis and his team, a typical cohort of wild chimpanzees has lived 95 percent of its years by age 37 but has not had 95 percent of its babies until age 45. That is to say, the reproductive lifespan in chimpanzees is actually longer, by this measure, than the "somatic" lifespan of the body itself (*soma* means "body" in Greek); that is, they do not have Post-Reproductive Viability. Post-Reproductive Representation among most groups of wild chimpanzees is only 0.018 (figure 3).[11]

As we learn more about wild chimpanzees, their demography becomes more complicated. The published studies of chimpanzee mortality cited previously are based on populations that are mostly declining, from disease and the catastrophic effects of humans on their environment; consequently, mortality is probably higher in these populations than has been historically true for most chimpanzees. Newly published

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studies of chimpanzees in healthier environments have shown much lower rates of mortality, especially for the Ngogo chimpanzees of Kibale National Park in Uganda, which are thriving.[12] This population is surrounded by other groups of chimpanzees and has little contact with humans, no large predators, no epidemic diseases, no history of logging in their forest, and an abundance of wild foods. As a result, its members live much longer on average than other groups of chimpanzees that have been observed, and perhaps longer than has been historically normal or average for chimpanzees. Average life expectancy at birth for Ngogo chimpanzees is 35.8 years for females and 29.6 years for males—similar to the range for human foragers (though the difference between male and female mortality is strikingly high and much greater than for humans). Early in life, mortality for this group of chimpanzees is actually lower than for human foragers.

However, even in this healthy and long-lived population, the contrast with humans at older ages is strong. Human foragers show much higher survival at ages past 40. Mortality begins to escalate earlier in the chimpanzee population than it does among humans, at about age 20. More chimpanzees in the Ngogo population outlive their reproductive lives than do members of other groups, but they apparently do not have a PrR comparable to that of humans.[13]

What, then, is the extent of the post-reproductive life stage among humans? Among the mid-twentieth-century !Kung, 95 percent of cohort years were lived by age 67—a full 25 years past the age at which 95 percent of fertility ended, at 42. Among foragers generally, the average age at which women last give birth is about 39, and life expectancy for those who reach that age is about 25 to 30 additional years. Typical Post-Reproductive Representation for foragers ranges between 0.35 and 0.5, though an unusually low figure of 0.256 has been calculated for the horticulturalist Yanomamo of Brazil. Among plantation slaves in eighteenth-century Trinidad, a very high-mortality population in which mortality exceeded fertility so that its numbers could only be maintained by importing more slaves, PrR was still 0.315. Post-Reproductive Representation among modern human societies is of course much higher, reaching about 0.76 in Japan today.[14]

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Thus, while humans and chimpanzees stop reproducing at about the same age, a 40-year-old chimpanzee—who still has a nearly 50 percent chance of giving birth again—is quite old. If humans had similar reproductive patterns, women would continue to bear children well into their 70s.

Besides chimpanzees, the long-suffering Rhesus macaque commonly used in laboratory experiments is among the most thoroughly studied of all primates. In 1938 researchers established a colony of Rhesus macaques imported from India on the Puerto Rican island of Cayo Santiago; originally intended as a source of laboratory animals, the colony, managed by the University of Puerto Rico, is now used to research the natural behavior and life cycle of macaques. Other research colonies of macaques have lived since the 1970s on Key Lois and Raccoon Key in Florida, and since the 1950s in Japan, where many wild monkey parks have conserved populations of Japanese macaques (a different species) for both tourism and research. Particularly well studied among these are the monkeys of Arashiyama ("Stormy Mountain").[15] All of these macaque communities are "provisioned"—that is, supplied with food by people. For this reason the demographic patterns observed may be somewhat different from what is typical in the wild—though it is hard to say how much, and the difference may be slight.

Although there is more evidence for a post-reproductive life stage in macaques than in chimpanzees, it is still small. An analysis of 50 years of data from the Arashiyama population of Japanese macaques found that fertility declined steeply after age 22 in this animal, reaching zero by age 26. Nineteen percent of female macaques who reached maturity survived to age 26—past the upper limit of fertility—but only about 8 percent lived beyond age 30. A few, mostly from one female lineage, survived to age 33.[16]

The average lifespan after last birth for the Arashiyama macaques was about 4.5 years. This is three times the average interval between births of about 1.5 years, but results were skewed because a few females lived much longer than the rest; in comparison, the median lifespan after last birth was fewer than three years. The researchers concluded that although females who survive long enough will outlive their reproductive

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capacity, and some individuals can live much longer than that, post-reproductive lifespan is not in general an important part of the life history of Japanese macaques.[17] Post-Reproductive Representation for Japanese macaques is 0.054, higher than that of chimpanzees (and statistically significant, meaning that the researchers are 95 percent confident that it reflects a real tendency for macaques to outlive their reproductive lives), but it is a tiny fraction of any value found for humans.[18]

How unusual is the long human post-reproductive life stage? Very, as it turns out. It is true that many or most mammals—and possibly other animals and organisms (though mammals have been studied the most)—can outlive their reproductive lives, as Fifi or the long-lived lineage of macaques at Arashiyama did. This is also the conclusion of an exhaustive survey by Alan A. Cohen published in 2004[19] and based on older methods of calculation from before the invention of PrR. For the purposes of his study, Cohen defined "post-reproductive lifespan," or PRLS, as the period of time between the average age at the birth of an animal's last offspring and the average age at death for animals living past that age. That is, if we call the first number x and the second number y, PRLS is equal to $y - x$. By this definition all animals that survive their last birth have some post-reproductive lifespan; Cohen defined a significant PRLS as a figure greater than the average interval between births for that animal, plus one standard deviation.

Cohen's study identified a pattern across many species, from lions and baboons to polar bears, ground squirrels, and several other mammals: fertility tends to cease before the end of the natural lifespan, and the oldest females may live significantly beyond the age at which they give birth for the last time.[20] Cohen counted 35 mammals that met his criteria for post-reproductive lifespan, out of 42 studied in the papers he surveyed. These studies included captive animals, laboratory animals, and domestic animals as well as wild animals, and some of their conclusions have been challenged by more recent evidence. Still, it is fair to say that reproductive lifespan and somatic lifespan can evolve independently, and that, in many mammals, fertility ends significantly before death. For most of these animals, though, post-reproductive lifespans are short and PrR, where this has been calculated, is small. For

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example, a recent study comparing seven primates that have been observed over long periods of time in the wild—including chimpanzees, baboons, gorillas, three kinds of monkey, and one lemur—calculated small PrRs of between 0.01 (for baboons) and 0.06 (for spider monkeys).[21]

To sum up, it is not unusual for individual nonhuman animals to outlive their reproductive lives, and reproductive lifespan does not always exactly match somatic lifespan, suggesting that the two can evolve separately. But the more we learn about other animals, and the more we develop good methods of calculation, the more divergent humans seem to be, with Post-Reproductive Representation that is much higher than that of our nearest relatives and of almost all other animals. Old arguments that menopause is only an artifact uncovered by recent medical advances that have lowered mortality and that few premodern humans lived past menopause can be relegated to the garbage heap of scholarship. Humans have a very significant, naturally occurring post-reproductive life stage.

As far as we know, among undomesticated mammals, only two species of whales have a post-reproductive life stage comparable to that of human females.[22] Several demographic studies on whales date to the 1980s, before commercial whaling was banned by the International Whaling Commission in 1986. In this period, whale drive fisheries corralled and killed whole pods at once, allowing researchers to study the demography of the populations that were hunted. More humane studies based on photographic surveys of pods over years or decades have also been published.

One of these photographic-survey studies analyzed data about orcas, or killer whales, living off the coast of British Columbia and Washington state from 1973 through 1987.[23] Two separate ("northern" and "southern") communities of orcas lived in the area year-round; a "transient" community also visited the region but was not studied. Each community was made up of several pods of orcas; the northern resident community had a larger number of pods of smaller average size than the southern community.[24] Observations of the "southern resident" whale population are still ongoing, and the Center for Whale Research in Friday

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Harbor, Washington, has trained many amateur volunteers to recognize individual whales by sight.

On average, female orcas give birth to calves about five years apart, beginning around age 15. The average age at last birth for females is 39, similar to the age at last birth for humans and chimpanzees. But mortality rates remain very low for females of this age. Several females reached ages beyond 60 during the study, and the researchers estimated the ages of the two oldest females as 76.5 and 77; maximum lifespans for females, they concluded, might be around 80 or even 90. Female orcas, then, have a post-reproductive life stage comparable to that of humans. One team of researchers has calculated orca PrR at 0.22, lower than that of most human foragers but higher than that of any other wild animal except the short-finned pilot whale.[25] The ages of male orcas were harder to estimate, but researchers did determine that they had much shorter lifespans, with maximums of about 50 or 60 years.

Orcas live in complex matrilineal societies in which each pod is composed of several families and pods cooperate in communities. Calves of both sexes continue to live with their mothers in adulthood, so families may be large, extending to as many as four generations.[26] It is possible that this social structure is connected to the evolution of a post-reproductive life stage in orcas. Having a living mother is highly beneficial even to adult orcas: adult females are 2.7 times more likely to die, and males 8 times more likely to die, in the year after their mother's death.[27] Post-reproductive females are more likely than others to lead salmon hunts, especially when salmon are scarce—perhaps because of their accumulated knowledge and experience. In this way, their skills may enhance survival for their descendants in the group.[28] In one charming story broadcast on National Public Radio, a grandmother orca seems to have helped deliver her daughter's baby by pulling on its dorsal fin, and she continued to swim with the baby afterward.[29] It is possible that post-reproductive female orcas help their descendants survive in other ways that may be hard to observe or understand.

It is less clear why female orcas do not continue to reproduce as they age. One theory is that when a mother and daughter are reproducing at the same time in the same group, there is too much competition for

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resources and higher mortality for juvenile orcas. Researchers have observed that when calves are born into groups with this kind of reproductive competition, the offspring of the older female has a greater chance of dying; the offspring of the younger female actually has stronger chances of survival than when no competition is present, probably because of the benefits of having a grandmother in the group. Also, because of orcas' social structure, older females are more related to the others in their group, who are all likely to be these females' own descendants, than are younger females, whose fathers are likely to be males outside the group. For these reasons, researchers argue, kin selection favors suppressed reproduction in older females rather than younger ones.[30]

Short-finned pilot whales (*Globicephala macrorhyncus*) were hunted at Taiji in Japan through the early 1980s. Studies published by Toshio Kasuya and Helene Marsh in 1984 analyzed data from the carcasses of more than 800 whales stranded or killed in the drive fishery from 1965 through 1981. Because the fishery captured whole groups, including pregnant females and juveniles, the researchers were able to study the demography and reproductive life cycle of this species. They dissected the reproductive organs of both males and females and also recorded length, weight, age (determined by layers of growth in the teeth), and other characteristics.[31]

Like orcas, short-finned pilot whales live in matrilineal groups in which females spend their entire lives; some males migrate to other groups at adulthood. Females become sexually mature much earlier than males, at around age nine (compared to the late teens for males). The oldest pregnant female in Kasuya and Marsh's sample was 34, and the oldest female still ovulating was about 40. The youngest post-reproductive female was 29, and all the females over 40 were post-reproductive. But females of this species, the researchers found, often lived decades past this age. The oldest female in the sample was 63, and they calculated the average post-reproductive lifespan for females at about 14 years. Some 25 percent of adult females in the sample, in fact, were post-reproductive.[32]

While most calves of young females were weaned by age three, post-reproductive females sometimes nursed their last offspring much

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longer, up to 15 years. The average interval between births was about seven years but was much lower (around five years) for young females under age 24. Males of this species lived much shorter lives. The oldest male in the sample was 46, and Kasuya and Marsh estimated that the male lifespan was about 15 years shorter than that of females for this species.

Because studies on whales in the wild are so difficult to conduct, we don't know whether these results showing long post-reproductive life stages for two species would hold true over time and in different ecological conditions. But they suggest that in rare cases, other animals have developed a female reproductive life cycle similar to that of humans. In both of these whale species, it is noteworthy that males die much earlier than females and continue to reproduce throughout their shorter lives. This suggests that females do not stop reproduction early; rather, some selection pressure has caused female lifespans to lengthen *beyond* reproduction. Whatever this pressure is, it has not affected the lifespans of male orcas or pilot whales.

Like humans, these two whale species are long-lived—at least the females are. So do all animals with long lifespans have a post-reproductive life stage? Is there some hard age limit for reproduction in mammals—say, age 40 or 45—that evolution cannot get around? Few animals live longer than humans, and the life cycles of long-lived animals are especially difficult to study because of the vast spans of time necessary to track changes. But we do know of at least two mammals that reproduce long past the human maximum of about age 45.

Cynthia J. Moss has studied African elephants in the Amboseli National Park in Kenya since 1972.[33] In 2001, based on observations and records of that population (1,778 individuals in total, including those who died in the course of the research), she published the most comprehensive and reliable study of wild elephant demography available today. On average, African elephants at Amboseli gave birth for the first time around age 14. Infant mortality (death in the first year after birth) was relatively low—almost 90 percent of calves born to mothers over 20 survived their first year. Calves were usually born about 4.5 years apart.

Elephant fertility began to decline around age 40, and this decline accelerated late in life, after age 55 or so. But only 9 of the 38 elephants

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who survived to age 50 stopped reproducing (that is, only these 9 females survived longer than seven years past their last birth). Of 12 females who survived past age 60, 5 gave birth. Maximum life expectancy for female elephants was around 65, and for males it was a little less, around 60. Males faced much higher mortality rates throughout the lifespan, and only a minority survived to reproductive age, which is late for male elephants—only mature bulls, usually over age 30, have a good chance of reproducing.

Another study has focused on a population of Asian elephants used for logging in Myanmar, based on records of the Myanma Timber Enterprise dating as far back as 1900. While these elephants worked for humans during the day until the retirement age of 54, they were otherwise unsupervised and allowed to forage and breed naturally. Results were similar to those published by Moss. Fertility in these elephants decreased after age 50 but did not end abruptly. Ninety-nine percent of elephant births were not complete until age 57, 10 years later than in the nonindustrialized human population to which researchers compared them (a dataset representing over 5,000 Finnish women born between 1595 and 1839), and the latest elephant birth on record occurred at age 65. Furthermore, mortality was higher in older elephants than in humans, and elephants were less likely to outlive their reproductive lives for that reason. Elephants over 40 years old had somewhat shorter intervals between births—less than five years—compared to younger elephants, even when researchers controlled for every confounding factor they could think of. Among the Asian elephants of Myanmar, PrR was 0.13—relatively high for a nonhuman mammal—but in the human population used for comparison, it was almost four times greater, at 0.51.[34]

Studies of wild African elephants have shown that very old matriarchs (over age 55 or 60) are better at protecting their herd from lions, at discriminating the signal calls of friends from those of strangers, and possibly (though this is harder to prove) at finding food and water during periods of drought. In one study of elephant behavior during a 1993 drought in Kenya, the oldest elephants seemed to remember water sources from a drought that had occurred 40 years earlier! In Myanmar, elephants born to young, inexperienced mothers were eight times more

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likely to survive to age five if their grandmother lived in the same group; in fact, 93 percent of newborn elephants survived to age five when their grandmother lived with them. Although elephants do not have long post-reproductive lifespans, these studies remind us that it is important to include the value of experience when calculating the benefits of longer lives in foraging populations.[35]

Another long-lived species that reproduces late in life is the fin whale (*Balaenoptera physalus*), which is the second-largest animal in the world, after the blue whale. The fin whale was hunted commercially until 1987, and studies of this species' life cycle have been based on carcasses; no long-term observational studies have been attempted, and these would be difficult, because fin whales live a very long time. In a publication from 1981, Sally Mizroch calculated the age of the whales by counting growth layers in their earplugs, which, along with the ovaries, had been preserved by the Japanese expeditions that killed them. The whalers also recorded other information about their catch, such as length and whether the females were pregnant. Twelve years of whaling data produced information on 1,556 female whales. Using these figures, Mizroch estimated the age of the oldest whale in her dataset to be 111. Four of the next oldest were in their 80s.

Fin whales reach sexual maturity early, around age six or seven. Calves are born around 2.5 years apart on average. Although Mizroch's examination of the ovaries suggested that ovulation rates declined with age, pregnancy rates told a different story: some pregnant females were more than 70 years old, and rates of pregnancy did not seem to change with age.[36]

Reproduction in long-lived mammals, then, can continue to very advanced ages. Furthermore, in some mammals with much shorter lifespans than humans—laboratory rodents, for instance—fertility declines and rates of abnormal oocytes, stillbirth, and genetic abnormalities in offspring increase in old age.[37] That is, mammalian eggs do not have a standard shelf life; "old eggs" alone cannot explain why reproductive life ends so early for women.

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HOW DOES MENOPAUSE HAPPEN?

To understand how it is possible for animals—even closely related ones, like humans and chimpanzees, or certain species of whales—to have different reproductive life cycles and post-reproductive lifespans, we must consider the physiology of reproduction. I should caution, though, that at this point—when we try to explain *why* certain things happen—answers become more complex and debatable, and it will be impossible to avoid oversimplifying. Most theories of reproductive senescence (a scientific term for "aging") rely on the idea that, in mammals, ovarian follicles containing "oocytes," immature eggs, become depleted over time. Because individual animals, including humans, vary widely in the number of follicles their ovaries contain, and because follicles can only be counted by dissection and cannot be counted for any individual more than once, it is difficult to get a clear picture of this process of depletion over time. Nevertheless, the physiology of reproduction in mammals offers an obvious way for nature to select for fertile lifespan separately from somatic lifespan, at least in females.

It is still the scientific consensus that in mammals and birds, males continue to produce sperm cells throughout life, but females produce all their oocytes early in embryonic life. In humans, the number of follicles containing oocytes reaches a maximum of about 600,000 at around five months of fetal development—around 295,000 per ovary on average, but with wide variation—and declines from this peak until menopause. There is some debate about the best model for this decline, but both leading candidates postulate an exponential decline that accelerates with age, even if they reject the more old-fashioned "broken stick" theory that saw a sharp increase in the rate at which oocytes are lost around age 38. Because of the exponential nature of the decline, however, even though it speeds up with age *as a percentage of remaining follicles*, the *absolute number* of follicles lost is much higher per month in youth, with the rate of loss peaking at age 14 or 19 depending on the model used.[38]

A maximum of only about 400 follicles mature for ovulation over a woman's lifetime (fewer in women who have many pregnancies). The remaining follicles degenerate at different points in the process of

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development; this degeneration is sometimes called "follicular atresia," and sometimes "apoptosis," a more general name for the kind of programmed cell death that is presumed to cause this process. These latter, doomed follicles produce estrogen, progestin, and other hormones necessary for reproductive cycling. Menopause occurs in humans when about 1,000 follicles are left. Most researchers believe that variation among individuals in the number of follicles they are born with explains variation in the age at menopause—women born with fewer follicles reach menopause sooner.

There is growing evidence from several independent studies that some female mammals—including laboratory rodents, some primates, and humans—may produce new oocytes throughout their reproductive lives.[39] Though this "eggs forever" hypothesis is still debated, scientists are working on new infertility treatments that may one day use stem cells from adult human ovaries ("oogonial stem cells") to generate new oocytes that can be fertilized.

In the traditional model of mammalian reproductive physiology, natural selection can act on the reproductive lifespan by increasing the number of oocytes produced before birth or by the relatively less costly method of slowing down the rate of atresia. The evidence that natural selection has, in fact, acted this way is strong. Larger mammals with longer lifespans have more follicles and lose them more slowly than smaller mammals, and mammals with both short and long lifespans show a similar pattern of declining fertility that eventually ends as the number of follicles decreases and the quality of oocytes declines.[40] If the creation of new follicles during reproductive life is an important factor in some mammals' fertility, presumably nature could also select for the production of more follicles over a longer period by delaying or turning off whatever changes are responsible for the decline of this process. We do not yet know what those changes are, but the new "eggs forever" model certainly begs the question: If both men and women produce sex cells throughout life, why do women stop, while men do not? If ovaries really do renew their eggs during adulthood, it should have been even easier for nature to select for a longer reproductive life, were it advantageous to do so.

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Whatever causes reproductive senescence in women, age at menopause is both variable among individuals and heritable. Menopause can happen as early as age 40 (if not earlier; 40 is the arbitrary cutoff for "premature" menopause) or as late as 60. Furthermore, we tend to reach menopause at an age similar to that at which our mothers experienced it. Seventeen genes have so far been identified that relate to age at menopause, although they explain only a small part of its heritability, which is estimated at 40 to 60 percent (that is, inherited genes are thought to account for about half of the individual variation in age at menopause, whereas other influences account for the other half).[41] Both of these conditions—variability and heritability—are important for natural selection to happen, and they are clearly present. We begin to see the evolutionary puzzle of menopause: it is hard to imagine a greater and more straightforward fitness benefit than a longer reproductive life. But although our lifespans have lengthened, age at menopause apparently has not changed since before our ancestors diverged from the lineage we share with chimpanzees.

As we have seen, there is no reason to believe that nature cannot select for shorter or longer fertile lifespans, and, more importantly, *nature has in fact done this*: when we compare the reproductive and post-fertile lifespans of other mammals, we find broad variation. "Pleiotropic" arguments about menopause—including the Patriarch Hypothesis discussed later—rely on the idea that nature *cannot* modify or extend reproductive life, but this is clearly not the case.[42] Furthermore, reproductive aging can evolve independently from general somatic aging (aging of the body). Natural selection can favor ending reproduction at a certain age, while the aging of the body is controlled mostly by other mechanisms and can be selected for separately. In most animals, the pressures of selection have, *on average*, placed age at reproductive cessation close to the maximum lifespan or a little before that, when somatic senescence is advanced—that is, when the animal is old. But in every population, some individual animals outlive their reproductive lifespans for a longer time than average (like Fifi the chimpanzee or the four female macaques at Arashiyama who lived to age 33), just as some reproduce longer than average. Those individuals provide an

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opportunity for nature to favor longevity past the reproductive lifespan, if they have a fitness advantage. This has happened at least a few times, in humans and in two species of whales. But it is unusual.

MENOPAUSE AND THE EVOLUTION OF AGING

It is not surprising that most animals do not outlive their reproductive lifespans for very long, because theories of senescence—aging—strongly predict this. Modern theories of senescence trace back to 1951, when Sir Peter Medawar delivered a famous lecture at University College, London, called "An Unsolved Problem in Biology," in which he addressed the question: Why does aging occur, given that nature should select for longevity and against mortality? His answer, although based on a much simpler model of genetics than the one that prevails today, remains foundational to evolutionary theory. Even without aging or mortality of the body, Medawar postulated, old animals are rare because organisms tend to die as a result of external causes (predation, accident, disease). Given this condition, harmful genes that act on the organism late in life can only be selected against weakly, and it is the accumulation of these genes over time that causes aging.[43]

This idea was strengthened and developed further in a well-known 1957 article in the journal *Evolution* called "Pleiotropy, Natural Selection, and the Evolution of Senescence," by George C. Williams. "Pleiotropy" refers to a gene's ability to cause "many turnings" or outcomes, some of which may be "antagonistic"; that is, they have opposing effects under different conditions and, specifically in Williams's theory, at different ages. If a gene is beneficial early in an organism's lifespan (when its reproductive potential is high) *but also* harmful later (when its reproductive future is shorter), nature will select for that gene. Because such genes will inevitably arise, they will inevitably accumulate, causing aging. Nature will continue to select against senescence in other ways, but the effects of this selection decrease with the organism's age as its reproductive future declines and it has fewer opportunities to pass on the gene.[44]

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Variations in longevity and aging among different species of animals reflect different balance points between these two types of selection, and organisms with high "extrinsic mortality," such as insects and rodents, tend to age faster and live for much shorter periods than organisms with low extrinsic mortality. This is because it is important for them to reproduce earlier and faster, and because there is little selection pressure against aging when few animals in the species survive for very long. Williams's theory predicts that large animals and those with unique protection from predators should have longer natural lifespans than smaller, more vulnerable animals; real-life examples include elephants, whales, some birds and bats (which can fly away from predators), and tortoises. Animals that reproduce early should age and die faster than animals with long periods of sexual immaturity. Where there are differences in extrinsic mortality between the sexes, the sex with higher mortality (usually males, who often compete for mates) should age and die faster. Most of these predictions hold up pretty well, and some of them are important for the hypotheses discussed later.

In 1966, an influential paper by William D. Hamilton built on Williams's work by developing mathematical formulae to express the effects of natural selection across the reproductive lifespan and the relationship between reproduction and mortality. Because Hamilton's model agrees with Williams's in predicting that animals will not long outlive their reproductive lives, some scholars call it the "Wall of Death" model.[45]

Finally, in 1977, Thomas B. L. Kirkwood added the concept of the "disposable soma" to senescence theory.[46] Previous theories had not considered that maintaining the body's cells is costly and requires energy and resources that could be used for other things, such as growing or reproducing. Because of these costs, nature tends to select against maintenance longer than the animal can reasonably survive and reproduce in the wild. This theory emphasizes that the body is only a vehicle for reproducing the germ cells (egg and sperm cells) that carry our genes to future generations and will tend to become disposable. The body, that is, is manufactured cheaply and designed to be used for a relatively short time. Again, if extrinsic mortality is high, there will be little payoff to investing in the maintenance of a body that probably won't

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survive for long anyway, and nature should select against maintaining the body beyond the point at which it can reproduce.

Indeed, for the most part, powerful selective pressures seem to have kept reproductive lifespans close to the natural lifespan in most animals. Where differences arise, they can result from two main causes. Pleiotropy, as described by Williams, and "kin selection," a concept developed largely by Hamilton, are common sources of such counterintuitive effects in evolution.

With kin selection, a trait that may be disadvantageous to an individual—an early end to reproduction, for instance—might still be selected for (or at least not selected against) if it is advantageous to close relatives of that individual who have a good chance of sharing the gene. In groups in which relatedness is high, some traits or behaviors that benefit the group more generally, but not the individual, may be selected for. Kin selection is one reason that humans and other animals often behave altruistically; that is, they help others at a cost to themselves.

Integral to kin selection is the concept of "inclusive fitness." This is an extension of the idea of evolutionary "fitness," which refers mainly to survival and reproduction—how many copies of its genes an organism passes on to offspring. An individual's genes are shared not only by offspring, but also by grandchildren, siblings, nieces, nephews, and so forth. Some groups with high "relatedness" share many genes, even among individuals who are not close family members. Hamilton coined the term "inclusive fitness" to describe this factor in natural selection. "Hamilton's rule" models mathematically how nature will select for a trait or behavior if its cost to the organism is outweighed by its benefit to related organisms, according to the likelihood that they share the gene for the trait. In an often-quoted reference to earlier versions of this idea, the geneticist J.B.S. Haldane is supposed to have quipped that he would lay down his life for two brothers or eight cousins.

Sometimes a gene that is selected for because it is advantageous also controls other traits that are not advantageous, or are even disadvantageous; Williams's theory of the evolution of aging depends on this concept of pleiotropy. One well-known example of pleiotropy is the case of sickle-cell anemia, in which a single mutation to a gene controlling the

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production of hemoglobin causes a cascade of physiological effects. Even with modern medicine, this mutation is highly lethal and devastating for people with two copies of the gene, but those with one copy are resistant to malaria; thus the gene persists despite conferring severe disadvantages on some who inherit it. Disadvantageous or neutral by-products of natural selection for advantageous traits are sometimes called "epiphenomena." Some researchers have argued that menopause is such an epiphenomenon,[47] but most current theories see it as adaptive in some way.

Whether we see menopause as an epiphenomenon or as an adaptation carries important implications. If menopause is an epiphenomenon, the "menopause as disease" approach that pervades much of modern medicine might make some sense. If it is adaptive, however, then it is more appropriate to see menopause as a normal, even healthy development that calls for little, if any, intervention.

The amount of dispute, investigation, testing, and theorizing that has gone into the question of the origin of menopause in recent decades is staggering. Emotions run high; camps are large and entrenched. Whatever one's conclusion, it is clear that the issue is an important one currently exercising some of evolutionary biology's best minds. It is fair to say that the Grandmother Hypothesis, described in the next section, is the dominant theory: even those who disagree with it must address it. Thus, even though I am going to propose something a little different myself, I will describe the Grandmother Hypothesis first.

The Grandmother Hypothesis challenged influential theories about the importance of hunting and monogamous marriage in human evolution, and debate on it continues to rage today. Whatever one concludes, the debate is significant in itself: menopause is obviously a defining feature of our species—a feature demanding explanation. My own conclusion is that, regardless of whether we accept all of the Grandmother Hypothesis, menopause is not only adaptive; it is related to other unique features of human life history and to our extraordinary success in almost every terrestrial environment.

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