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Fitness benefits of prolonged post-reproductive lifespan in women

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Most animals reproduce until they die, but in humans, females can survive long after ceasing reproduction[1,2]. In theory, a prolonged post-reproductive lifespan will evolve when females can gain greater fitness by increasing the success of their offspring than by continuing to breed themselves[3–6]. Although reproductive success is known to decline in old age[1–6], it is unknown whether women gain fitness by prolonging lifespan post-reproduction. Using complete multi-generational demographic records, we show that women with a prolonged post-reproductive lifespan have more grandchildren, and hence greater fitness, in pre-modern populations of both Finns and Canadians. This fitness benefit arises because post-reproductive mothers enhance the lifetime reproductive success of their offspring by allowing them to breed earlier, more frequently and more successfully. Finally, the fitness benefits of prolonged lifespan diminish as the reproductive output of offspring declines. This suggests that in female humans, selection for deferred ageing should wane when one's own offspring become post-reproductive and, correspondingly, we show that rates of female mortality accelerate as their offspring terminate reproduction.

Life-history theory generally predicts that there should be no selection for living beyond one's reproductive capacity[1,2]. That female humans show a prolonged post-reproductive lifespan is therefore puzzling. The most compelling hypothesis so far predicts that selection will favour a prolonged post-reproductive lifespan if this enables individuals to increase their fitness through assisting their own offspring to reproduce successfully (the grandmother hypothesis)[3,4]. Such helping by post-reproductive individuals is unusual in the animal kingdom: helpers are typically pre-reproductive offspring that delay their own dispersal and help their parents to breed[7]. Nevertheless, evidence of helper effects from cooperatively breeding animals can be used to predict the benefits that mothers may confer by helping offspring to reproduce. Helpers may 'lighten the reproductive load' of breeders (allowing them to breed earlier and/or more often[8,9]) or provide care that is additive to breeders (causing survival improvements to their offspring[9–11]).

Previous research on humans provides some evidence that post-reproductive mothers can benefit the reproductive output of their offspring[12–15]. However, it has not yet been possible to test whether prolonged post-reproductive longevity in humans is associated with greater grandchild production, and hence greater fitness, because data covering the complete reproductive histories of several generations of individuals are scarce. Here we investigate the fitness benefits of prolonged post-reproductive lifespan using complete, multi-generational individual-based data sets from humans living in two different countries (Finland, $n = {\sim}500$ women and Canada, $n = {\sim}2,300$ women) during the eighteenth and nineteenth centuries (see Methods). We concentrate on the fitness benefits of post-reproductive lifespan for females, because the post-reproductive lifespan of males cannot easily be defined. Our data come from historical farming communities, where grandparent(s) are known to have been an integral part of the family, residing in the same house as at least one of their offspring and near to virtually all others[16,17]. Evidence from contemporary human populations shows that grandparents may assist philopatric offspring by transferring knowledge and participating in household tasks and child care, and that such help may increase offspring breeding probability[12], and grandchildren nutrition and survival[4,14].

We first investigate the effect of a woman's post-reproductive lifespan (age at death after ${\sim}50$, see Methods) on the number of grandchildren that she leaves in the population (that is, fitness). Second, using the Finnish data set, we investigate the effect that the presence of a post-reproductive mother has on the lifetime reproductive performance of all her offspring: lifetime fecundity, lifetime reproductive success (number of children produced and raised to 15) and individual λ[18] (a fitness measure incorporating the timing of reproduction and the lifetime reproductive output) (see Methods). Third, we investigate the mechanism(s) through which post-reproductive females influence the fitness of their offspring (and hence themselves) by comparing the effect of post-reproduc-

tive mother presence/absence on offspring key life-history traits (age at first reproduction, inter-birth intervals and reproductive tenure length) and grandchildren survival probability. Analyses are conducted using general linear (mixed) models (GLMs or GLMMs) in which we control for a large range of potentially confounding effects (see Methods). These include socio-economic status (rich, wealthy, average, poor), temporal (birth cohort) and geographic (population) differences in living conditions[19], post-reproductive mother's age (or potential age had she been alive), offspring sex, number of competing siblings, and birth order, as well as the inclusion of different offspring from the same mother.

First, the length of a woman's post-reproductive lifespan has a significant positive effect on the number of grandchildren that she gives rise to in both Finns and Canadians (Fig. 1). In each country, the strength of this relationship is similar, and equates to the equivalent of post-reproductive women gaining two extra grandchildren for every ten years that they survive beyond age 50. This similarity arises despite the social, cultural and life-history differences between the two countries (Table 1 and Methods).

These findings are not confounded by a long post-reproductive lifespan being related to the production of more offspring before age 50. No relationship occurs between the number of offspring delivered by a female in her lifetime and her post-reproductive longevity (Finland: $F_{1,351} = 0.04$, $P = 0.84$; Canada: $F_{1,2360} = 0.11$, $P = 0.74$), and the effect of post-reproductive longevity on number of grandchildren remains significant after controlling for the number of offspring produced (Finland: $\beta = 0.18 \pm 0.05$, $F_{1,325} = 15.29$, $P = 0.0001$; Canada: $\beta = 0.20 \pm 0.04$, $F_{1,2357} = 23.68$, $P < 0.0001$). Moreover, our results are unlikely to be confounded by between-family differences in living conditions or health. Significant effects of socio-economic status as well as temporal and geographical differences in living conditions on grandchild numbers are controlled (Finnish analysis: $F_{3,326} = 4.97$, $P = 0.0022$; $F_{4,326} = 4.82$, $P = 0.0009$; $F_{4,326} = 14.57$, $P < 0.0001$, respectively). Neither socio-economic status, nor temporal or geographic differences in living conditions influences female post-reproductive lifespan (all values $P > 0.1$). The probability of a Finnish mother dying of the most common cause of death, an infectious disease, is unrelated to either the probability of her offspring ($n = 574$) dying of an infectious disease (GLMM: $\chi_1^2 = 0.33$, $P = 0.56$) or the fecundity of her offspring (GLMM: $\chi_1^2 = 0.09$, $P = 0.77$).

Second, further analysis of the Finnish data set reveals that post-reproductive mothers living when their offspring begin to reproduce have a significant positive effect on the three components of fitness measured. In the presence of a living post-reproductive mother, both sons and daughters have a greater number of offspring in their lifetime (Fig. 2a), and raise more to adulthood (age 15) (that is, greater lifetime reproductive success) (Fig. 2b). Additionally, a living post-reproductive mother has a significant positive effect on her offspring's individual λ[18] (GLMM: $F_{1,524} = 4.22$, $P = 0.04$). Finally, the longer a post-reproductive mother survives after the offspring started reproducing (controlling for mother's age) the greater her offspring's lifetime reproductive success (GLMM: $F_{1,281} = 8.42$, $P = 0.004$). Previous studies have suggested that post-reproductive mothers might direct their care primarily towards daughters[3–4], but our results imply that sons and daughters benefit similarly from the presence of a post-reproductive mother. This is likely to arise in our study populations because both sexes usually remained in their natal population and resided near to their mothers.

Again, our results are unlikely to be confounded by either genetic or non-genetic sources of variation (see above). (1) We control for individual differences in socio-economic status, temporal and geographic differences in living conditions, offspring sex, number of competing siblings and birth order (see Methods); (2) we used a mixed modelling framework, which enables comparisons of the success of different offspring from the same family, when their mother was alive versus when she was dead, while controlling for significant within-family effects ($P = 0.05–0.001$)[20]; (3) further comparison of the reproductive success of offspring who lived in the same village as their post-reproductive mother versus those that lived elsewhere (>20 km away) reveals that those living near to their mother produce more offspring (Fig. 2c). These analyses therefore provide convincing evidence that it is the presence of a post-reproductive mother in itself that causes offspring to reproduce more successfully.

Third, we found that these fitness effects result from the beneficial effects that a living post-reproductive mother has on (1) the key-life-history traits of her offspring; and (2) the survival of her
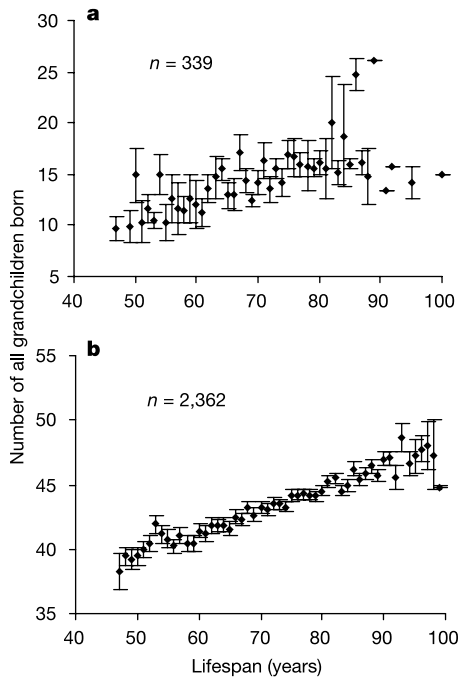

Figure 1 Female lifespan and total number of grandchildren contributed to the following generation in Finland and Canada. **a**, Finland (GLM: $\beta = 0.18 \pm 0.05$, $F_{1,326} = 14.32$, $P = 0.0002$); **b**, Canada (GLM: $\beta = 0.18 \pm 0.05$, $F_{1,2358} = 13.67$, $P = 0.0002$). Graphs show predicted means (± 1 s.e.) after controlling for effects of socio-economic status, and geographic (Finland) and temporal differences in living conditions (Finland and Canada).

Table 1 **Life-history parameters of the pre-modern post-reproductive women studied**

	Finland			Canada		
	Mean	s.d.	Range	Mean	s.d.	Range
Age at first reproduction (years)	25.4	4.6	16–43	22.8	4.3	15–44
Age at last reproduction (years)	39.3	5.0	19–52	38.7	6.1	16–50
Number of offspring born	6.8	3.0	1–18	9.1	3.9	1–22
Number of adult offspring	3.8	2.2	0–12	5.1	2.9	1–16
Number of grandchildren	11.3	10.8	0–53	38.2	28.0	0–157
Longevity (for those surviving to 50)	67.5	10.2	50–100	74.0	10.9	50–100

Number of adult offspring is the number of offspring raised to age 15 in Finland and the number of offspring surviving to marry in Canada. s.d., standard deviation.

grandchildren. In the presence of a living mother, offspring reproduce earlier, with the difference in ages at first reproduction in the presence and absence of a post-reproductive mother being 2.4 yr (Fig. 2d). This effect is evident after controlling for mother's age (or potential age if dead), and hence is not confounded by the possibility that offspring who begin to breed earlier are more likely to have a younger, living mother. Furthermore, in the presence of a living mother, offspring have significantly reduced inter-birth intervals (first three intervals only; Fig. 2e), and increased reproductive tenures (time between first and last childbirth) (GLMM: $F_{1,534} = 4.5$, $P = 0.035$). These effects do not differ according to offspring gender, again indicating that such benefits are common to both sons and daughters.

In addition, grandchildren have significantly higher survival probabilities if their grandmother is alive at their birth (Fig. 2f). However, the significance of this effect depends on both the age of the grandmother and the grandchild. Grandchild survival to adulthood is enhanced by 12% when grandmothers are under 60 at their birth, but by only 3% when grandmothers are over this age. Grandmothers have no effect on the survival probability of their grandchildren between birth and two years of age (GLMM: $\chi_1^2 = 0.08$, $P = 0.78$), but have significant positive effects when offspring are between two and five (GLMM: $\chi_1^2 = 7.09$, $P = 0.008$), and between five and 15 (GLMM: $\chi_1^2 = 4.18$, $P = 0.041$). That offspring survival is unaffected by grandmother presence pre-weaning (birth to two years), when offspring are suckled by their own mother, but is affected thereafter, provides strong evidence that the grandchild survival effect observed is again caused by the grandmother in itself, and not by differences in individual quality, or maternal or environmental conditions.

In conclusion, our results lend strong support for the hypothesis that prolonged female post-reproductive lifespan is adaptive[3,4], to our knowledge revealing for the first time the substantial fitness benefits that females accrue by living beyond reproductive age. However, the results of this study have broader implications regarding the evolution of cooperative breeding[20], menopause[5] and senescence[6]. First, as this study measures the effects of helping on an individual's complete contribution to a following generation, it represents one of the most detailed studies of fitness conducted in a cooperative breeding vertebrate. Second, although grandmother effects alone are suggested to be insufficient to account for the evolution of menopause[5], our results suggest that they can be sufficient to account for the evolution of the substantially prolonged post-reproductive lifespan observed in humans[21].
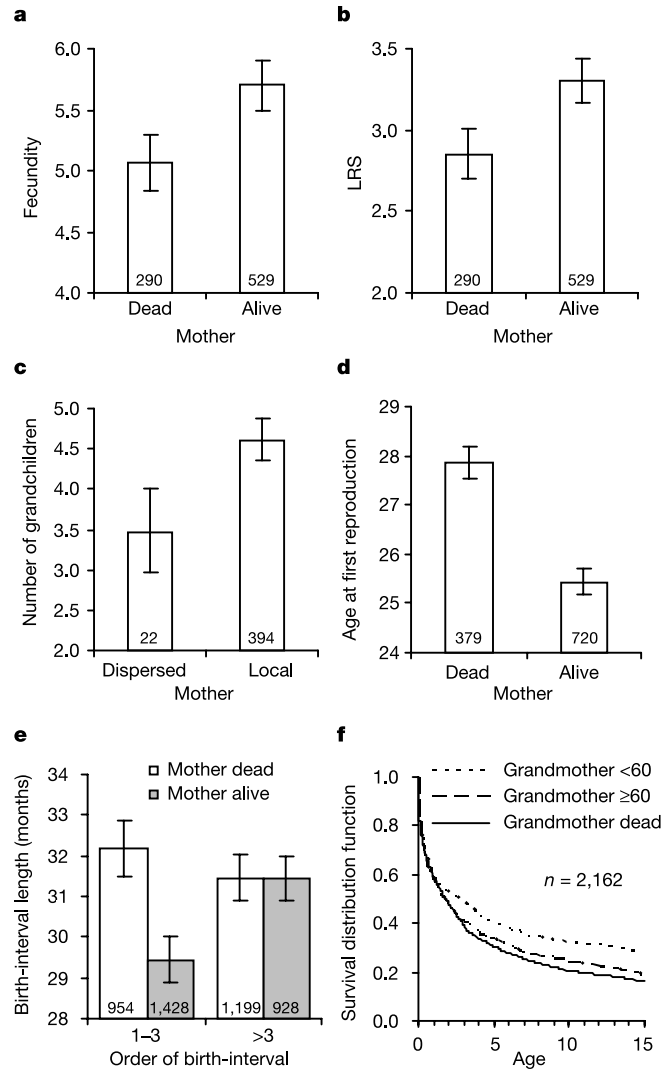

Figure 2 Post-reproductive mother presence (at the time that each offspring began to reproduce) and correlates of each offspring's (son and daughter) fitness and key life-history traits in Finland. **a–c**, Offspring fitness; **d–f**, Key life-history traits. A living post-reproductive mother is associated with: **a**, increased lifetime fecundity of offspring ($F_{1,607} = 9.44$, $P = 0.0022$); **b**, increased lifetime reproductive success of offspring (LRS) ($F_{1,593} = 8.23$, $P = 0.0043$); **c**, increased numbers of grandchildren produced when post-reproductive mother was living in the same village versus elsewhere ($F_{1,293} = 3.98$, $P = 0.047$); **d**, reduced ages at first reproduction of offspring ($F_{1,814} = 52.65$, $P < 0.0001$); **e**, reduced first three inter-birth intervals ($F_{1,977} = 6.45$, $P = 0.011$), but not those thereafter ($F_{1,711} = 0.84$, $P = 0.36$); and **f**, increased survival of grandchildren until age 15 (log-rank test: $\chi_2^2 = 19.78$, $P < 0.0001$). Panels **a–e** show predicted means (± 1 s.e.) from GLMMs after controlling for effects of offspring socio-economic status, geographic and temporal differences in living conditions, birth order, sex, number of siblings, mother's age and repeated measures of mother, where appropriate. Panel **f** shows Kaplan–Meier survival curves for grandchildren depending on the age and presence of a post-reproductive grandmother.
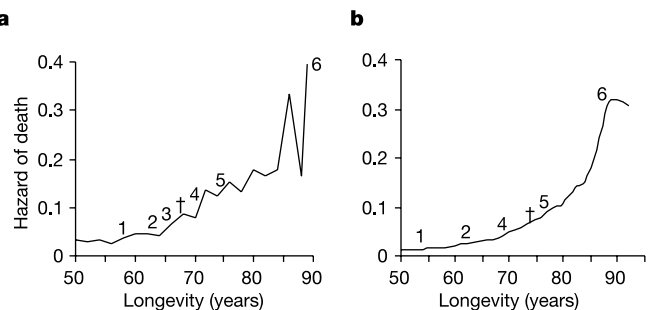

Figure 3 Age-specific hazards of death for post-reproductive mothers and the timing of different life-history events of their offspring and grandchildren. **a**, In Finland; **b**, in Canada. Dagger indicates average age at death post-reproduction. 1, average age when offspring have first offspring; 2, average age when offspring have their fourth offspring; 3, maximum age when grandchild survival can be significantly improved; 4, average age when offspring produce their last offspring; 5, average age when last offspring have their last offspring; 6, average age when 50% of all grandchildren start producing great-grandchildren. Note that female mortality rates are relatively low when most increments to fitness can be gained through helping offspring but high when fitness could be gained through helping grandchildren, to whom they are half as related.

Finally, our results not only show that selection may act to increase post-reproductive longevity, but also indicate at what age such selection might be expected to wane (Fig. 3). The mean lifespan of post-reproductive women from Finland and Canada was 68 and 74 yr respectively, which is close to the maximum age at which women can gain fitness in the two countries and the age at which offspring cease reproducing. That mortality rates accelerate from the time that offspring begin to terminate reproduction (Fig. 3) suggests that selection for post-reproductive longevity is deferred only until a woman's own offspring finish reproducing and can become the future generation of helpers. □

Methods

The Finnish women

The Finnish data were collected using historical population registers. The Lutheran Church has been obliged by law to submit accurate census registers of all births, marriages and deaths in each parish in the country since the seventeenth century[22], making the Finnish church registers one of the most reliable sources of demographic data on historical humans[23]. Our data contain two complete generations of pedigree data for 537 reproductive women from five farming/fishing communities, varying substantially in their ecological conditions[19].

We recorded the survival and lifetime reproductive details (Table 1) of 537 women born during the years 1702–1823 ($n = 3,629$ offspring born, 1,186 marrying and reproducing in the population, 6,002 grandchildren born). The study period therefore ended before industrialism and more liberal economics, healthcare improvements and modern birth-control methods influenced standard of living, survival and reproduction[24]. The occupation of each woman's husband (at the time the children were born, for example, priest, landowner, tenant farmer, servant, and so on) allowed us to rank the socio-economic status (rich, wealthy, average or poor) of each family, which is a correlate of resources available[25].

The Canadian women

The Canadian data were obtained using the BALSAC population register based at the University of Quebec, Chicoutimi[26]. The register, internationally recognized for its quality, contains demographic and genealogical information collected from baptism, marriage and death certificates from all individuals in the Saguenay region of Quebec during the nineteenth and twentieth centuries[26]. The population is mostly French-speaking and Catholic, and until the beginning of the twentieth century, mainly agricultural. This study includes all women ($n = 3,290$) born in the Saguenay region from 1850 to 1879 (inclusive) who got married in the region and had at least one offspring who also married in the region ($n = 29,895$ children born, 16,618 marrying and reproducing in the population, 100,074 grandchildren born; Table 1; ref. 27). Detailed data on the reproductive history of each woman, other than the number, survival and subsequent reproductive success of their offspring, were unavailable to us, enabling us to conduct the analyses shown in Fig. 2 for Finns only.

Statistical analyses

Statistical analyses were conducted using SAS (SAS Institute Inc., release 8.02, 1999–2001). Relationships between a female's post-reproductive lifespan and the number of grandchildren born to her were analysed using general linear models, in which number of grandchildren born was fitted as the response term to a normal error structure and female longevity was fitted as the main fixed effect. In these analyses, we restricted our data to include only those women who lived past menopause ($n = 339$ for Finland and $n = 2,362$ for Canada)—the age at which 99% of females had finished reproducing ($\sim$49 yr). The analyses control for socio-economic status and geographic differences in living conditions (population)[19] in Finland and temporal differences in living conditions (birth cohort in both countries).

Effects of post-reproductive mother presence on fitness correlates (Fig. 2a–c) and underlying life-history traits of offspring (Fig. 2d, e) were analysed using GLMMs, which allow both fixed and random terms to be fitted to a model, with random terms controlling for repeated measures within mother[28] (and grandmother in Fig. 2e). Satterthwaite's formula[29] was used to approximate the denominator degrees of freedom of each fixed effect. In these analyses, the response terms were fitted to a normal error structure and mother presence/absence was fitted as the main fixed effect. We defined presence/absence as whether a post-reproductive mother was alive versus dead (Fig. 2a, b, d), or living in the same village versus elsewhere (Fig. 2c), when each offspring started reproducing. In Fig. 2e, the presence of a post-reproductive (grand)mother was defined as whether or not she was alive when the grandchild was born. We controlled for confounding effects (where appropriate) of: mother's age, offspring's socio-economic status, population[19], birth cohort, sex, birth order, the number of competing siblings, the survival status of the directly previous child born in the family and the repeated measures of the same mother.

The effect of post-reproductive grandmother presence on grandchild survival was analysed using log-rank test and survivorship functions estimated using the Kaplan–Meier method. To investigate the period when the presence of the post-reproductive woman was most important for the survival of grandchildren, GLMMs were performed, where the response term for whether or not the grandchild survived to a certain age was fitted to a binomial error structure and logit-link function. Analyses controlled for socio-economic status of a parent, population, birth cohort and order, sex of grandchildren and repeated measures within parents.

In all models, significant model terms were determined using the backward elimination technique, and subsequently checked using the forward technique. The residuals of all models were normally distributed (GLMs, GLMMs) and the variances were equal (GLM: Levene's test $P > 0.05$). All statistics are from the GLM unless otherwise indicated.

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