NATIONAL CENTER FOR CASE STUDY TEACHING IN SCIENCE

Is It Hot in Here, or Is It Just Me?

The Evolutionary Conundrum of Menopause

by

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Part I – The Conundrum

Menopause, the total cessation of ovulation, is a part of life for nearly every woman who lives long enough. Across all human societies, women reach menopause around the same age (~50 years old) after 10–15 years of declining fertility. With an average life expectancy of almost 79 years for women in the United States today, this means that many women will spend more than a third of their lives unable to have children. In contrast, men can have children throughout their entire lives. In fact, several men have fathered children well into their nineties!

If we measure fitness by counting the total number of offspring born, menopause presents an evolutionary conundrum. Why do women lose the ability to have children, and thus presumably have decreased fitness, while men do not?

Questions

1. What are some hypotheses you can come up with for why women cannot have children beyond a certain age, while men can? Consider both ultimate (evolutionary) and proximate (physiological) hypotheses.
2. What other species do you think might have similar reproductive patterns to humans? Why?
3. How common do you think this pattern is in the animal kingdom? Why?
4. How would you test your hypotheses? What kinds of data would you collect?

Part II – The Mother Hypothesis

Menopause is quite rare in the animal kingdom, even within primates (Figure 1). Apart from humans, only a few species of cetaceans (whales and dolphins) and a few species of insects have a post-reproductive period of life for females in the wild, although fertility does decline with age in many mammal species. The male equivalent to menopause is not known in any vertebrate species. Other species, including some primates and fish, show some evidence of reproductive senescence in females (the scientific term for the loss of the ability to reproduce well before death), but this has only been definitively documented in captive animals; it is unclear if menopause occurs in natural populations of these species.

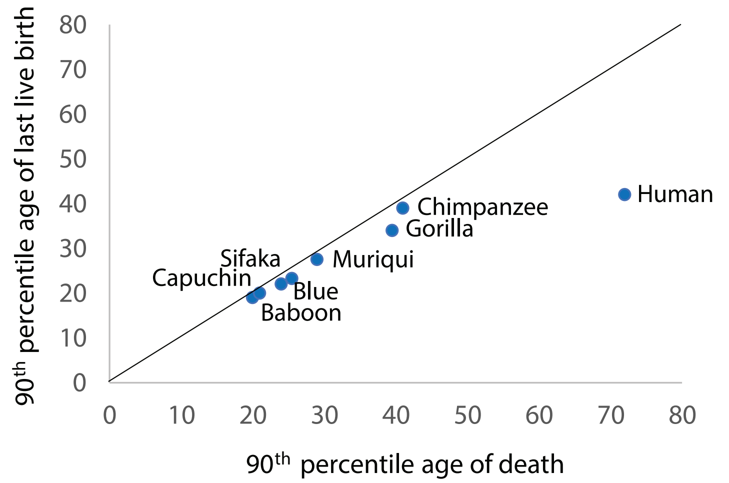


Figure 1. Data showing the age of death and the age at the birth of the last live offspring for females in eight primate species. The solid black line represents the points where the x and y axis are equal and is shown to aid comparisons between age at death and age at last live birth. Human data is from a study of !Kung people, a population of hunter-foragers living in the Kalahari desert, although their life history parameters are similar to other hunter-forager populations. Modified from Alberts *et al.* (2013).

One hypothesis for the evolution of menopause is the "mother hypothesis." This hypothesis rests on two assumptions: 1) that having children at an older age is more likely to cause maternal death, and 2) death of a child's mother before the child is able to care for itself is detrimental to that child's survival. Thus, if mortality goes up as mothers get older, they should stop reproducing to ensure they can take care of the children they already have. Otherwise, if the mother dies in childbirth, her older, but still dependent, children will risk dying themselves. Thus, a mother's fitness is greater if she stops reproducing but survives long enough to raise her youngest child to independence.

Questions

1. Summarize the data shown in Figure 1 in your own words. How are humans different than other primates in this graph?

2. Does this data rule out any of the hypotheses you suggested in Part I?

3. How would you test the mother hypothesis? Be specific about the predictions you would make; consider making a graph or graphs of data that would support your hypothesis.

4. Why do you think that Alberts *et al.* (2013) used data from the !Kung people to represent humans? Would you expect to see the same pattern if they choose modern New Yorkers, for example?

Part III – Testing the Mother Hypothesis

An innovative study by Lahdenperä *et al.* (2011) combined demographic data from two datasets to test the mother hypothesis. One dataset came from church records in Finland from the 18th century and included demographic data on births, marriages, and deaths of women in fishing and farming communities. The second dataset came from baptism, marriage, and death certificates from women born in Quebec, Canada between 1850 and 1879.

Using this data, the authors tested each of the assumptions of the mother hypothesis. First, they calculated the maternal mortality risk by age, and used the relationship between death rate and age to estimate what the risk of death would be if reproduction continued throughout a mother's life. Second, they measured the risk of child mortality for two groups, those children whose mothers died and those whose mothers survived until the child reached 15 years old (and thus was considered independent). For this second test, they evaluated both the short-term effects of maternal mortality (whether a child died within a year after their mother died) and the long-term effects of maternal mortality (child mortality that occurred more than one year after their mother died). Below is the data they collected on the risk of maternal mortality during childbirth (Figure 2) and the risk of child mortality (Figure 3).

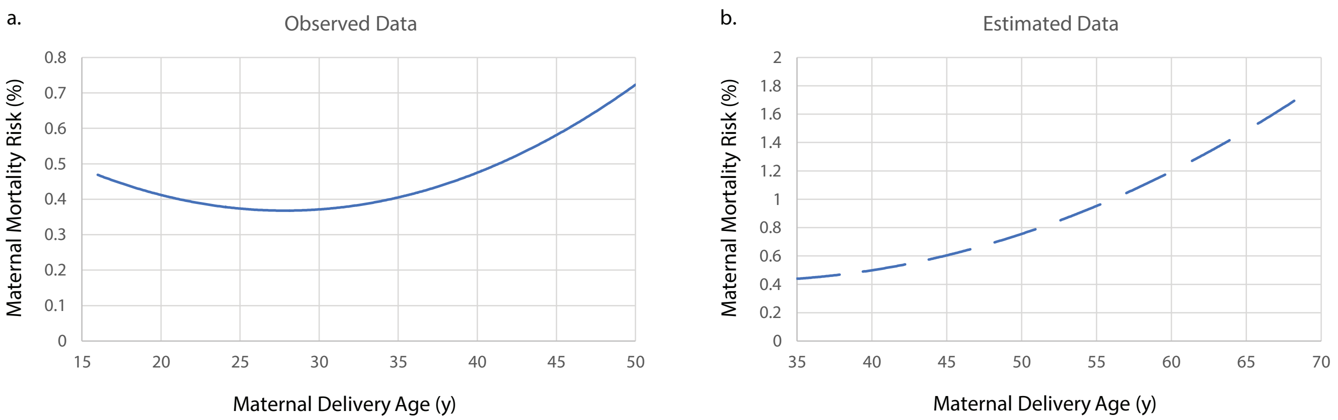


Figure 2. Data on the risk of death to mothers at each age of delivery from the ages of 15–50 (a), and the estimated risk of death if reproduction continued to the age of 70 (b) based on the observed relationship between death rates and age. Data is shown for the Finnish population only; the results from the Canadian population were similar. Data is estimated and simplified from Lahdenperä *et al.* (2011).

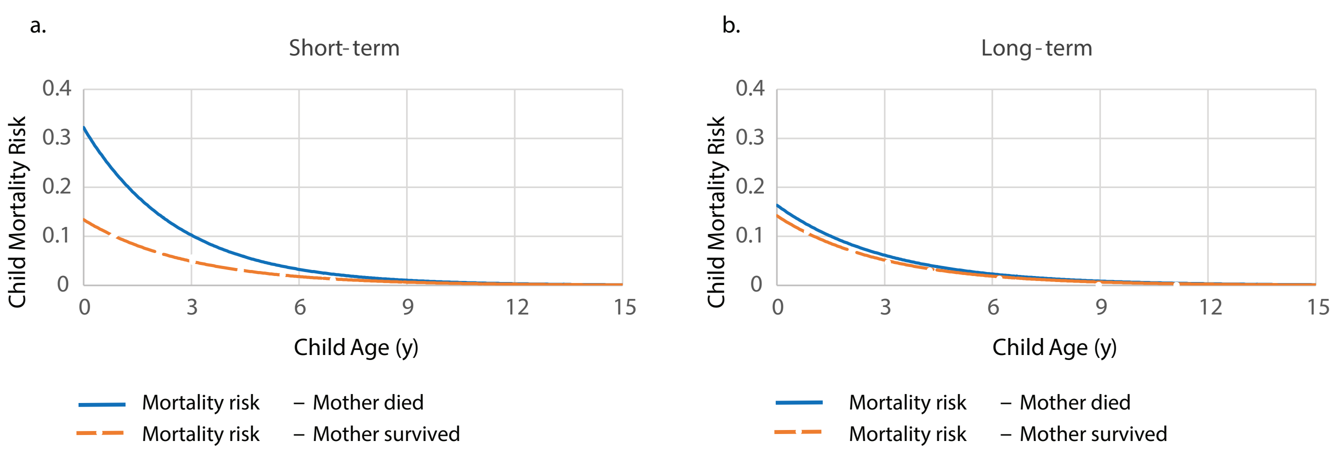


Figure 3. The risk of child mortality by age when mothers died for both (a) short term consequences of mother loss (risk of dying within one year of their mother's death) and (b) long term consequences (risk of dying more than one year after their mother's death). Offspring face a significantly greater risk of dying after their mother's death over the short-term (within the next calendar year, $p < 0.0001$), although the risk of dying decreases with increasing offspring age ($p < 0.01$). After the first year following maternal death, however, offspring face no increased risk of dying compared to children whose mothers survived ($p = 0.30$). Data estimated and simplified from Lahdenperä *et al.* (2011).

Questions

1. Interpret the data shown in each figure for a non-specialist audience. Does anything surprise you about this data?

2. Do you think the data above supports the mother hypothesis as an explanation for menopause in humans? Why or why not?

Part IV – The Grandmother Hypothesis

Based on the evidence shown in Part III, the mother hypothesis is not sufficient by itself to explain the length of menopause in humans. A second hypothesis, the "grandmother hypothesis," has also been proposed. Under this hypothesis, a mother's role in raising young extends to her grandchildren. If a grandmother's care helps more grandchildren survive, this would increase the grandmother's inclusive fitness even though she has stopped reproducing herself.

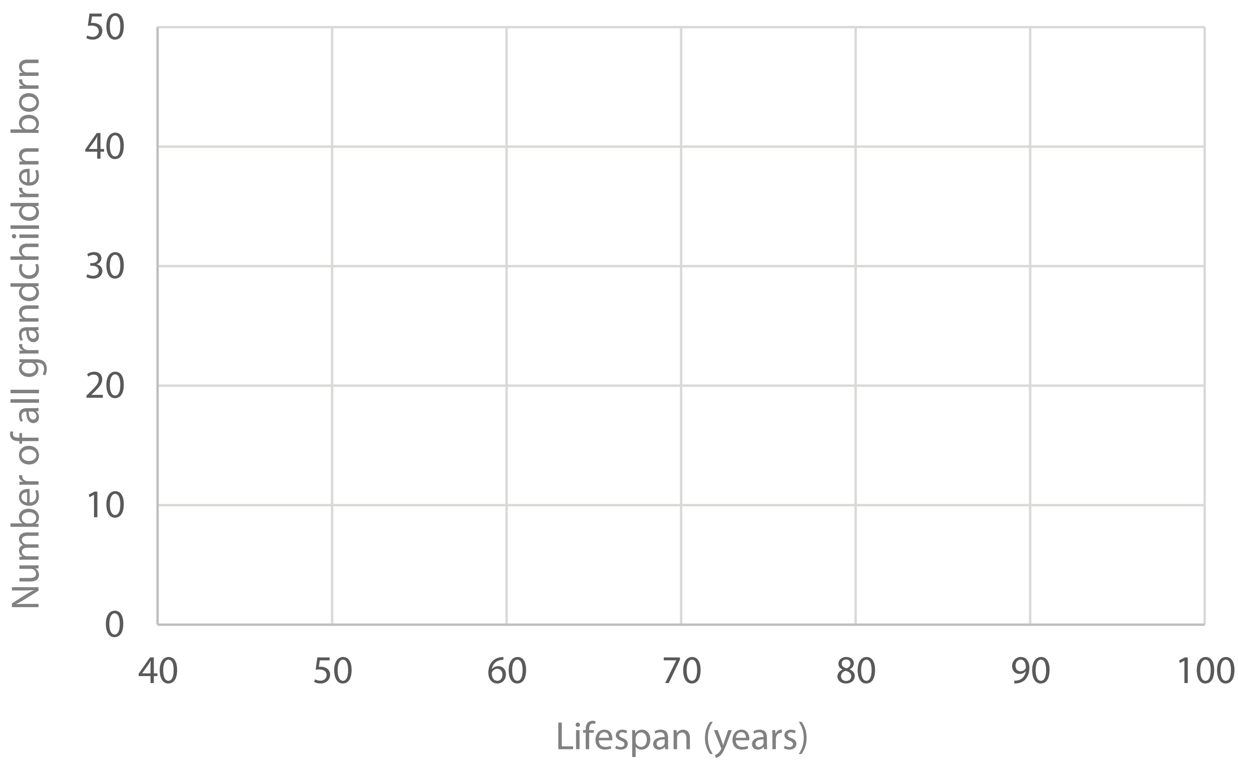
A different study by Lahdenperä *et al.* (2004) used the same combined dataset mentioned in Part III to test the grandmother hypothesis. In these pre-industrial, rural communities, grandparents were often an integral part of the family and lived near, or even with, their offspring and grandoffspring.

Using this data, the authors were able to calculate the lifespan of each woman in the study, the number of children and grandchildren she had, and the proportion of her lifetime that was spent post-reproductive (from the age of 50 until death).

Questions

1. In what ways might a grandmother help increase the number of children her offspring have?

2. If an extended post-reproductive life span does positively benefit children and grandchildren, what relationship would you expect to see? Draw it on the graph below.



Part V – Testing the Grandmother Hypothesis

Lahdenperä *et al.* (2004) found a large impact of grandmothers' survival on the total number of grandchildren born. Women had, on average, two more grandchildren for every decade that they survived after the age of 50. The total number of grandchildren includes those grandchildren born before, and those born after, a grandmother's death. For example, women in the Canadian dataset who died at age 50 had a total of around 38 grandchildren on average, while those who survived to 80 had an average total of 44 grandchildren. The data suggests that the longer a woman lives after she has finished reproducing, the more children her children are able to raise to adulthood (considered age 15 in this study). Importantly, this data is not the result of women having more children while they were still reproducing (so it is not that women who lived to 90 had more children than those that died at 50). Children of the women studied (both sons and daughters) had more children overall, started having children sooner, and had children closer together if their mother was alive when they started reproducing than if their mother died before they reached reproductive age. Having a living grandmother also increased the likelihood of survival of grandchildren after the age of 2 (but not for younger children).

Questions

1. Does the grandmother hypothesis explain the evolution of menopause based on this data? Why or why not?

2. Go back to your original hypotheses in Part I. Does the data presented above eliminate any of your original hypotheses, or could there be other factors that contributed to the evolution of menopause?

3. The existence of menopause has been studied in other long-lived species. In resident killer whales, females stop reproducing in middle age but can live into their 90s or even 100s. In elephants, however, females continue reproducing until their death. In fact, elephant grandmothers can be raising newborn calves at the same time their daughters are raising their calves. How might the hypotheses you generated for humans be applied to these other species? What might be some differences between whales (that have menopause) and elephants (that do not)?

4. Can you think of any critiques of the data shown in Parts III and V that might affect the conclusions the authors reached?

5. What is the most important thing that you have learned about evolutionary processes after doing this case study?

References

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