The Grandmother Effect

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Key Words

Cultural evolution • Modal age at death • Grandmothers

Abstract

Two classes of explanation have been advanced to explain women's long post-menopausal life span – that it is an epiphenomenon of increased longevity or an evolved adaptation. While there is no decisive evidence to choose between them, the latter appears more likely. Two mechanisms for the evolved adaptation have been proposed, the 'mother effect' and the 'grandmother effect'. It is argued that both these effects, insofar as they have been shown to occur, are likely to be culturally rather than genetically evolved.

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Human females are highly unusual, possibly unique, in their prolonged life expectancy following the menopause and the end of their reproductive life. This phenomenon has long fascinated anthropologists and there is an extensive literature speculating about its causes and its meaning (reviewed in [1]). Three papers in this journal [2–4] have also put forward opposing views.

Two principal explanations have been explored: 'the epiphenomenon of longer lifespan' and 'the evolutionarily selected adaptation'.

The Epiphenomenon of Longer Lifespan

The pros and cons of this idea are thoroughly discussed by Peccei [5]. The length of female reproductive life is determined by the supply of ova. All ova that a woman ever has are present at birth and they diminish in number rapidly thereafter. The menopause occurs when there are no more ova available for ovulation [6]. This is believed to have occurred at around the age of 50 ± 10 years of age throughout history. These physiological mechanisms are surely genetically determined and may show quantitative variation so that differences in age at menopause can be subject to selective pressures. Peccei [5] also points out that the first mention of the menopause is in the bible (Genesis) and we can be sure of its occurrence only for some 3,000 years. Since *Homo sapiens sapiens* emerged about 160,000 years ago, this would represent only the last 2% of the time span of human existence.

The analyses are based largely on median life spans which may not be the best choice as this statistic was, until recent times, dominated by infant and childhood mortality. A better statistic is the 'adult modal age at death' [7]. This is a much more robust measure of the life expectancy of those who live beyond the menopause. Wilkie [pers. commun., Prof. David Wilkie, Heriot-Watt University] points out that the adult modal age at death in 1840, when the first UK mortality statistics were recorded, was

72, much higher than most people would expect, and that it has risen to around 80 in the intervening 170 years. Urban mortality was probably only a little different in 1840 than it had been in Roman times [8] so that prolonged survival after the menopause is unlikely to be of only recent origin. This inclines one to be hesitant about accepting the longer lifespan hypothesis.

The Evolutionarily Selected Adaptation

The alternative explanation is that prolonged survival after the menopause is a selected adaptation. Those who take this view have suggested at least two mechanisms, the 'mother effect' and the 'grandmother effect'.

The Mother Effect

Darwinian evolution by natural selection favours the survival of those who leave the most progeny who will themselves successfully reproduce. It is therefore wrong to believe that selective advantage will always cease to operate immediately after the end of active reproductive life. While this may be true of fish, which abandon their progeny immediately after the eggs have been laid and fertilised, it is clearly untrue in species where the young require parental care. Human offspring are dependent on their parents before becoming sexually, and, perhaps even more importantly, 'economically' independent (i.e. capable of existing successfully within the society in which they live) for about 25% of their lifespan, and this has probably changed little in historical times, as both average life span and the period of dependency have increased. Amongst the great apes this period is appreciably shorter, at around 15% for gorillas [pers. commun., Dr. D.A. Field, Zoological Director, Zoological Society of London].

The 'mother effect' could therefore be sufficient to explain a selective advantage in women living active lives for some 15–20 years after giving birth to their last child, simply in order to raise this child to sexual and economic maturity. Van Bodegom et al. [4] supply data to support this, taken from contemporary populations in northern Ghana.

The Grandmother Effect

The other explanation is the 'grandmother effect', which takes the view that having a grandmother to help with childcare or to gather food is a selective advantage to producing more progeny. Evidence for and against is reviewed but inconclusive [1]. Herndon [2] argues in fa-

vour of the grandmother hypothesis, suggesting that this may be associated with a prolonged maintenance of cognitive ability in humans, as opposed to their great ape ancestors. Bateson and Martin [9] propose that it is selectively advantageous for women to care for their grandchildren rather than to attempt to breed again after a certain age and point out that in some pre-industrial human tribes in Tanzania [10] it was common for post-menopausal women to gather food, which contributed to enhancing their daughters' fertility. van Bodegom et al. [4] take the opposing view, and argue that while the presence of mothers is associated with a greater probability of survival of offspring, the presence of grandmothers is not.

It would be inappropriate for someone who is not an anthropologist to enter into these long-standing controversies and I provide these comments, at the invitation of the editor, to make just one significant point: if the 'mother effect' and/or the 'grandmother effect' can be shown to exist and to be of selective advantage, they are unlikely to have arisen as a result of genetic evolution but rather as the product of cultural evolution.

Cultural Evolution

Cultural evolution is defined as the transmission of information (most typically of behavioural prescriptions) both horizontally and vertically by all means other than through the genome [11].

One of the principal advantages of cultural evolution is that it acts over a much shorter time scale since it does not depend on reproduction. In the 160,000 years (4,800–6,400 generations) that *H. sapiens sapiens* has existed, there has been little time for genetic evolution to produce major innovations, but cultural evolution has taken humans from the Palaeolithic to the modern age in just over 10,000 years. Cultural evolution has been described in monkeys, but in its highly developed form is a characteristic of humans. It is largely dependent on the development of language and was greatly accelerated by the development of writing. It acts on groups of humans and group selection is at the core of cultural evolution. The building blocks of cultural evolution are to a large extent enshrined in religious prescriptions. This is what gives religion its evolutionary significance [12].

The real test for whether a group behavioural trait is genetically or culturally inherited is the 're-queening experiment' [13]. In bees, variations in colony behaviour can be shown to be genetically determined by re-

placing the queen in a colony with a mated queen from another colony with more desirable traits. The workers that are bred from the new queen grow up among the original workers but learn nothing from them. They behave entirely according to their genetic background. When analogous 'experiments' (for example moving children from the New Guinea Highlands to the United States) have been done with humans, the result has always been the reverse. Humans acquire the behavioural group characteristics of those amongst whom they grow up.

It does, therefore, seem an entirely reasonable hypothesis that some populations have adopted an important role for grandmothers and that this adaptation has proved advantageous for them; while others with no obvious role for grandmothers have succeeded as well in their particular circumstances. This is entirely consistent with the way

that cultural evolution operates and there is no reason not to believe the conclusions of both Herndon [2] and van Bodegom et al. [4]. However, since the adaptations are cultural, they are not necessarily associated with developments of cognition, which are genetically evolved.

In present-day Western society, it seems plausible that there is an advantage in the 'grandmother effect' since it is increasingly required that both parents work to make an adequate living. Stable geographical localisation of multi-generation families would be an advantage here. In some countries there has been a marked tendency among the middle classes for families to move away from their parents, making the option of the 'grandmother effect' less possible. This provides an opportunity for a sociologist to look critically at whether the 'grandmother effect' has measurable advantages in contemporary society.

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