Behav Ecol Sociobiol
DOI 10.1007/s00265-013-1630-6

ORIGINAL PAPER

Effects of remarriage after widowhood on long-term fitness in a monogamous historical human population

Jenni E Pettay · Anna Rotkirch · Alexandre Courtiol · Markus Jokela · Virpi Lummaa

Received: 14 May 2013 / Revised: 30 August 2013 / Accepted: 30 August 2013

Abstract The fitness benefits of multiple mating determine the strength of sexual selection in each sex. This is traditionally quantified by the number of offspring born to once versus multiply mated individuals. In species with (bi)parental care, however, this measure may overestimate the benefits of multiple mating since having several mates can increase offspring number but decrease offspring quality. We analyzed short- and long-term fitness consequences of multiple marriages for both sexes in humans in preindustrial Finnish populations, where monogamy was socially enforced and remarriage was possible only after widowhood. Remarriage increased the lifetime number of offspring sired by men by lengthening their reproductive span but was unrelated to the lifetime number of births for women. However, neither men's nor women's long-term fitness, measured as their number of grandchildren, was significantly increased or decreased by remarriage. These associations were not modified by individual wealth. Our results suggest that despite increasing the number of offspring sired by men, the long-term fitness benefits of serial monogamy may be negligible for both sexes when parental investment is crucial for offspring success and continues to adulthood. They also demonstrate the importance of incorporating long-term fitness measures when quantifying the benefits of mating and reproductive strategies.

Keywords Human evolution · Mating system · Sexual selection · Parental care

Communicated by P. M. Kappeler

Electronic supplementary material The online version of this article (doi:10.1007/s00265-013-1630-6) contains supplementary material, which is available to authorized users.

J. E. Pettay (✉)
Department of Biology, Section of Ecology, University of Turku,
20014 Turku, Finland
e-mail: jenni.pettay@utu.fi

A. Rotkirch
Population Research Institute, Väestöliitto, 00101 Helsinki, Finland

A. Courtiol · V. Lummaa
Wissenschaftskolleg zu Berlin, Wallotstraße 19, 14193 Berlin,
Germany

A. Courtiol
Leibniz Institute for Zoo and Wildlife Research, 10252 Berlin,
Germany

M. Jokela
Institute of Behavioural Sciences, University of Helsinki,
00014 Helsinki, Finland

V. Lummaa
Department of Animal and Plant Sciences, University of Sheffield,
Sheffield S10 2TN, UK

Introduction

Sexual selection refers to the struggle between individuals of one sex for reproductive access to the other sex (Darwin 1899). The strength of sexual selection acting on each sex is predicted to vary across species and populations and to be reflected in the mating system by the degree of polygamy (Emlen and Oring 1977). Sex differences in the benefits of multiple mating were first demonstrated by Bateman (1948) in his experiments using fruit flies (*Drosophila melanogaster*). From his work, three “Bateman's principles” were postulated, according to which the variance in the number of (1) offspring and (2) mates should be greater and (3) the relationship between mating success and number of offspring stronger in males than in females, indicating that males experience more intense sexual selection than females (Arnold 1994; Arnold and Duvall 1994; Schuster and Wade 2003). In particular, the stronger the association between mating and reproductive success, the stronger sexual selection is predicted to influence characteristics enhancing mating success.

Humans offer an excellent opportunity to test predictions related to sexual selection. As a species, humans represent several mating systems—strictly imposed monogamy, serial monogamy, polygyny, and polyandry—depending on the ecological and social conditions of the populations (Marlowe 2000; Mealey 2000). Sexual selection can act more powerfully under polygyny than monogamy because highly competitive and attractive men in polygynous populations may mate with many women and thus gain more offspring than other men (Huxley 1938; Kirkpatrick and Ryan 1991; Arnold and Duvall 1994). Current evidence suggests, however, considerable variation between populations in the maximal strength of sexual selection experienced by each sex (Brown et al. 2009). In men, partner number has been positively associated with measures of reproductive success among the polygynous Brazilian Xavante (Salzano et al. 1967), Kenyan Kipsigis (Borgerhoff Mulder 1987), historical polygynous, or serially monogamous Utahns in US (Moorad et al. 2011) and in the contemporary US (Jokela et al. 2010), as well as in monogamous preindustrial Sami (Käär et al. 1998), Finns (Courtiol et al. 2012), and Swedes (Low 2000) but negatively associated with measures of reproductive success in serially monogamous Tanzanian Pimbwe (Borgerhoff Mulder 2009). In women, partner number had a positive association with reproductive success in Pimbwe (Borgerhoff Mulder 2009) and in historical Utah where women had a small fitness benefit from remarriage after divorce or widowhood as measured by their total number of offspring (Moorad et al. 2011) but not in historical Finland (Courtiol et al. 2012) or the contemporary US (Jokela et al. 2010) or Sweden (Forsberg and Tullberg 1995). Thus, the strength and focus of selection varies extensively between populations, and general conclusions have been difficult to draw (Brown et al. 2009), partly because data on the effects of various marriage systems on the strength of sexual selection in humans is limited, and very few studies have measured the fitness benefits of multiple mating simultaneously in both sexes in a given population (but see Borgerhoff Mulder 2009; Jokela et al. 2010; Moorad et al. 2011; Courtiol et al. 2012).

Importantly, the effects of multiple mating may also depend on the level of parental investment required to successfully raise offspring and on its distribution between both parents (e.g., Trivers 1972; Emlen and Oring 1977; Clutton-Brock 2007). Maternal care is universally important for human offspring, while the importance and level of paternal care vary dramatically between and within populations (Flinn et al. 2007; Quinlan and Quinlan 2007; Nettle 2008). The benefits of extended (grand)parental care by each sex also vary (Lahdenperä et al. 2007; Sear and Mace 2008).

All previous studies assessing the strength of sexual selection in humans have measured reproductive success as the numbers of children born or children surviving to a certain age in childhood, including our own previous study on historical Finns (Courtiol et al. 2012). Thus, they have ignored the possible long-term trade-offs between quantity and quality of children, which arise with multiple mating (Emlen and Oring 1977; Marlowe 2000). Fitness gains from multiple mating can be predicted to diminish especially in societies with high parental investment. First, given the larger overall number of children produced by several simultaneous wives, polygyny can lead to higher offspring competition for resources within a household and, thereby, to higher child mortality (Gyimah 2009; Strassmann 2011). Second, under monogamy, remarriage can lower the investment in offspring from the first union due to either the child's loss of one biological parent or due to diminished investment following divorce (Amato and Keith 1991a, b; Brown 2006), as well as exposure to potentially harmful stepparenting (Willführ 2009). The number of offspring born or surviving early childhood may therefore be an insufficient measure of long-term fitness in humans or other species with extensive (bi)parental care (Gillespie et al. 2008).

We investigate the short-term and long-term fitness consequences of multiple marriages for men and women in a monogamous human population in preindustrial Finland. In this population, monogamy was socially and culturally imposed so that extramarital affairs were condemned, divorce was forbidden, and individuals were able to remarry only if widowed. Since the common custom required a couple (rather than, e.g., a widow or widower) as the head of the household in these agrarian populations (Moring 2002), remarriage was culturally approved of. The obligations of widows towards their parents-in-law, and the rights of the first-born children to inheritance, remained and were usually respected after the death of a spouse (Moring 2002). We explore the sex differences in mating success and reproductive success and the relationship between (re)marriage and reproductive success assessed by (a) offspring number (number of children born) and (b) their long-term quality, that is, number of offspring raised to adulthood and the number of grandchildren born. To determine causes for any effects of remarriage on reproductive success, we also investigated survival of offspring in relation to parental loss and remarriage. Finally, we investigate whether the associations between the number of marriages and measures of fitness varied between the wealthy (landowners) and the poor (landless).

Methods

Data

We compared men's and women's reproductive success in relation to marriage success by using demographic data collected from Finnish population registers of the preindustrial era (see, e.g., Lummaa et al. 1998; Lahdenperä et al. 2004; Lummaa et al. 2007; Courtiol et al. 2012). The Lutheran Church has kept census, birth/baptism, marriage, and death/burial registers of each parish in the country since the seventeenth century, covering practically the whole population of Finland from 1749 onwards (Gille 1949; Luther 1993). Using these registers, it is possible to follow the reproductive and marital details of each individual from birth to death, as practically the whole population practiced the Lutheran religion and all who died (in most cases including also stillborn and infants who died before baptism) were buried in a cemetery and recorded in the book of deaths (Gille 1949). Migration rates were relatively low, and in most cases, the parish migration registers allow the life events of those moving away from natal parish to be determined. The predominant household was composed of the eldest son, his wife, their children, his parents, and one or more unmarried siblings (Moring 2003). All siblings usually lived close by (Moring 1993), but while the presence of elder siblings was beneficial for childhood survival (Nitsch et al. 2013), the presence of same-sexed siblings in adulthood decreased mating and reproductive opportunities of both males and females (Nitsch et al. 2013). Instead, previous studies on this population have documented positive effects of grandmothers (Lahdenperä et al. 2004) but not grandfathers (Lahdenperä et al. 2007) on child survival.

We used demographic data collected from four geographically separate populations, one inland parish (Ikaalinen) and three coastal parishes (Hiittinen, Kustavi, and Rymättylä) of the eighteenth to nineteenth centuries (Soininen 1974; Karskela 2001). We obtained complete life history records for all individuals born 1732–1860; in total, the sample consisted in 3,069 married individuals with full life history details known. We could track the number of grandchildren for 2,825 individuals. During the study era, the main source of livelihood was farming, supplemented by fishing in coastal areas (Soininen 1974; Heervä and Joutsamo 1983), and the populations experienced high mortality and high fertility, exacerbated by the lack of modern medical care and contraceptive methods (Liu and Lummaa 2011). Only 62 % of all children born in our study populations during the study period survived to the age of 15. Furthermore, 78 % of men and 82 % women who survived to age 15 married at least once in their lifetime. We assigned the socioeconomic status of each married women according to the profession of her husband, simplified into two groups according to those owning land versus those either renting or having no access to land at all (landowners vs. landless) (Pettay et al. 2007). Although there is likely to be variation within our landownership groups, this broad categorization allowed us to observe the major effects of differences in access to resources between individuals (Gillespie et al. 2008; Rickard et al. 2010).

We used marriage status as a proxy measure for mating success. This approximation is likely reliable because (1) the number of premarital sexual partners was presumably low due to strict social regulation of sexual behavior (Sundin 1992)—only 1.9 % of unmarried women had registered children in our dataset; (2) extra-pair copulation rates are also expected to have been low for the same sociocultural reasons, given that extra-pair paternity rates are usually lower than 3 % in most contemporary European populations (Anderson 2006) with less strict sexual norms than in our study population. In preindustrial Finland monogamy was socially imposed and divorce forbidden so that men and women could remarry only if widowed (Saarimäki 2010). Thus, our study focuses exclusively on the consequences of remarriage following widowhood. In our sample, the proportion of married men whose wife died before them was 45 % for landowners and 49 % for landless. In addition, 28 % of men were under 40 years of age when they became widowers and 29 % of women were under 40 years when widowed. Thus, widowhood, and potential remarriage, during fertile period was common in this population. Most of those who remarried did so only once: 14.5 % of all marriages were the second marriage for at least one of the spouses, while only 1 % of marriages were the third or the fourth for any of the spouses. We therefore combined two, three or four times married and call this sample remarried. In an earlier paper on the same population (Courtiol et al. 2012), we found that the remarriage probability was affected by sex (men were more likely to remarry) but not by socioeconomic status. In the sample analyzed in the current paper, too, widowed men were more likely to remarry than widowed women (generalized linear model (GLM): $F_{1,1118}$=85.81, p=<0.0001), but the probability of remarriage was similar in both social classes ($F_{1,1117}$=0.30, p=0.6). Remarriage probability was also lower in later birth cohorts ($F_{6,1117}$=2.28, p=0.03) and declined with the age when widowed, especially for women (age effect: $F_{1,1117}$=258.81, p=<0.0001; age× sex: $F_{1,1117}$=8.89, p=0.003). The mean number of marriages for all at least once-married individuals was (mean±SE) 1.20±0.20 and 1.20±0.18 for landowner men and women and 1.20±0.20 and 1.12±0.11 for landless men and women, respectively. The mean age at first marriage corresponded to 25.3±0.4 and 23.0±0.1 for landowner men and women and 26.5±0.5 and 25.5±0.5 for landless men and women. For age at first remarriage, the corresponding values were 43.7±1.1 and 37.1±0.9 for landowner men and women and 43.8±0.9 and 40.5±0.9 for landless men and women. Both men and women remarried younger spouses than themselves, the corresponding values being 12.4±1.1 and 6.7±1.2 years younger for landowner men and women and 10.5±0.8 and 2.8±1.4 for landless men and women, respectively.

Statistical analyses

To study Bateman's key prediction that mating success is more strongly correlated with reproductive success in men than in women, we investigated the association between the numbers of marriages with lifetime number of children born, as commonly done in previous studies (Brown et al. 2009). To assess whether high-mating success increased long-term fitness, we also investigated the relationship between the number of marriages and lifetime reproductive success (measured as the number of children surviving to adulthood at age 15, the youngest age people were able to marry and reproduced in our population) as well as the number of grandchildren born.

Because the numbers of offspring born or surviving to adulthood as well as the number of grandchildren are count variables, the effect of marriage number on fitness measures was assessed with a GLM using a negative binomial error structure and a log-link function (Allison 1999). We distinctly separate GLM for each fitness measure (number of born children, survived children, and grandchildren).

Our main terms of interest in each model were the number of marriages (once vs. multiply married, see above), sex, and their interactions. In cases of statistically significant sex interaction effects (p value<0.05), post hoc pairwise comparisons were conducted using the Scheffe procedure, which adjusts p values for multiple comparisons (Ruxton and Beauchamp 2008). In case of a nonsignificant interaction term between sex and other covariates, the model was refitted omitting interaction terms that included sex in order to assess whether or not marriage number influenced the fitness measures irrespectively of sex.

Since in this population, remarriage was possible only after the spouse died, to disentangle the effect of widowhood from remarriage; all analyses were also rerun including only individuals that had lost their spouse and these were divided into two groups; those who remarried (remarried) and those who did not remarry (single).

In order to investigate the effect of remarriage on fitness measures, we also included in our model covariates susceptible to influence fitness. First, lifespan is known to affect family size in our study populations (Pettay et al. 2007) and was therefore fitted as a covariate. Second, we included a 20-year birth cohort (nine levels) and study parish (four levels) as independent categorical variables in the analyses in order to control for temporal and spatial variation in the variables studied (Lummaa et al. 1998; Liu et al. 2012). Furthermore, to study the possible effects of wealth, we constructed a second set of three models including social class (two levels, see above) and its interaction with sex and marriage number, modeled as a triple interaction.

We compared reproductive span (time in years between first and last birth for women or that of their spouse's for men) of once-married and remarried men and women by a GLM to assess how remarriage affected reproductive tenure. This analysis was conducted in a similar manner as the analyses described above by fitting sex, marriage status, parish, birth cohort, social class, and their interactions in the initial model.

Finally, to disentangle the effect of remarriage and parent loss on child survival, we compared survival of children with two parents, mother only, father only, no parents, mother and stepfather, father and stepmother, mother and stepfather with children from the new union, and father and stepmother with children from the new union. To do so, we analyzed survival using a logistic regression framework following Allison (1982). This technique implies to express the data as individual year observations ($N=165{,}544$) from which we predicted the probability of a child death per year. As the data were entered longitudinally, the status of parents was entered as a time varying factor with the aforementioned eight categories. In addition to this independent variable, we also considered that the death probability is a quadratic function of the age of children and that both sex and the parental social class could modify the basal death rate. The survival analysis was conducted using R (2011), and all other analyses were conducted with SAS version 9.2 (SAS Institute Inc., Cary, NC, USA).

In all of the analyses above, we included only individuals with complete life history over the entire potential reproductive period and complete life history of at least one offspring when analyzing the number of grandchildren. Limiting the sample to only those individuals with complete records may introduce a bias, but our previous study has shown that such data sampling procedures affect little the ability to correctly measure the overall opportunity to selection in this study population (Courtiol et al. 2012). We were able to track ~97 % of offspring until their adulthood (married and remarried men, 97.5 and 97.2 %; married and remarried women, 97.8 and 97.2 %) and 85 % of offspring until the end of their potential reproductive lifespan (married and remarried men, 85.2 and 85.7 %; married and remarried women, 84.1 and 84.5 %). Due to such missing values, grandchild numbers were slightly underestimated for some individuals. Consequently, we weighted the analyses of lifetime reproductive success with percentage of offspring with known survival to age 15 (e.g., if survival was unknown for one out of five children born, the weight received the value 0.8). In a similar way, the number of grandchildren was weighted with the percentage of offspring of whom we have complete life history data. This is a better method than omitting families with missing information, since such an omission could potentially bias the data towards small families which are less likely to have missing information; however, we found qualitatively similar results if the weights were omitted from the analyses. In any case, given that the slight underestimation of grandchild numbers due to incomplete records of some offspring does not differ between the sexes or marriage status groups, there is little reason to expect that the underestimation would bias our results. Note that because the sample only includes reproductive individuals and men experience larger variance (skew) in reproductive success in this population (Courtiol et al. 2012), the average numbers of children or grandchildren produced by men and women are not necessarily equal.

Results

We found clear evidence that remarriage brought benefits in men but not in women when measured by their lifetime number of offspring born (interaction between the marriage status and sex: $F_{1,3053}$=5.66, p=0.02, Fig. 1a, supplementary Tables S1 and S2). The model-based average number of children produced over a lifetime by reproductive men and women were 5.13±0.2 and 4.6±0.2, respectively, but remarried men had 1.12 (25 %) children more than did once-married men (post hoc pairwise comparison between married and remarried men: t_{3053}=−4.24, p<0.0001). By contrast, multiple marriages did not increase significantly the number of offspring born to women, with remarried women having only 4 % more children born than once-married women (t_{3053}=−0.69, p=0.9). The pattern remained similar when only individuals that had lost their spouse were included in the analysis and comparisons were made between those individuals that were widowed and remarried versus those individuals that were widowed and did not remarry, suggesting that it was only remarried widowed men but not remarried widowed women who were able to increase their parity (see supplementary Tables S3 and S4 for details). Although social class had an overall effect on the lifetime number of offspring born—with landowners having 12 % more children than the landless (model-based means: 5.18±0.22 vs. 4.6±0.2, $F_{1,3053}$=2.62, p=0.0003)—the effect of remarriage on lifetime number of children born was similar among both landowners and landless (interaction between social class and marriage status: $F_{1,3050}$=3.33, p=0.07). Nor did the sex-specific benefits of multiple marriages on the lifetime number of children born significantly differ between the socioeconomic groups (triple interaction between sex, marriage status, and social class: $F_{1,3050}$=0.94, p=0.3). To assess if the higher parity of remarried men was due to a prolonged reproductive period, we compared the reproductive span of married and remarried men and women (interaction between sex and marriage status: F_1= 41.16, p<0.0001). Remarried men had on average 5 years longer reproductive lifespan than did once-married men (t_{2608}= −9.59, p<.0001), whereas the reproductive span of married and remarried women did not differ (t_{2608}=−0.27, p=0.8) (Fig. 2).

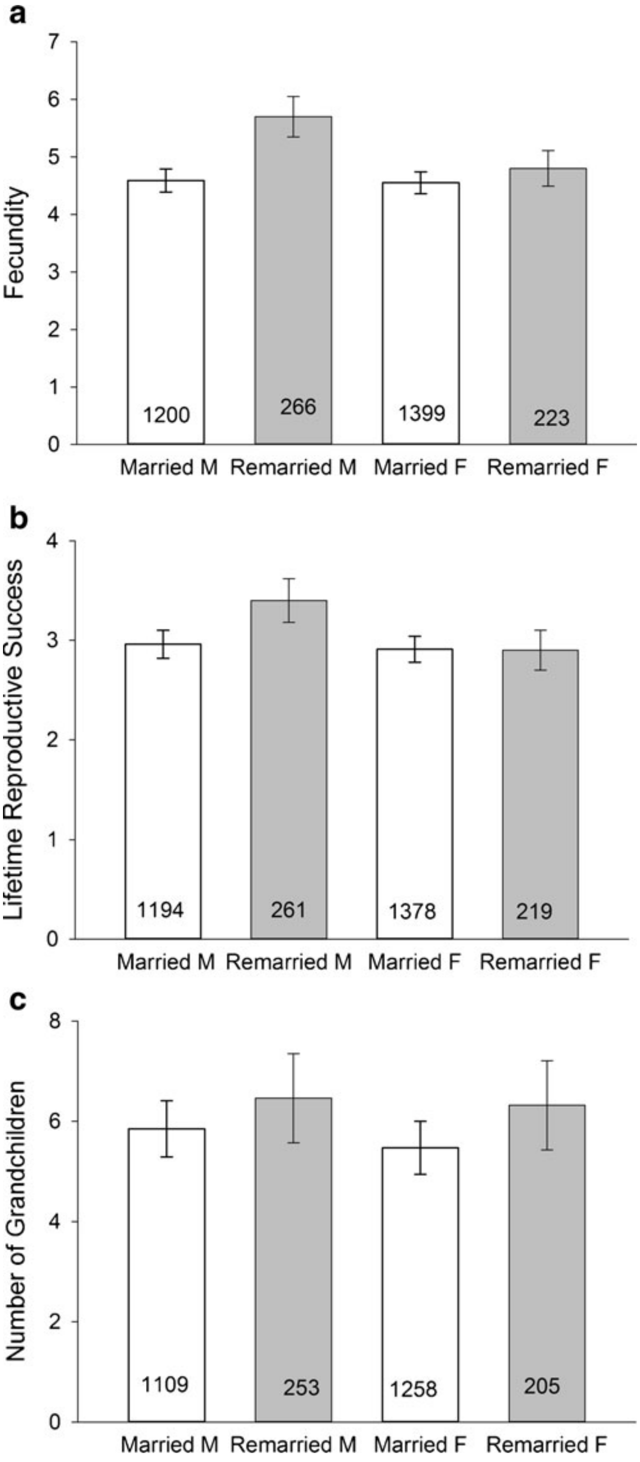

Fig. 1 Male (*M*) and female (*F*) reproductive success relative to their mating success. *Married* refers to the men and women who were only married once in their lifetime, *remarried* refers to individuals who were married twice or more. **a** Number of children born or sired, **b** number of children raised to age 15, and **c** long-term fitness measured as the number of grandchildren born or sired. Figures show predicted means (±SE) and values in *bars* indicating the number of men and women in each category

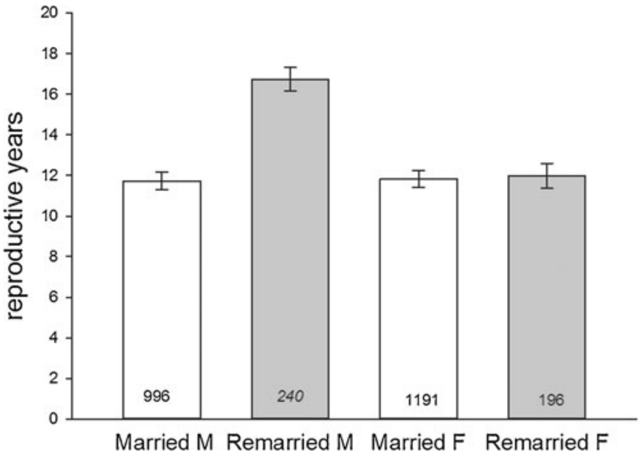

Fig. 2 Male (*M*) and female (*F*) reproductive years (time span between the first and last birth) relative to their marriage status. Figure shows predicted means (±SE) and values in *bars* indicating the number of men and women in each category

Once we incorporated offspring quality into the measure of reproductive success and investigated the ability to raise offspring to age 15, the benefits for remarriage gained only marginal statistical support (main marriage status effect: $F_{1,3037}=3.46$, $p=0.06$) and did not any longer strongly differ between men and women (interaction between number of marriages and sex: $F_{1,3035}=3.33$, $p=0.07$, Fig. 1b, Table S1). Reproductive men and women raised on average (model-based means) 3.23±0.22 and 3.011±0.2 offspring to adulthood (age 15), respectively. Remarried men raised 0.44 (15 %) offspring more than did once-married men, whereas once-married women raised 0.01 (1 %) fewer children than did remarried women. However, when limiting the sample to only those that lost their spouse (widows and widowers), remarried widowed men were able to raise more children to adulthood compared to widowers that remained single, whereas for female widows remarriage did not bring additional reproductive success (Tables S3 and S4). Overall, landowner men had higher lifetime reproductive success than did landless men (model-based means: 3.29±0.15 vs. 2.82±0.13, $F_{1,\ 3035}=19.76$, $p<.0001$) and landless women raised the lowest number of children to adulthood (interaction between sex and social class: $F_{1,3033}=5.98$; $p=0.01$; model-based means for landless women: 2.5±0.14). However, once again remarriage benefited landowners and landless alike (interaction between marriage status and sex: $F_{1,3033}=2.49$, $p=0.11$), and the benefits between sexes of multiple marriages to the number of children raised to adulthood were not modified by socioeconomic class (triple interaction between sex, marriage status, and social class: $F_{1,3033}=1.62$, $p=0.2$).

We further found that the composition of the family had a noticeable influence on the survival of children (Likelihood Ratio Test: $\chi^2=110$, $df=7$, $p<0.0001$). All family arrangements involving at least the presence of one parent led to a significantly higher survival rate than when both parents were dead (z tests on model estimates: all $p<0.001$). Rerunning the model omitting this latter category shows that child survival rates were still different between the remaining seven categories ($\chi^2=18.9$, $df=6$, $p=0.004$). Taking children with two parents as a reference category in this latter model showed that all family arrangements for which the mother was missing had significantly lower survival rate of children (all $p<0.03$), but child survival did not differ depending on whether the father remarried or rebred ($\chi^2=1.64$, $df=2$, $p=0.44$). While children with a single mother did show a higher death rate ($p=0.008$), those with a remarried mother (rebred or not) had a similar survival rate as children with both parents alive (both $p>0.78$). In both the model including the “no parent” category (model 1) and in the one without (model 2), sons presented death rates significantly higher than daughters (model 1: $\chi^2=43.2$, $df=1$, $p<0.0001$; model 2: $\chi^2=14.5$, $df=1$, $p<0.0001$), children from landowners tended to survive better than children from landless individuals but differences were not significant (model 1: $\chi^2=3.49$, $df=1$, $p=0.062$; model 2: $\chi^2=0.39$, $df=1$, $p=0.53$), and we found strong support for the U-shaped effect of age on the death rate (model 1: $\chi^2=2155.7$, $df=2$, $p<0.0001$; model 2: $\chi^2=1464.7$, $df=2$, $p<0.0001$).

We then studied the long-term fitness consequences of multiple mating by measuring the total number of grandchildren born, which incorporates offspring number, their longevity, and their reproductive output in adulthood into one measure. Remarriage did not appear to bring additional grandchildren ($F_{1,2811}=0.77$, $p=0.4$) and this was true for both men and women (interaction between sex and the marriage status: $F_{1,2810}=0.06$, $p=0.8$, Fig. 1c, Table S1). Men and women had on average 5.3±0.8 and 6.9±1.12 grandchildren, respectively. The trend was positive for both sexes: once-married and remarried men had model-based means of 5.26±0.85 and 7.02±1.27 grandchildren (33 % difference), respectively, whereas once-married and remarried women had 5.34±0.83 and 6.86±1.25 grandchildren (28 % difference), respectively. Restricting analysis to widowers and widows led to similar conclusions (details in Table S3 and S4). Although landowners had more grandchildren compared to the landless (model-based means: 8.02±0.79 vs. 4.51±0.45, $F_{1,2810}=67.83$, $p<.0001$), the marriage status had a similar effect on grandchildren numbers among both landowners and the landless ($F_{1,2807}=2.10$, $p=0.27$), and this was true for both men and women (triple interaction between sex, marriage status, and social class: $F_{1,2807}=1.24$, $p=0.26$).

Discussion

The relationship between mating success and reproductive success is a key question for assessing sexual selection and understanding the marked variability in human mating systems, but such calculations may be sensitive to the fitness measures used. We investigated how serial monogamy related to short- and long-term fitness among men and women in preindustrial Finland. Previous studies on the effects of multiple mating on fitness in humans have either measured short-term fitness (births) (e.g., Brown et al. 2009; Courtiol et al. 2012) or measured long-term fitness (grandchildren) only for one sex (e.g., Lahdenperä et al. 2011), and we therefore lack comparisons of long-term fitness benefits of multiple mating for men and women in a given population. Our results show that remarried men had 25 % more offspring born than did once-married men. However, men's benefits of multiple marriages were smaller and not statistically significant when measured as numbers of offspring raised to adulthood or as numbers of grandchildren born. We found that survival of offspring from previous marriage for remarried men was lower compared to children with both parents alive or mother alive. However, such lower survival of offspring of remarried men was due to loss of mother rather than remarriage, since survival of offspring of widowed men who did not remarry was similar. Women neither benefited nor suffered from their own multiple marriages with regards to both short-term and long-term fitness. The results were similar for landowners and landless men and women, regardless of the overall higher fitness of landowners, suggesting the effects of remarriage to be similar in both social classes.

When using the numbers of offspring born over lifetime as a fitness measure, our findings are in line with the prediction derived from Bateman's third principle (Bateman 1948). Remarried men had more children over their lifespan compared to men who had only one wife during their lifetime, taking into account any differences in longevity. Similar results have been reported in earlier studies of historical societies with socially imposed monogamy (e.g., Käär et al. 1998; Low 2000; Moorad et al. 2011; Courtiol et al. 2012). These short-term reproductive benefits are largely explained by differences in the reproductive lifespan of once-married and remarried men. Men who remarried could prolong their reproductive lifespan, since widowers typically married a woman younger than their first wife at death (see also Lahdenperä et al. 2011; Courtiol et al. 2012).

Differences in long-term fitness measured by the number of grandchildren revealed that multiple marriages did not significantly increase men's fitness. In the long run, the Bateman gradient did not apply to married people in this population. Such negative findings must always be interpreted with caution, given that a lack of significance might be dependent upon sampling procedure, sample size, or inability to control for confounding effects. While such possibilities remain open, our data on grandchild numbers was equally complete for both men and women of different marriage categories (see "Methods"). Moreover, our models adjusted for missing data and a range of potentially confounding factors, such as geographic and temporal variation, differences in lifespan, or access to resources. Overall, our sample included over 2,800 individuals, and while the vast majority of those married only once, the analyses include a minimum of 205 remarried women and 253 remarried men. Consequently, even if a small benefit of remarriage for long-term fitness would be true in the population but not detected in our sample, the reduced difference between sexes in benefits of remarriage for the numbers of children appears robust.

The reason why men did not gain additional grandchildren from their second marriages was likely due to the lack of maternal presence for the children born from the first marriage. Survival of offspring suffered when the mother died, which is not surprising as maternal presence was crucial in this population for infant and child survival during the first 2 years of life (Lahdenperä et al. 2010). Furthermore, maternal presence during adulthood improved reproductive success (Lahdenperä et al. 2004), and this may have affected the children of remarried men, e.g., through lower prospects of marriage or potential help with childcare. Other possible mechanisms explaining the lack of noticeable long-term fitness benefits of serial monogamy for both sexes might include lower paternal investment due to remarriage and possible abuse by the stepmother. However, men's remarriage and presence of stepmother with or without additional children (half-siblings) was not associated with improved or lowered survival of offspring. On the other hand, for offspring survival, it was better if widowed women remarried rather than stayed single and survival of children of remarried women did not differ from those children who had both parents alive. This result is in line with a study of historical Sweden, where remarriage appeared to improve rather than decrease child survival (Andersson et al. 1996). However, effects of stepparents are likely to be population specific, for example, a study from a historical German population found that time spent with stepparents increased the mortality rate of children (Willführ 2009). It also remains open how comparable these results are to populations where remarriage is possible after divorce (and therefore does not imply total loss of one parent).

Recently, Courtiol et al. (2012) showed that investigation of the potential strength of sexual selection should incorporate all individuals born, including those never reproducing, to accurately reflect selection pressures acting on mating behavior. Here, we further demonstrate that in species with high parental care, one should incorporate measures of both offspring quantity and quality to assess the potential strength of sexual selection. Our results also suggest that in humans, the apparently large discrepancy in previous studies regarding sex-specific benefits of multiple mating might arise from long-term differences in these benefits for men and women, which in turn may vary between populations depending on their ecology. The level of parental and grandparental investment, sibling competition, and effects of stepparents all differ depending on demography and social structure, distribution of resources, and the marriage system, among other factors (Kaplan and Lancaster 2003). In preindustrial Finland, resources were limited, parental support was important for offspring success into adulthood, and this support often included help, advice, and reputation building in addition to wealth.

A lack of long-term fitness benefits from multiple mating does not preclude sexual selection. Much of the overall fitness variation due to sexual selection in the study population arose through individual differences in their ability to find any mate in their lifetime (Courtiol et al. 2012), and we have here only focused on the mated individuals. Nevertheless, our results do not support the predicted difference between sexes in relationship between mating and reproductive success called the Bateman gradient. This could result from lower asymmetry in the importance of maternal and paternal investment in this population than in most other mammals. However, since also other factors such as the operational sex ratio, population density, and relative resource-holding power have been predicted to influence the Bateman gradient, only replication of studies similar to this one in other human populations will shed light on the respective influence of these different factors (Brown et al. 2009). Furthermore, because historical studies like this one are unable to address causality directly, the correlation of widowhood with higher child mortality may arise from underlying factors such as disease exposure and crop failures that are known to vary dramatically through time in this population (Hayward et al. 2012). Indeed, death and remarriage are unlikely to occur randomly, but instead, health outcomes are correlated within families. Nevertheless, our study controlled for social class as well as general temporal and geographic variation in mortality, reducing the likelihood that our findings would be distorted by temporal variation in conditions increasing both the risks of widowhood and offspring mortality. Moreover, child and adult mortality in the population were usually caused by different factors and diseases (Hayward et al. 2012).

The next step will be to integrate explicitly the effect of multiple mating on the long-term fitness of individuals within the quantitative framework of sexual selection (e.g., Moorad et al. 2011; Courtiol et al. 2012). This is necessary to assess the selective pressures acting on the mating strategies and their potential implications for the evolution of traits influenced by sexual selection, but represents a methodological challenge because the traditional framework does not allow the use of fitness components spread across generations (Arnold and Wade 1984). Nonetheless, the recent development of methods based on contextual analyses (Moorad 2013) is a good step in this direction.

In sum, our results suggest that in some environments, the costs of monogamy should not be high for either sex when parental investment is crucial for offspring success and its effects continue to maturation and adulthood. The spread of social norms enforcing monogamy may have been easier in these conditions, but as both the mating system and parental investment evolve jointly, the actual picture is complex. We demonstrate that in species with high parental care, investigations of the strength of sexual selection should incorporate measures of both offspring quantity and quality to accurately reflect long-term selection pressures acting on mating behavior. More empirical studies are needed to understand how mating systems and demands on parental investment affect the evolution of sexual strategies. The large variation in the results of previous studies on sex-specific benefits of multiple mating in humans may partly reflect between-population differences in the benefits to offspring of biparental care and the costs of stepparenting and thus in the long-term fitness benefits for men and women from multiple mating.

Acknowledgments We thank K. Pokkinen, A. Siitonen, L. Iso-Iivari, and V. P. Toropainen for data collection and two anonymous reviewers for helpful comments. This work was funded by the European Research Council, the Kone foundation (Helsinki, Finland), the Wissenschaftskolleg (Berlin, Germany), the Royal Society (UK), and the University of Helsinki Research Funds.

References

Allison PD (1982) Discrete-time methods for the analysis of event histories. Sociol Methodol 13:61–98

Allison PD (1999) Logistic regression using the SAS® System: theory and application. SAS Institute Inc., Cary, NC

Amato PR, Keith B (1991a) Parental divorce and the well-being of children: a meta-analysis. Psychol Bull 110:26–46

Amato PR, Keith B (1991b) Parental divorce and adult well-being: a meta-analysis. J Marriage Fam 53:43–58

Anderson KG (2006) How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. Curr Anthropol 47:513–520

Andersson T, Hogberg U, Akerman S (1996) Survival of orphans in 19th century Sweden—the importance of remarriages. Acta Paediatr 85: 981–985

Arnold SJ (1994) Bateman's principles and the measurement of sexual selection in plants and animals. Am Nat 144:S126–S149

Arnold SJ, Duvall D (1994) Animal mating systems: a synthesis based on selection theory. Am Nat 143:317–348

Arnold SJ, Wade MJ (1984) On the measurement of natural and sexual selection: applications. Evolution 38:720–734

Bateman AJ (1948) Intra-sexual selection in Drosophilia. Heredity 2: 349–368

Borgerhoff Mulder M (1987) On cultural and reproductive success: Kipsigis evidence. Am Anthropol 89:618–634

Borgerhoff Mulder M (2009) Serial monogamy as polyandry or polygyny? Marriage in the Tanzanian Pimbwe. Hum Nat 20:130–150

Brown SL (2006) Family structure transitions and adolescent well-being. Demography 43:447–461

Brown GR, Laland KN, Borgerhoff Mulder M (2009) Bateman's principles and human sex roles. Trends Ecol Evol 24:297–304

Clutton-Brock TH (2007) Sexual selection in males and females. Science 318:1882–1885

Courtiol A, Pettay JE, Jokela M, Rotkirch A, Lummaa V (2012) Natural and sexual selection in a monogamous historical human population. Proc Natl Acad Sci U S A 109:8044–8049

Darwin C (1899) The descent of man, and selection in relation to sex, 2nd edn. John Murray, London

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223

Flinn MV, Quinlan RJ, Coe K, Ward CV (2007) Evolution of the human family: cooperative males, long social childhoods, smart mothers, and extended kin networks. In: Salmon CA, Shackleford TK (eds) Family Relationships: An Evolutionary Perspective. Oxford University Press, Oxford, pp 16–38

Forsberg AJL, Tullberg B (1995) The relationship between cumulative number of cohabitating partners and number of children for men and women in modern Sweden. Ethol Sociobiol 16:221–232

Gille H (1949) The demographic history of the Northern European countries in the eighteenth century. Pop Stud 3:3–65

Gillespie DOS, Russell AF, Lummaa V (2008) When fecundity does not equal fitness: Evidence of a quantity-quality trade-off in pre-industrial humans. Proc R Soc Lond B 275:713–722

Gyimah OS (2009) Polygynous marital structure and child survivorship in Sub-Saharan Africa: some empirical evidence from Ghana. Soc Sci Med 68:334–342

Hayward AD, Holopainen J, Pettay JE, Lummaa V (2012) Food and fitness: associations between crop yields and life-history traits in a longitudinally-monitored pre-industrial human population. Proc R Soc Lond B 279:4165–4173

Heervä J, Joutsamo T (1983) Kustavin historia. Uudenkaupungin Kirjapaino Oy, Uusikaupunki, Finland

Huxley J (1938) Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research. Am Nat 72:416–433

Jokela M, Rotkirch A, Rickard IJ, Pettay J, Lummaa V (2010) Serial monogamy and reproductive success in a contemporary human population. Behav Ecol 21:906–912

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, Lancaster JB (2003) An evolutionary and ecological analysis of human fertility, mating patterns and parental investment. In: Wachter KW, Bulatao RA (eds) Offspring: Fertility Behavior in Biodemographic Perspective. National Research Council, National Academies Press, Washington D.C., pp 170–223

Karskela S (2001) Sukututkijan tietokirja. Jyväskylä, Finland

Kirkpatrick M, Ryan MJ (1991) The evolution of mating preferences and the paradox of the lek. Nature 350:33–38

Lahdenperä M, Lummaa V, Helle S, Tremblay M, Russell AF (2004) Fitness benefits of prolonged post-reproductive lifespan in women. Nature 428:178–181

Lahdenperä M, Russell AF, Lummaa V (2007) Selection for long lifespan in men: benefits of grandfathering? Proc R Soc Lond B 274:2437–2444

Lahdenperä M, Russell AF, Tremblay M, Lummaa V (2010) Selection on menopause in two pre-modern human populations: no evidence for the Mother hypothesis. Evolution 65:476–489

Lahdenperä M, Lummaa V, Russell AF (2011) Selection on male longevity in a monogamous human population: late-life survival brings no additional grandchildren. J Evol Biol 24:1053–1063

Liu J, Lummaa V (2011) Age at first reproduction and probability of reproductive failure in women. Evol Hum Behav 32:433–443

Liu J, Rotkirch A, Lummaa V (2012) Maternal risk of breeding failure remained low throughout the demographic transitions in fertility and age at first reproduction in Finland. PLoS ONE 7:e34898

Low BS (2000) Why sex matters. Princeton University Press, Princeton, NJ

Lummaa V, Haukioja E, Lemmetyinen R, Pikkola M (1998) Natural selection on human twinning. Nature 394:533–534

Lummaa V, Pettay JE, Russell AF (2007) Male twins reduce fitness of female co-twins in humans. Proc Natl Acad Sci U S A 104:10915–10920

Luther G (1993) Suomen Tilastotoimen Historia vuoteen 1970. WSOY, Helsinki, Finland

Marlowe F (2000) Paternal investment and the human mating system. Behav Process 51:45–61

Mealey L (2000) Sex differences: development and evolutionary strategies. Academic, London

Moorad JA (2013) Multi-level sexual selection: individual and family-level selection for mating success in a historical human population. Evolution 67:1635–1648

Moorad JA, Promislow DEL, Smith KR, Wade MJ (2011) Mating system change reduces the strength of sexual selection in an American frontier population of the 19th century. Evol Hum Behav 32:147–155

Moring B (1993) Household and family in Finnish coastal societies 1635–1895. J Fam Hist 467:395–414

Moring B (2002) Widowhood options and strategies in preindustrial northern Europe—socioeconomic differences in household position of the widowed in 18th and 19th century Finland. Hist Fam 7:79–99

Moring B (2003) Nordic family patterns and the north–west European household system. Contin Chang 18:77–109

Nettle D (2008) Why do some dads get more involved than others? Evidence from a large British cohort. Evol Hum Behav 29:416–423

Nitsch A, Faurie C, Lummaa V (2013) Are elder siblings helpers or competitors? Antagonistic fitness effects of sibling interactions in humans. Proc R Soc Lond B 280(1750):20122313

Pettay JE, Helle S, Jokela J, Lummaa V (2007) Wealth class-specific natural selection on female life-history traits in historical human populations. PLoS ONE 2:e606

Quinlan RJ, Quinlan MB (2007) Evolutionary ecology of human pair-bonds: cross-cultural tests of alternative hypotheses. Cross-Cult Res 41:149–169

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/

Rickard IJ, Holopainen J, Helama S, Helle S, Russell AF, Lummaa V (2010) Food availability at birth limited reproductive success in historical humans. Ecology 91:3515–3525

Ruxton GD, Beauchamp G (2008) Time for some a priori thinking about post hoc testing. Behav Ecol 19:690–693

Saarimäki P (2010) The Norms, Practices and conflicts of sex and marriage—premarital and marital sexual Activity in Rural central Finland in the Late Nineteenth Century. Dissertation, Jyväskylä University, Jyväskylä

Salzano FM, Neel JV, Maybury-Lewis DI (1967) Demographic data on two additional villages: genetic structure of the tribe. Am J Hum Genet 19:463–489

Schuster SM, Wade MJ (2003) Mating systems and strategies. Princeton University Press, Princeton

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 AM (1974) Old traditional agriculture in Finland in the 18th and 19th centuries. Forssan Kirjapaino Oy, Forssa, Finland

Strassmann BI (2011) Cooperation and competition in a cliff-dwelling people. Proc Natl Acad Sci U S A 108:10894–10901

Sundin J (1992) Sinful sex: legal prosecution of extramarital sex in preindustrial Sweden. Soc Sci Hist 16:99–128

Trivers R (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man 1871–197. Aldine, Chicago, pp 136–179

Willführ KP (2009) Short- and long-term consequences of early parental loss in the historical population of the Krummhörn (18th and 19th century). Am J Hum Biol 21:488–500