



Original Article

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 coresident 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 intrafemale 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 coresided 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.

Key words: anthropology, conflict, cooperative breeding, fertility, joint family.

INTRODUCTION

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 1982; Plard et al. 2011; Clutton-Brock and Huchard 2013). 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). Intrafemale 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 and 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).

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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 cowives compete for resources (Strassmann 1997); and in historical joint-families—where several unrelated women of reproductive age coresided in the same households—the risk for offspring mortality before adulthood increased by 23% when coresident 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 minimize the costs of cobreeding 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 and Schmidt 2005), although not all studies have found associations between self-reported stress and conception rate (Lynch et al. 2012). However, studies of high-income and low-fertility societies may not represent reproductive strategies typical in the past. The causes and outcomes of social and physical stress in modern high-income societies are likely to differ from patterns in more traditional societies, due to increases in living standards, higher energy intake, reduced physical activity, and the postponement of reproduction (Jasienska 2013), as well as the disappearance of large households and ensuing lower daily involvement of close kin in the lives of mothers (Sear and Coall 2011).

One opportunity to study the consequences of female reproductive competition on fertility outcomes is provided by family systems in which women of the same age share resources and potentially compete for reproductive opportunities. Mating patterns affect the degree of genetic relatedness of group members, which in turn shape kin altruism and competition (Cant and Johnstone 2008). Individuals are predicted to behave more altruistically when they are closely related, compared to less genetically related individuals (Hamilton 1964). At the same time, kin and affinal kin also compete for shared resources, and kin competition may sometimes override the effects of kin altruism on behavior (West et al. 2002). Human dispersal patterns include patrilocality, where the young woman moves to her husband's residence and male kin are highly genetically related, and matrilocality, where the young husband moves into the woman's parents' house and female kin are highly related

(Hill et al. 2011). Human families can also consist of parents and offspring only (nuclear family), include grandparents (extended stem family), or include siblings and their families alongside with grandparents (joint family). Furthermore, the parents may be a monogamously married couple raising their offspring or a polygynous man (or polyandrous woman) with multiple spouses. Such a wide range of residence and mating patterns in humans offers possibilities for advancing our understanding of how reproductive conflict affects fertility suppression in different socioecological contexts. To our knowledge, however, no previous study has investigated whether coresident 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 intrafemale 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 coresiding 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 were coliving 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 coliving 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 coliving, 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 preindustrial 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 2 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 study period and child mortality was high: approximately 45% of children died before age 15. Age at first birth was 23.77 ± 0.16 (mean \pm standard error) on average for women in this population and they had given birth to 5.05 ± 0.11 children during their lifetime.

The study area is situated east of the Hajnal line, which is characterized by patrilocal joint households—laterally extended families where married brothers coreside with their ageing parents (Hajnal 1965; Moring 1999). This family type is associated with labor intensive slash-and-burn agriculture. Family compositions changed over time, and the same house could be inhabited by joint- and nuclear family types at different periods (Moring 1999). We identified households with multiple reproductive-aged women from women's houses of residence, as recorded in the parish registers. In some cases, these numbers may refer to a small compound of households, rather than households in which members ate at the same table. Reproductive-aged women in the same household were usually daughters-in-law, while a very small minority would have consisted of daughters of the house. It was also possible to be part of a household by contract as an equal partner (a man and his family) without biological family ties (Partanen 2004). Although the degree of relatedness between cohabiting reproductive women is not the focus of our analysis, very few reproductive women would have been close kin and their children would usually be paternal cousins.

Since socioeconomic status is known to affect survival and other life-history traits in historical Finns (Pettay et al. 2007), socioeconomic status of each house was robustly categorized as landowner (wealthy) or landless (poor); larger tenant farms (lampuoti) were placed in the same category with landowners. Servants were seldom hired in joint-families (Moring 1999), and therefore the majority of women in our data set were categorized as landowners (only 16% of women were classified as landless). The sample of women included in this study corresponds closely with Pettay et al. (2016) study investigating effects of competition on the coresident women's offspring survival, with the exception that the current study question and design enabled including also women censored before the end of their potential reproductive life, leading to an inclusion of a further maximum of 98 women (depending on the study question, see statistical analysis) not part of the previous study.

Statistical analysis

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

Presence of competitor and first birth interval

We tested differences in the interval from marriage to first birth in women who married into a house either with or without at least one resident and already married women of reproductive age (termed “competitor”). The sample consisted of all women with known house number, marriage date and timing of first birth ($N = 662$) born 1801–1917. We considered only the first marriages of these women. We included only women who married before the year of 1937, since the beginning of the Finnish Winter War in 1939 and the ensuing absence of men was likely to affect conception rate. Four hundred and thirty-eight women married into a house without a competitor, 114 to a house with one, 30 with 2, and 11 with 3 competitors. We grouped women with 1, 2, and 3 competitors together, to get a 2-category factor: competitor present against no competitor present. The focal women, or newcomers who married into a house, were usually younger than the other females already present in that household; only in 10 marriages was the newcomer older than another married woman already residing in that house. First birth interval was measured as months from date of marriage to date of delivery of first child, rounded to the nearest full month. To exclude premarital conceptions and thus an unknown starting point of our first birth interval (as well as for female coresidence), we removed from the sample women who gave birth to a child less than 9 months after marriage. The mean first birth interval after these exclusions was 20.39 months (standard error ± 0.8 , $N = 593$). Competitor in the house was, for this analysis, defined as a woman residing in the same house who was under 51 years of age. We identified 155 women who married into a house which already had at least one competitor defined this way.

The response variable in this analysis was first birth interval, which was quantified as the number of months between a female marrying and delivering her first child. Since the length of first birth interval is a non-normally distributed count variable, the analysis was conducted by using generalized linear-mixed effects model (GLMMs) with negative binomial errors and a logit link function. Our main term of interest was whether there were other reproductive-aged women present in the same household at the time of the focal woman's marriage (yes vs. no). To control for possible confounding terms affecting fertility, we included the following terms in the regression model: socioeconomic status (2 levels, landowners and landless), parish (2 levels), birth year (1801–1917 as a continuous covariate), and the focal woman's age at marriage (as a continuous covariate; woman's age at marriage as quadratic term was also tested but was dropped since it did not reach statistical significance of $P < 0.05$). Month of marriage (to take into account possible seasonal fluctuations of physical work, Nenko et al. 2014) and husband's age were also investigated, but similarly dropped as nonsignificant. We also tested for the interaction between competitor presence and age of focal woman to determine if, for example, younger women were more affected by the competitor than older women, but this too was dropped from the final model as nonsignificant.

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

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 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 the section “Presence of competitor and first birth interval”. 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 (2 levels, competitor present or not) at each age. In 26.48% of records (person years), one competitor was present, in 10.60% 2 competitors, and in 2.60% 3 competitors were present, in contrast to 60.32% of records without recorded competitor present. Our sample thus consists of 2790 records (observation years) with competitor present versus 4296 records without competitor present. A mother-in-law under 51 years was only found in 94 records of person-years. Preliminary analyses suggested no difference in fertility between having one or more competitor present. Competition was therefore analyzed as none present versus at least one competitor present (pooling records of one, 2 or 3 competitors with variable sample sizes). Since we were especially interested in whether competition affected a female’s birth rate across different ages and whether the competition had different effects at different female ages, we fitted the focal woman’s age and quadratic term of age as well as interactions between age and the competition variable.

We included time since last event as years from last birth in order to account for multiple events (Steele 2005). If the time since last event exceeded 10 years, these years were grouped following Mace and Alvergne (2012). Parity (range 1–14) was fitted as a fixed factor to account for order of events, and 7 or more births were grouped since parities above 7 were relative rare (10% of records). Parish (2 levels) and socioeconomic status (2 levels) were fitted to adjust for variation from geographic and socioecological sources and year to adjust for temporal variation in fertility patterns. Since currently having a baby and breastfeeding are likely to reduce the probability to give birth, we included a term (nursing) to indicate whether each woman, at each age, had a living child under the age of 2 years to nurse and its interaction with woman’s age (Steele 2005). For example, if a child died the following year from his/her birth, for the next year of the mother’s life this term was scored as zero. The term was also zero for the third year after birth, even if the child was still alive. Survival to age two was unknown for 378 records, and we assigned these years of the focal woman’s life a third level “nursing unknown” in order to include in the model otherwise valuable data points. We also tested for time effect (year) and biologically interesting interactions (e.g., between socioeconomic status and nursing status), but since these were not statistically significant they were dropped from the model.

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.

To study the possibility that the age of a potential competitor would affect fertility, we reran 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 2 years in either direction of the focal woman’s birth. A younger woman was defined as being born at least 2 years after, and an older woman at least 2 years before the focal individual’s birth. In this sample, the potential competitor was absent in 4295 records, at least 2 years younger than the focal woman in 1195 records, at least 2 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.

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 6 months to 2 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 6 (rather than 9) months before as having the possibility to affect the focal woman’s birth rate is that first trimester spontaneous abortions could be caused by conflict between females (Neugebauer et al. 1996). Our data had 733 records with reproductive competition thus defined, compared to 6353 observation years with no competition. Our primary term of interest was whether the other resident women recently reproducing versus not reproducing affected our focal women’s probability of giving birth at each age (as in section “Presence of competitor and age-specific fertility”). We also investigated the interaction between competition and focal woman’s age, in case the effect of competitor reproduction on the focal woman’s probability to give birth herself changes with her age.

In a similar manner to previous model of presence of competitor and age-specific fertility (GLMM, see full definition above), we fitted age and age squared, time since last birth, parity, nursing status (3 levels, see definition above) and its interaction with age, parish (2 levels), and socioeconomic status (2 levels) in the model as covariates, and focal female identity as a random term nested into house identity.

RESULTS

Presence of competitor and first birth interval

The mean first birth interval (from marriage to first birth) in our sample was 20.39 months (SE \pm 0.8), indicating that the new wife typically became pregnant toward the end of her first year in the new household. The length of the first birth interval was not affected by the presence of other married women of reproductive age in the household at the time of marriage (21.70 \pm 1.06 months

without competitor compared to 20.06 ± 1.4 with competitor present) (Table 1). This result is robust to 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.

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 2 years of age, her probability to give birth was low even at young ages, when otherwise the probability to give birth was high (Supplementary Figure 1). Other confounding factors are presented in Table 2.

Rerunning 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-specific fertility ($F_{3,6632} = 0.91$, $P = 0.2$), or that the age of competitors had a varying effect at different focal woman ages (interaction between age class of competitor and focal woman's age; $F_{3,6632} = 0.84$, $P = 0.5$) (Supplementary Table 4).

Presence of reproducing competitor and scheduling of births

In the last analysis, we investigated whether women were adjusting their birth schedule to avoid the adverse effects of simultaneous

reproduction with other coresident women. The mean interbirth interval of all births in our sample was 2.70 ± 0.31 years but with considerable variance between different women and also between the births of the same woman. This variation offered possibilities to adaptively schedule births so as to avoid reproducing close to another woman in the household. However, when investigating competition as recent reproduction by a potential competitor, we did not find that reproduction of another woman in the house in the previous year or earlier the same year (more than 6 months before) would have affected the focal woman's probability to give birth; this lack of effect remained similar across all ages of the focal woman (Table 3). The effects of other factors included in the analysis were similar to those reported in section "Presence of competitor and age-specific fertility" (Table 3).

DISCUSSION

Simultaneous reproduction of several women in a given household is known to have negative consequences for their infants' survival, raising the question of whether such costly competition may have promoted birth scheduling in order to avoid resource competition with other reproductive females in the family (Cant and 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

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

Term	Estimate	SE	Mean	SE	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				
Socioeconomic 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

Table 2

Age-specific fertility, after the first birth, in relation to presence of other women of reproductive age (competitor) ($N = 7086$)

Term	Estimate	SE	Mean	SE	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	<0.0001
Age²	0.00	0.00			1	6637	11.84	<0.001
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	<0.0001
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	<0.0001
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	<0.0001
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	<0.0001
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	<0.001
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				

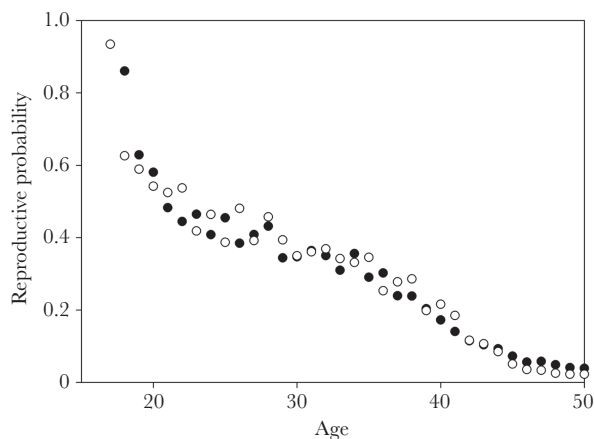


Figure 1

Age-specific fertility of married women from first birth to age 50 in relation to presence (open symbols) or absence (filled symbols) of potential competitor (other woman of reproductive age) in the household. Figure shows predicted values of the model drawn according to reference categories of controlled variables in the final model (Table 2).

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 of 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

Table 3

Age-specific fertility, after the first birth, in relation to competition overlap (whether another woman in the household gave birth to a child 2 to 0 years before) (N = 7086)

Term	Estimate	SE	Mean	SE	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	<0.0001
Age²	0.00	0.00			1	6636	11.35	<0.001
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	<0.0001
2 years	2.12	0.11	0.60	0.066				
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	<0.0001
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	<0.0001
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	<0.0001
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	<0.0001
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				

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 coresiding 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 nonmutually 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 any possible adjusting behavior 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 coresidence are realized only when the infants are most vulnerable, while coresidence 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 coresidence 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 (Strassmann and Gillespie 2002; Sear et al. 2003). 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), while 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 preindustrial Finland, only 6.6% 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 birth again (Mace and Alvergne 2012). This lack of reproductive overlap between generations is achieved through menopause and further enhanced by social norms, such as late age at marriage (Mace and Alvergne 2012) or customs for the older generation to refrain from reproduction when daughters or sons start their families (reviewed in Cant et al. 2009).

Why, then, has similar avoidance of reproductive conflict not evolved against peers who are reproductive competitors, even though it is likely that in our evolutionary past residence patterns would also have exposed women to such group competition? In the case of competing generations of women in patrilocal populations, the older women face an evolutionary disadvantage resulting from kinship dynamics. However, in the joint families investigated here, the competing women were typically equally unrelated to each other's offspring, and of the same generation, which means that there can be no selection to "win" the conflict.

In most mammal populations, age increases social status and competitive ability (Clutton-Brock and Huchard 2013). However, age did not interact with the presence of competitors in any of our analysis, indicating that the effects of competition did not vary according to the focal woman's age. Our results thus differ from those from rural Gambia, where young women had lower fertility in the presence of unrelated reproductive-aged women in their compound compared to older women (Mace and Alvergne 2012). The lack of an age effect in our data could either reflect the social equality of Finnish brothers and their families, as suggested in historical research (Moring 1999; Waris 1999), or that elder women were indeed likely to be dominant but this did not translate to fertility differences in this population. There were also cultural means to avoid conflict between in-laws. Joint families were already becoming rarer during the study period (Moring 1999), so that women who lived in joint families had perhaps chosen this family type over others due to expected benefits of the ensuing lifestyle, such as extra land resources. Our study individuals had a possibility to split farms when necessary or to migrate if they did not get along; farms were occasionally split between brothers (Moring 1999). Therefore, due to a rather equal share of resources and relatedness, any costs of conflict were likely identical to all participants, and rather than reproductive restraint, a behavioral solution to severe costs of conflict may have been to split the group (Hughes 1988).

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Pettay et al. (2017).

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