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Effects of female reproductive competition on birth rate and reproductive scheduling in a historical human population

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Costly reproductive competition among females is predicted to lead to strategies that reduce these costs, such as reproductive schedules. Simultaneous births of co-resident women in human families can reduce their infant survival, but whether such competition also affects overall birth rates and whether females time their pregnancies to avoid simultaneous births remain unknown, despite being key questions for understanding how intra-female competition affects reproductive strategies. Here, we used detailed parish registers to study female reproductive competition in historical Finnish joint − families, where brothers stayed on their natal farms and sisters married out, and consequently unrelated daughters-in-law often co-resided and competed for household resources. We quantified the time-varying effects of having reproductive-aged competitor(s) on a woman's interval from marriage to first childbirth, on age-specific fertility, and on birth scheduling. Contrary to our hypothesis, the presence of one or several potential female competitors did not lead to longer first birth intervals or lower age-specific probability of reproduction. We also found no evidence that women would schedule their reproduction to avoid the real cost of simultaneous births on their offspring mortality risk; age-specific reproductive rates were unaltered by changes in the presence of other infants in the household. These results raise interesting questions regarding the evolution of fertility suppression in social mammals in different contexts, the costs and benefits of extended families for female reproductive success and strategies deployed, and the cultural practices that may help to avoid the negative outcomes of female reproductive competition in human families.

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Competition for reproduction among females is one of the cornerstones of the theory of natural selection (Clutton-Brock and Huchard 2013). Nevertheless, breeding competition between males has gained much more attention than competition between females, maybe because male competition often involves observable contests or distinguishable secondary sexual characteristics, such as antlers in deer, while female competition is less visible (Clutton-Brock and Huchard 2013; Clutton-Brock 1982; Plard et al. 2011). Compared to the profound variance in male reproductive success caused by such competition, differences in female reproductive success are usually less pronounced, requiring long-term data over several breeding attempts in order to be detected (Clutton-Brock and Huchard 2013). In social species, female competition arises over reproductive resources such as food, mates and breeding sites (Cant et al. 2009; Stockley and Bro-Jorgensen 2011). Intra-female competition may lower the reproductive success of some females, especially subordinates, through reduced fertility or offspring survival, consequently increasing variation in female reproductive success (Clutton-Brock 2009; Stockley and Bro-Jorgensen 2011). In extreme cases only dominant females breed, while subordinates have their own reproduction suppressed to help rear the dominants' young (Clutton-Brock 2007).

Female competition in primates is common (Isbell & Young 2002), suggesting it may also have posed a significant selective pressure during human evolution. Group size and ecological conditions are known to affect primate female fertility and reproductive success. For example, wild female baboons (*Papio cynocephalus*) from Amboseli, Kenya, had lower conception rates when they were living in large groups, but only in drought conditions (Beehner et al. 2006). Aggression from other females can also lead to increased rates of abortion and reductions in juvenile survival in many mammalian species

(Stockley and Bro-Jorgensen 2011). In line with this, studies on humans have found that reproductive competition among women can increase infant mortality in some populations: simultaneous reproduction of daughter-in-law and mother-in-law in historical Finnish households led to significantly reduced survival of the resulting babies of both parties (Lahdenperä et al. 2012); child condition and survival can be compromised in polygamous families where co-wives compete for resources (Strassmann 1997); and in historical joint-families – where several unrelated women of reproductive age co-resided in the same households – the risk for offspring mortality before adulthood increased by 23 per cent when co-resident women reproduced close to each other (Pettay et al. 2016).

Such costly competition may have promoted the evolution of birth scheduling in order to avoid resource competition with other reproductive females in the household (Pettay et al. 2016). However, with the exception of research on the evolution of female menopause due to intergenerational reproductive competition of women in patrilocal populations (Cant and Johnstone 2008; Lahdenperä et al. 2012; Mace and Alvergne 2012; Mace 2013; Snopkowski et al. 2014), relatively few studies have investigated the effects of reproductive competition among women on their birth rates in general, and on adaptive birth scheduling that could minimise the costs of co-breeding in particular. Female competition may manifest itself as increased social stress, which may in turn affect the likelihood of conception, full-term pregnancy and child survival. The possibility of such effects is suggested by studies showing that, among contemporary Western women, lower self-esteem and lack of support from family and friends are associated with reproductive problems such as infertility, ovulatory delay, and habitual spontaneous abortions, as well as with complications at and following parturition, abandonment, and even child abuse (Wasser and Barash 1983). A Danish study found substantially reduced fecundability among women undergoing infertility treatments if they were distressed (Boivin

86 and Schmidt 2005), although not all studies have found associations between self-reported stress and

87 conception rate (Lynch et al. 2012). However, studies of high-income and low-fertility societies may

88 not represent reproductive strategies typical in the past. The causes and outcomes of social and physical

89 stress in modern high-income societies are likely to differ from patterns in more traditional societies,

90 due to increases in living standards, higher energy intake, reduced physical activity, and the

91 postponement of reproduction (Jasienska 2013), as well as the disappearance of large households and

92 ensuing lower daily involvement of close kin in the lives of mothers (Sear and Coall 2011).

93 One opportunity to study the consequences of female reproductive competition on fertility outcomes is

94 provided by family systems in which women of the same age share resources and potentially compete

95 for reproductive opportunities. Mating patterns affect the degree of genetic relatedness of group

96 members, which in turn shape kin altruism and competition (Cant and Johnstone 2008). Individuals are

97 predicted to behave more altruistically when they are closely related, compared to less genetically

98 related individuals (Hamilton 1964). At the same time, kin and affinal kin also compete for shared

99 resources, and kin competition may sometimes override the effects of kin altruism on behaviour (West

100 et al. 2002). Human dispersal patterns include patrilocality, where the young woman moves to her

101 husband's residence and male kin are highly genetically related, and matrilocality, where the young

102 husband moves into the woman's parents' house and female kin are highly related (Hill et al. 2011).

103 Human families can also consist of parents and offspring only (nuclear family), include grandparents

104 (extended stem family), or include siblings and their families alongside with grandparents (joint

105 family). Furthermore, the parents may be a monogamously married couple raising their offspring or a

106 polygynous man (or polyandrous woman) with multiple spouses. Such a wide range of residence and

107 mating patterns in humans offers possibilities for advancing our understanding of how reproductive

108 conflict affects fertility suppression in different socio-ecological contexts. To our knowledge, however,

no previous study has investigated whether co-resident women adaptively schedule their births in order to avoid costly simultaneous breeding (in terms of offspring survival) with other women (Pettay et al. 2016). Understanding how the presence of other women affects overall birth rates and whether females of reproductive age specifically time their pregnancies to avoid simultaneous births with their rivals are key questions for advancing our understanding of how intra-female competition affects reproductive strategies.

Here, we investigate whether female-female reproductive competition affected fertility behavior in a patrilocal monogamous society in historical Finland, characterized by joint families. These joint families included brothers with their families who lived in the same household, so that most co-residing women were sisters-in-law who were not genetically closely related. This family type was connected to lower dispersal possibilities, and also to wealth accumulation within families, so that richer families could afford to have more people under the same roof and thus larger manpower for fieldwork, which was crucial in this agrarian society (Moring 1999). In a previous study, we found that simultaneous reproduction (within 2 years) among sisters-in-law in joint families was associated with lower offspring survival (Pettay et al. 2016). Here, we investigate whether the negative effect of female competitors on offspring survival was associated with behavioral changes in childbearing patterns. We use detailed longitudinal demographic data on family reproductive histories from Eastern Finland (see Pettay et al. 2016) in order to test whether the fertility of the females in joint families decreased when several women of reproductive age women were co-living in the same household.

Specifically, our hypothesis is that competition between unrelated women may suppress their fertility, and/or women may also adaptively time their births so as to avoid costly simultaneous births with other-co-resident women. First, we determine the interval from marriage to first birth in the presence of co-living women. Interval from marriage to first birth is a good measure for reproductive capability,

since no modern contraceptive methods were available, and children in marriage were seen as highly desirable and raised the new wife's status in the family (Sirén 1999). Even if some methods of birth spacing or contraception were used after the desired number of children had been achieved, this was highly unlikely to happen before the first birth (Nenko et al. 2014). Second, we examine whether age-specific fertility of women was affected by the presence of female competitors. We are interested in age patterns in relation to the possible effects of competition, since women's social prestige and other abilities to compete for joint resources can be assumed to increase with age in traditional populations (Mace and Alvergne 2012). Third, we estimate if women were scheduling births to avoid costly simultaneous reproduction arising from co-living, by assessing the dynamics of the birth timings between all reproductive women in the household at each time point.

METHODS

Study population and data

We use demographic data collected from Finnish population registers in order to study female reproductive competition within households of the pre-industrial era. The Lutheran Church kept census, birth/baptism, marriage and death/burial registers of each parish in the country since the 17th century, covering almost the whole population of Finland from 1749 onwards (Gille 1949; Luther and Erjos 1993). These registers allow for the construction of detailed reproductive and marital histories of each individual from birth to death (Gille 1949). This study uses data collected from church book records from two parishes, Rautu and Jaakkima. They are now situated in the Republic of Karelia of the Russian Federation but were part of the Finnish province of Vyborg until 1945. The main source of livelihood in the area was farming (Moring 2003). Living standards were generally modest during the

154 study period and child mortality was high: approximately 45% of children died before age 15. Age at

155 first birth was 23.77±0.16 (mean±standard error) on average for women in this population and they had

156 given birth to 5.05±0.11 children during their lifetime.

157 The study area is situated east of the Hajnal line, which is characterized by patrilocal joint households –

158 laterally extended families where married brothers co-reside with their ageing parents (Hajnal 1965;

159 Moring 1999). This family type is associated with labor intensive slash-and-burn agriculture. Family

160 compositions changed over time, and the same house could be inhabited by joint- and nuclear family

161 types at different periods (Moring 1999). We identified households with multiple reproductive-aged

162 women from women's houses of residence, as recorded in the parish registers. In some cases these

163 numbers may refer to a small compound of households, rather than households in which members ate

164 at the same table. Reproductive-aged women in the same household were usually daughters-in-law,

165 while a very small minority would have consisted of daughters of the house. It was also possible to be

166 part of a household by contract as an equal partner (a man and his family) without biological family ties

167 (Partanen 2004). Although the degree of relatedness between cohabiting reproductive women is not the

168 focus of our analysis, very few reproductive women would have been close kin and their children

169 would usually be paternal cousins.

170 Since socioeconomic status is known to affect survival and other life-history traits in historical Finns

171 (Pettay et al. 2007), socioeconomic status of each house was robustly categorized as landowner

172 (wealthy) or landless (poor); larger tenant farms (lampuoti) were placed in the same category with

173 landowners. Servants were seldom hired in joint-families (Moring 1999), and therefore the majority of

174 women in our data set were categorized as landowners (only 16% of women were classified as

175 landless). The sample of women included in this study corresponds closely with Pettay et al. (2016)

176 study investigating effects of competition on the co-resident women's offspring survival, with the

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177   exception that the current study question and design enabled including also women censored before the

178   end of their potential reproductive life, leading to an inclusion of a further max. 98 women (depending

179   on the study question, see below) not part of the previous study.

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181   **Statistical analysis**

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183   All statistical analyses were conducted using SAS (SAS Institute Inc., release 9.4).

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185   **(i) Presence of competitor and first birth interval**

186   We tested differences in the interval from marriage to first birth in women who married into a house

187   either with or without at least one resident and already married women of reproductive age (termed

188   "competitor"). The sample consisted of all women with known house number, marriage date and

189   timing of first birth (N=662) born 1801–1917. We considered only the first marriages of these women.

190   We included only women who married before the year of 1937, since the beginning of the Finnish

191   Winter War in 1939 and the ensuing absence of men was likely to affect conception rate. 438 women

192   married into a house without a competitor, 114 to a house with one, 30 with two, and 11 with 3

193   competitors. We grouped women with 1, 2, and 3 competitors together, to get a two-category factor:

194   competitor present against no competitor present. The focal women, or newcomers who married into a

195   house, were usually younger than the other females already present in that household; only in 10

196   marriages was the newcomer older than another married woman already residing in that house. First

197   birth interval was measured as months from date of marriage to date of delivery of first child, rounded

198 to the nearest full month. To exclude premarital conceptions and thus an unknown starting point of our

199 first birth interval (as well as for female co-residence), we removed from the sample women who gave

200 birth to a child less than nine months after marriage. The mean first birth interval after these exclusions

201 was 20.39 months (standard error.±0.8, N=593). Competitor in the house was, for this analysis, defined

202 as a woman residing in the same house who was under 51 years of age. We identified 155 women who

203 married into a house which already had at least one competitor defined this way.

204 The response variable in this analysis was first birth interval, which was quantified as the number of

205 months between a female marrying and delivering her first child. Since the length of first birth interval

206 is a non-normally distributed count variable, the analysis was conducted by using generalized linear

207 mixed effects model (GLMMs) with negative binomial errors and a logit link function. Our main term

208 of interest was whether there were other reproductive-aged women present in the same household at the

209 time of the focal woman's marriage (yes vs no). To control for possible confounding terms affecting

210 fertility, we included the following terms in the regression model: socioeconomic status (two levels,

211 landowners and landless), parish (two levels), birth year (1801-1917 as a continuous covariate), and the

212 focal woman's age at marriage (as a continuous covariate; woman's age at marriage as quadratic term

213 was also tested but was dropped since it did not reach statistical significance of $p < 0.05$). Month of

214 marriage (to take into account possible seasonal fluctuations of physical work, Nenko et al. 2014) and

215 husband's age were also investigated, but similarly dropped for non-significance. We also tested for the

216 interaction between competitor presence and age of focal woman to determine if e.g. younger women

217 were more affected by the competitor than older women, but this too was dropped from the final model

218 as non-significant.

219 Household identity was fitted as a random factor to account for the cluster effect from the same

220 household.

221

(ii) Presence of competitor and age-specific fertility

The effect of competitor presence on the focal woman's age-specific fertility was investigated by a discrete time event model, where women's fertile period was partitioned annually, consisting of 7086 records from 427 women. We implemented this with a generalized linear mixed-effects model (GLMM) with binomial error and a logit link function with fertility status each study year set as the response variable (binomial: no birth vs. birth). This method allows a sensitive analysis of the effects of time-dependent factors, such as the presence of competitor(s) changing from year to year (Allison 1999; Steele 2005). Only women whose year of first marriage was known were included and the sample was limited to women who had given birth at least once during their lifetime. We included only years from the first birth, since factors affecting the probability of the first birth might differ from subsequent births, and the interval to first birth is covered in section (i). Censored individuals were included until the year of departure even if they were not followed until age of 50, as long as the marital and reproductive histories of these women were known until the censoring year. We further restricted our analysis to years when the husband was alive in the previous year. As in the previous analysis, we again included only years from 1820 to 1938, since the beginning of the Finnish Winter War in 1939 and the ensuing absence of men was likely to affect conception rates.

Our main term of interest in this analysis, competition, was measured as the presence of one or more married women of reproductive age (aged under 51) living in the house with the focal woman (two levels, competitor present or not) at each age. In 26.48% of records (person years) one competitor was present, in 10.60% two competitors, and in 2.60% three competitors were present, in contrast to 60.32% records without recorded competitor present. Our sample thus consists of 2790 records

243 (observation years) with competitor present versus 4296 records with competitor present. A mother-in-

244 law under 51 years was only found in 94 records of person-years. Preliminary analyses suggested no

245 difference in fertility between having one or more competitor present. Competition was therefore

246 analysed as none present vs. at least one competitor present (pooling records of one, two or three

247 competitors with variable sample sizes). Since we were especially interested in whether competition

248 affected a female's birth rate across different ages and whether the competition had different effects at

249 different female ages, we fitted the focal woman's age and quadratic term of age as well as interactions

250 between age and the competition variable.

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252 We included time since last event as years from last birth in order to account for multiple events (Steele

253 2005). If the time since last event exceeded 10 years, these years were grouped following Mace &

254 Alvergne (2012). Parity (range 1-14) was fitted as a fixed factor to account for order of events, and 7 or

255 more births were grouped since parities above 7 were relative rare (10% of records). Parish (two

256 levels) and socioeconomic status (two levels) were fitted to adjust for variation from geographic and

257 socio-ecological sources and year to adjust for temporal variation in fertility patterns. Since currently

258 having a baby and breastfeeding are likely to reduce the probability to give birth, we included a term

259 (nursing) to indicate whether each woman, at each age, had a living child under the age of two years to

260 nurse and its interaction with woman's age (Steele 2005). For example, if a child died the following

261 year from his/her birth, for the next year of the mother's life this term was scored as zero. The term was

262 also zero for the third year after birth, even if the child was still alive. Survival to age two was

263 unknown for 378 records, and we assigned these years of the focal woman's life a third level "nursing

264 unknown" in order to include in the model otherwise valuable data points. We also tested for time

265 effect (year) and biologically interesting interactions (e.g. between socioeconomic status and nursing

266 status), but since these were not statistically significant they were dropped from the model.

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Focal female identity was nested into house identity as a random term, and was fitted to take into

account both repeated measures from the same woman and the cluster effects of households.

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To study the possibility that the age of a potential competitor would affect fertility, we re-ran the above

model, but this time classified competitor to be either none, younger, older, or of similar age. In case

more than one competitor was simultaneously present, we used the age of the competitor closest to the

focal individual's own age. A competitor of similar age was defined as one born within two years in

either direction of the focal woman's birth. A younger woman was defined as being born at least two

years after, and an older women at least two years before the focal individual's birth. In this sample, the

potential competitor was absent in 4295 records, at least two years younger than the focal woman in

1195 records, at least two years older than the focal person in 981 records, and the potential competitor

was approximately of the same age as the focal woman in 614 records.

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(iii) Presence of reproducing competitor and scheduling of births

In order to investigate whether reproduction of other resident women in the household (in contrast to

simply their presence as in the analyses above) affected the birth scheduling (age-specific fertility) of

our focal woman, we lastly defined immediate competition as a situation when another woman in the

same household had given birth within 2 years of each focal woman's follow-up years. In the years

where the focal individual had given birth herself, we considered reproductive overlap to have occurred

when a competitor had given birth six months to two years before her, in order to restrict competition

to situations where the competitor could affect the fertility of the focal person. Our rationale for

considering competitor births at least six (rather than nine) months before as having the possibility to

290   affect the focal woman's birth rate is that first trimester spontaneous abortions could be caused by

291   conflict between females (Neugebauer et al. 1996). Our data had 733 records with reproductive

292   competition thus defined, compared to 6353 observation years with no competition. Our primary term

293   of interest was whether the other resident women recently reproducing vs. not reproducing affected our

294   focal women's probability of giving birth at each age (as in section ii). We also investigated the

295   interaction between competition and focal woman's age, in case the effect of competitor reproduction

296   on the focal woman's probability to give birth herself changes with her age.

297   In a similar manner to the previous model ii (GLMM, see full definition above), we fitted age and age

298   squared, time since last birth, parity, nursing status (3 levels, see definition above) and its interaction

299   with age, parish (two levels), and socioeconomic status (two levels) in the model as covariates, and

300   focal female identity as a random term nested into house identity.

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303   **RESULTS**

304   **(i) Presence of competitor and first birth interval**

305   The mean first birth interval (from marriage to first birth) in our sample was 20.39 months (S.E.±0.8)),

306   indicating that the new wife typically became pregnant toward the end of her first year in the new

307   household. The length of the first birth interval was not affected by the presence of other married

308   women of reproductive age in the household at the time of marriage (21.70±1.06 months without

309   competitor compared to 20.06±1.4 with competitor present) (Table 1.). This result is robust to

310   adjustments for a number of potential confounding terms included in our model. For example, the first

birth interval was on average 4.55 months shorter for women from Jaakkima (N=450) compared to

women from Rautu (N=143) and this regional effect was considered in our analyses (Table 1.). The

birth year of the newcomer also had a small but statistically significant effect on her birth interval

length, indicating a shorter first-birth interval later in the study period also documented in other parts of

Finland (Nenko et al. 2014). In contrast, the effect of socioeconomic status or focal woman's age at

marriage did not reach statistical significance. Mean age at marriage in this sample was 22.04±0.16

years, ranging between 15 and 39 years (95% quantile before age 30), and thus most women in this

sample were in their peak fertile years when marrying. This might explain the somewhat surprising

result that age at marriage was not significantly associated with the time span between marriage and

first birth.

(ii) Presence of competitor and age-specific fertility

We did not find any effect of reproductive competition, defined as the presence of other reproductive-

aged married women in the household, on overall age-specific fertility (chance to give birth at given

ages) of our focal women, nor that the effect of reproductive competition would change with the focal

woman's age (Table 2). As was to be expected, the probability to give birth was affected by the focal

woman's age, and probability of giving birth in this sample of married and once reproduced women

declined with age (Figure 1). If the focal woman had a child less than two years of age, her probability

to give birth was low even at young ages, when otherwise the probability to give birth was high (SI

Figure 1.). Other confounding factors are presented in Table 2.

Re-running the same analysis with the competitor status split into groups (no competitor present,

younger, of similar age, and older), we did not find that the relative age of competitors affected age-

333   specific fertility ($F_{3,6632}=0.91$, $P=0.2$), or that the age of competitors had a varying effect at different

334   focal woman ages (interaction between age class of competitor and focal woman's age; $F_{3,6632}=0.84$,

335    $P=0.5$ (SI Table 4.).

336

337   **(iii) Presence of reproducing competitor and scheduling of births**

338   In the last analysis, we investigated whether women were adjusting their birth schedule to avoid the

339   adverse effects of simultaneous reproduction with other co-resident women. The mean inter-birth

340   interval of all births in our sample was 2.70 ± 0.31 years but with considerable variance between

341   different women and also between the births of the same woman. This variation offered possibilities to

342   adaptively schedule births so as to avoid reproducing close to another woman in the household.

343   However, when investigating competition as recent reproduction by a potential competitor, we did not

344   find that reproduction of another woman in the house in the previous year or earlier the same year

345   (more than six months before) would have affected the focal woman's probability to give birth; this

346   lack of effect remained similar across all ages of the focal woman (Table 3). The effects of other

347   factors included in the analysis were similar to those reported in section ii (Table 3).

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350   **DISCUSSION**

351   Simultaneous reproduction of several women in a given household is known to have negative

352   consequences for their infants' survival, raising the question of whether such costly competition may

353   have promoted birth scheduling in order to avoid resource competition with other reproductive females

in the family (Cant & Johnstone 2008, Lahdenperä et al. 2012, Mace and Alvergne 2012, Pettay et al. 2016). We studied whether the presence and/or reproductive timing of unrelated, reproductive-aged female competitors in laterally extended families in historical Finland, usually sisters-in-law, suppressed the fertility of other women in the family. Despite the documented negative effects of simultaneous births of such women on their infant survival rates (Pettay et al. 2016), we found no evidence of reproductive scheduling, nor did we discover overall reductions in fertility, among women faced with female competition. These results raise interesting questions regarding the evolution of fertility suppression in humans and other social mammals in different contexts, the costs and benefits of extended families in humans for female reproductive success and strategies deployed, and the cultural practices that may help to avoid the negative outcomes of reproductive competition in human families.

First, we measured first-birth intervals in relation to whether a house already had women of reproductive age when a newly married wife moved in. Marriage marks the official right to start childbearing in many societies, including our study population; indeed, children were desired and expected in marriage. The first birth interval, or time between marriage and first birth, is a known measure of reproductive ability in different conditions (Nenko and Jasienska 2013): a previous study found that poor women take longer to conceive after marriage during periods with low food availability, while the birth intervals of wealthier women are less sensitive to variation in food availability at the time of marriage (Nenko et al. 2014). Given that the vast majority of already-present women in our study families were older than the newcomer and had established families and positions within the household, we might expect the young wife's competing power to be low compared to that of a woman already resident in the house, with potential effects on her fertility. In particular, lack of family support or stress are known to lead to a range of reproductive problems, including ovulatory delays and spontaneous abortions (Wasser and Barash 1983), that could lengthen the first birth interval.

However, the fertility of young brides was not affected by the presence other reproductive-aged women in the household in our population. Of course, the lack of association might be explained by confounding factors not considered in our analysis. However, our models did adjust for a number of key traits such as temporal, spatial and socioeconomic differences in fertility, and any variation due to age. It could also be argued that the presence of older, more experienced wives in the household might have served as help and guidance to the new bride or could have reduced her workload and aided fertility, since more "working hands" increased net productivity of a farm in Finland during this period (Moring 1999). However, given that the simultaneous childbearing among females is known to reduce infant survival in the same population (Pettay et al. 2016), we see this as an unlikely scenario. We also found no overall positive effect on fertility of co-residing females. It thus appears that the motivation and capacity of young married women to give birth soon after the wedding outweighed any negative effects that reproductive competition might have posed on her fecundity or the resulting child's survival prospects (Pettay et al. 2016). One crucial factor is the importance of the first-born child in tying the woman into her new family, and the status and respect this provided from the husband's family and in society at large (Sirén 1999). There was also no evidence that the women's overall fertility across lifetime, measured as her age-specific probability to reproduce, would have been reduced by the presence of other reproductive-aged women in the household at a given time, or that possible effects of competition on fertility would vary according to her own age.

Although neither the initial nor the overall fertility of women was hampered by the presence of reproductive competitors in the household, women could still have aimed to adaptively time their pregnancies so as to avoid direct competition for resources with their potential rivals. Given that offspring survival was 23% lower if women reproduced within 2 years of each other in these households (Pettay et al. 2016), such birth scheduling would have likely resulted in higher overall

reproductive success. In other species, adaptive timing of pregnancies relative to other females in the group can be very elaborate: for example, in banded mongooses (*Mungos mungo*) all females in the group aim to give birth simultaneously in the same burrow to avoid infanticide by dominant females (Cant et al. 2014). However, we did not find any indication that women schedule their reproduction by not giving birth after a child had been born to another woman in the house: age-specific reproductive rates were unaltered by time-varying changes in the presence of other infants in the household. Several non-mutually exclusive possibilities could explain this finding. First, the costs of occasionally giving birth simultaneously with another woman in the household might not have been big enough to select for physiological or behavioral mechanisms to avoid simultaneous reproduction. It is still largely unknown how sensitive human female reproduction is to environmental cues and how heritable possible adjusting behaviour is (Vitzthum 2009). Alternatively, one could also expect women to give birth to more babies when a competitor was reproducing, given that simultaneous births increased child mortality (Pettay et al. 2016) – in theory, this could result in replacement births since women are more likely to become pregnant again once they stop breastfeeding. Indeed, probability of giving birth at a given time was higher for women who did not currently have young children themselves compared to women with infants. However, adjusting for the presence of nursing children in our analysis did not reveal any positive or negative effects of competitor's reproduction on a woman's fertility.

It could also be that the negative effects of female co-residence are realized only when the infants are most vulnerable, while co-residence at other times brings benefits or is neutral, or that infant survival is more sensitive to the costs posed by competition than the conception rate. The physiological costs of nursing infants exceed those of pregnancy (Butte and King 2005), and thus we might have only been able to detect negative effects of co-residence on the former. Indeed, several studies suggest that in natural fertility societies, variation in child mortality might be more important than variation in fertility

in determining reproductive success (Sear et al. 2003; Strassmann and Gillespie 2002). Therefore, women may not have suffered the costs of reproductive competition themselves in the form of reduced ability to conceive, but rather those costs were transferred to their offspring. Additionally, females in our agrarian population may have faced special constraints on reproductive scheduling that have been absent from other preindustrial populations. For example, our population had cultural practices discouraging infanticide, which in some societies has been a way of spacing children (Hrdy 1999).

Finally, it could also be that the presence of several infants in the household increased the likelihood of infection by childhood infectious diseases, the main cause of mortality in our population (Hayward et al. 2016), whilst older children would have already been immune and not act as carriers. Overall, reproductive conflict in many situations can be caused by extrinsic causes such as dilution of resources or susceptibility to diseases or predators, rather than active competition between females (Clutton-Brock 2016).

Our results are of interest in light of the current theories for the evolution of menopause (ceased reproduction at older age). Cant and Johnston (2008) have suggested that female menopause evolved due to intergenerational reproductive competition of women in patrilocal populations, where women marry outside their own natal group and cohabit with their in-laws. Because a mother-in-law is related to the offspring of her daughter-in-law through her son but not *vice versa*, daughters-in-law would win an evolutionary conflict over breeding priority. The evolution of menopause would resolve this conflict. Simultaneous reproduction of daughter- and mother-in-law can indeed reduce the survival of infants from both parties (Lahdenperä et al. 2012), and consequently such reproductive events in historical and contemporary high-fertility populations are rare: in pre-industrial Finland, only 6.6 per cent of mothers delivered a child within 2 years of their first grandchild (Lahdenperä et al. 2012), and in rural Gambia becoming a maternal grandmother significantly decreased the probability of giving

446   birth again (Mace and Alvergne 2012). This lack of reproductive overlap between generations is

447   achieved through menopause and further enhanced by social norms, such as late age at marriage (Mace

448   and Alvergne 2012) or customs for the older generation to refrain from reproduction when daughters or

449   sons start their families (reviewed in Cant et al. 2009).

450   Why, then, has similar avoidance of reproductive conflict not evolved against peers who are

451   reproductive competitors, even though it is likely that in our evolutionary past residence patterns would

452   also have exposed women to such group competition? In the case of competing generations of women

453   in patrilocal populations, the older women face an evolutionary disadvantage resulting from kinship

454   dynamics. However, in the joint families investigated here, the competing women were typically

455   equally unrelated to each other's offspring, and of the same generation, which means that there can be

456   no selection to "win" the conflict.

457   In most mammal populations age increases social status and competitive ability (Clutton-Brock and

458   Huchard 2013). However, age did not interact with the presence of competitors in any of our analysis,

459   indicating that the effects of competition did not vary according to the focal woman's age. Our results

460   thus differ from those from rural Gambia, where young women had lower fertility in the presence of

461   unrelated reproductive-aged women in their compound compared to older women (Mace and Alvergne

462   2012). The lack of an age effect in our data could either reflect the social equality of Finnish brothers

463   and their families, as suggested in historical research (Moring 1999, Waris 1999), or that elder women

464   were indeed likely to be dominant but this did not translate to fertility differences in this population.

465   There were also cultural means to avoid conflict between in-laws. Joint families were already

466   becoming rarer during the study period (Moring 1999), so that women who lived in joint families had

467   perhaps chosen this family type over others due to expected benefits of the ensuing lifestyle, such as

468   extra land resources. Our study individuals had a possibility to split farms when necessary or to migrate

469 if they did not get along; farms were occasionally split between brothers (Moring 1999). Therefore, due

470 to a rather equal share of resources and relatedness, any costs of conflict were likely identical to all

471 participants, and rather than reproductive restraint, a behavioral solution to severe costs of conflict may

472 have been to split the group (Hughes 1988).

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483 Data accessibility: Analyses reported in this article can be reproduced using the data provided by Pettay

484 et al. (2017).

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486 **REFERENCES**

487 Allison PD. 1999. Logistic regression using the SAS System: theory and application SAS Institute Inc.,
488 cary, NC

489 Beehner JC, Onderdonk DA, Alberts SC, Altmann J. 2006. The ecology of conception and pregnancy
490   failure in wild baboons. Behav Ecol 17:741-50.

491 Boivin J1, Schmidt L. 2005. Infertility-related stress in men and women predicts treatment outcome 1
492   year later. Fertil Steril. 83:1745-52.

493 Bove RM, Vala-Haynes E, Valeggia C. 2014. Polygyny and women's health in rural mali. J Biosoc Sci
494 46:66-89.

495 Butte NF1, King JC. 2005. Energy requirements during pregnancy and lactation. Public Health Nutr
496   8(7A):1010-27.

497 Cant MA and Johnstone RA. 2008. Reproductive conflict and the separation of reproductive
498   generations in humans. Proc Natl Acad Sci U S A 105:5332-6.

499 Cant MA, Johnstone RA, Russell AF. 2009. Reproductive skew and the evolution of menopause. In:
500   Hager R and Jones CB, editors. Reproductive skew in vertebrates. Cambridge (UK): Cambridge
501   University Press. p. 24-50.

502 Cant MA, Nichols HJ, Johnstone RA, Hodge SJ. 2014. Policing of reproduction by hidden threats in a
503   cooperative mammal. Proc Natl Acad Sci U S A 111:326-330.

504 Clutton-Brock T and Huchard E. 2013. Social competition and its consequences in female mammals. J
505   Zool 289:151-71.

506 Clutton-Brock T. 1982. The functions of antlers. Behaviour 79:108.

507 Clutton-Brock T. 2007. Sexual selection in males and females. Science 318:1882-5.

508 Clutton-Brock T. 2009. Cooperation between non-kin in animal societies. Nature 462:51-7.

509 Clutton-Brock T. 2016. Mammal societies. John Wiley & Sons Ltd, Chicester, UK. p. 60-63.

510 Gille H. 1949. The demographic history of the northern european countries in the eighteenth century.
511   Pop Stud. 3:3-65.

512 Hajnal J. 1965. European marriage pattern in historical perspective. In: Glass DV and Eversley DEC,
513   editors. Population in history. London: Arnold. p.101.

514 Hamilton WD. 1964. Genetical evolution of social behaviour. J Theor Biol 7:1.

515 Hill KR, Walker RS, Bozicevic M, Eder J, Headland T, Hewlett B, Hurtado AM, Marlowe FW,
516   Wiessner P, Wood B. 2011. Co-residence patterns in hunter-gatherer societies show unique human
517   social structure. Science 331:1286-9.

518 Hrdy SB. 1999. Mother Nature: Natural selection and the female of the species. London: Chatto and
519   Windus, Great Britain. p.288-317.

520 Hughes AL. 1988. Evolution and human kinship. Oxford University Press, Oxford, England

521 Isbell LA, Young TP. 2002. Ecological models of female social relationships in primates: Similarities,
522   disparities, and some directions for future clarity. Behaviour 139:177-202.

523 Jasienska G. 2013. The Fragile Wisdom. An Evolutionary View on Women's Biology and Health.
524   Harvard University press, cambridge, Massachusetts

525 Ji T, Wu J, He Q, Xu J, Mace R, Tao Y. 2013. Reproductive competition between females in the
526   matrilineal mosuo of southwestern china. Philos Trans R Soc Biol Sci. 368:20130081.

527 Lahdenperä M, Gillespie DOS, Lummaa V, Russell AF. 2012. Severe intergenerational reproductive
528   conflict and the evolution of menopause. Ecol Lett. 15:1283-90.

529 Lawson DW, James S, Ngadaya E, Ngowi B, Mfinanga SGM, Borgerhoff Mulder M. 2015. No
530   evidence that polygynous marriage is a harmful cultural practice in northern Tanzania. Proc Natl
531   Acad Sci USA. 112:13827-13832.

532 Luther G and Erjos M. 1993. Suomen tilastotoimen historia vuoteen 1970. Helsinki: Tilastokeskus.

533 Lynch CD, Sundaram R, Louis GMB, Lum KJ, Pyper C. 2012. Are increased levels of self-reported
534   psychosocial stress, anxiety, and depression associated with fecundity? Fertil Steril. 98:453-8.

535 Mace R. 2013. Cooperation and conflict between women in the family. Evol Anthropol. 22:251-8.

536 Mace R and Alvergne A. 2012. Female reproductive competition within families in rural gambia. Proc
537 Biol Sci. 279:2219-27.

538 Moring B. 2003. Nordic family patterns and the north-west european household system. Contin
539   Change. 18:77-109.

540 Moring B. 1999. Land, labor, and love: Household arrangements in nineteenth century eastern Finland
541   - cultural heritage or socio-economic structure? Hist Fam. 4:159-84.

542 Nenko I, Hayward AD, Lummaa V. 2014: The effect of socio-economic status and food availability on
543 first birth interval in a pre-industrial human population. Proc Biol Sci 281:20132319.

544 Nenko I, Jasienska G. 2013. First birth interval, an indicator of energetic status, is a predictor of
545   lifetime reproductive strategy. Am J Hum Biol 25:78–82.

546 Neugebauer R, Kline J, Stein Z, Shrout P, Warburton D, Susser M. 1996. Association of stressful life
547   events with chromosomally normal spontaneous abortion. Am J Epidem 143: 588-596.

548 Partanen J. 2004. Isän tuvasta omaan tupaan : Väestö ja kotitaloudet karjalankannaksen maaseudulla
549   1750-1870. Helsinki (Finland): Suomalaisen Kirjallisuuden Seura.

550 Pettay JE, Lahdenperä M, Rotkirch A, Lummaa V. 2016. Costly reproductive competition between co-
551   resident females in humans. Behav Ecol 2016; 27: 1601-1608.

552 Pettay JE, Helle S, Jokela J, Lummaa V. 2007. Natural selection on female life-history traits in relation
553   to socio-economic class in pre-industrial human populations. Plos One 2(7):e606.

554 Pettay JE, Lahdenperä M, Rotkirch A, Lummaa V.. 2017. Data from: Effects of female reproductive
555 competition on birth rate and reproductive scheduling in a historical human population. *Dryad Digital*
556 *Repository.* http:// doi:10.5061/dryad.vv08k.

557 Plard F, Bonenfant C, Gaillard J. 2011. Revisiting the allometry of antlers among deer species: Male-
558   male sexual competition as a driver. Oikos 120:601-6.

559 Sear R, Coall D. 2011. How much does family matter? Cooperative breeding and the demographic
560   transition. Popul Dev Rev 37 (s1), 81-112

561 Sear R, Mace R, McGregor I. 2003. The effects of kin on female fertility in rural gambia. Evol Hum
562   Behav 24:25-42.

563 Silk JB. 2007. The adaptive value of sociality in mammalian groups. Philos Trans R Soc B-Biol Sci
564   362:539-59.

565 Sirén K. 1999. Suuresta suvusta pieneen perheeseen : Itäsuomalainen perhe 1700-luvulla. Helsinki
566 (Finland): Suomen historiallinen seura.

567 Skjaervo GR and Roskaft E. 2013. Menopause: No support for an evolutionary explanation among
568   historical norwegians. Exp Gerontol 48:408-13.

569 Snopkowski K, Moya C, Sear R. 2014. A test of the intergenerational conflict model in indonesia
570   shows no evidence of earlier menopause in female-dispersing groups. Proc Biol
571   Sci. 281(1788):20140580.

572 Solomon NG FJ. 1997. Cooperative breeding in mammals. Cambridge (UK): Cambridge University
573   Press.

574 Steele F. 2005. Event history analysis. ESRC National Centre for Research Methods Briefing Paper. In
575   NCRM Methods Review Papers (NCRM/004). Bristol, UK: University of Bristol.

576 Stockley P and Bro-Jorgensen J. 2011. Female competition and its evolutionary consequences in
577   mammals. Biolog Rev 86:341-66.

578 Strassmann BI. 1997. Polygyny as a risk factor for child mortality among the dogon. Curr Anthropol.
579   38:688-95.

580 Strassmann BI. 2011. Cooperation and competition in a cliff-dwelling people. Proc Natl Acad Sci U S
581   A 108:10894-901.

582 Strassmann B and Gillespie B. 2002. Life-history theory, fertility and reproductive success in humans.
583   Proc Biol Sci 269:553-62.

584 Voland E and Beise J. 2002. Opposite effects of maternal and paternal grandmothers on infant survival
585   in historical krummhorn. Behav Ecol Sociobiol 52:435-43.

586 Vitzthum V J. 2009. The ecology and evolutionary endocrinology of reproduction in the human female.
587   Am J Physicl Anthropol. 140 Suppl, 95–136.

588 Waris E. 1999. Yksissä leivissä: Ruokolahtelainen perhelaitos ja yhteisöllinen toiminta 1750-1850.
589   Helsinki (Finland): Suomen historiallinen seura.

590 Wasser S and Barash D. 1983. Reproductive suppression among female mammals - implications for
591   biomedicine and sexual selection theory. Q Rev Biol 58:513-38.

592 West SA, Pen I, Griffin AS. 2002. Cooperation and competition between relatives. Science 6:72-5.

593 rsbl.2006.0463.

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606 Table 1. First interbirth interval (in months) in relation to presence of other women of reproductive age
607 in the house at the time of marriage of the focal woman (N=593).

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term	estimate	s.e.	mean	s.e.	Num DF	Den DF	F value	p-value
competitor presence at time of marriage					**1**	**399**	**1.61**	**0.2**
no competitor	0.078	0.06	21.70	1.06				
competitor present	0.000	.	20.06	1.4				
parish					**1**	**399**	**7.13**	**0.01**
Jaakkima	-0.218	0.08	18.71	0.98				
Rautu	0.000	.	23.26	1.8				
socio economic status					**1**	**399**	**2.09**	**0.15**
wealthy	-0.105	0.07	19.79	0.92				
poor	0.000	.	21.99	1.69				
birth year	**-0.004**	**0.00**			**1**	**399**	**10.37**	**0.002**
age at marriage	**-0.008**	**0.01**			**1**	**399**	**1.41**	**0.24**

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Table 2. Age-specific fertility, after the first birth, in relation to presence of other women of

reproductive age (competitor) (N=7086).

term	estimate	s.e.	mean	s.e.	Num DF	Den DF	F value	p-value
Competition					1	6637	1.95	0.16
no competitor present	-0.67	0.48	0.43	0.07				
competitor present	0.00	.	0.51	0.08				
age	-1.01	0.09			1	6637	118.49	<.0001
age²	0.00	0.00			1	6637	11.84	<.001
age*competition					1	6637	0.57	0.45
age*no competitor present	0.01	0.01						
age*competitor present	0.00	.						
time since last birth					9	6637	44.84	<.0001
2 years	2.11	0.11	0.58	0.065				
3 years	0.31	0.17	0.19	0.04				
4 years	0.60	0.20	0.24	0.06				
5 years	0.84	0.25	0.28	0.07				
6 years	1.45	0.30	0.42	0.09				
7 years	1.82	0.37	0.51	0.11				
8 years	2.79	0.41	0.73	0.09				
9 years	2.73	0.54	0.73	0.09				
10 or more years	3.76	0.48	0.88	0.06				
1 year	0.00	.	0.15	0.03				
Parity					6	6637	49.8	<.0001
2	2.59	0.20	0.23	0.01				
3	4.46	0.29	0.13	0.03				
4	6.42	0.39	0.52	0.08				
5	8.14	0.49	0.86	0.05				
6	9.56	0.57	0.96	0.02				
7	12.22	0.71	1.00	0.00				
1	0.00	.	0.00	0.00				
Nursing status					2	6637	68.31	<.0001
previous child under 2 years	-5.60	0.48	0.16	0.04				
status of previous child not known	-0.87	0.97	0.31	0.08				
no child under 2 years	0.00	.	0.88	0.03				
Age*Nursing status					2	6637	10.37	<.0001
previous child under 2 years	0.06	0.02						
status of previous child not known	-0.06	0.03						
no child under 2 years	0.00	.						
socioeconomic status					1	6637	14.06	<.001

landowner	-1.68	0.45	0.28	0.05				
landless	0.00	.	0.67	0.11				
Parish					**1**	**6637**	**0.2**	**0.65**
Jaakkima	-0.16	0.35	0.45	0.07				
Rautu	0.00	.	0.49	0.10				

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632 Table 3. Age-specific fertility, after the first birth, in relation to competition overlap (whether another

633 woman in the household gave birth to a child 2-0 years before) (N=7086).

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term	estimate	s.e.	mean	s.e.	Num DF	Den DF	F value	p-value
Competition (reproductive overlap)					1	6636	2.15	0.14
no competition overlap	-0.73	0.50	0.46	0.08				
competition overlap	0.00	.	0.50	0.08				
age	-1.01	0.10			1	6636	115.4	<.0001
age²	0.00	0.00			1	6636	11.35	<.001
age*competition					1	6636	1.21	0.27
age*no competition overlap	0.02	0.01						
age*competition overlap	0.00	.						
time since last birth					9	6636	44.85	<.0001
2 years	2.12	0.11	0.60	0.06 6				
3 years	0.30	0.17	0.20	0.05				
4 years	0.59	0.20	0.25	0.06				
5 years	0.82	0.25	0.29	0.07				
6 years	1.44	0.30	0.43	0.09				
7 years	1.79	0.37	0.52	0.11				
8 years	2.75	0.41	0.74	0.91				
9 years	2.69	0.53	0.73	0.12				
10 or more years	3.73	0.49	0.88	0.06				
1 year	0.00	0.00	0.15	0.04				
Parity					6	6636	48.62	<.0001
2	2.56	0.20	0.02	0.01				
3	4.42	0.29	0.14	0.04				
4	6.37	0.39	0.53	0.08				
5	8.08	0.49	0.86	0.05				
6	9.50	0.57	0.96	0.02				
7	12.13	0.71	1.00	0.00				
1	0.00	.	0.00	0.00				
Breastfeeding status					2	6636	67.81	<.0001
previous child under 2 years	-5.57	0.48	0.02	0.05				
status of previous child not known	-0.93	0.97	0.33	0.09				
no child under 2 years	0.00	.	0.89	0.03				
Age*Breastfeeding status					2	6636	10.00	<.0001

previous child under 2years	0.06	0.02						
status of previous child not known	-0.06	0.03						
no child under 2 years	0.00	.						
socioeconomic status					1	6636	15.72	<.0001
landowner	-1.84	0.46	0.27	0.27				
landless	0.00	.	1.81	0.70				
Parish					1	6636	0.21	0.65
Jaakkima	-0.16	0.35	0.46	0.07				
Rautu	0.00	.	0.50	0.10				

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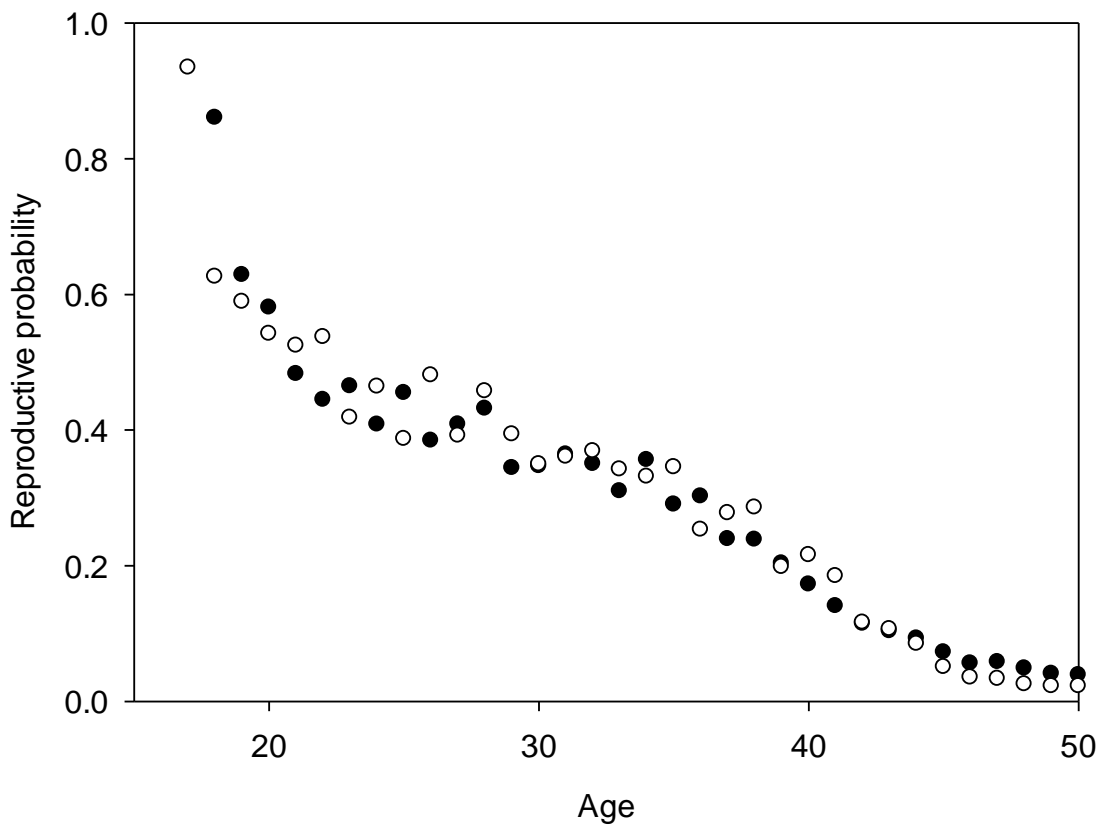640

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652   Figure 1. Age specific fertility of married women from first birth to age 50 in relation to presence (open

653   symbols) or absence (filled symbols) of potential competitor (other woman of reproductive age) in the

654   household. Figure shows predicted values of the model drawn according to reference categories of

655   controlled variables in the final model (Table 2.).

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