

Reproductive biology

**Print title: Whale clues to how menopause evolved**

**Online title: Whales make waves in the quest to discover why menopause evolved**

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Why do several species of whale experience menopause? Why does menopause occur at all? Analysing whale demography may help answer these questions, and perhaps shed light on why menopause evolved in our own species.

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Many a menopausal woman has no doubt longed to take a cold bath to ease her hot flushes, but cold baths are the natural habitat of the few known species which experience menopause apart from our own. Menopause — identified in non-human species by an extended period of life after the production of offspring ends — is an unusual characteristic, shared by just a handful of species. Writing in *Nature*, Ellis *et al.*<sup>1</sup> shed light on factors that might drive the evolution of menopause

Most of the known species that have menopause are whales. Five types of toothed whales (those who prey on fish, shellfish and marine mammals, unlike plankton-feeding baleen whales) seem to show long periods of post-reproductive life. These five examples are killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*), short-finned pilot whales (*Globicephala macrorhynchus*), beluga whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*). Many other toothed whales, including dolphins (members of the family Delphinidae) and porpoises (members of the family Phocoenidae), do not. Ellis and colleagues exploit this variation in the experience of menopause within a group of closely related species to help resolve the question of why menopause evolved. By comparing the characteristics of those toothed whale species which experience menopause to those which do not, Ellis *et al* find support for the hypotheses that menopause evolved because it allows post-menopausal females to help their younger relatives while also avoiding too much competition for resources between generations, for example, by reducing the number of mouths which need to be fed.

The evolution of menopause is considered a puzzle by many biologists<sup>2</sup>. An intuitive assumption is that reproducing until the end of one's lifespan should result in greater reproductive success — more of one's genes passed on to future generations — than stopping reproduction many years or even decades before death. This assumption is overly simplistic. Successfully passing genes on to future generations isn't just about producing offspring, but it is also about grandoffspring (and great-grandoffspring, and so on). Investing in existing offspring and grandoffspring to make sure that they survive to adulthood and produce offspring themselves might sometimes be a better strategy than continuing to produce offspring of one's own. This is known as the grandmother hypothesis for the evolution of menopause<sup>3</sup>.

An alternative, although not mutually exclusive, hypothesis is that menopause evolved to reduce competition for resources between generations<sup>4</sup>. Species which experience menopause tend to be long-lived and live in groups in which multiple generations live together. Although group-living has many benefits, it necessitates having to share limited resources. Continuing to produce offspring which will compete with grandoffspring for resources might sometimes result in fewer descendants than would be the case for giving up on reproduction. Both cooperation and competition between post-menopausal females and their younger relatives have therefore been proposed to explain the evolution of menopause.

To test these hypotheses, Ellis and colleagues searched through published scientific literature for data which could be used to reconstruct whale mortality and fertility patterns, and then compared these patterns between species with and without menopause. Toothed whales have relatively long lifespans, with many species capable of living for several decades and the results indicated that species which have menopause typically live longer than those without menopause. The reproductive lifespan (the period of time during which females can produce offspring) was around the same length of time in both groups, however. This means that, in species with menopause, there is a greater likelihood that mothers, adult offspring and grandoffspring are alive at the same time, so there is substantial overlap between generations. There is not a greater likelihood of mothers and daughters reproducing at the same time in species with menopause; the reproductive overlap between mothers and daughters is about the same in species with and without menopause. In other words, in species with menopause, older females have greater opportunity for helping their offspring and grandoffspring but there is less opportunity for competition between generations in these species. This is because whale grandmothers spend at least some time alive but not producing offspring which would compete with grandoffspring for resources. Altogether, these demographic patterns suggest both the cooperation and competition hypotheses for the evolution of menopause are plausible.

The comparative method harnessed by the authors, comparing closely related species with and without a particular characteristic, is a powerful way to test hypotheses about evolution. But this method requires that the data used for these analyses is good enough to generate evidence from which one can draw rigorous conclusions. Studying whale demography is not easy. Observing 'natural' mortality and fertility events directly is rarely possible, meaning the authors had to estimate demographic parameters using data from 'unnatural' mortality events, mainly from mass strandings or whales accidentally caught

by commercial fishing activities. Lifespans, for example, were modelled from data on the age distributions of such deceased whales. Reproductive lifespans were estimated from inspections of the ovaries of these whales. The data therefore contain biases and might involve small sample sizes; several assumptions are then required to reconstruct the demographic patterns of interest. Contemporary whale populations are also often highly affected by human activities, so their demography may not reflect demographic patterns throughout most of their evolutionary history. While the effort and expertise needed to produce these analyses are impressive, it's worth being cautious in interpreting the results and not conclude that they are definitive answers to the puzzle of why menopause evolved.

The authors end by concluding that the evolution of menopause in whales and humans is an example of convergent evolution — a situation in which similar pressures of natural selection lead to the evolution of the same characteristic in notably different species. This perhaps overstates what we know about menopause in humans. We're limited in the analyses we can do to explore the evolution of menopause in our own species; comparative analysis has not been possible given the established view that other primates don't experience menopause. Or so we thought until last year, when a paper was published demonstrating a long post-reproductive lifespan for females in one population of chimpanzees<sup>5</sup>. This was surprising, given that chimps don't seem to provide much help to their grandoffspring.

Research on menopause in humans has tended to focus mainly, though not exclusively<sup>6</sup>, on searching for evidence for helpful grandmothering, and found this in abundance<sup>7,8</sup>. However, direct evidence for help between generations only provides limited support for hypotheses about the evolution of menopause. Contemporary grandmothers might help grandchildren either because menopause evolved to create helpful grandmothers, or because menopause means older women have no choice but to invest in grandchildren rather than children. Multiple other hypotheses exist to explain menopause, including that it is simply an artefact of declines in mortality which have extended lifespans, but have not extended reproductive lifespans.

Research demonstrating the helpfulness of grandmothers in our own species is useful, but perhaps more-so for informing policy than for evolutionary models. Human grandmothers, like whale grandmothers<sup>8</sup>, are important in the lives of their adult children and grandchildren, but older women are too often ignored in policy circles and public health research<sup>9</sup>.

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