

1 Evolution: Grandmothering in space and time

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14 Grandparents, though no longer fertile, may yet promote (or impede) the welfare of their
15 grandchildren, and so influence the mode of propagation of their genes. A gene for
16 grandmotherly indulgence should therefore prevail over one for callous indifference, in spite of
17 the fact that the gene is propagated *per procurationem* and not by the organism in which its
18 developmental effect appears.

19 P.B. Medawar. 1952

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22 In a footnote to his essay *An unsolved problem of biology* [1], the British biologist
23 Peter Medawar outlined what is now known as the ‘grandmother hypothesis’ for the
24 evolution of human menopause. Menopause – the cessation of reproduction midway
25 through life – is a universal feature of human life history, but demands explanation
26 because classic evolutionary theory suggests there should be no selection for
27 survival past the end of reproduction. Medawar compared post-reproductive
28 grandmothers to sterile bee workers, arguing that selection could favour helping by
29 post-reproductive women as a means of propagating copies of their genes via kin,
30 just as sterile workers propagate their genes by aiding the reproduction of their
31 queen. The puzzle of menopause thus inspired one of the first explicit examples of
32 ‘inclusive fitness’ reasoning, a decade before W.D. Hamilton’s landmark papers on
33 the topic [2]. In recent years evidence has accumulated from detailed studies of
34 hunter gatherers and other ‘natural fertility’ human populations that grandmothers do
35 indeed boost the fitness of their reproductive offspring [3-5]. Now two studies
36 published in *Current Biology* use two different historical datasets on pre-industrial
37 humans to show that space and time (or more precisely, age) set limits on the

38 benefits of grandmothing. Together these findings provide important new insights
39 into how kin selection has shaped human life history and social structure.

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41 First consider spatial constraints on grandmothing. If grandmothers are to boost the
42 fitness of their descendants, they need to live close enough to their adult children to
43 help with resources and childcare. But in many small-scale human societies,
44 daughters (and frequently sons too) disperse away from their natal family group [6].
45 Daughters may also have commonly dispersed from their family in the societies of
46 ancestral humans, as they do in chimpanzees, bonobos, and gorillas. On the face of
47 it, female dispersal appears to be incompatible with (maternal) grandmothing, but
48 until now there has been no detailed information on how grandmothing benefits
49 vary with the dispersal distance of daughters. How far can a grandmother's helping
50 hand reach?

51

52 Engelhardt et al address this question using a remarkable dataset on a population of
53 17th and 18th Century French settlers to the St Lawrence Valley area of modern-day
54 Canada. The Catholic clergy kept a watchful eye on these settlers, and
55 systematically recorded baptisms, marriages, and deaths in local parish records.
56 These records have been assembled into a multigenerational database of the life
57 history of thousands of settler families living from 1621 to 1799 in parishes across 'La
58 Nouvelle-France'. Engelhardt et al use this database to test for fitness benefits of
59 (maternal) grandmothing, and whether these benefits declined with the geographic
60 distance between mothers and their adult daughters. To control for fitness
61 correlations that arise from genetic or shared-environment effects, rather than the
62 efforts of helpful grandmothers, they carried out a *within-family* analysis, in which
63 they compared the reproductive success of a daughter who began to reproduce while
64 her (post-reproductive) mother was still alive, with the reproductive success of one of
65 her sisters who began to reproduce after their mother was already dead.

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67 In support of the grandmother hypothesis, Engelhardt et al. found that daughters who
68 started to reproduce with a living mother gave birth to more offspring across their
69 lifespan (2.08 more, on average), and succeeded in raising more offspring to 15
70 years of age (1.14 more). Their study also revealed that the fitness benefits conferred
71 by grandmothers depended on how far daughters dispersed. Sisters who dispersed
72 further started reproducing later, and produced fewer surviving offspring across their
73 lifetime than sisters who stayed close to their mother. For example, sisters who

74 settled 325 km away from their mother (the maximum dispersal distance recorded)
75 had around 30% fewer surviving offspring than their stay-at-home sisters.

76

77 Engelhardt et al's study confirms the prediction that grandmothering is less effective
78 from afar [4]. However, it also challenges the assumption of demographically explicit
79 kin selection models (reviewed in [7]) that dispersal is an insurmountable barrier to
80 helping. In the St Lawrence Valley population, daughters who dispersed 25 km away
81 from their mother had almost as many surviving offspring as their non-dispersing
82 sisters. This finding is relevant to the ongoing debate about the level of female
83 dispersal in ancestral humans and its influence on selection for post-reproductive
84 lifespans [8, 9]. Some authors have argued that post-reproductive grandmothering
85 should select against female dispersal, on the assumption that grandmothers can
86 only help their daughters if they remain nearby [10]. However, Engelhardt's study
87 shows that grandmothers can still provide substantial help to their daughters even
88 after they disperse. The potential for distant grandmothering following dispersal
89 should in principle strengthen selection for female dispersal, since daughters that
90 disperse can escape the costs of local kin competition and inbreeding, while retaining
91 the benefits of grandmotherly assistance. Other factors that promote female dispersal
92 are a male-biased adult sex ratio, and higher costs of male compared to female
93 dispersal [11]. Male dispersal may have been particularly costly in human
94 populations that show evidence of intense intergroup conflict [12].

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Figure 1 around here

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98 The new study by Chapman et al [13] focuses on a second constraint on
99 grandmothering, the frailties and limitations of advanced age. From the perspective
100 of the evolutionary theory of aging, post-reproductive helping can be treated as a
101 form of reproductive effort, and selection should favour greater helping effort early in
102 the post-reproductive period compared to later [14]. Thus one might predict that the
103 fitness benefits conferred by post-reproductive helpers will decline with age,
104 weakening selection for survival. On the other hand, where grandmothers help
105 through the transfer of knowledge and accumulated wisdom (e.g. [15]), older
106 grandmothers may provide more valuable help than younger ones, which could in
107 principle halt or even reverse the process of senescence (a form of 'negative
108 senescence' [16]), if only temporarily.

109

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

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

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Figure 2 around here

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139 To conclude, the two studies provide important confirmation of the dynamic nature of
140 kin selection as a force shaping human life history. Selection for late-life survival and
141 helping is weaker when there are few grandchildren to help, those grandchildren live
142 far away, and grandmothers have become great-grandmothers. To understand how
143 kin selection changes across the lifespan in family groups we need to zoom out to
144 consider which individuals disperse from the family and how far, and how the life
145 stages of family members are overlaid in time and space (Figure 2; [17, 18]). These
146 studies are further evidence that fundamental features of our physiology and patterns

147 of aging are explained by our evolutionary history of family life, with all its
148 opportunities for cooperation and conflict.

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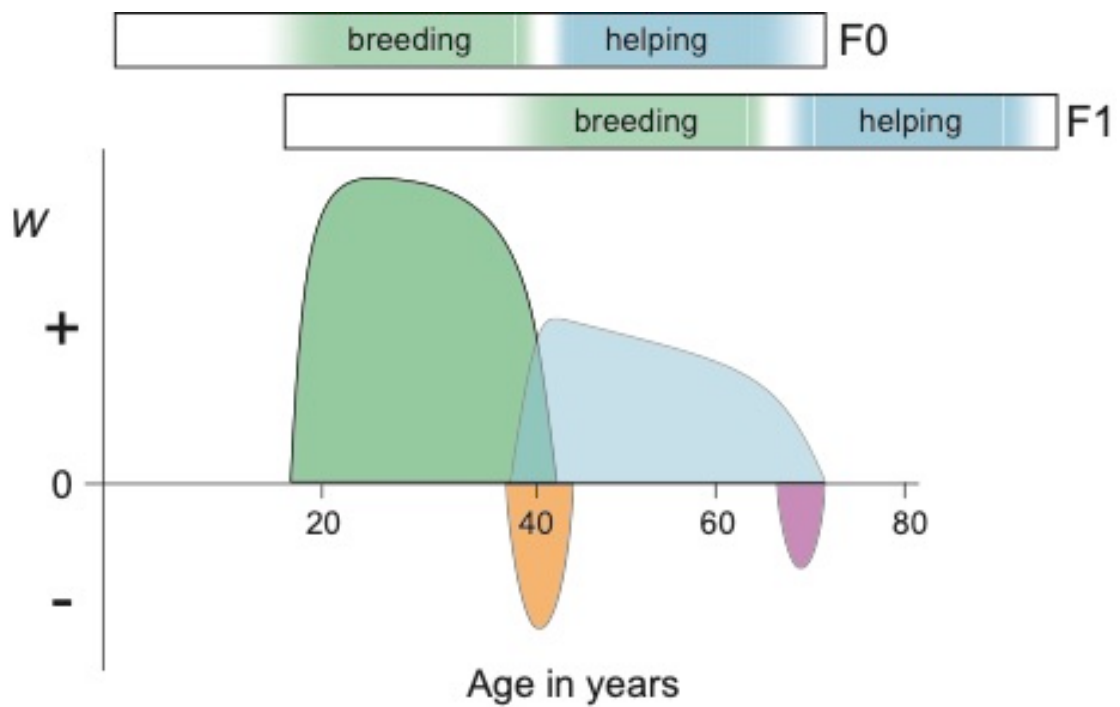
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212 Figure 1. Finnish grandparents with grandoffspring, Date and location unknown.

213 Image courtesy of The Human Life History Group, University of Turku, Finland.

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217 Figure 2. Schematic schedule of inclusive fitness costs (negative values of W) and
 218 benefits (positive values of W) for a focal female (F0) across two generations, based
 219 loosely on findings from the Finnish dataset [13, 19]. Bars depict overlapping life
 220 histories of F0 and F1 females; reproductive and post-reproductive periods are
 221 shown in green and blue; periods of potential intergenerational conflict over
 222 reproduction and grandmothering are shown in orange and purple, respectively.

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