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Post-reproductive survival in a polygamous society in rural Africa

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Chapter 9

When grandmothers matter

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In a recent issue of *Gerontology*, Herndon discussed the grandmother hypothesis and its implications for studies on cognitive ageing¹. According to this hypothesis the long post-reproductive life span in human females is an adaptive mechanism that evolved to maximize female fitness by investing resources in the care of their grandchildren rather than by continuing to reproduce themselves. From this Herndon deduces that special cognitive robustness to be maintained until after the age of menopause must have co-evolved because grandmothers can only exert the beneficial effect if their cognitive abilities remain intact. He therefore pleads to compare cognitive ageing in humans with other primates, especially chimpanzees, because they lack a long post-reproductive life span and would therefore not have evolved this cognitive robustness. Here, we question the important role of grandmothers in our evolutionary past, first because of the different family structures during this time and second because of the low number of females that actually lived to experience a post-reproductive lifespan. We also show that in a population that reflects our evolutionary past, grandmothers do not have an important role for child survival. Finally we react on the implications for the study of cognitive ageing as put forward by Herndon.

From an evolutionary perspective the long post-reproductive period in human females is a puzzle. Since the length of the reproductive period is a variable trait with a genetic basis² with obvious consequences for reproductive success, why did human females evolve such a long post-reproductive period? One of the theories put forward to explain this phenomenon is the grandmother hypothesis³⁻³. In this theory the human species evolved a post-reproductive life span as an adaptive mechanism because women who stop reproducing around 50 can assist their children to raise the grandchildren. Ultimately, this strategy would result in a larger number of grand-offspring than continuing to reproduce themselves. In support of the grandmother hypothesis, numerous studies have found a positive effect of grandmothers on offspring survival, which were summarized in a recent review⁶.

Our first remark concerns the nature and family structure of the populations of our evolutionary past. Both anthropological and genetic y-chromosomal analyses indicate that the human species until recently lived in polygynous extended families in which one man lives together with multiple wives and a large group of kin^{7,8}. In these populations with polygynous extended families, the wives can

divide the task of childcare with the other kin members and an important role for grandmothers is less likely to be expected. Most studies that have found an effect of grandmothers were conducted in historic populations dating from 1600 to the present. We think that these populations are very different from the populations that constitute our evolutionary past up to recent cultural changes. The study populations were already developed enough to leave written historical records of child survival and genealogical information. These societies are mostly Christian, monogamous agricultural societies. It is possible that in these populations, with three generational nuclear families, composed of man, wife, grandparents and children, grandmothers have a larger influence⁹, because there is only one wife to take care of all children and household tasks, who would greatly benefit from an assisting grandmother.

Some studies were conducted in populations with a polygynous extended family structure. These studies found contrasting results for the effects of both maternal and paternal grandmothers⁶. We studied a large polygynous extended family population of 26,170 individuals in the north of Ghana for five years, which is described in more detail elsewhere^{10,11}. We investigated the effect of different kin members on child survival up to reproductive age (eighteen years). The results in figure 1 show that, the presence of grandmothers did not have a significant effect on the survival of children in this population. Also when we stratified the grandmothers into those below 65 years and those above 65 years, we saw similar patterns. As expected, the mother did have a large effect on the survival of the children. Children whose mother was present during all five years had a 30% survival benefit compared to children of whom the mother was not present during all five years of follow-up. This is a further indication that in polygynous extended family populations, the role of grandmothers on child survival is probably limited and the role of grandmothers in evolution seems to be limited to recent times. Given the remarkably contrasting results, especially in matrilineal and patrilineal societies, we stress the importance of anthropological differences in tribal, clan and family structures. Which kin members influence child survival seems by a large extent determined by cultural factors.

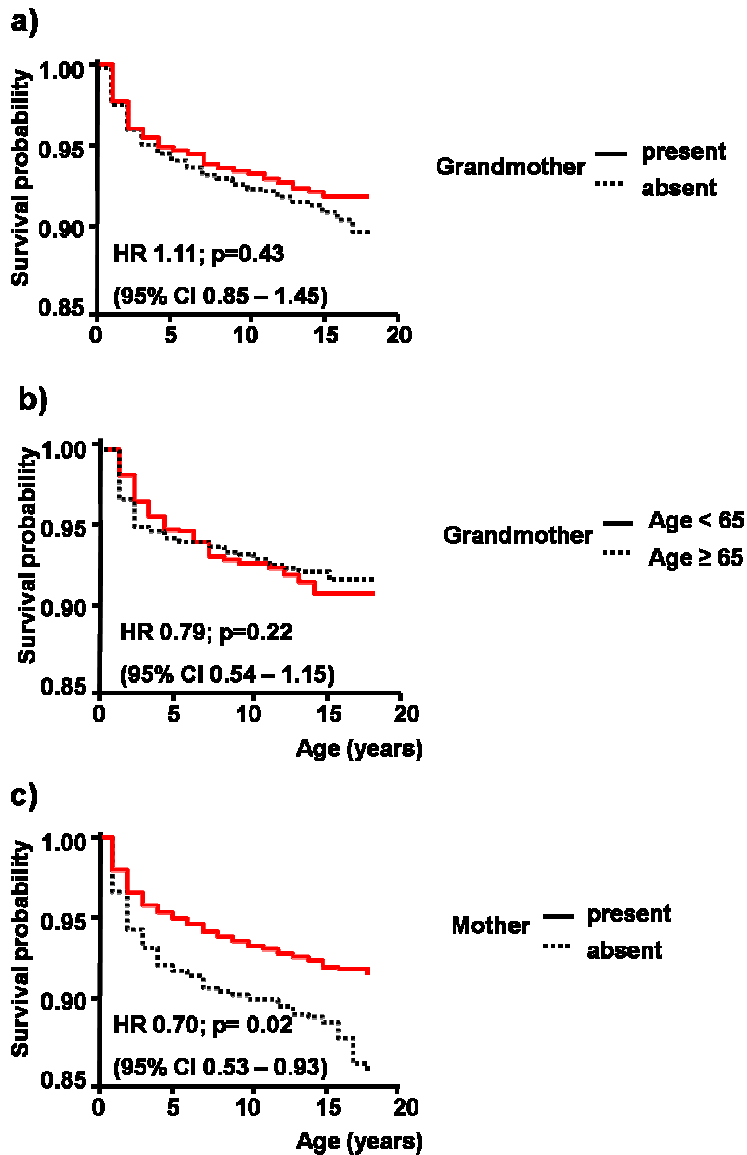


Figure 1. Survival probabilities for children up to eighteen years dependent on the presence of different kinmembers. a) grandmothers; b) grandmothers above 65 years and below 65 years; c) mothers. Left-censored Kaplan Meier plots, hazard ratios (HR) derived from multivariate Cox regression analysis, adjusted for sex, all other kinmembers, socioeconomic status and tribe. All analyses were performed with Stata 9.0, Statacorp, USA.

A second remark to the role of grandmothers in our evolutionary past is that in earlier civilizations, with high extrinsic mortality, only very few individuals would live long enough to experience a post-reproductive life span beyond the age of 50^{12,13}. Variants that yield an increase in female fertility at younger ages would be preferentially selected over variants that result in a fitness benefit at old age, when only a few individuals are left to experience this advantage¹⁴. The post-reproductive life span in this reasoning is not so much an evolutionary puzzle but a recent epiphenomenon of our increased life span. Some argue that these few old individuals could have had a very important function in the community, by transferring special knowledge or skills. This theory is however dependent on group selection which can execute only a small selective advantage, because of the low amount of shared genetic material on a community level.

We would like to make two remarks on the implications for the study of cognitive ageing as put forward by Herndon. Many characteristics of the human species as we know it today, evolved during a long period of evolution. A recent role of grandmothers, as has been found in some populations cannot have given rise to the co-evolution of maintenance of cognitive robustness until after the age of menopause as Herndon implies. The evolution of our brain which separates us from other primates, evolved during a long period of evolution. It is possible that the presence of grandmothers has an advantage for children nowadays, but we think that this effect is too recent to have given rise to a co-evolved maintenance of cognitive robustness until after the age of menopause. Instead the existence of age-associated diseases, such as Alzheimer, cancer and cardiovascular diseases, in our view strongly argues against selection for robustness at higher age. This is in line with the classic theory of ageing as put forward by Medawar which indicates that selective pressure decreases very rapidly after the time of reproduction and rearing of offspring which is therefore called the selection shadow¹⁴.

As a second reaction to the implications, we also think that human life history does not stand out very differently from other primate species. During our evolution in the past 10.000 generations, with the exception of the last ten, the median life span of humans was probably not 80 years as noted in figure 1 of Herndon's paper, but much lower, around 40 years¹⁵. Human life history in this case would be very similar to the life history of chimpanzees or rhesus monkeys, because most humans would also not live long enough to experience a post reproductive life span.

Concluding, we question the important role of grandmothers in our evolutionary past up to recent times, which was characterized by polygynous extended families. In line with this reasoning, we also do not find an effect of grandmothers in a polygynous extended family population. Consequentially we question whether humans developed special cognitive robustness to be maintained until after the age of menopause which is also inconsistent with current theories of ageing. Also, we question whether human life history is very different from other primate life histories. Although it is possible that the study of the chimpanzee brain can teach us many things about cognitive ageing, we do not think that the role of grandmothers in our evolution provides us with good reasons to believe this.

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