

Selection on male longevity in a monogamous human population: late-life survival brings no additional grandchildren

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Abstract

Humans are exceptionally long-lived for mammals of their size. In men, lifespan is hypothesized to evolve from benefits of reproduction throughout adult life. We use multi-generational data from pre-industrial Finland, where remarriage was possible only after spousal death, to test selection pressures on male longevity in four monogamous populations. Men showed several behaviours consistent with attempting to accrue direct fitness throughout adult life and sired more children in their lifetimes if they lost their first wife and remarried. However, remarriage did not increase grandchild production because it compromised the success of motherless first-marriage offspring. Overall, grandchild production was not improved by living beyond 51 years and was reduced by living beyond 65. Our results highlight the importance of using grandchild production to understand selection on human life-history traits. We conclude that selection for (or enforcement of) lifetime monogamy will select for earlier reproductive investment and against increased lifespan in men.

Introduction

Evolutionary theory proposes that, in iteroparous organisms, individual fitness will be maximized through optimizing the trade-off between investment in reproduction and self-maintenance (Williams, 1966; Stearns, 1992). It therefore follows that hypotheses proposed to account for the evolution of senescence should predict a strong degree of synchrony between the rates of senescence in reproductive and somatic systems (Williams, 1957; Hamilton, 1966). Humans provide an interesting case because women show a radical de-coupling of senescence in the two systems, leading to an unparalleled proportion of life being spent post-reproductive. By contrast, men show the more classic senescence patterns of synchronous germ and soma deterioration. Under-

standing sex differences in rates of senescence in reproduction and survival, both key life-history traits, will provide an important insight into how differing selection pressures can mould rates of senescence and ultimate longevity within a species (Williams, 1957; Charlesworth, 2001; Bonduriansky *et al.*, 2008).

Human life-expectancy has increased significantly with advancements in medicine and sanitation, but such advancements fail to account fully for our exceptional longevity (Hawkes *et al.*, 1998; Gurven & Kaplan, 2007). For example, in hunter-gatherers and/or pastoralists living in pre-industrial mortality conditions, 60–80% of individuals that survive childhood reach 45 years, and survivors to 45 are expected to live for at least another 20 years. This contrasts with the lifespan of our closest primate relatives, which seldom exceeds 50 years even in zoos where individuals have access to health care (Ricklefs, 2008). Empirical studies testing the evolutionary hypotheses of human longevity are principally conducted in women, whose menopause and post-reproductive lifespan can be partly explained by the

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fitness benefits of providing prolonged care to children and grand-children (Williams, 1957; Hawkes *et al.*, 1998; Lahdenperä *et al.*, 2004, 2011; Sear & Mace, 2008). However, men live almost as long as women, but the evolutionary explanations for male longevity have primarily received theoretical rather than empirical attention (Kaplan *et al.*, 2000; Marlowe, 2000; Tuljapurkar *et al.*, 2007; Bonduriansky *et al.*, 2008).

The predominant explanation for the evolution of male lifespan in humans is here called the Continued Reproduction Hypothesis, formulated by Williams (1957). This hypothesis proposes that male lifespan is a function of age-specific selection pressures on reproductive success, with men living to an age when their ability to gain direct fitness through reproduction begins to wane. Positive selection on male lifespan is suggested to be strong in humans because resource acquisition has significant effects on fitness correlates and is age-dependent (Kaplan *et al.*, 2000; Marlowe, 2000). Indeed, the benefits of continued reproduction for men late in life have been suggested to be strong enough to drive a significant increase in human lifespan in both sexes (Marlowe, 2000; Tuljapurkar *et al.*, 2007). Empirical evidence shows that the number of wives (either concurrently or cumulatively) can increase with male age and men who reproduce late in life (e.g. into their 60s) commonly sire more children in their lifetimes (Dupâquier *et al.*, 1981; Boone, 1986; Low, 1990; Paget & Timaeus, 1994; Forsberg *et al.*, 1995; Käär *et al.*, 1998; Marlowe, 2000). However, studies have yet to test whether increasing male lifespan correlates positively with grandchild production, a more appropriate measure of evolutionary fitness incorporating both the quantity and quality of offspring produced (Stearns *et al.*, 2010). In addition, selection on male lifespan might be expected to differ between societies where men tend to remain with a single woman throughout their lives and those where multiple partners are possible and common.

Our aim is to provide the first test of both the short- and long-term 'fitness' consequences of remarriage for men living under enforced monogamy. Monogamy is practised by the majority of the world's population, either because it is enforced (socially or religiously) or because men have insufficient resources to support multiple wives (Mealey, 2000; Pollet & Nettle, 2009). We use a three-generational life-history dataset on four pre-industrial Finnish populations living in conditions of natural fertility and mortality (1714–1908); wherein monogamy was strictly enforced by the Lutheran church and remarriage was permitted only following spousal death (Moring, 2002). We examine whether (i) following spousal death, men show remarriage patterns consistent with attempting to increase fitness in late-life. We then investigate the consequences of such patterns for (ii) late-life reproductive schedules, and (iii) lifetime breeding success and offspring survival. Finally, we investigate (iv) the association between male marriage pattern and

lifespan on lifetime grandchild production, one of the strongest correlates of evolutionary fitness readily available (Stearns *et al.*, 2010). We acknowledge that many of our results are based on an assumption of paternity. However, given the serious punishments dealt to men accused of adultery in the study society (Sundin, 1992), it is unlikely that it would have exceeded the current world-wide mean of 3% for populations with high paternity certainty (Anderson, 2006), and such low levels of extra-pair paternity are insufficient to bias our results qualitatively.

Methods

The data were collected using historical Finnish church records. The Lutheran Church has been obliged to submit accurate registers of all births, inter-parish movements, marriages and deaths in the country since the 17th century (Luther, 1993). From these records, we compiled life-long marriage and reproductive details of a random sample of 484 men born between 1714 and 1839 (mean = 1775, SD = 25 years) in four geographically distinct farming/fishing communities. These men sired 3177 offspring in their lifetimes between 1741 and 1882 (mean = 1808; SD = 26 years), which led to 6717 grandchildren born between 1766 and 1908 (mean = 1842, SD = 25 years). Thus, all data were collected between 1714 and 1908; hence preceding the onset of fertility declines, significant improvements to standards of living and the demographic transition which arose primarily during the 20th century in Finland (Soininen, 1974; Korpelainen, 2003). The lifetime breeding success was known for all 484 men and for 97% of them we recorded the survivorship to adulthood (age 15 years) of all of their offspring. In addition, because the Church also maintained migration registers that allow the tracking of individuals who dispersed among parishes, we were able to determine the lifetime breeding success of almost all children born, irrespective of whether they remained in their natal parish throughout their lives or dispersed to a new one. Knowledge of the lifetime breeding success of children born to the first generation sample of men, even if they dispersed, meant that we are able to use the total number of grandchildren ever produced as our approximation of evolutionary fitness (Stearns *et al.*, 2010).

All analyses were conducted in Genstat Release 11 (VSN International Ltd, Hemel Hempstead, UK). Investigations of male marriage patterns and their consequences for male reproductive success and grandchild production were principally investigated using general and generalized linear models (GLM) following F and χ^2 distributions, respectively. All GLM analyses control for potential ecological differences among men by fitting birth cohort, study population and socio-economic status of first generation men as co-factors. Birth cohort was considered in approximately 20-year blocks (1714–1750, 1751–1770, 1771–1790, 1791–1839; Lahdenperä *et al.*,

2004, 2007). The first and last block included more than 20 years of data because prohibitively few individuals were born before 1730 ($N = 16$) and after 1810 ($N = 15$) for additional categorizations within these birth years. Additionally, the results were qualitatively similar when birth year was considered as an ordinal variable or as a factor in 50-year blocks (results not shown). Study populations varied in food quality and predictability (Lummaa *et al.*, 1998, 2001) and socio-economic status was determined using male occupation (Lahdenperä *et al.*, 2007; Pettay *et al.*, 2007). Unless otherwise stated, all GLM analyses also control for any inherent differences in male (and first wife) quality; captured by variation in male age at first reproduction (AFR), the age difference (and direction of difference) between the man and his first wife as well as their respective lifespans (van de Pol & Verhulst, 2006). Age differences were fitted instead of both male and female AFR to avert problems of collinearity with AFR within the same pair. Quadratic terms were fitted to control for nonlinear effects where appropriate, but only presented if significant. Interactions between marriage status (the primary term of interest in all GLM analyses, see below), and both study population and socio-economic status were fitted in all models to elucidate the generality of the findings across populations differing in ecology and life history, as well as across individuals varying in resource availability. The statistical significance of model terms was determined using influences on model deviance and log likelihood ratio tests (Zar, 2010).

Remarriage patterns

We conducted three analyses to address whether or not men showed behaviours consistent with attempting to increase their lifetime fitness following spousal death. These include the probability that men vs. women remarry following spousal loss, whether or not men who lose their first wife late in life attempt to secure a fertile-aged woman as a subsequent wife and the factors that affect the probability that men are able to obtain such a wife.

To investigate whether men are more likely than women to re-marry following spousal death (and thus maintain the potential for breeding), we documented remarriage probabilities for men and women using a GLM in which remarriage status (0/1) following spousal death was fitted as the response term to a binomial error structure with logit link function and where 1 was fitted as the binomial denominator and dispersion parameter. Only those who lost their first spouse were included ($N = 224$ men and 250 women). Birth cohort, study population and socio-economic status were fitted as potential ecological confounding terms. Individual sex and the age at which spouses were lost were fitted as the primary terms of interest. It is unlikely that men and women differ inherently in quality, and so we did not

control for AFR, differences in AFR or lifespan in this analysis.

We investigate whether men who lost their first wife after the age of 40 and subsequently remarried, preferentially did so with women under 40 years given the availability of such women under this age in the population ($N = 62$ men). Our rationale here is that if men show preferences for enhancing their fitness through re-marriage, they should choose women under the age by which the average woman (and man outlived by their first wife) has ceased reproduction (i.e. approximately 40 years). The probability that widowed men are able to secure an unmarried woman under the age of 40 will obviously be influenced by the availability of such women in the population. We calculated the annual availability of unmarried women under and over the age of 40 within each of the four parishes by counting the number of unmarried women aged 19 to 39 years and those 40 and above. Our calculations reveal that in each year of each parish, on average, 33% of unmarried women in our populations are under the age of 40, whereas 67% are over this age. Using these expected values, we then used a contingency table to determine whether men who lost their first wife after the age of 40 showed preferences for marrying women under the age of 40.

Finally, we investigate the factors associated with a man's ability to secure a subsequent wife under the age of 40 years, when he lost his former wife over the age of 40 ($N = 62$ men). The probability that a subsequent wife was obtained under the age of 40 was analysed using a GLM with binomial error structure and logit link function in which both the binomial denominator and dispersion parameter were set at 1. Explanatory terms of interest included all correlates of ecological and inherent differences outlined above, as well as the number of offspring delivered in the first marriage and the age at which men lost their first spouse and this age squared.

Reproductive patterns

Preference for women under the age of 40 as subsequent wives will only be beneficial if men maintain fertility into late life and are able to reproduce for longer through remarriage. First, we investigated the effects of male age at spouse loss on the probability that he would reproduce in a subsequent marriage. All men who chose a new spouse under the age of 40 years were included irrespective of their own age ($N = 96$). The probability that men would sire a child in a subsequent marriage was investigated by fitting male reproductive status after remarriage (0/1) as a response term in a GLM with binomial error structure and logit link function, in which 1 was set as the binomial denominator and the dispersion parameter. Male age and male age squared were fitted as the primary terms of interest. All ecological correlates

were controlled as was the number of years for which men survived following remarriage and spousal age. Inherent differences (AFR and ultimate lifespan) were not necessary to consider in this analysis since there is no reason to suspect that these should relate to male fertility late in life.

We then investigated whether male marriage patterns might influence the age at which men last reproduce (ALR). Men were categorized into four marriage classes: 'married' (men who were outlived by their first spouse); 'single' (men who lost their first wife but did not remarry); 'remarried' (men who remarried but did not rebreed with their new wife); and 'rebred' (men who both remarried and rebred). We investigated the effect of marriage status on the age at which men last reproduced in a GLM with normal error structure ($N = 484$ men). Potential confounders included all ecological and inherent differences among men. Marriage status was fitted as the primary fixed effect of interest.

Lifetime breeding success and offspring survival

Lifetime reproductive success is a composite of the lifetime breeding success (number of children born) and the proportion of those children that survive to adulthood (age 15 years; Lahdenperä *et al.*, 2004, 2007). Using the marriage categorizations outlined above, we first investigated whether men were able to increase their lifetime breeding success by rebreeding with a new wife following the loss of their first one. To do so, we used a GLM in which the lifetime number of children sired by men was fitted as the response term with a normal error structure ($N = 484$ men). Marriage status was fitted as the primary fixed effect of interest and potential confounders included all measures of ecological and inherent differences among men (see above).

Marriage patterns are likely to have significant consequences for offspring survival. Men who remained married throughout life are likely to have high child survival because of maternal presence, whereas, at the other extreme, men who remarry and rebreed might compromise the survival of existing offspring because of preferential treatment of new offspring (Volland, 1988; Borgerhoff Mulder, 1998; Jankowiak & Diderich, 2000; Pollet, 2007). We examine the effect of marriage patterns on the proportion of offspring surviving to age 15 from 480 first marriages for which full offspring survival data were known (four men were dropped because the fate of some of their offspring were unknown). The number of children surviving was fitted as the response term in a GLM with binomial error structure and logit link function in which the number of children born in the first marriage was fitted as the binomial denominator. Marriage status was fitted as the primary fixed effect of interest. We included all

potential correlates of ecological and inherent differences among men as additional explanatory terms, and weighted the analysis by the number of children born in the first marriage to ensure homogeneity of variance structures.

Grandchild production: an estimate of fitness

Finally, we investigated whether enforced monogamy influences estimates of age-specific fitness by examining the association between both marriage status and male lifespan with total grandchild production. The total number of grandchildren arising from a given father (irrespective of whether he was alive or dead at the time of their production) was used where known with precision, including most of those produced in other parishes following dispersal ($N = 468$ men). The total number of grandchildren was fitted as the response term to a GLM with normal error structure following 1 + logarithm transformation. Marriage status, male lifespan and male lifespan squared were fitted as the primary terms of interest. All potential correlates of ecological and inherent differences among men were included as potential confounders.

Results

Remarriage patterns

On average, Finnish men who were married survived to 59 years (± 14 SD, $N = 484$), those who reached 40 survived to 62 (± 12 SD, $N = 424$), and the maximum lifespan was 94 (Fig. 1a). Men showed a number of behaviours consistent with attempting to accrue direct fitness throughout adult life. Compared with women, men were three times more likely to remarry following the death of a spouse on average (59% vs. 18%; main sex effect: GLM; $\chi^2_1 = 54.85$, $P < 0.001$; Fig. 1b). This difference arose because, unlike women, men continued to show strong tendencies to remarry late in life (sex \times age interaction: GLM; $\chi^2_1 = 7.11$, $P = 0.008$). Birth cohort, study population and socio-economic status did not significantly influence remarriage patterns (cohort: $\chi^2_3 = 1.34$, $P = 0.26$; population: $\chi^2_3 = 3.96$, $P = 0.27$; socio-economic status: $\chi^2_2 = 4.36$, $P = 0.11$).

When men remarried, they tended to marry younger women. On average, men were less than a year older than their first wife (mean age difference \pm SD = 0.03 ± 7 years, $N = 424$ for which the age of both men and women were known), but 10 years older than their subsequent wife (10.4 ± 11 , $N = 119$) (Student's *t*-test; $T_{1,21} = 12.43$, $P < 0.0001$). This change suggests that men prefer fertile women as subsequent wives. In accordance, men over the age of 40 were significantly more likely to choose a subsequent wife under the age of 40, given the availability of unmarried women under this age in the population (Contingency table; $\chi^2_1 = 68.95$, $P < 0.0001$;

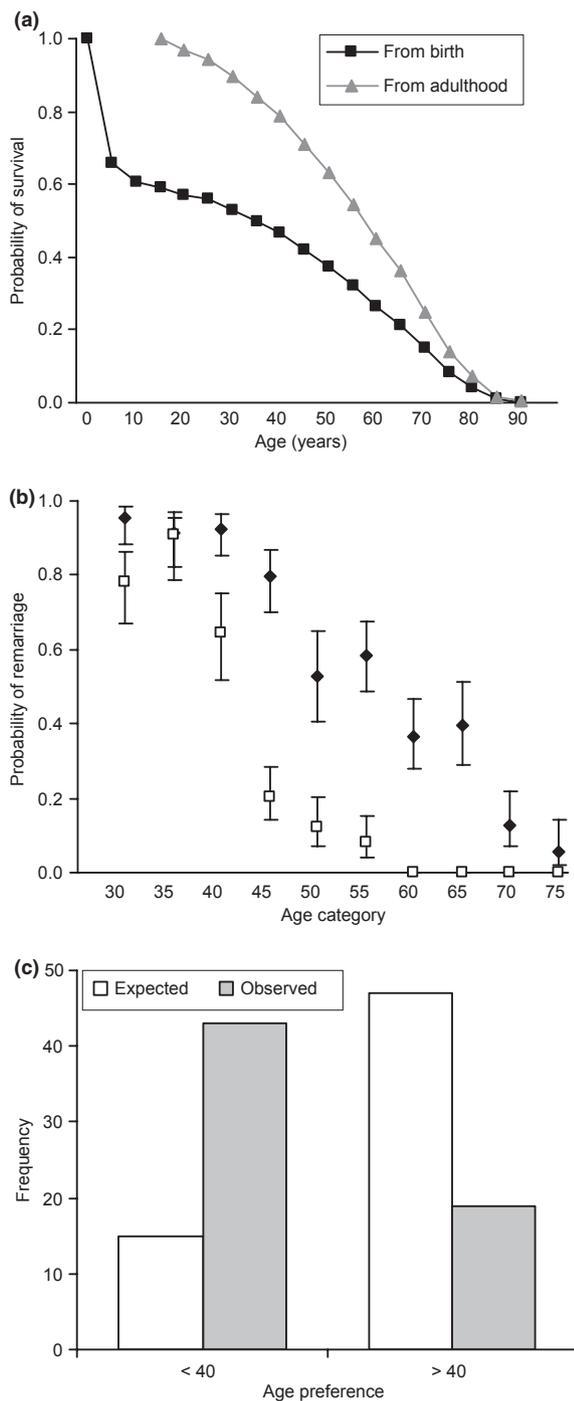


Fig. 1 Survival and fitness maximizing behaviours. (a) Male age-specific survival probability from birth ($N = 1652$) and from adulthood (age 15, $N = 954$). Survival curves were estimated using the Kaplan–Meier procedure. (b) A man's probability of remarriage declined linearly with age (closed diamonds), whereas a woman's probability plummeted around age 40 (open squares), generating a significant interaction between sex and age on remarriage probability. (c) Men over the age of 40 showed a significant preference for remarriage women under the age of 40, given the availability of such women in the population.

Fig. 1c). Marrying women under the age of 40 is significant because 92% ($N = 90$) vs. 40% ($N = 25$) of men who remarried women under vs. over 40 years, respectively, sired subsequent offspring (Goodness of fit; $\chi^2_1 = 34.5$, $P < 0.001$).

The mean age at which men over the age of 40 years remarried women under 40 years was 51 years (range = 41–77, SD 7 years) and the mean age of the women they married was 31 years (range = 19–39; SD 4 years). The probability that men remarried women under the age of 40 was related to their own age, with the probability decreasing linearly as they aged beyond 40 themselves (GLM; linear effect $\chi^2_1 = 8.41$, $P = 0.004$, estimate \pm SE = -0.11 ± 0.039 , $R^2 = 11\%$). We found no evidence to suggest that the probability of securing a second wife under the age of 40 years was influenced by ecological differences among men (cohort $\chi^2_3 = 1.36$, $P = 0.25$; population $\chi^2_2 = 0.85$, $P = 0.47$; socio-economic status $\chi^2_3 = 2.75$, $P = 0.25$), inherent differences among men (AFR $\chi^2_1 = 0.02$, $P = 0.89$; age difference with first wife $\chi^2_1 = 0.09$, $P = 0.77$; lifespan $\chi^2_1 = 1.72$, $P = 0.18$) or the number of children sired in the first marriage ($\chi^2_3 = 2.75$, $P = 0.25$).

Reproductive patterns

The eldest new father in our population was 77 years old. We found no effects of the following on the probability that men married to women under the age of 40 would reproduce: cohort (GLM; $\chi^2_3 = 2.23$, $P = 0.53$), population ($\chi^2_3 = 1.99$, $P = 0.58$), socio-economic status ($\chi^2_2 = 0.01$, $P = 0.99$); or the number of years for which men survived following remarriage ($\chi^2_2 = 1.73$, $P = 0.19$). Unsurprisingly, a man's probability of siring offspring in a subsequent marriage decreased with increasing spousal age ($\chi^2_1 = 4.64$, $P = 0.031$; estimate \pm SE = -0.18 ± 0.085) as well as his personal age (GLM: $\chi^2_1 = 12.0$, $P < 0.001$; Fig. 2a). Nevertheless, the negative effect of male age on reproductive probability was modest until at least the age of 60: men of 60 years old had an 80% chance of siring offspring if currently married to a woman under 40.

The ALR of men varied across birth cohorts and increased with increasing socio-economic status, AFR, lifespan, first wife's lifespan, and positive age differences with their first wife (Table 1). After controlling for these effects, we found that ALR varied significantly according to marriage status (GLM: $F_{3,453} = 77.50$, $P < 0.0001$; Fig. 2b). Men who rebred with a subsequent spouse were able to sire offspring 12–15 years (30–40%) later than those who remained married to their first wife throughout life, lost their first wife and did not remarry or lost their first wife and remarried but did not rebreed. This result did not differ across populations or among men in different socio-economic stratum (i.e. interaction terms with marriage status were nonsignificant) (Table 1).

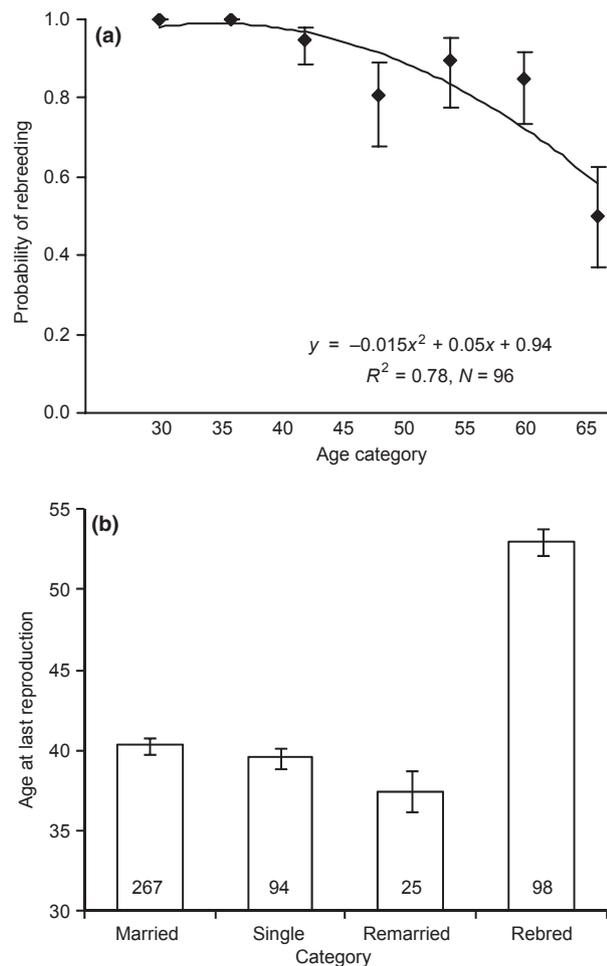


Fig. 2 Male reproductive schedules according to marriage status. (a) The probability that men (married to woman under 40) produced offspring declined with increasing age, but men over the age of 65 still had a > 50% probability of siring offspring, indicating that they maintained fertility late in life. (b) Men from the rebred category bred for the last time at significantly older ages than men from the other three categories. ‘Married’ refers to men who were outlived by their first spouse, whereas ‘single’, ‘remarried’ and ‘rebred’ refer to men who outlived their first wife and remained single, remarried but did not rebrand and remarried and rebred, respectively. Figures show means (± 1 SE) predicted from the model after controlling for significant confounders indicated in Methods/Results (a) and Table 1 (b). Values in bars of b indicate numbers of men in each category.

Lifetime breeding success and offspring survival

The lifetime breeding success of men (number of offspring sired over lifetime) averaged 6.4 offspring (range = 0–18, SD = 3.2). Lifetime breeding success varied across birth cohorts and study populations, declined with increasing male AFR, and increased when socio-economic status was high, men were older than their first wife and with increasing lifespan up to a point, after

Table 1 Factors affecting male age at last reproduction. SE, standard error; Vr (%), % of variance explained by a given term; AFR, age at first reproduction. Age difference, difference in age between husband and first wife, with a positive effect denoting a benefit when males are older than females; M. status, marriage status; SES, socio-economic status; SP, study population.

Term	Estimate \pm SE	F	d.f.	P-value	Vr (%)
Birth cohort		3.70	3,453	0.012	1
Study population		1.65	1,450	0.18	< 1
SES	\uparrow wealth	3.62	2,452	0.028	1
Male AFR	0.20 ± 0.048	17.37	1,451	< 0.0001	2
Male lifespan	0.21 ± 0.024	72.87	1,451	< 0.0001	8
Age difference	0.46 ± 0.051	82.61	1,451	< 0.0001	9
1st wife lifespan	0.10 ± 0.028	13.01	1,451	< 0.001	2
Marriage status	Fig. 2b	77.50	3,453	< 0.0001	23
M. status \times SP		0.64	9,447	0.76	0
M. status \times SES		1.90	6,450	0.080	< 1
Constant	46.14 ± 3.72				

Table 2 Effects of marriage status on male lifetime breeding success (number of children born). See Table 1 legend for key.

Term	Estimate \pm SE	F	d.f.	P-value	Vr (%)
Birth cohort		3.08	3,469	0.027	1
Study population		10.26	1,469	< 0.001	3
SES	\uparrow wealth	3.70	2,468	0.025	1
Male AFR	-0.25 ± 0.019	170.46	1,467	< 0.0001	19
Age difference	0.14 ± 0.018	62.75	1,467	< 0.0001	7
Male lifespan	0.32 ± 0.050	72.09	1,468	< 0.0001	8
Male lifespan ²	-0.0022 ± 0.00044	24.68	1,467	< 0.0001	3
1st wife lifespan	0.0090 ± 0.011	0.73	1,456	0.39	0
Marriage status	Fig. 3a	18.28	3,469	< 0.0001	6
M. status \times SP		0.55	9,466	0.84	0
M. status \times SES		1.79	6,455	0.10	0
Constant	6.42 ± 0.14				

AFR, age at first reproduction; M. status, marriage status; SES, socio-economic status; SP, study population.

which it began to decline (Table 2). After controlling for significant effects of the above terms, we found that the number of offspring sired varied with marriage patterns (GLM; $F_{3,469} = 18.28$, $P < 0.0001$), but was not modified by either population or socio-economic circumstances (i.e. interaction terms with marriage status were non-significant) (Table 2). Men who rebred in their second marriage had a 26–49% increase in lifetime breeding success compared with men who were outlived by their first wife, men who outlived their first wife but thereafter remained single or men who did not rebrand with a subsequent wife (Fig. 3a).

On average, 60% of offspring from first marriages survived to adulthood at age 15 (SD = 27%). The proportion of offspring from first marriages reaching age 15 varied across populations and increased with socio-economic status and male lifespan (Table 3). After controlling for these effects, we found that the proportion

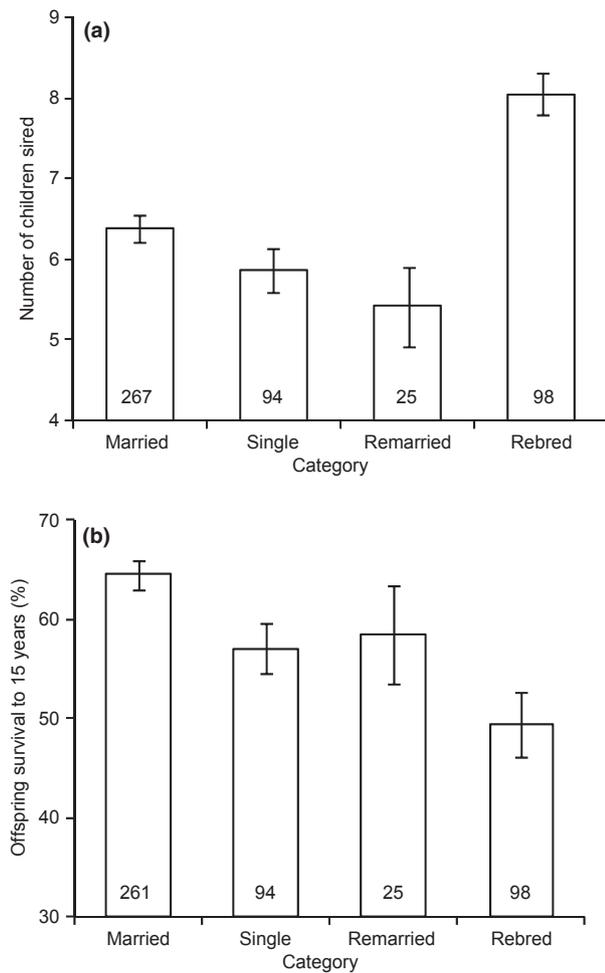


Fig. 3 Reproductive consequences of marriage behaviour. (a) Men who rebred sired more offspring than those in other categories (see Table 2). (b) Offspring from first marriages had reduced survival when their father rebred with a subsequent wife (see Table 3). Marriage status on the x-axis of each figure is as defined in Fig 2 legend. Figures show means (± 1 SE) predicted by the models after controlling for confounders illustrated in Tables 2 (a) and 3 (b). Values in bars indicate numbers of men.

of offspring surviving to age 15 varied across marriage status categories (GLM: $\chi^2_1 = 6.12$, $P < 0.001$), and this was not modified by population or socio-economic status (i.e. interaction terms with marriage status were non-significant) (Table 3). The proportion of offspring reaching 15 years from first marriages decreased by 13–23% in those men who rebred with a subsequent wife compared with those who maintained their first wife throughout their life or who lost their first wife but either remained single or remarried without rebreeding (Fig. 3b).

Grandchild production: an estimate of fitness

The number of grandchildren descending from first generation men averaged 14.2 (range = 0–69;

Table 3 Effect of marriage status on offspring survival from the first wife. See Table 1 for key.

Term	Estimate \pm SE	χ^2	d.f.	P-value	Vr (%)
Birth cohort		0.58	3	0.63	0
Study parish		5.66	3	< 0.001	3
SES	\uparrow wealth	5.71	2	0.004	2
Male AFR	-0.011 ± 0.011	0.97	1	0.32	0
Age difference	0.062 ± 0.082	0.58	1	0.45	0
Male lifespan	0.016 ± 0.0042	14.34	1	< 0.001	3
1st wife lifespan	0.0047 ± 0.0041	1.30	1	0.25	0
Marriage status	Fig. 3b	6.12	3	< 0.001	4
M. status \times SP		0.66	9	0.74	0
M. status \times SES		0.80	6	0.57	0
Constant	0.41 ± 0.049				

AFR, age at first reproduction; M. status, marriage status; SES, socio-economic status; SP, study population.

Table 4 Marriage status, male lifespan and grandchild production. See Table 1 for key.

Term	Estimate \pm SE	F	d.f.	P-value	Vr (%)
Birth cohort		0.54	3,439	0.66	0
Study population		16.58	3,442	< 0.0001	7
SES	\uparrow wealth	13.66	2,441	< 0.001	4
Male AFR	-0.046 ± 0.0073	40.42	1,440	< 0.0001	7
Age difference	0.038 ± 0.0065	34.62	1,440	< 0.0001	6
1st wife lifespan	0.0069 ± 0.0026	7.21	1,440	0.008	2
Male lifespan	0.078 ± 0.020	23.21	1,441	< 0.0001	4
Male lifespan ²	-0.00055 ± 0.00017	10.33	1,440	0.001	3
Marriage status	Fig. 4a	1.02	3,439	0.38	0
M. status \times SP		0.40	9,436	0.94	0
M. status \times SES		1.80	6,436	0.097	0
Constant	8.78 ± 0.49				

AFR, age at first reproduction; M. status, marriage status; SES, socio-economic status; SP, study population.

SD = 12.1). Grandchild numbers varied across study populations and were greater among men from wealthy social classes as well as those who began reproducing early in life, were older than their first wife at marriage and whose first wife had high survival (Table 4). After controlling for such effects we found no evidence to suggest that marriage patterns influenced total grandchild production (GLM; $F_{3,439} = 1.02$, $P = 0.38$; Fig. 4a). In addition, although men continued to increase grandchild production towards the age at which their first wife would reach menopause (GLM: lifespan linear effect, $F_{1,441} = 23.21$, $P < 0.001$), those who survived into late life suffered a reduction in grandchild production (lifespan quadratic effect $F_{1,440} = 10.33$, $P = 0.001$) (Fig 4b). Subsequent analyses using restrictions on the male lifespans included in the analyses revealed a positive relationship between lifespan and grandchild production up to the age of 51 years, but not beyond, as well as a negative relationship from the age of 65 years. These results indicate that men fail to increase grandchild

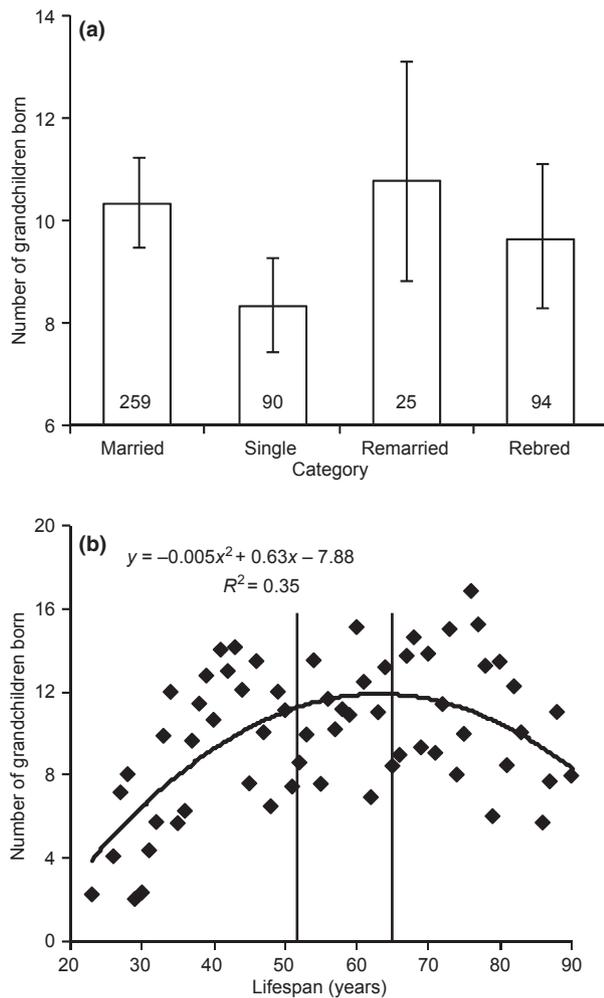


Fig. 4 Male reproductive behaviour, lifespan and grandchild production. (a) We found no evidence to suggest that remarriage offered fitness benefits in terms of grandchild production (see Table 4). (b) Grandchild production showed a significant quadratic relationship with male lifespan (see Table 4). (a) Means (± 1 SE) predicted by the models after controlling for confounders illustrated in Table 4. Values in bars of (a) indicate numbers of men. In (b) the first and second vertical lines represent the ages after which further survival fails to increment grandchild production (51 years) and is associated with reductions (65 years), respectively.

production by surviving beyond 51 years and begin to be associated with negative effects on grandchild production from the age of 65 years.

Discussion

In the strict monogamous society of pre-industrial Finland, individuals were only permitted to remarry following the death of their spouse. Following spousal death, men appeared to employ several tactics aimed at increasing the probability of gaining fitness late in life through direct reproduction. These included having a

greater probability than women of remarriage following spousal death, particularly late in life, and showing a preference for premenopausal women. As a consequence of both of these remarriage patterns and of the retention of fertility late in life, men who lost their first wife and rebred with a subsequent wife extended their reproductive lifespan and sired significantly more children in their lifetimes. Nevertheless, the survival of children from the first marriage was compromised by breeding with a subsequent wife and consequently men were unable to gain a fitness advantage from reproducing with a new wife, on average. Moreover, survival beyond the age of 51 years did not improve grandchild production, and survival beyond 65 appeared to be associated with reduced grandchild production, suggesting no (or negative) fitness consequences of living beyond 51 years.

Marriage patterns and their effects on reproductive schedules, success and ultimate measures of fitness could be confounded by differences in the ecologies experienced by men and/or inherent differences in their (or their wife's) quality. However, we think this is unlikely in this study. First, in all analyses we controlled for ecological differences arising from being born in a given cohort, population and socio-economic stratum, all of which have ecological relevance in our populations (Lummaa *et al.*, 1998, 2001; Lahdenperä *et al.*, 2007; Pettay *et al.*, 2007). Second, we controlled for male AFR, as well as age differences between first spouses and their lifespans, which are used routinely to control for inherent differences in individual quality/condition (van de Pol & Verhulst, 2006; Nussey *et al.*, 2008). Third, men assigned to each marriage class appeared to be inherently unbiased, for they neither differed in AFR (ANOVA; $F_{3,480} = 0.38$, $P = 0.77$) nor reproductive rates with their first wife (GLM; $F_{3,418} = 0.49$, $P = 0.69$). (Reproductive rates were considered as the number of births per year between marriage and last reproduction after controlling for any ecological or inherent individual differences. Marriages were excluded if they showed signs of sterility problems (i.e. < 2 children delivered or > 2 delivered with birth intervals outside 95% confidence intervals, $N = 51$) or if women died in childbirth ($N = 4$), although inclusions of those excluded had no influence on the results).

Our evidence suggests that men show multiple behaviours reflecting selection for continued reproduction throughout adult life (Williams, 1957). Men had a high probability of marrying following spousal loss, a preference for marrying women under the age of 40, maintenance of fertility into their 60s and an increase in age at last reproduction following remarriage. By contrast, the probability that women remarried plummeted from age 40 coinciding with the onset of menopause. These sex-differences in remarriage resulted in older men acquiring younger women as subsequent spouses. Such age differences have been suggested to be beneficial for both parties, where older men have accumulated

resources important for reproductive success (Kaplan *et al.*, 2000; Marlowe, 2000). Although we agree with this hypothesis, our results do not wholly support its predictions. For example, that first spouses were the same age on average, men became less likely to remarry with increasing age and there was no effect of socio-economic status on this probability, suggests a female preference against older men irrespective of their resources. These results might be particular to populations with enforced monogamy. In such populations, fertile women might be selected against marrying older men since such men are likely to have their own children and might have a higher chance of dying before the end of the woman's reproductive potential (Gillespie *et al.*, 2010). Similarly, menopausal women might benefit more from living with the family of one of her offspring and helping to rear grandchildren than marrying a man with existing unrelated offspring (Moring, 2002; Lahdenperä *et al.*, 2004). We suggest that it is important to consider the possibility that the principle reason for remarriage by older men in monogamous populations is to procure help with rearing existing children rather than to produce more children, perhaps in return for supplying material benefits to women. Under this hypothesis, the tendency of older men to marry younger, fertile women might simply be attributed to the fact that such women are the only age category of unmarried women willing to marry. In support, acquiring fertile women as subsequent spouses compromised the success of existing offspring and did not enhance the fitness of men on average (see below).

Nevertheless, remarriage following spousal death has been shown to permit men to breed later in life and sire extra offspring (Dupâquier *et al.*, 1981; Boone, 1986; Low, 1990; Forsberg *et al.*, 1995; Käär *et al.*, 1998). However, these studies failed to investigate whether increased lifetime breeding success translated into increased grandchild production (i.e. a closer approximation to fitness; Stearns *et al.*, 2010). This is particularly problematic in long-lived species like humans, where offspring quality is likely to be an important contributor to overall fitness (Williams, 1966; Lack, 1968). Despite increasing lifetime breeding success through remarriage, we failed to show that this translated into increased fitness, as measured in term of grandchild production. The most likely explanation is that men who remarry (or the wives of such men) favour new offspring over those from previous marriages, reducing the survival and success of the latter (Volland, 1988). That the offspring of first marriages had reduced survival if their father rebred with a new wife following the death of his first wife, compared with when he remained single or remarried but did not re-breed, is consistent with this idea. In addition, we found no evidence to suggest that competition between half-sibs leads to reduced survival of offspring in the new marriage, as has been shown previously (Borgerhoff Mulder, 1998; Jankowiak &

Diderich, 2000; Pollet, 2007). For example, the number of offspring produced in a previous marriage did not influence the proportion of offspring surviving to adulthood in a current marriage (GLM; $\chi^2_1 = 0.30$, $P = 0.59$, $N = 87$, after controlling for changes in maternal and paternal age and differences between the two). Although the offspring-party which suffers from male marriage patterns might vary between societies, it would appear essential that offspring success is considered before one concludes whether or not a given male reproductive strategy is adaptive.

Overall, men failed to improve grandchild production by surviving beyond age 51 years and even appeared to have negative effects if surviving beyond 65, possibly because of competition for resources. Although compromising the success of existing offspring explains why men cannot gain fitness by remarriage and re-breeding following spousal death, it does not explain why men cannot gain fitness by increasing the quality of existing offspring, as is the case with women (Sear & Mace, 2008). The explanation appears to be that Finnish men are unable or unwilling to improve the quality of existing independent offspring through parenting and grandparenting (Lahdenperä *et al.*, 2007), in stark contrast to women (Lahdenperä *et al.*, 2004, 2011). This is a general finding: of those studies to have considered potential (grand) paternal effects on early (grand) child survival, after due consideration of potential confounds, only 40% ($N = 15$) and 10% ($N = 10$) reported an overall positive influence of fathers and grandfathers, respectively (Sear & Mace, 2008). This general lack of (grand) paternal effect on (grand) offspring contrasts markedly with that of (grand) maternal effects. All studies conducted so far ($N = 23$) show that mothers have positive effects on early child survival, and ca. 60% ($N = 15$) show positive effects of grandmothers. These sex differences in the effects of parents and grandparents on child survival are significant (parental sex-difference: Fisher Exact test $P < 0.001$; grandparental sex-difference; $P = 0.040$). These results suggest that men are relatively insensitive to the needs of young compared with women, presumably because in our recent evolutionarily past, they maximized fitness by concentrating on securing matings rather than caring for offspring (Hawkes *et al.*, 1995).

In conclusion, we agree that male lifespan has been shaped by selection on reproduction throughout adult life in humans, and found several behaviours consistent with the Continued Reproduction Hypothesis of Williams (1957). Nevertheless, that these behaviours did not result in fitness gains under enforced monogamy has important implications for selection on male and female life history in monogamous populations. First, we have shown previously that the length of the pair-bond is an important determinant of fitness in our monogamous populations (Gillespie *et al.*, 2010) and here we show that both early reproduction and increasing spouse lifespan had positive effects on male fitness estimates, suggesting

that there should be positive selection on men to first marry young, similarly aged spouses. Second, negative genetic correlations can exist between AFR and lifespan in humans (Pettay *et al.*, 2005). That selection appears to be acting on early reproduction and not late-life survival in these men suggests that enforced monogamy will select for genes facilitating early reproduction at the expense of those combating late-life senescence. This hypothesis predicts that, all else being equal, men in populations with enforced monogamy will have an earlier onset of late-life health problems and reduced lifespans in adulthood than in those populations where polygyny or serial monogamy is possible without spousal loss.

Finally, it has been suggested that positive selection on late-life reproduction in men could be strong enough to drive a concomitant increase in female lifespan (Marlowe, 2000; Tuljapurkar *et al.*, 2007). If true, we might also predict that monogamy should lead to a reduction in lifespan of women, but the data are currently unresponsive. Not only does female lifespan typically exceed male lifespan, but it does so particularly in populations with enforced monogamy (Maklakov, 2008). We suggest that although male and female lifespan will be linked, lifespan is largely a consequence of independent selection pressures in men and women, with lifespan an evolved response to selection for increasing offspring quantity through prolonged reproduction in men (Williams, 1957) and for increasing offspring quality through prolonged care in women (Hawkes *et al.*, 1998; Penn & Smith, 2007). Such a difference in fitness maximizing strategies would be expected to give rise to substantial sexual conflict in humans, and might explain the apparent differences in contributions to parental care between men and women (Brown *et al.*, 2009; Lahdenperä *et al.*, 2011).

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References

Anderson, K.G. 2006. How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. *Curr. Anthropol.* **48**: 511–518.

Bonduriansky, R., Maklakov, A., Zajitschek, F. & Brooks, R. 2008. Sexual selection, sexual conflict and the evolution of ageing and lifespan. *Funct. Ecol.* **22**: 443–453.

Boone, J.L. III 1986. Parental investment and elite family structure in preindustrial states: a case study of late medieval-early modern Portuguese genealogies. *Am. Anthropol.* **88**: 859–878.

Borgerhoff Mulder, M. 1998. Brothers and sisters: how sibling interactions affect optimal parental allocations. *Hum. Nat.* **9**: 119–162.

Brown, G.R., Laland, K.N. & Borgerhoff Mulder, M. 2009. Bateman's principle and human sex roles. *Trends Ecol. Evol.* **24**: 297–304.

Charlesworth, B. 2001. Patterns of age-specific means and genetic variances of mortality rates predicted by the mutation-accumulation theory of ageing. *J. Theor. Biol.* **210**: 47–65.

Dupâquier, J., Hélin, E., Laslett, P., Livi-bacci, M. & Sogner, S. (eds.) 1981. *Marriage and Remarriage in Populations of the Past*. Academic Press, London.

Forsberg, A., Lindqvist, J. & Tullberg, B.S. 1995. The relationship between cumulative number of cohabiting partners and number of children for men and women in modern Sweden. *Ethol. Sociobiol.* **16**: 221–232.

Gillespie, D.O.S., Lahdenperä, M., Russell, A.F. & Lummaa, V. 2010. Pair-bonding modifies the age-specific intensity of natural selection on human female fecundity. *Am. Nat.* **176**: 159–169.

Gurven, M. & Kaplan, H. 2007. Longevity among hunter-gatherers: a cross-cultural examination. *Popul. Dev. Rev.* **33**: 321–365.

Hamilton, W.D. 1966. The moulding of senescence by natural selection. *J. Theor. Biol.* **12**: 12–45.

Hawkes, K., Rogers, A.R. & Charnov, E.L. 1995. The male's dilemma: increased offspring production is more paternity to steal. *Evol. Ecol.* **9**: 662–677.

Hawkes, K., O'Connell, J.F., Blurton Jones, N.G., Alvarez, H. & Charnov, E.L. 1998. Grandmothering, menopause, and the evolution of human life histories. *Proc. Natl Acad. Sci. USA* **95**: 1336–1339.

Jankowiak, W. & Diderich, M. 2000. Sibling solidarity in a polygamous community in the USA: unpacking inclusive fitness. *Evol. Hum. Behav.* **21**: 125–139.

Käär, P., Jokela, J., Merilä, J., Helle, T. & Kojola, I. 1998. Sexual conflict and remarriage in preindustrial human populations: causes and fitness consequences. *Evol. Hum. Behav.* **19**: 139–151.

Kaplan, H., Hill, K., Lancaster, J. & Hurtado, M. 2000. A theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol.* **9**: 156–185.

Korpelainen, H. 2003. Human life histories and the demographic transition: a case study from Finland, 1870–1949. *Am. J. Phys. Anthropol.* **120**: 384–390.

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. Methuen, London.

Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M. & Russell, A.F. 2004. Fitness benefits of prolonged post-reproductive lifespan in women. *Nature* **428**: 178–181.

Lahdenperä, M., Russell, A.F. & Lummaa, V. 2007. Selection for long lifespan in men: benefits of grandfathering? *Proc. R. Soc. Lond. Ser. B* **274**: 2437–2444.

Lahdenperä, M., Russell, A.F., Tremblay, M. & Lummaa, V. 2011. Selection on menopause in two pre-modern human populations: no evidence for the Mother hypothesis. *Evolution* **65**: 476–489.

- Low, B.S. 1990. Occupational status, landownership, and reproductive behavior in 19th-Century Sweden: Tuna Parish. *Am. Anthropol.* **92**: 457–468.
- Lummaa, V., Haukioja, E., Lemmetyinen, R. & Pikkola, M. 1998. Natural selection on human twinning. *Nature* **394**: 533–534.
- Lummaa, V., Jokela, J. & Haukioja, E. 2001. Gender difference in benefits of twinning in pre-industrial humans: boys did not pay. *J. Anim. Ecol.* **70**: 739–746.
- Luther, G. 1993. *Suomen tilastotoimen historia vuoteen 1970*. WSOY, Helsinki.
- Maklakov, A.A. 2008. Sex difference in life span affected by female birth rate in modern humans. *Evol. Hum. Behav.* **29**: 444–449.
- Marlowe, F.W. 2000. The patriarch hypothesis: an alternative explanation of menopause. *Hum. Nat.* **11**: 27–42.
- Mealey, L. 2000. *Sex Differences: Developmental and Evolutionary Strategies*. Academic Press, San Diego.
- Moring, B. 2002. Widowhood options and strategies in pre-industrial northern Europe. Socioeconomic differences in household position of the widowed in 18th and 19th century Finland. *Hist. Fam.* **7**: 79–99.
- Nussey, D.H., Coulson, T., Festa-Bianchet, M. & Gaillard, J.-M. 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. *Funct. Ecol.* **22**: 393–406.
- Paget, W.J. & Timaeus, I.M. 1994. A relational Gompertz model of male fertility: development and assessment. *Popul. Stud.* **48**: 333–340.
- Penn, D.J. & Smith, K.R. 2007. Differential fitness costs of reproduction between sexes. *Proc. Natl Acad. Sci. USA* **104**: 553–558.
- Pettay, J.E., Kruuk, L.E.B., Jokela, J. & Lummaa, V. 2005. Heritability and genetic constraints of life-history trait evolution in pre-industrial humans. *Proc. Natl Acad. Sci. USA* **102**: 2838–2843.
- Pettay, J.E., Helle, S., Jokela, J. & Lummaa, V. 2007. Natural selection on female life-history traits in relation to socio-economic status in pre-industrial human populations. *PLoS ONE* **7**: e606.
- van de Pol, M. & Verhulst, S. 2006. Age-Dependent traits: a new statistical model to separate within- and between- individual effects. *Am. Nat.* **167**: 764–771.
- Pollet, T.V. 2007. Genetic relatedness and sibling relationship characteristics in a modern society. *Evol. Hum. Behav.* **28**: 176–185.
- Pollet, T.V. & Nettle, D. 2009. Market forces affect patterns of polygyny in Uganda. *Proc. Natl Acad. Sci. USA* **106**: 2114–2117.
- Ricklefs, R.E. 2008. The evolution of senescence from a comparative perspective. *Funct. Ecol.* **22**: 379–392.
- Sear, R. & Mace, R. 2008. Who keeps children alive? A review of the effects of kin on child survival. *Evol. Hum. Behav.* **29**: 1–18.
- Soininen, A.M. 1974. *Old Traditional Agriculture in Finland in the 18th and 19th Centuries*. Forssan Kirjapaino Oy, Forssa.
- Stearns, S. 1992. *The Evolution of Life Histories*. Oxford University Press, New York.
- Stearns, S.C., Byars, S.G., Govindajaru, D.R. & Ewbank, D. 2010. Measuring selection in contemporary human populations. *Nature Rev. Genet.* **11**: 611–622.
- Sundin, J. 1992. Sinful sex: legal prosecution of extramarital sex in preindustrial Sweden. *Soc. Sci. Hist.* **16**: 99–128.
- Tuljapurkar, S.D., Puleston, C.O. & Gurven, M.D. 2007. Sexual selection effects on the evolution of senescence. *PLoS ONE* **2**: e785.
- Voland, E. 1988. Differential infant and child mortality in evolutionary perspective: data from late 17th to 19th century Ostfriesland. In: *Human Reproductive Behavior* (L. Betzig, M. Bergerhoff Mulder & P. Turke, eds), pp. 253–261. Cambridge University Press, Cambridge.
- Williams, G.C. 1957. Pleiotropy, natural selection and the evolution of senescence. *Evolution* **11**: 398–411.
- Williams, G.C. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. *Am. Nat.* **100**: 687–690.
- Zar, J.H. 2010. *Biostatistical Analysis*, 5th edn. Pearson Prentice-Hall, Upper Saddle River, NJ.

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