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Life-History Evolution: Grandmothering in Space and Time

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The evolutionary puzzle of the extended post-reproductive life of female humans has been explained by indirect fitness benefits gained by grandmothers helping raise their grandchildren. Two new studies support this 'grandmother hypothesis' and explore its limits in space and time.

> *"Grandparents, though no longer fertile, may yet promote (or impede) the welfare of their grandchildren, and so influence the mode of propagation of their genes. A gene for grandmotherly indulgence should therefore prevail over one for callous indifference, in spite of the fact that the gene is propagated* per procurationem *and not by the organism in which its developmental effect appears".*
>
> Peter B. Medawar. 1952 [1]

In a footnote to his essay '*An unsolved problem of biology*' [1], the British biologist Peter Medawar outlined what is now known as the 'grandmother hypothesis' for the evolution of human menopause. Female menopause — the cessation of reproduction midway through life — is a universal feature of human life history, but demands explanation because classic evolutionary theory suggests there should be no selection for survival past the end of reproduction. Medawar compared post-reproductive grandmothers to sterile bee workers, arguing that selection could favour helping by post-reproductive women as a means of propagating copies

Figure 1. Finnish grandparents with their offspring.
Photo courtesy of The Human Life History Group, University of Turku, Finland.

of their genes via kin, just as sterile workers propagate their genes by aiding the reproduction of their queen. The puzzle of menopause thus inspired one of the first explicit examples of 'inclusive fitness', a decade before William D. Hamilton's landmark papers on the topic [2]. In recent years evidence has accumulated from detailed studies of hunter gatherers and other 'natural fertility' human populations that grandmothers do indeed boost the fitness of their reproductive offspring [3–5]. Now, two recent studies published in *Current Biology*, by Sacha Engelhardt and colleagues [6] and Simon Chapman, Mirkka Lahdenperä and colleagues [7], use two different historical datasets on pre-industrial humans to show that space and time (or more precisely, age) set limits on the benefits of grandmothering. Together these findings provide important new insights into how kin selection has shaped human life history and social structure.

First consider spatial constraints on grandmothering. If grandmothers are to boost the fitness of their descendants, they need to live close enough to their adult children to help with resources and childcare. But in many small-scale human societies, daughters — and often sons, too — disperse away from their natal family group [8]. Daughters may also have dispersed from their family in the societies of ancestral humans, as they do in chimpanzees, bonobos and gorillas. On the face of it, female dispersal appears to be incompatible with (maternal) grandmothering, but until now there has been no detailed information on how grandmothering benefits vary with the dispersal distance of daughters. How far can a grandmother's helping hand reach?

Engelhardt and colleagues [6] address this question using a remarkable dataset on a population of 17th and 18th Century French settlers to the St Lawrence Valley area of modern-day Quebec. The Catholic clergy kept a watchful eye on these settlers and systematically recorded baptisms, marriages and deaths in local parish records. These records have been assembled into a multigenerational database of the life history of thousands of settler families living from 1621 to 1799 in parishes across 'La Nouvelle-France'. Engelhardt and colleagues [6] use this database to test for fitness benefits of maternal grandmothering, and whether these benefits declined with the geographic distance between mothers and their adult daughters. To control for fitness correlations that arise from genetic or shared-environment effects — rather than the efforts of helpful grandmothers — they carried out a within-family analysis, in which they compared the reproductive success of a daughter who began to reproduce while her (post-reproductive) mother was still alive, with the reproductive success of one of her sisters who began to reproduce after their mother was already dead.

In support of the grandmother hypothesis, Engelhardt and colleagues [6] found that daughters who started to reproduce with a living mother gave birth to more offspring across their lifespan (2.08 more, on average), and succeeded in raising more offspring to 15 years of age (1.14 more). Their study also revealed that the fitness benefits conferred by grandmothers depended on how far daughters dispersed. Sisters who dispersed further started reproducing later and produced fewer surviving offspring across their lifetime than sisters who stayed close to their mother. For example, sisters who settled 325 km away from their mother (the maximum dispersal distance recorded) had around 30% fewer surviving offspring than their sisters that stayed near home.

The study by Engelhardt and colleagues [6] confirms the prediction that grandmothering is less effective from afar [4]. However, it also challenges the assumption of demographically explicit kin-selection models [9] that dispersal is an insurmountable barrier to helping. In the St Lawrence Valley population, daughters who dispersed 25 km away from their mother had almost as many surviving offspring as their non-dispersing sisters. This finding is relevant to the ongoing debate about the level of female dispersal in ancestral humans and its influence on selection for post-reproductive lifespans [10,11]. Some have argued that post-reproductive grandmothering should select against female dispersal, on the assumption that grandmothers can only help their daughters if they remain nearby [12]. However, Engelhardt's study shows that grandmothers can still provide substantial help to their daughters even after they disperse. The potential for distant grandmothering following dispersal should in principle strengthen selection for female dispersal, as daughters who disperse can escape the costs of local kin competition and inbreeding, while retaining the benefits of grandmotherly assistance. Other factors that promote female dispersal are a male-biased adult sex ratio and higher costs of male compared to female dispersal [13]. Male dispersal may have been particularly costly in human populations that show evidence of intense conflict between groups [14].

The new study by Chapman and colleagues [7] focuses on a second constraint on grandmothering, the frailties and limitations of advanced age. From the perspective of the evolutionary theory of aging, post-reproductive helping can be treated as a form of reproductive effort, and selection should favour greater helping effort early in the post-reproductive period compared to later [15]. Thus one might predict that the fitness benefits conferred by post-reproductive helpers will decline with age, weakening selection for survival. On the other hand, where grandmothers help through the transfer of knowledge and accumulated wisdom [16], older grandmothers may provide more valuable help than younger ones, which could in principle halt or even reverse the process of senescence — a form of 'negative senescence' [17] — if only temporarily.

Chapman and colleagues [7] test how the benefits change with grandmother age using another invaluable historical dataset from pre-industrial Finland (Figure 1). Again, this dataset is the product of an assiduous clergy: in this case the Lutheran Church kept detailed records on the demography and major life events of most of the population of Finland for over 150 years, starting in the mid 1700s. Chapman and colleagues [7] show that the availability of grandchildren towards whom ageing women could direct their care peaked when they were in their early 60s but then rapidly declined. By age 75 most of a woman's grandchildren had already been born, because their daughters had ceased reproduction. Moreover, the survival benefit to offspring conferred by the presence of a grandmother declined with grandmother age, starting at around 70 years of age. This age-related decline in the availability of recipients and the effectiveness of help coincides with a rise in the mortality rates of older women as they entered their 70s — just what we might predict if rates of senescence were moulded by the magnitude of kin-selected benefits that grandmothers can confer on their offspring.

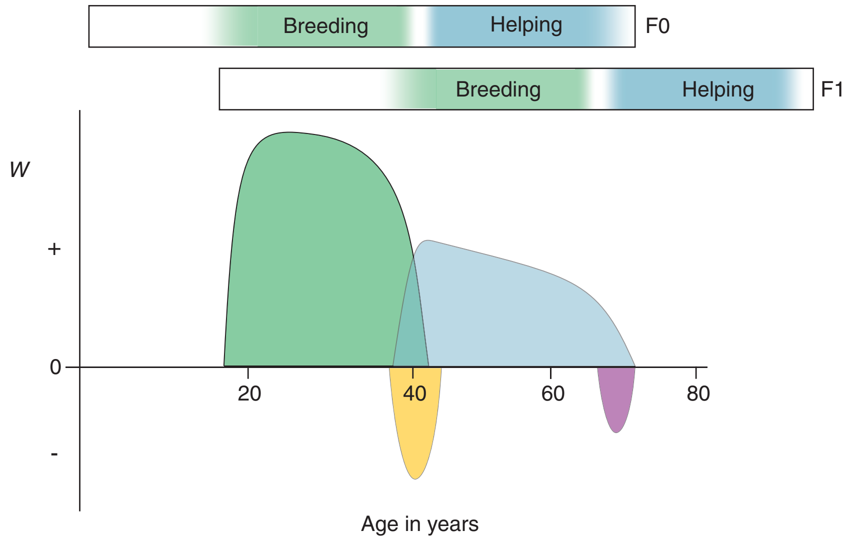

Figure 2. Inclusive fitness across the lifespan.
Schematic schedule of inclusive fitness costs (negative values of *W*) and benefits (positive values of *W*) for a focal female (F0) across two generations, based loosely on findings from the Finnish dataset [7,20]. Bars depict overlapping life histories of F0 and F1 females; reproductive and post-reproductive periods are shown in green and blue; periods of potential intergenerational conflict over reproduction and grandmothering are shown in orange and purple, respectively.

A striking finding of the study of Chapman and colleagues [7] is that grandmothers can also inflict costs on their grandchildren. Specifically, the presence of paternal (but not maternal) grandmothers over the age of 75, or paternal (but not maternal) grandmothers that were within one year of death, had a negative impact on the survival of grandchildren (Figure 2). The authors suggest these costs do not result from disease transmission, but rather that conflicts over the allocation of parental resources may arise between aging grandmothers and grandchildren. The fact that only paternal grandmothers inflicted these costs in late life is further evidence that sex-biased dispersal can have important implications for within-family conflict and life history evolution.

Both studies [6,7] provide important confirmation of the dynamic nature of kin selection as a force shaping human life history. Selection for late-life survival and helping is weaker when there are few grandchildren to help, those grandchildren live far away and grandmothers have become great-grandmothers. To understand how kin selection changes across the lifespan in family groups we need to zoom out to consider which individuals disperse from the family and how far, and how the life stages of family members are overlaid in time and space (Figure 2) [18,19]. These studies are further evidence that fundamental features of our physiology and patterns of aging are explained by our evolutionary history of family life, with all its opportunities for cooperation and conflict.

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Conservation: Bye-Bye to the Hihi?

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Theoretically, small populations should be less capable of adapting to environmental change, yet empirical evidence is mixed. A new study on a rare New Zealand bird, the Hihi, uses genomics and long-term demographic data to reveal low adaptive potential.

Populations of many animal species are declining at an unprecedented rate across the world [1]. To prevent extinction, a thorough understanding of the factors affecting the persistence of small populations is paramount. Small populations are more likely to go extinct due to stochastic effects [2] and may face additional threats due to inbreeding depression, the loss of genetic diversity and the accumulation of deleterious mutations [3, 4]. Given the rapid rate of global environmental change, a particular concern is that small populations are predicted to have lower *adaptive potential*, that is, a reduced capacity to change genetically in response to environmental changes [5]. The adaptive potential of a population is ultimately determined by the amount of heritable genetic variation for fitness available in the population [6]. Despite the importance of adaptive potential in predicting population persistence, measuring adaptive potential in natural populations is exceedingly difficult, and rigorous studies of adaptive potential in threatened populations remain rare [7]. A recent paper in *Current Biology* by Pierre de Villemereuil, Anna W. Santure, and colleagues [8] uses multiple methods to assess the adaptive potential of an endemic New Zealand bird, the hihi (*Notiomystis cincta*).

The hihi, or stitchbird, is a small songbird that is one of New Zealand's rarest birds and the sole member of the endemic family Notiomystidae [9]. Males have white ear tufts and a black head ringed by bright yellow shoulders, while females are a drab olive (Figure 1). These curious birds flit through the forest canopy, tails cocked, often emitting the distinct 'stitch' call that gave the stitchbird its English name [10]. The hihi feeds on nectar, fruits and invertebrates, but their food choice is largely determined by local competitors — the larger, more dominant tui and bellbirds get the first pick in foraging sites [11]. Hihi have unusual reproductive behavior: they have a highly variable and promiscuous mating system and are the only known bird that mates face to face [12]. Its Maori name, hihi, means 'ray of sunshine'. In Maori folklore, the demigod Maui asked the hihi to fetch him some water after he tamed the sun. When the bird refused, Maui picked him up and threw him into the fire, burning his feathers. The male hihi's yellow and black plumage now serves as a reminder of the sun and fire, a permanent lesson about disobedience [13].