

# 1 Evolution: Grandmothering in space and time

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4 Michael A. Cant<sup>1\*</sup> and Darren P. Croft<sup>2</sup>

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6 1. Centre for Ecology and Conservation, University of Exeter, Penryn Campus,  
7 Penryn, Cornwall TR10 9FE, UK

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9 2. Centre for Research in Animal Behaviour, University of Exeter, Exeter EX4 4QG,  
10 UK

11  
12 \* Author for correspondence, [m.a.cant@exeter.ac.uk](mailto:m.a.cant@exeter.ac.uk)

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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.

66

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.

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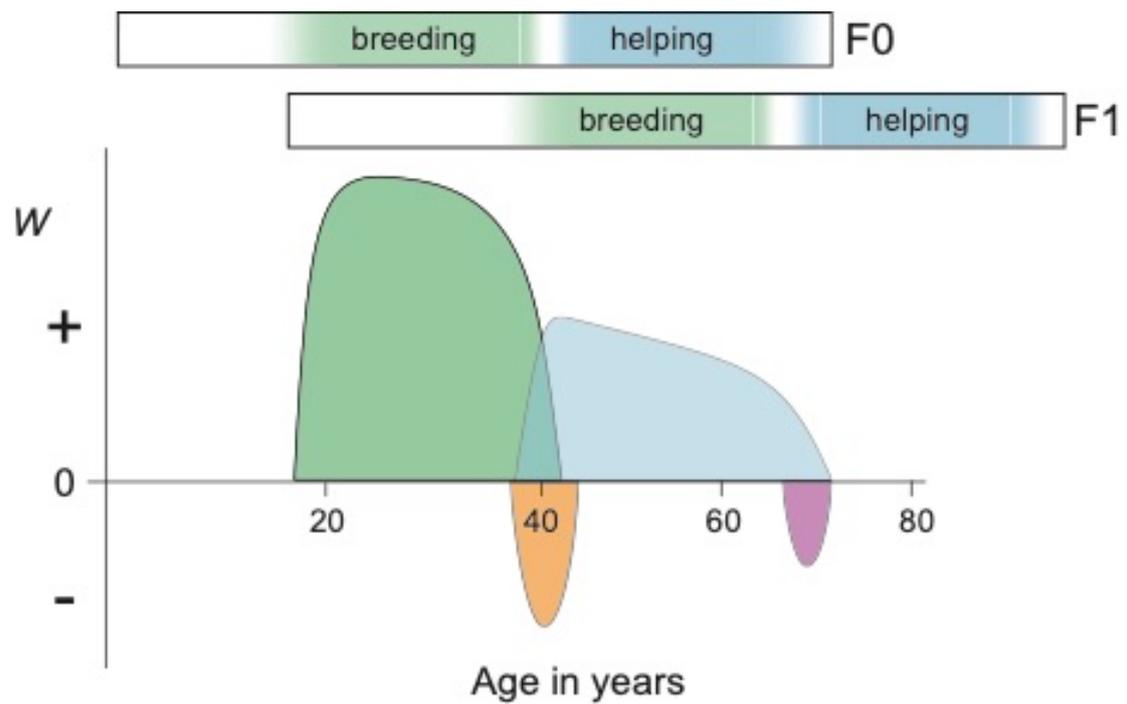
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212 Figure 1. Finnish grandparents with grandoffspring, Date and location unknown.

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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