Family dynamics and age-related patterns in marriage probability

Jenni E. Pettay[*], Simon N. Chapman, Mirkka Lahdenperä, Virpi Lummaa

Department of Biology, University of Turku, 20014 Turku, Finland

A R T I C L E   I N F O

A B S T R A C T

In cooperatively breeding species, extended living in natal families after maturity is often associated with limited breeding possibilities and the ability to gain indirect fitness from helping relatives, with family dynamics, such as parental presence and relatedness between family members, playing a key role in determining the timing of own reproduction. How family dynamics affect marriage and the onset of reproduction in humans is complex and less well-understood. While paternal absence can be associated with both earlier puberty and reproductive behaviour, or with delayed reproduction if marriage requires parental resources, in step-parent families, half-siblings could further decrease the benefits from helping and delaying own reproduction compared to families with only full-siblings. Such costs and benefits are likely age-dependent, but have not been addressed in previous studies. Using data from pre-industrial agrarian Finland, we investigated if parental loss and remarriage affected marriage probabilities of their differently-aged sons and daughters. We found that parental composition had divergent effects across adulthood: loss of a parent resulted in a higher probability to marry in early adulthood, whereas parental presence increased later adulthood marriage probability. Whilst the death of either parent was linked to an overall lowered marriage probability, remarriage of the widowed parent, especially mother, could mitigate this effect somewhat. Additionally, the presence of underage full-siblings lowered marriage probability, suggesting postponement of one's own reproduction in favour of helping parental reproduction. Overall, our results support the idea that humans are cooperative breeders, and show the importance of considering both relatedness and age when investigating family dynamics.

1. Introduction

Parental investment is a key variable in evolutionary biology and is involved in an important life history trade-off: parents expend resources to benefit current offspring (e.g. time, energy) at a cost to their ability to invest in other components of fitness (Trivers, 1972). For cooperatively breeding animals with long lifespans, parental investment can even extend beyond the period that offspring are incapable of independent feeding. In killer whales *Orcinus orca*, for example, mothers can help their adult offspring to find food (Brent et al., 2015), thereby increasing their adult son survival (Foster et al., 2012), and in Asian elephants *Elephas maximus*, the presence of an experienced mother increases the likelihood of her young daughter's offspring to survive to adulthood (Lahdenperä, Mar, & Lummaa, 2016). In humans, due to an extremely long childhood and the importance of cultural transmission, parental care is vital in early life (Sear & Mace, 2008), can influence mate choice (Apostolou, 2007) and reproductive careers of offspring (Lahdenperä, Lummaa, Helle, Tremblay, & Russell, 2004), and can even extend to care of grandchildren (Hawkes, O'Connell, Jones, Alvarez, & Charnov, 1998).

Conversely, offspring can also help their parents in breeding attempts when ecological constraints force offspring to delay their own reproduction, and fitness can also be gained by remaining in the family group (Emlen, 1994). In many cooperatively breeding animals, parents usually dominate breeding, while offspring can help their parents by caring for their younger siblings. This breeding style is likely related to limited breeding possibilities (e.g. lack of suitable breeding sites) and the possibility of gaining indirect fitness from helping relatives (Clutton-Brock, 1998; Emlen, 1995; Kokko & Ekman, 2002). Helpers in many cooperative species are pre-reproductive previous offspring of the breeding parents, and helping might, therefore, not be particularly costly before maturation, since reproducing oneself is not yet an option for immature young. Rather, helping can benefit an individual by giving them the opportunity to learn skills later needed to raise their own future offspring successfully (Komdeur, 1996). However, after reaching maturity, the initiative for breeding might be stronger, and conflict between family members can then arise. This is seen in some human societies, where older non-mature siblings can provide care for their younger siblings (Crognier, Baali, & Hilali, 2001; Kramer, 2011; Nitsch, Faurie, & Lummaa, 2013), but can have the opposite, negative effect on

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[*] Corresponding author.
E-mail address: jenni.pettay@utu.fi (J.E. Pettay).

their siblings once they have reached sexual maturity (Nitsch et al., 2013), especially if siblings compete for heritable resources (Gibson & Gurmu, 2011). Despite this, parents will generally 'win' reproductive conflicts with their offspring when resources constrain reproductive opportunities within family: there are greater incentives for older siblings to help rear their younger siblings (relatedness = 0.5) when only parents can reproduce, than for the parents to give up own reproduction in favour of helping their offspring reproduce (and subsequently rearing their own grandoffspring, $r = 0.25$).

The dynamics of family groups are not static, however, and the nature of reproductive conflict can change if the status quo of parental dominance over reproduction is affected. Parental loss may be expected to lead to greater change in family dynamics due to conflict over who fills the resulting reproductive vacancy. This can result in changes in kinship relations if the replacement breeder comes from outside the group (Emlen, 1995). If a parent produces offspring with an unrelated mate instead of the other parent, the relatedness of future siblings would decrease (i.e. half-siblings). This means that adult offspring can gain more fitness by reproducing themselves than by helping their parents to produce half-siblings. Therefore, in humans, parental loss and remarriage could reduce adult offspring age at maturity and at first reproduction. This theory predicts that offspring age at first reproduction would be highest when both parents are present ($r_{sibling} = 0.5$). In contrast, age at first reproduction would be lowest when the parent is widowed and with no prospects of further siblings being born, so there is no incentive to delay reproduction. Finally, intermediate ages at first reproduction would dominate when the parent is with a new partner and likely to produce half-siblings ($r_{sibling} = 0.25$) (Moya & Sear, 2014). However, the effect of parental loss on reproduction does not depend solely on relatedness, as parental investment can be important for decreasing constraints on offspring reproduction. In some societies, for example, parents may act as negotiators for finding a spouse or provide the resources required for marriage, and therefore a decreased parental investment following parental death could lead to a later age at reproduction. Whether the loss of a parent affects the age at reproduction of their offspring thus depends heavily on the ecological constraints, societal structure, and customs of a population.

Additionally, stepparents can force unrelated subordinates to disperse in order to reduce reproductive competition (Hannon, Mumme, Koenig, & Pitelka, 1985). In the cooperatively breeding Seychelles warbler *Acrocephalus sechellensis*, for example, offspring were more likely to disperse when a parent was replaced by a stepparent from outside the territory than when both parents remained in the group (Eikenaar, Richardson, Brouwer, & Komdeur, 2007). Helpers are not always losers in reproductive conflicts, however, and the death of one parent can lead to the eviction of the other by reproductively active offspring (Hatchwell et al., 2004). Timing of reproduction in cooperative breeders is therefore dependent on many factors: age, resource availability, and parental presence which, as well as affecting parental investment, may also limit breeding opportunities.

Research into the evolutionary effects of human family dynamics has concentrated on the timing of puberty and reproductive behaviour when looking at whether both parents are present, or only one parent, either solo or with a step-parent. Several studies have reported earlier puberty is associated with father absence (Sheppard, Garcia, & Sear, 2014; Voland & Willführ, 2017; Webster, Graber, Gesselman, Crosier, & Schember, 2014), with the adoption of a faster life-history strategy in more unfavourable circumstances proposed as an explanation for this phenomenon (Chisholm, 1993). However, results are mixed across studies, and this phenomenon cannot therefore be claimed as ubiquitous (Sear, Sheppard, & Coall, 2019; Sohn, 2017). The effects of changing family dynamics on the reproductive timing of already matured offspring have received less attention in humans. Despite commonly appearing in animal literature on cooperative breeders, the effects of offspring age, sex, parental presence, birth order, sibling number, sibling relatedness, and resources on reproductive timing have

rarely been studied in humans at the same time in the same population and when including mature offspring of all ages, even though these can have important effects on the evolution of families and life history traits such as the onset (Moya & Sear, 2014) and end of fertility (Cant & Johnstone, 2008).

Here, we examine the effects of family dynamics on offspring age-specific marriage probability in a pre-industrial Finnish population. Reproduction was almost exclusively within marriage in historical Finland, and marriage was therefore a key fitness decision, with remarriage only possible after the spouse's death (Moring, 1996). Though marriage was the norm, not everyone who survived to adulthood married in their lifetime, and there was a skew in marriage probability between the sexes: a higher proportion of men never married during their lifetime compared to women, and more men remarried after spousal death than women (Courtiol, Pettay, Jokela, Rotkirch, & Lummaa, 2012; Lahdenperä, Lummaa, & Russell, 2011). Here, we concentrate on the effects of parents' presence or absence during adulthood (> 15 years) on daughter and son marriage age, rather than possible early childhood effects that are well-documented elsewhere (e.g. Alvergne, Faurie, & Raymond, 2008; Nettle, Coall, & Dickins, 2011; Quinlan, 2003; Sheppard, Snopkowski, & Sear, 2014). We examine if the loss of male or female parent and parental remarriage (or lack thereof) affected the marriage probability of offspring depending on the offspring age. For those with a parent who remarried, we further investigated whether the age of the mother/step-mother at remarriage/ marriage affected marriage prospects of offspring, since only a premenopausal stepmother or remarried mother could produce half-siblings and thus be in reproductive competition with adult children. We would expect parental presence helped offspring to marry, whilst remarriage of a parent could create conflict over family resources and affect help between generations. As well as offspring age and sex, we might expect to find effects of social class, as transfer of land to the next generation favoured the eldest son amongst landowners (Moring, 2003b). Similarly, there may be effects of birth order: the presence of same-sex elder siblings increased survival of younger siblings when they were pre-reproductive (Nitsch et al., 2013), but competed for mates as adults (Faurie, Russell, & Lummaa, 2009; Nitsch, Faurie, & Lummaa, 2014). By exploring the dynamic effects of kinship, resources, and age on marriage probability in a pre-industrial population where marriage was essential for reproduction, we can increase our understanding on family dynamics in humans.

2. Methods

2.1. Study population

Our study sample, recording birth, marriage, death and socioeconomic status data over the lifetime of individuals across several generations, is collected from Finnish Lutheran church book records (Gille, 1949) from families originating from eight parishes in Finland (Rymättylä, Hiittinen, Kustavi, Ikaalinen, Tyrvää, Pulkkila, Rautu and Jaakkima). Our dataset not only tracks life events of family members who remained in their natal parish in adulthood, but also records marital, reproductive, and death information of those individuals who dispersed elsewhere in the country (see e.g. Nitsch, Lummaa, & Faurie, 2016), thus reducing the likelihood that selective migration after parental loss/remarriage might have affected our results. During the study period (1700–1910), Finland was predominantly a patrilocal agrarian society with high fertility and child mortality (Turpeinen, 1979). The oldest son often stayed in his natal farm, helping his parents as a compensation for receiving the farm at the time of his parents' retirement, while younger siblings often sought service elsewhere before marriage (Moring, 1996, 2003b, 2006). The social system was monogamous, with remarriage only possible after spousal death. When a husband died, his property was divided between his widow and the children. The legal share of the widow after her spouse's death was one

third of the property. The widow could hold the headship when children were young, and was able to remarry (Moring, 2006). Though the oldest son typically inherited the farm, other sons and daughters inherited other resources such as crofts, money, or cattle, with equal shares for sons, and half shares for daughters (Moring, 1998). In the case of parental remarriage (and in the presence of half-siblings), offspring from the first marriage still got their legal share, and this was usually uncontested. The heir to the farm generally married before succeeding to headship, and would then be responsible for the upkeep of younger siblings until they married and left their natal house (Moring, 1998). Orphans were typically taken care of by relatives, neighbours, or godparents. In the absence of these alternative caregivers, orphaned children could have been fostered in farms, where they were expected to work in return of their up-keep (Pulma & Turpeinen, 1987). Men did not retire particularly early, around age 60 (Moring, 2006), except in eastern Finland (study parishes Jaakkima and Rautu), where the father remained as head of the household until his death, with brothers sharing household resources (Moring, 1999; Pettay, Lahdenperä, Rotkirch, & Lummaa, 2016). Co-residence between parents and one married child was common, and delayed departure from the parental household by younger children could be rewarded by a croft and security of life (Moring, 2003a).

Based on the occupation of the father, we categorised individuals into two socioeconomic classes - landed (farm owners) and landless (tenant farmers, crofters, servants) - because social class (and resources) is associated with many life-history traits, including later age at first reproduction, amongst the landless population (Pettay, Helle, Jokela, & Lummaa, 2007).

We selected individuals for our sample if they met all of the following criteria: a) born between 1700 and 1870 to include individuals before records became sparser (i.e. elevated level of censoring) and before the demographic transition (Anderson, Kaplan, David, & Lancaster, 1999; Bolund, Hayward, Pettay, & Lummaa, 2015; Hjerppe, 1985; Scranton, Lummaa, & Stearns, 2016), b) survived to 15 years of age (earliest age at marriage), c) born from the first marriage of both parents, and d) had the survival status (alive or dead) of both parents known.

2.2. Statistical analysis

All statistical analysis was conducted with R statistical software version 3.5.1 (R Core Team, 2018).

We first analysed how parental marriage status affected when adult children had their first marriage using discrete time-event analyses (n_{sons} = 7998, total of 94,529 observations; $n_{daughters}$ = 8026, total of 86,217 observations). We used separate models for sons and for daughters, implemented as binomial generalised linear mixed-effects models (GLMMs), using the *lme4* package version 1.1-12 (Bates, Maechler, Bolker, & Walker, 2015). Yearly marriage status was set as the response variable (time-varying binary: 0, not married; 1, married). Individuals entered the analysis at age 15 and remained in the analyses until they were married, were no longer recorded (i.e. censored or died), or until they reached 40 years old, whichever came first. An interaction between parental marriage status (time-varying 6-level factor: both parents alive, both parents dead, only mother dead, only father dead, mother remarried, and father remarried) and offspring age (time-varying continuous) was included as an explanatory factor to test the prediction that parental marriage status will differentially affect the marriage prospects of their offspring depending on the offspring age. As divorce was forbidden by the church except in exceptional circumstances (Sundin, 1992), and as the sample contained no divorcees, remarriage of either parent indicates their spouse was deceased. It should be noted that the different statuses are not independent from each other and are correlated with time of observation. For instance, individuals whose fathers remarried must have first suffered maternal loss, and the older an individual, the more likely they were to experience parental

loss. Our main explanatory variable, the interaction of age with parental status, allowed us to deal with this: as both of these variables are time-dependent in our model, the parental status is allowed to change with age within the same individual. Similarly, the model also takes into account that the probability of belonging to each parental status grouping changes with offspring age.

Social class (2-level factor: landed, landless), number of living older same-sex siblings (i.e. older brothers for sons, older sisters for daughters; time-varying continuous), number of younger siblings of either sex under the age of 15 (time-varying continuous), half-siblings (time-varying continuous), and parental marriage status and age were included as fixed effects. Birth order was not explicitly controlled for, as it was highly correlated with the number of living older same-sex siblings. Father ID was added as a random effect to control for variation between families (shared family-level effects), as were study parish (8-level factor) and birth cohort (17-level factor, in 10 year bins e.g. 1700–1709, 1710–1719 etc.), to control for spatial and temporal variation respectively.

We then further investigated the role of social status as a mediator of parental status effects on marriage probability, amongst those who could potentially inherit land, and separately amongst those who could not inherit because their family did not own land. We first subset both the son and daughter datasets into those with the social class 'landed' (n_{sons} = 4157, 50,556 observations; $n_{daughters}$ = 4162, 43,749 observations) and 'landless' (n_{sons} = 3841, 43,973 observations; $n_{daughters}$ = 3864, 42,468 observations). These GLMMs did not include social class as a fixed effect, but were otherwise the same as the base models for sons and daughters.

Following this, we investigated how the effect of parental status on marriage probability could be affected by whether an individual was the oldest child of their sex (thus being able to inherit/benefit most from parental investment), or not the oldest child of their sex. As for the social status models, we subset the son and the daughter datasets into 'first living child' (n_{sons} = 5110, 57,438 observations; $n_{daughters}$ = 5260, 53,690 observations) and 'not first living child' (n_{sons} = 3324, 37,091 observations; $n_{daughters}$ = 3219, 32,527 observations). These GLMMs were largely identical to the above models, differing only in that the number of living older same-sex siblings term was removed. Additionally, for the 'first living child' models, individuals could enter the analysis older than 15 if an older same-sex sibling had died in that year (and thus were no longer the oldest living sibling). Likewise, the death of an older same-sex sibling could lead to individuals being censored in the 'not first living child' models if they then became the oldest living child of their sex.

Finally, to explore how parental remarriage and the possibility of competing half-siblings affected marriage probability, we created two further subsets for the main son and daughter datasets - one subset including all individuals with both parents alive plus those individuals (and years) with their mother remarried (n_{sons} = 5524, 49,487 observations; $n_{daughters}$ = 5491, 44,527 observations), and the other subset including all individuals with both parents alive plus those individuals with their father remarried (n_{sons} = 5637, 51,700 observations; $n_{daughters}$ = 5539, 46,173 observations). We then calculated the age at which the mother married the stepfather and the age of the stepmother when she married the father. If this was before 45, she was considered potentially reproductive (mother remarried analysis: n_{sons} = 404, 4045 observations, $n_{daughters}$ = 398, 3238 observations; father remarried analysis: n_{sons} = 496, 4582 observations, $n_{daughters}$ = 449, 3832 observations) i.e. capable of producing competing half-siblings. If after, she was classed as post-reproductive (mother remarried analysis: n_{sons} = 151, 1108 observations, $n_{daughters}$ = 151, 1002 observations; father remarried analysis: n_{sons} = 326, 2784 observations, $n_{daughters}$ = 259, 2054 observations). All individuals with both parents alive were included as the reference level for a baseline probability of remarriage (both analyses: n_{sons} = 5006, 44,334 observations; $n_{daughters}$ = 4992, 40,287

observations). We then ran models with the nearly the same terms as the base models: the parental marriage status term was replaced with a term for mother/step-mother age at the mother/father's second marriage (3-level factor: "pre-45", "post-45", "control").

To select the simplest model for each analysis, we sequentially removed terms based on differences in Akaike information criterion (AIC), with the lowest AIC the best-fitting. The use of AIC was to avoid overfitting (see Burnham & Anderson, 2002 for further details). The key variable is the parental marriage status by age interaction, and all others are potential confounders. The AIC process identifies which of these terms do not improve the fit of the model (and therefore which terms will be of minor importance at best). Terms retained in each model following this procedure can be found in Tables S1–S4. Significance of interaction terms were assessed with likelihood ratio testing using the function *mixed* from package *afex* (Singmann, Bolker, Westfall, & Aust, 2017), as parametric bootstrapping can have unfeasibly long computational times.

We note here that a family-fixed effects Cox regression (Allison, 2009) can be used as an alternative, complementary modelling approach to that used here. However, we did not include this for several reasons. First, analysis would have been limited to only those individuals with living same-sex adult siblings. In pre-industrial Finland, the number of children surviving to adulthood was variable, but generally low (2 or 3), and thus we would lose a lot of statistical power from dropping all individuals who were the only adult offspring of their sex in the family. Second, later-born siblings are always more likely to experience the loss of parents (s) or parental remarriage. This could introduce greater biases when variation is limited to within-family and disregards between-family variation, as is the case for a family-fixed effect approach (Allison, 2009). Lastly, unobserved heterogeneity at the family level is already accounted for with random effect (see Willführ & Gagnon, 2013) – here, father ID.

3. Results

Overall, 67.4% of adult children in this study married at or before age 40: 66% of men (n = 5279) and 68.8% of women (n = 5529) (Fig. 1). Only 7.7% (n = 613) of men and 8.7% (n = 699) of women remained unmarried at age 40. The remainder were unmarried but died or were censored before age 40. Mean age at marriage was 26.2 ± 4.4 for men and 24.7 ± 4.8 for women. Both men and women tended to marry earlier than this when both parents were still alive
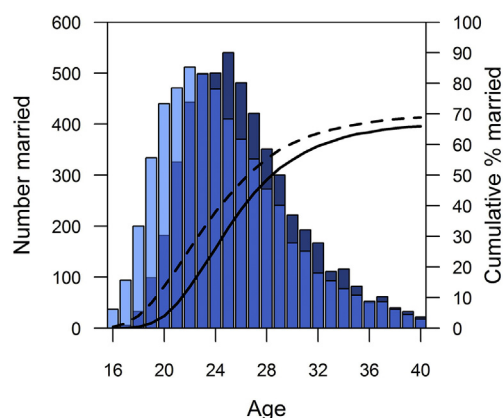

Fig. 1. Number and cumulative percentage of adult children marrying by age. Women generally married younger than men. Light blue bars indicate women, dark blue indicate men, and intermediate colour of blue indicates an overlap. Solid line refers to cumulative percentage of men in the sample who married, and dashed line refers to the same but for women. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
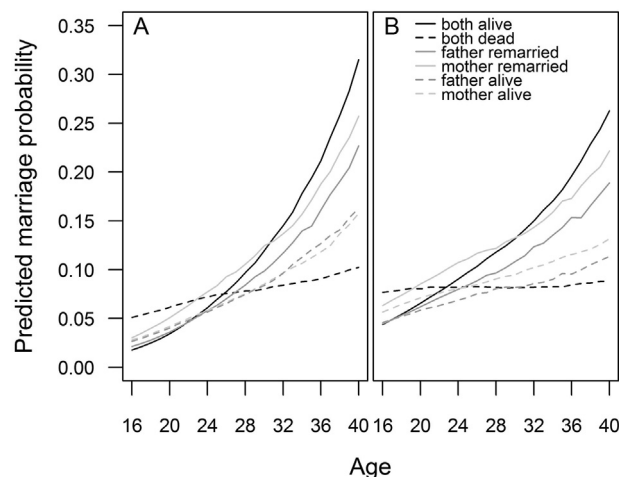

Fig. 2. Age-specific marriage probability by parental status for adult children. a) sons, and b) daughters. For both a) sons and b) daughters, parental death or remarriage increased marriage probability compared to when both were alive in early adulthood. Later adulthood marriage probability was highest when both parents were still living. Lines indicate parental status: solid black = both parents alive, dashed black = both parents dead, solid dark grey = father remarried, solid light grey = mother remarried, dashed dark grey = only father alive, and dashed light grey = only mother alive.

(mean$_{sons}$ = 25.3 ± 4.0, mean$_{daughters}$ = 23.5 ± 4.2). Of those who married, 39.8% (n = 2102) of sons and 43.6% (n = 2411) of daughters married before the death of either parent, whilst 14.5% (n = 767) and 13.4% (n = 739) of sons and daughters married after parental remarriage.

In cooperative species, changes in family structure can lead to either delays or acceleration in reproduction. In support of this, we find parental status affected marriage probability of their children. There was a significant interaction between age and parental status for both men (χ^2_5 = 311.96, p < 0.001) and women (χ^2_5 = 197.95, p < 0.001) (Fig. 2, Table S1). Marriage probability was highest in early adulthood for sons if both parents were dead (at age 20, 78.6% higher probability of marrying than when both parents were alive), but was lower than when both parents were alive by the mean age of marriage (age 26, 2.5% lower) (Table 1). Whilst the death of either parent was linked to a lowered marriage probability, remarriage of the widowed parent could mitigate this effect somewhat (Fig. 2, Table 1). For both men and women, higher numbers of younger siblings under age 15 reduced marriage probability (β = −0.060 ± 0.015, p < 0.001 and β = −0.070 ± 0.013, p < 0.001 respectively).

As decisions to marry could relate to inheritance and wealth in this population, with landed offspring gaining more resources from parents than landless offspring, we tested for the effects of parental status in

Table 1
Percentage difference between marriage probability with each parental status compared to both parents alive for sons and daughters at age 20, average age of marriage (24 for women, 26 for men), and age 35.

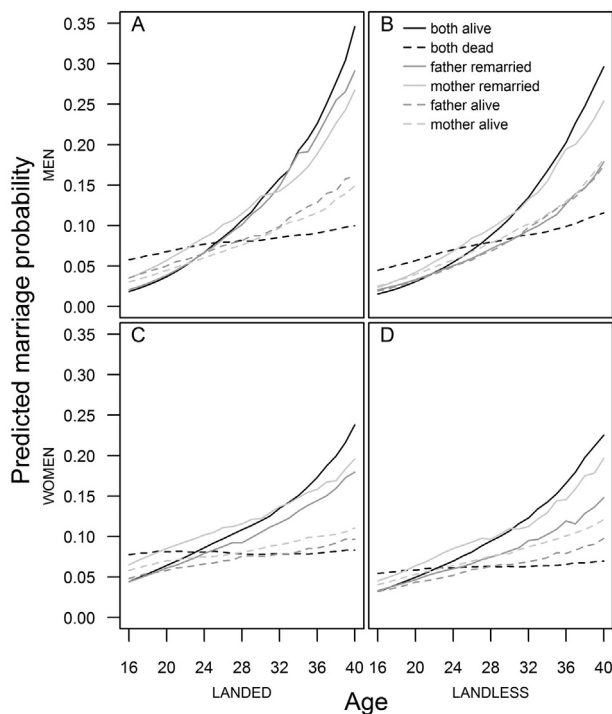| Parental status	Focal sex	Age 20 (%)	Average age of marriage (%)	Age 35 (%)
Both dead	Male	+78.6	−2.5	−54.4
	Female	+22.5	−9.3	−54.6
Only mother alive	Male	+22.1	−14.1	−42.1
	Female	+8.4	−11.0	−38.1
Mother remarried	Male	+47.7	+19.6	−11.6
	Female	+30.0	+18.8	−6.3
Only Father alive	Male	+17.1	−12.0	−38.0
	Female	−10.8	−23.9	−47.2
Father remarried	Male	+4.9	−9.6	−25.4
	Female	−5.7	−11.4	−21.3

Fig. 3. Age-specific marriage probability by parental status for adult children with different social statuses. For a) landed sons, b) landless sons, c) landed daughters, and d) landless daughters, parental death or remarriage increased marriage probability compared to when both were alive in early adulthood. In all models, later adulthood marriage probability was highest when both parents were still living. Lines indicate parental status: solid black = both parents alive, dashed black = both parents dead, solid dark grey = father remarried, solid light grey = mother remarried, dashed dark grey = only father alive, and dashed light grey = only mother alive.

Table 2
Percentage difference between marriage probability with each parental status compared to both parents alive for sons and daughters at age 20, average age of marriage, and age 35 for social class models.

Parental status	Focal sex	Model	Age 20	Average age of marriage	Age 35
Both dead	Male	Landed	+83.3	−7.3	−57.2
		Landless	+84.5	+8.1	−48.1
	Female	Landed	+25.9	−6.5	−51.6
		Landless	+17.9	−12.3	−57.9
Mother alive	Male	Landed	+21.1	−20.7	−46.3
		Landless	+29.3	−2.3	−34.2
	Female	Landed	+8.8	−13.4	−38.7
		Landless	+7.2	−8.1	−36.6
Father alive	Male	Landed	+35.9	−12.4	−40.5
		Landless	+4.5	−17.4	−34.6
	Female	Landed	−9.4	−23.4	−47.2
		Landless	−12.5	−25.2	−47.6
Mother remarried	Male	Landed	+54.7	+18.2	−16.8
		Landless	+38.1	+21.5	−4.8
	Female	Landed	+32.8	+18.4	−8.6
		Landless	+28.6	+22.1	−5.5
Father remarried	Male	Landed	+4.3	−2.3	−7.9
		Landless	+8.3	−14.4	−38.6
	Female	Landed	−4.8	−8.3	−14.2
		Landless	−6.2	−13.5	−28.6

different social classes. The parental status by age interaction was significant for both landed and landless men (landed: $\chi_5^2 = 214.30$, $p < 0.001$; landless: $\chi_5^2 = 116.33$, $p < 0.001$) and women (landed: $\chi_5^2 = 109.30$, $p < 0.001$; landless: $\chi_5^2 = 89.05$, $p < 0.001$). The highest overall probability of marriage in all the social class models was

when both parents were alive (Fig. 3, Table 2 & Table S2), but, again, the highest probability in earlier adulthood was when both parents were dead. Father's remarriage significantly lowered marriage probability compared to both parents being alive for landless men ($\beta = -0.056 \pm 0.014$, $p < 0.001$), but did not significantly lower marriage probability for landless women ($\beta = -0.026 \pm 0.015$, $p = 0.076$), landed men ($\beta = -0.020 \pm 0.014$, $p = 0.169$), or landed women ($\beta = -0.015 \pm 0.014$, $p = 0.274$). Mother's remarriage also did not significantly lower marriage probability compared to both parents being alive for landless men ($\beta = -0.027 \pm 0.018$, $p = 0.128$), landless women ($\beta = -0.014 \pm 0.018$, $p = 0.446$), or landed women ($\beta = -0.027 \pm 0.018$, $p = 0.058$), but it did significantly decrease marriage probability of landed men ($\beta = -0.049 \pm 0.014$, $p < 0.001$). Number of older brothers decreased marriage probability in landed men ($\beta = -0.067 \pm 0.024$, $p = 0.004$).

As inheritance and distribution of wealth is unequal for offspring in this population, we tested marriage probability for the oldest living child of each sex, and for those who were not the oldest living child of that sex. The interaction of parental status and age was significant for sons (oldest: $\chi_5^2 = 174.52$, $p < 0.001$; not oldest: $\chi_5^2 = 129.08$, $p < 0.001$) and daughters (oldest: $\chi_5^2 = 113.16$, $p < 0.001$; not oldest: $\chi_5^2 = 84.79$, $p < 0.001$), regardless of whether they were the oldest living or not. In other words, firstborns (farm inheritors) did not disproportionally benefit or suffer from parental death and remarriage as compared to laterborns. For children who were the oldest living, marriage probability was similar to that of the overall model (Fig. 4, Table 3
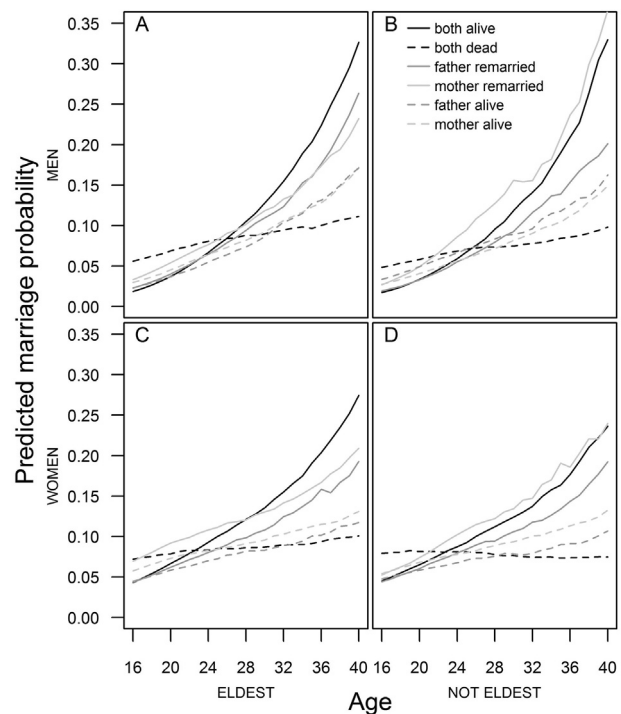

Fig. 4. Age-specific marriage probability by parental status for adult children with different sibling ranks. For a) oldest living sons, b) not oldest living sons, c) oldest living daughters, and d) not oldest living daughters, parental death or remarriage increased marriage probability compared to when both were alive in early adulthood. For sons and daughters who were not the oldest, mother remarriage increased marriage probability across adulthood (albeit insignificantly), whilst all other parental statuses decreased marriage probability. All parental statuses decreased marriage probability later in life for the oldest children. Lines indicate parental status: solid black = both parents alive, dashed black = both parents dead, solid dark grey = father remarried, solid light grey = mother remarried, dashed dark grey = only father alive, and dashed light grey = only mother alive.

Table 3
Percentage difference between marriage probability with each parental status compared to both parents alive for sons and daughters at age 20, average age of marriage, and age 35 for sibling models.

Parental status	Focal sex	Model	Age 20	Average age of marriage	Age 35
Both dead	Male	Oldest	+85.1	−0.4	−52.5
		Not oldest	+73.3	−4.3	−55.5
	Female	Oldest	+18.0	−10.5	−52.0
		Not oldest	+24.9	−7.4	−55.0
Mother alive	Male	Oldest	+22.4	−13.3	−39.5
		Not oldest	+21.5	−15.2	−45.1
	Female	Oldest	+9.9	−10.7	−41.0
		Not oldest	+4.6	−10.9	−33.3
Father alive	Male	Oldest	−0.5	−24.2	−37.5
		Not oldest	+47.7	−1.7	−37.9
	Female	Oldest	−12.2	−24.6	−47.2
		Not oldest	−9.9	−22.9	−44.8
Mother remarried	Male	Oldest	+45.6	+7.1	−20.5
		Not oldest	+47.2	+43.8	+10.0
	Female	Oldest	+37.9	+16.5	−16.1
		Not oldest	+13.9	+16.9	+16.7
Father remarried	Male	Oldest	+7.9	−6.8	−21.1
		Not oldest	−1.5	−12.1	−26.9
	Female	Oldest	−6.6	−13.4	−24.0
		Not oldest	−7.3	−9.0	−17.9

Fig. 5. Boxplots of marriage probability by remarriage age of mother/step-mother for adult children. a) sons were more likely to marry if their mother was older than 45 when she remarried, but b) stepmother age at father remarriage did not affect their marriage probability. For daughters, c) marriage probability was increased regardless of mother age at remarriage, whilst d) stepmother age at father remarriage also had no effect on marriage probability. From left to right, boxes refer to marriage probability with both parents alive, with remarriage when mother/step-mother was younger than 45 years old, and marriage probability with remarriage when mother/step-mother was 45 or more years old.

& Table S3). For children who were not the oldest, however, marriage probability when their mother was remarried did not significantly differ from the marriage probability when both parents were still living (men: β = −0.011 ± 0.020, p = 0.590; women: β = 0.002 ± 0.020, p = 0.939; Table 3).

Additionally, we ran the interaction models on only the individuals who had lost a parent, starting in the year of parental death, to independently estimate the effect of parental loss and of remarriage (see Willführ & Gagnon, 2013). As these results were similar to those in the full models (see Table S1, Figs. S1–S5), we are confident that no significant biases were introduced by the dependence of remarriage on parental death.

The timing of remarriage may have affected marriage decisions, as reproductive age mothers/mothers-in-law could potentially produce half-siblings (who might compete for parental resources). Sons were significantly more likely to marry if their mothers remarried when they were post-reproductive (age 45 and later) (β = 0.422 ± 0.145, p = 0.004; odds ratio 1.53 [1.15, 2.02]), but not if they remarried when they were younger than 45 (β = 0.008 ± 0.107, p = 0.937; odds ratio 1.01 [0.82, 1.24]) (Fig. 5a). If half-siblings were present, however, marriage probability was then significantly increased (β = 0.151 ± 0.054, p = 0.005); the possibility of a competing half-sibling alone was not enough to affect marriage probability. Whether a step-mother married a focal individual's father before or after age 45 did not, however, affect marriage probability of sons (Fig. 5b; Table S4). In all cases, for men and women when either their father or mother remarried, having more dependent (under age 15) younger full siblings reduced the probability of marriage (Table S4). Step-mother age at father remarriage similarly had no effect on the marriage probability of daughters (Fig. 5d; Table S4). The effect of mother remarriage, however, differed for daughters in that marriage probability significantly increased regardless of whether mother was older or younger than 45 at her age of remarriage (Fig. 5c; Table S4).

4. Discussion

Our results on family dynamics show signs of both cooperation and intergenerational conflict over family resources in this pre-industrial agrarian population. First, we found that parental death and remarriage did indeed affect offspring marriage probability, but such effects varied across different life-stages of the offspring, as indicated by the
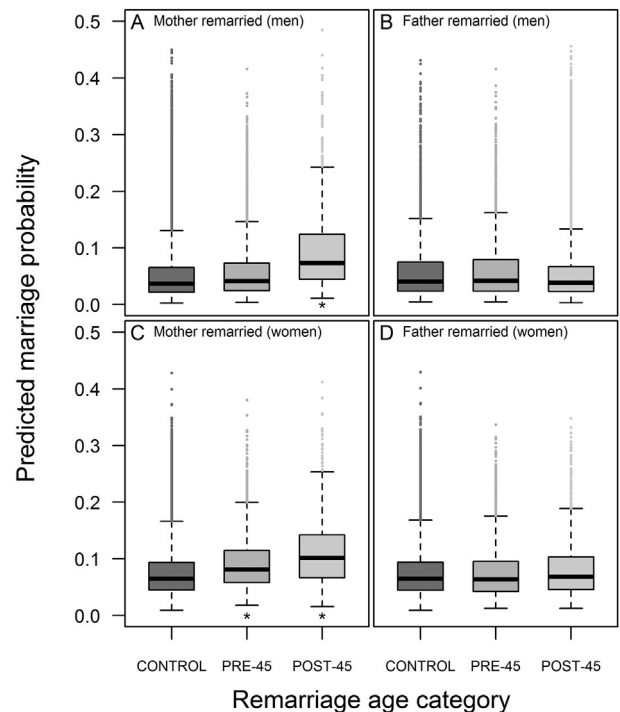
interaction with age in each model. In both sexes, marriage probability was highest in early adulthood if both parents were dead. However, by the mean age of marriage, the probability of marriage of orphans was lower than for those who had both parents alive. Whilst the death of either parent was linked to a lowered marriage probability, remarriage of the widowed parent, especially the mother, could mitigate this effect. It further seems that in peak marrying ages (in mid-twenties) the effect of parental death or remarriage was less important than in later ages, when marriage probability was highest if both parents were alive or the mother was remarried. Presence of underage full-siblings lowered offspring probability of marriage, suggesting postponement of their own reproduction in favour of helping parental reproduction in both men and women. For males, the presence of half-siblings increased the probability of marriage, which may result from greater expected fitness gains from personal reproduction in such situations, in contrast to when helping to raise full siblings. Overall, our results further support the idea that humans are cooperative breeders, and that family dynamics are affected by both relatedness and age. These should therefore be investigated in concert in any future studies.

Our finding that death of both parents increased marriage probability in early adulthood is in accordance with findings that parental absence expedites reproduction (Hatchwell & Komdeur, 2000; Quinlan, 2003; Voland & Willführ, 2017). Even though studies have mainly concentrated on the absence of the father, absence of both parents was not likely to be uncommon in the evolutionary past of our species. With these data, we cannot distinguish whether this may have been caused by an unfavourable environment, which selects for behaviours that favour early reproduction (Draper & Harpending, 1982), or by relaxed intergenerational conflict over reproduction (Moya & Sear, 2014). For

early adulthood (before mean marrying age), our results fit with the predictions by Moya and Sear (2014) about how relatedness in a family affects reproductive timing: the lowest probability of marriage is when parents are alive, and the highest when a parent is dead. For example, at age 18 men's and women's probability to marry was 128% and 46% higher when both parents were dead than when both parents were alive. One possibility is that, while young men and women with less parental investment were more likely to marry, they might have been marrying lower quality spouses, and therefore earlier marriage would indicate lesser parental allocation rather than relaxed competition (Shenk & Scelza, 2012). Orphaned adolescents were often living either with more distant relatives or non-related caregivers such as god-parents, who might have hastened the transition to marriage and independence to reduce the length of their own investment into up-keeping.

Furthermore, Moya and Sear (2014) predict that marriage probability would be intermediate if a step-parent is present. In our data this was true when the mother remarried. However, in the ages when most marriages were contracted (Fig. 1), a dead parent lowered marriage probability, rather than increased it, and mother remarriage increased marriage probability the most for both men and women, though the situation did not differ from when both parents were alive. After the typical ages for marriage were passed, parental presence and remarriage was positively associated with marriage, while marriage probability was lowest when both parents were dead. One way to interpret this is that amongst those who did not marry before or during peak marriage ages, parental presence helped to attract a spouse. For example, at age 30 men's marriage probability was 33% lower when both parents were dead compared to when both parents were still alive, and for women, the probability was 38% lower at age 30. Our findings are interesting since we found that parental presence or absence had age-variable effects on adult offspring, which has rarely been studied in the past.

As heritable resources were likely to be important for marrying, we also tested effects of parental presence in those who had a heritable resource (i.e. a farm), and also in landless people who had less wealth. We would expect potential for intergenerational competition for farm resources is stronger in landowning class. However, we did not find indications of this; parental status effects followed the general pattern in all categories, suggesting that inherited resources were not crucial for these effects. For landed men, the number of living older brothers decreased marriage probability, indicative of reproductive conflict between brothers, in accordance with a previous study in this population (Nitsch et al., 2013). Birth order is often important in terms of mating success and reproductive outcomes (Faurie et al., 2009; Kokko & Ekman, 2002; Nitsch et al., 2013), and societal practices in humans may have a strong mediating influence on the effects of birth order. However, parental status had largely similar effects on oldest living men and women compared to later born men and women in our study population.

For both men and women, higher numbers of underage younger full-siblings reduced marriage probability. This effect was small, but consistent over sexes, social classes, and birth orders, with the exceptions of landless men and 'not oldest' daughters, and was present after controlling for age and birth order amongst living same-sex siblings. This supports the general concept of cooperative breeding that young postpone their own reproduction in favour to help their parents to rear their siblings (Emlen, 1995), though may also reflect that the benefit-cost ratio of staying may outweigh the benefit-cost ratio of dispersing (Creel & Creel, 2015). That 'low-ranking' daughters would not stay to help may be related to group size: in some cooperative breeders, individuals, particularly helping females, lower their investment to young with larger group size (Legge, 2000; Woxvold, Mulder, & Magrath, 2006) Therefore, staying to help would not necessarily be beneficial for younger daughters. Landless men may not stay to help, as the costs of staying to help in a poor family will outweigh the benefits, e.g. higher

competition for limited resources.

When parents are producing half-siblings, offspring are theoretically not expected to invest as much in their parents' reproduction, instead focusing on their own (Green, Freckleton, & Hatchwell, 2016; Komdeur, 1994). In humans, the potential for a parent to produce half-siblings is dependent on the age of the remarrying mother or mother-in law. Theory suggests that offspring would have a higher initiative to reproduce themselves and a higher competitive effort for reproduction if their parent is going to produce half-sibling (Moya & Sear, 2014). We found that mother remarriage both before and after age 45 increased daughter's marriage probability compared to both parents being alive, suggesting that the possibility of competition due to potential future half-siblings was either not a driver of marriage decisions, or was not the only driver. For sons, marriage probability was increased only when the remarrying mother was over 45, indicating they had no higher initiative to reproduce when their mother was capable of producing half-siblings. However, we found partial support for lower investment to half-siblings; sons were more likely to marry if half-siblings by their mother were present, whereas a similar effect from the father's side was not present.

Reproduction was almost exclusively within marriage in historical Finland. Selection favoured younger age at first reproduction, at least in women (Pettay et al., 2007), though most people married in their mid-twenties. Reasons for this may have been lack of livelihood opportunities (e.g. availability of land) or the skills needed for running a farm. Contracting a marriage was likely affected by numerous factors, including age, wealth, personality, attractiveness, and availability of suitable mates. With historical data of the kind used in the present study, we can control for some of these to an extent (e.g. age and wealth), but personal attributes are not possible to assess in register information. Though we can assume spousal death to have been non-dependent on spousal qualities, those who remarried might have been more attractive as a spouse, and they might share these qualities with their offspring. In this population, women were less likely than men to marry after widowhood (Lahdenperä et al., 2011; Pettay, Rotkirch, Courtiol, Jokela, & Lummaa, 2014), so those who did remarry might have been especially attractive mates. This could explain the finding that mother remarriage appear to be better than widowed single mother in terms of probability to marry. One other possible driver of marriage patterns is the addition of resources a step-parent would have brought into the household. Our historical Finnish population differs from many populations, in that dowry or bridal wealth were not required for marriage, therefore parental power over marriage was probably not as high as it is in those populations where they are essential. While only one of the offspring (typically, but not always the oldest son) inherited the natal farm, other offspring and landless individuals had to try to save or wait for an opportunity to get a croft (Moring, 2003a). Furthermore, both sons and daughters were working in the farm in the landowning class, reducing need to hire outside workforce; sons and daughters were likely to be seen as a resource rather than as a burden.

To understand how family structure and dynamics are important for cooperation and conflict in human families, it is important to investigate how they interplay with relatedness, resource availability, and whether they differ by age patterns. We found that in this historical agrarian Finnish population, parental composition had age-specific effects on the marriage probability of their adult children, as did the presence of both younger and older siblings, supporting evolutionary models for dynamics of families.

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interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2019.09.001.

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