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Costly reproductive competition between co-resident females in humans

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Studying the evolution of cooperative breeding and group living requires simultaneous quantification of both helping benefits and competitive costs within groups. Although such research has traditionally focused on the fitness benefits of helping behavior, increasing evidence now highlights reproductive competition in cooperatively breeding animals including humans. Human groups consist of cooperative individuals of varying relatedness, predicted to lead to conflict when resources are limited and relatedness low. However, few studies exist that determine the costs of co-breeding to both parties sharing resources. Here, we studied female reproductive competition in historical Finnish joint-families where brothers stayed on their natal farms and sisters married out, so that several unrelated women of reproductive age co-resided in the same households. Using detailed parish registers we quantified the effects of simultaneous reproduction of these women on their offspring mortality. We found that the risk for offspring mortality before adulthood was increased by 23% if co-resident women reproduced within 2 years of each other, a risk that was not associated with the overall numbers of co-resident reproductive-aged women or children. Such costly competition may have promoted the evolution of birth scheduling, dispersal patterns and life-history traits including menopause that avoid resource competition with other reproductive females.

Key words: **anthropology, conflict, cooperative breeding, inter-birth interval, joint family, sibling competition, survival**.

INTRODUCTION

Cooperative breeding describes a situation where individuals in groups help other group members rear offspring (Solomon 1997). Such a breeding system has been documented among 9% of birds (Cockburn 2006) as well as in some fish, social insects, and mammals (Seger 1997; Russell 2004; Cockburn 2006; Wong and Balshine 2011; Eggert 2014). Most research on cooperative breeding systems has focused on helping behavior and its measurable benefits to the recipients, as well as any fitness payoff to the helpers. However, conflict is also universal in cooperative animal societies (Emlen 1982; Rubenstein and Shen 2009). Conflict in a group arises from competition over reproductive resources such as food, mates and breeding sites (Cant et al. 2009; Stockley and Bro-Jorgensen 2011). For example, if 2 females reproduce simultaneously in the same group, each offspring will receive less food compared with the offspring when only one of the women were to reproduce, provided that food availability is constant. In such groups, reproductive success can be highly variable among females (Clutton-Brock 2009; Stockley and Bro-Jorgensen 2011), and intra-female competition may lower the reproductive success of females,

especially subordinates (Clutton-Brock 1998). Competition in group living animals can in extreme cases manifest itself as egg-tossing in group-living birds such as acorn woodpeckers (*Melanerpes formicivorus*) (Mumme et al. 1983), and as killing of the offspring of the other females in the group in many mammalian taxa (Stockley and Bro-Jorgensen 2011). In chimpanzees (*Pan troglodytes*) living in male patrilocal groups with female dispersal, competition between unrelated females can be fierce and include infanticide (Pusey and Schroepfer-Walker 2013). Consequently, studies on the evolution of group living and cooperative breeding should investigate the competitive costs as well the helping benefits within a group (Sterck et al. 1997a; West et al. 2002).

A substantial body of evidence now shows that human mothers receive critical help from other group members in rearing their children, favoring the hypothesis that humans are a communally or cooperatively breeding species (Sear and Mace 2008). This help may have enabled women to simultaneously raise several differently aged, dependent children, and facilitated the evolution of human life-history traits such as a long childhood, high fertility, and long post-reproductive female lifespan (Hawkes et al. 1998; Burkart et al. 2009; Kramer 2010). However, the human breeding system is also very variable (Lummaa 2013). Although evidence suggests that in addition to the mother, other close relatives are important for children to thrive, the presence of relatives in the household

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may also be harmful to children (Lahdenperä et al. 2004; Sear and Mace 2008; Nitsch et al. 2013, 2014). Both the costs and the benefits of living with relatives can depend on the life stage of each group member (Emlen 1995; Nitsch et al. 2013). Yet our knowledge of the circumstances when children are, or are not, helped by other group members remains limited.

Research on cooperative breeding in humans has mainly focused on the benefits of cooperative behavior for reproductive success and survival. Only recently has the evolutionary conflict arising from communal breeding in humans garnered more interest (Strassmann 1997; Voland and Beise 2002; West et al. 2002; Cant and Johnstone 2008; Strassmann 2011; Lahdenperä et al. 2012; Mace and Alvergne 2012; Ji et al. 2013; Mace 2013; Skjaervo and Roskaft 2013; Snopkowski et al. 2014; He et al. 2016). For instance, having a co-resident sister decreased fertility in matrilineal Mosuo in China (Ji et al. 2013) and co-resident paternal grandmothers had adverse effects on child survival in Dogon of Mali (Strassmann 2011) and in historical Germany (Voland and Beise 2002). An evolutionary conflict within a family can manifest as reduced survival or reproductive success, and thus contribute to the evolution of human group living, behavior and life history. Understanding the circumstances that promote evolutionary conflict also enhances our understanding of the dynamics of cooperative breeding.

In the cooperative breeding context, previous studies on evolutionary conflict within extended human families have focused on conflicts between women of different generations. Cant and Johnstone (Cant and Johnstone 2008) predicted that because a mother-in-law is related to the offspring of her daughter-in-law, but the daughter-in-law is not related to her mother-in-law's offspring, daughters-in-law would win an evolutionary conflict between these generations over breeding priority. As a consequence, female menopause could have evolved to resolve this conflict in patrilocal human societies. Only a few studies have so far investigated this hypothesis (Lahdenperä et al. 2012; Mace and Alvergne 2012; Skjaervo and Roskaft 2013; Snopkowski et al. 2014). Among them, Lahdenperä et al. (Lahdenperä et al. 2012) showed that in historical Finland, simultaneous reproduction of daughter-in-law and mother-in-law in a household led to significantly reduced survival of the resulting babies of both parties. However, such conflict arising from 2 generations of women reproducing simultaneously seems to be rare: in pre-industrial 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, whilst becoming a paternal grandmother before reaching 50 years of age was too rare an event to even evaluate (Mace and Alvergne 2012). The lack of reproductive overlap between female generations in most human populations is often enhanced by social norms, such as late age at marriage (Mace and Alvergne 2012), or customs dictating that the older generation cease reproduction when daughters or sons become reproductive (reviewed in Cant et al. 2009). Consequently, the reproductive separation of generations in contemporary humans is so pronounced that it is difficult to obtain data on the costs of co-breeding. A more prevalent opportunity to study the potential consequences of reproductive competition between multiple women in a family is provided by family systems where women of the same generation share resources and compete for reproductive opportunities. Any evidence for costs of co-breeding for such women could also shed light on the hypotheses that reproductive conflict between unrelated women of different generations lead to the evolution of menopause (Cant and Johnstone 2008), because

the measured costs are likely to be of similar magnitude for both cases of unrelated co-resident reproductive women.

The type of group people live in is likely to affect the potential for reproductive conflict and how it is manifested. Human family types range from stem families to various forms of extended families (Hill et al. 2011). For example, in polygamous families co-wives and their children can compete severely for resources. Studies have documented how child condition and survival in such families are compromised by competition among unrelated women (Strassmann 1997). None have, however, investigated the timing of reproduction of each potentially competing woman. This is essential in order to clarify whether reduced child health and survival follow from larger group size alone, or from direct competition between women reproducing simultaneously.

Here, we seek evidence for female–female reproductive competition within the same household in humans by studying longitudinal demographic data from historical patrilocal populations of Eastern Finland. Specifically, we test whether the reproductive success of cohabiting non-related females in joint families decreases when one or more women in the household gave multiple births within a short time span. Joint families are laterally extended families where married siblings, typically brothers, live in the same household. In historical Finland this family type was connected to lower dispersal possibilities, and wealth accumulation within family (Moring 1999). We investigate conflict by analyzing the survival probability of offspring of cohabiting non-related women who reproduced within 2 years. Our analyses control for important confounding factors such as maternal age, overall number of cohabiting adult women and children in the household, socioeconomic status, household effects, and time trends.

METHODS
Study population and data

We used demographic data collected from historical Finnish population registers to study female-female reproductive competition within households. The Lutheran Church has kept census, birth/baptism, marriage, and death/burial registers of each parish in the country since the 17th century, covering practically the whole population of Finland from 1749 onwards (Gille 1949; Luther and Erjos 1993). Using these registers, it is possible to follow the detailed reproductive and marital histories of each individual from birth to death (Gille 1949). Our data is collected from church book records from the parishes of Rautu and Jaakkima, which are now situated in the Republic of Karelia of Russia but belonged to the Finnish province of Viborg until 1945. The main source of livelihood in the area was farming (Moring 2003). Our study sample includes 2485 individuals born 1821–1920 to 564 mothers in 418 households of the 2 study parishes. The study period was chosen so as to maximize the availability of house numbers and data quality, and to minimize the effects of the demographic transition on fertility and mortality rates (Bolund et al. 2015). During this period child mortality in the area was high; 45% of children died before age 15. On average women gave birth for the first time at age 22 and produced 5 children during their lifetime.

The study area is situated east of the so-called Hajnal line (defining family types in Europe), indicating prevalence of patrilocal joint households—laterally extended families where married siblings, typically brothers, live in the same household (Hajnal 1965; Moring 1999). This family type is associated with labor-intensive slash-and-burn agriculture (Moring 1999). Household composition

was dynamic by nature; the same house could be inhabited by joint- and nuclear-family types at different times (Moring 1999). Households with multiple reproductive-aged women at the same time were identified from women's houses of residence as recorded in the parish registers. Reproductive-aged women in the same household were usually daughters-in-law to the head of the household, whereas a very small minority were daughters of the house (in our sample there were only 6 sister pairs within 161 houses). It was also possible to be part of a household by contract as an equal partner (a man and his family) without family ties (Partanen 2004). Though the degree of relatedness between cohabiting reproductive women is not the focus of our analysis, very few coresiding reproductive women would have been close kin in this sample.

We study reproductive overlap between women, defined as at least 2 women giving birth within 2 years of each other in the same household, and the possible effect of such reproductive competition on the survival of their offspring. For the sake of simplicity, we refer to children in the house that are not siblings as cousins, although a minority of them may have been unrelated. Our rationale for the 2-year cut off at either side of birth is that this encapsulates the period when mothers are in greatest conflict over resources. Future mothers need to gain sufficient resources to conceive and nurture gestating offspring (Lumey 1992; Butte and King 2005; Jasienska 2009; Roseboom et al. 2011), whereas postpartum mothers need to provide substantial resources to suckling offspring (Butte and King 2005; Kramer 2005) until other helpers can also provision offspring following weaning (Sear and Mace 2008; Hrdy 2009). Additionally, children are most dependent upon their mothers in the first 2 years, and breastfeeding as a primary source of nourishment typically lasts approximately 2 years in pre-industrial societies (Lahdenperä et al. 2011; Sellen 2001). Including the birth interval between overlapping women in the analysis as a continuous variable (instead of the 2-year cut-off) was not possible, because children with no cousins would have had no value for such a variable, whereas other children were born close to several different cousins and would have had several values.

Socioeconomic status is known to affect survival and other life-history traits in contemporary and historical populations, including the Finns (Pettay et al. 2007). Therefore, the socioeconomic status of each house was categorized as landowner ($N = 2192$) or landless ($N = 293$); larger tenant farms (lampuoti) were placed in the same category with landowners. Because the joint families had large man-power, servants were seldom hired (Moring 1999), and therefore the majority of children who were categorized as being in reproductive overlap with a cousin (see above) were from landowning households. Although our analyses could not adjust for detailed measures of wealth such as farm size (not directly applicable to slash and burn agriculture), in addition to the socioeconomic status above our analyses do adjust for variation in household size (see below).

Statistical analyses

We investigated the consequences of simultaneous reproduction of women in the household for offspring survivorship by using Cox regression (or proportional hazards regression), which allows analyzing the effect of several risk factors on survival. Hazard ratio is a measure of how often a particular event happens in one group compared with how often it happens in another group in time. A hazard ratio over one means that mortality is higher compared with reference group, less than one means that mortality is lower compared with reference group, and a hazard ratio of one means

that there is no difference in survival between the group and reference group (Allison 2010). We confirmed that the assumption of proportional hazards was met: that is, that reproductive overlap effects acted proportionally to the baseline hazard at each offspring age (proportionality of the hazard for the overlap variable: $\chi^2_1 = 0.88$, $P = 0.3$). We analyzed offspring survival to 15 years. Although competition is predicted to have the strongest impact on offspring survival during the first 2 years of life, when mothers require substantial resources to support lactation, competition during the early years might also impose delayed mortality costs on offspring (Lummaa 2003; Roseboom et al. 2011). A single analysis of offspring survival to age 15 years avoids multiple testing, and ensures incorporation of the entire developmental period over which evolutionary implications of reproductive overlap can be manifested (Courtiol et al. 2012). Our main term of interest predicting the survival of children was birth overlapping with the birth of at least one other child in the household, who was not a sibling (termed overlap with 2 levels: no overlap and overlap; see above for full definition).

We also included sex (2 levels), socioeconomic status (2 levels: landowner and landless), and birth cohort of 30 years (3 levels: 1830–1859, 1860–1889, 1890–1920), study parish (2 levels: Jaakkima and Rautu), twinning status (single vs. twin; 3% offspring in this sample were twins) in the model, because these variables have been shown to be associated with variation in child survival in historical Finland (Lummaa et al. 1998; Pettay et al. 2007; Faurie et al. 2009; Liu et al. 2012; Gillespie et al. 2013). Since maternal presence during the first years of life was important for child survival in historical Finns (Lahdenperä et al. 2011), we fitted maternal survival status during the first 15 years in the model indicating if the mother died during the first 15 years of the focal individual's life (termed dead), or if she was alive at least until the focal individual turned 15 years of age (termed alive). Including alternatively also a category for mothers dying in the first 2 years did not change our conclusions. When maternal survival status was unknown, a third "unknown" category was assigned to prevent loss of otherwise valid data points (mother was alive until adulthood for 2057 children, 359 children lost their mother during the first 15 years, and in 69 cases the survival status of the mother was not known). These terms were retained, irrespective of statistical significance, to control most effectively for any confounding influences on the effect sizes of the terms of interest. To take into account cluster effects of offspring born in the same household, we used the marginal approach, which leaves the correlation structure unspecified and adjusts for the correlation by using a sandwich-type variance estimator (Lee et al. 1992).

We further controlled for the possibly confounding effects of maternal age at birth (Faurie et al. 2009; Gillespie et al. 2013), which ranged from 17.4 years to the maximum age of 47 years, with a mean ± standard error (SE) of 29.8 ± 0.13 years. We included in the analyses the number of other reproductive women, calculated as the number of women in the household that had given birth to a child 15 years or less before the birth of the focal child. This term "other women" was categorized as 0, 1, 2, and 3 other mothers (13 individuals, with more than 3 reproducing mothers merged into the last category). Overall, 29% of all offspring had at least one woman other than their own mother reproducing within this time range in the household. Furthermore, we included in the analyses the number of siblings that were alive and under 15 years of age at the birth of the focal child (range: 0–7, mean ± SE: 1.8 ± 0.03, grouped in 5 classes (0 to 5+; only 36 cases had

more than 5 siblings alive). We also included the number of cousins in a household, defined as the children who were alive and born maximum of 15 years before the birth of the focal child (range:0–12, mean ± SE:0.8±0.3, categorized as 0 to 4+ with those having more than 4 cousins included in category 4+). Since close sibling birth intervals of around or below 27 months are known to have adverse effect on pregnancy outcomes and infant health (Conde-Agudelo et al. 2012) we also included a factor indicating if the focal child's mother had given birth within 2 years before the birth of the focal child (overlap with sibling). Such a sibling was born for 588 offspring. Because short birth intervals of succeeding siblings often result from the early death of the first child (reverse causality), we only consider the previous (but not succeeding) birth to a mother as a possible confounding factor in our analysis. However, for cousin effects also close births after the focal child were considered, because there is no reason to expect similar reverse causality between mothers as within the same mother. Finally, since reproductive competition might affect the survival of male and female offspring differently, an interaction between sex and reproductive overlap was also investigated. In these cases terms were dropped when they failed to reach $P < 0.10$.

In addition, we conducted a separate analysis to test whether competition from several cousins had cumulative effects. We ran a similar survival analysis as the one described above but compared cases where one cousin was born within 2 years of the focal individual and survived until the birth of the focal child ($N = 241$) to cases with 2 alive closely born cousins ($N = 45$, including 2 cases with 3 alive closely born cousins). Because of the smaller sample size, we included only maternal status (alive, dead, unknown) and birth cohort as confounding factors in this model.

RESULTS

We found that offspring risk of death before adulthood (15 years) was significantly higher when 2 or more mothers from the same household gave birth within 2 years of each other [Hazard ratio (95% confidence intervals [CIs]): 1.23 (1.03, 1.48)] as compared

with offspring whose birth did not overlap with the birth of a child to another woman in the household (Table 1, Figure 1).

In contrast, the total number of cousins, the number of siblings, or the number of reproductive women present in the household as such did not affect offspring survivorship significantly (Table 1). This suggests that the negative effects of competition between women on their offspring survival were only apparent when their reproductive timings overlapped, whereas the presence of other women (or their offspring) alone was not significantly related to offspring survival.

Our results are not confounded by differences in survivorship caused by differing maternal survival, socioeconomic status, twinning status, or temporal or geographic variations, which were all controlled for. Maternal survival status was positively and statistically significantly associated with offspring survival to age 15; the child's risk of death was highest when the mother died during the first 15 years compared with when she was alive or her status was not known (Table 1). Family socioeconomic status was a statistically significant predictor of survivorship, with a 25% higher risk of death among the landless compared with the landowners (Table 1). Survival of different birth cohorts also varied significantly, with the earliest birth cohort (1830–1859) experiencing the highest risk and the latest birth cohort having the lowest risk (Table 1). Being a twin was associated with almost 3 times higher risk of death than being born as a single. However, survival was not affected if the mother gave birth to a sibling in the previous 2 years (Table 1). Maternal age at birth, study parish, offspring sex or its interaction with overlap with cousin were not significant predictors of survivorship to age 15 in this sample (Table 1).

Whether there were one or 2 closely aged cousins did not further reduce survival as tested with a subsample containing only those individuals who had one or 2 cousins alive and who were under 2 years of age (Hazard ratio (95% CIs):0.74 (0.39, 1.42); $\chi_1^2 = 0.81$, $P = 0.4$), suggesting that the negative effect of simultaneous closely aged cousins in the household might not be cumulative; however the sample size in this analysis was relatively small.

Table 1

Cox regression model of the effects of reproductive overlap on offspring mortality from birth to age 15 years

Term	Parameter estimate ± SE	Hazard ratio (95% CIs)	df	χ^2	P value
Overlap (0 = no overlap)	0.21±0.09	1.23 (1.03, 1.48)	1	4.99	0.03
Twin (0 = single)	1.07±0.21	2.90 (1.93, 4.37)	1	26.1	<0.0001
Birth cohort (0 = 1830–1859)			2	42.51	<0.0001
1860–1889	−0.11±0.10	0.89 (0.72, 1.01)			
1890–1920	−0.56±0.11	0.57 (0.46, 0.71)			
Maternal status (0 = mother dead)			2	36.85	<0.0001
Mother alive	−0.52±0.09	0.60 (0.50, 0.71)			
Mothers status not known	−0.26±0.23	0.77 (0.49, 1.20)			
Family SES (0 = landowner)	0.22±0.10	1.25 (1.02, 1.53)	1	4.56	0.03
Sex (0 = male)	0.71±0.08	1.07 (0.93, 1.24)	1	0.9	0.34
Parish (0 = Jaakkima)	−018±0.11	0.84 (0.67, 1.05)	1	2.36	0.12
Maternal age at birth	0.002±0.01	1.002 (0.99, 1.01)	1	0.081	0.78
Number of siblings alive (0 = 0 vs. 2 sibling)	−0.26±0.12	0.85 (0.61, 0.99)	4	7.023	0.13
Other mothers (0 = 0 vs. 2 other mother)	−0.05±0.17	1.05 (0.76, 1.45)	3	4.59	0.2
Number of cousins alive (0 = 0 vs. 2 cousins)	−0.09±0.20	1.09 (0.74, 1.61)	4	4.12	0.39
Overlap with sibling (0 = no overlap)	−0.35±0.22	0.71 (0.46, 1.09)	1	0.6	0.44
Sex × overlap	−0.05±0.20		1	0.07	0.8

$N = 2485$ offspring. Positive and negative estimates for the categorical variables mean that the mortality is higher and lower than in the reference group (0), respectively. When a nonsignificant variable had more than 2 levels, one of levels is shown and indicated in the parenthesis. For continuous variables, positive estimates indicate an increase in mortality risk, whereas negative estimates indicate a decreasing mortality function. Terms retained in the final model are shown above the dashed line and those below the line denote to terms dropped from the final model as nonsignificant. SES, socioeconomic status.
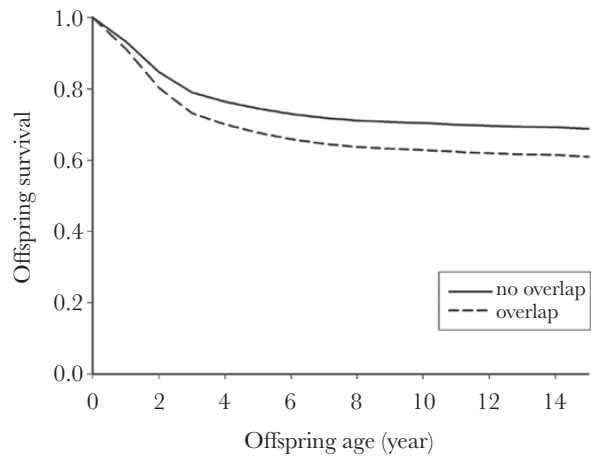
Figure 1
Presence of reproductive overlap and offspring survival to maturity (15 years). Reproductive overlap was defined as the birth of another child to a different mother within 2 years of each other in the same household. Solid line refers to births with no overlap ($N = 1991$) and dashed line to cases with overlap ($N = 494$). The figure shows the predicted rates from a Cox regression adjusting for a range of possible confounders (Table 1).

DISCUSSION

Although the prevalence, mechanisms and evolutionary consequences of reproductive competition among males are well understood, intrasexual competition among females has only recently begun to attract wider attention in evolutionary biology (Clutton-Brock and Huchard 2013). We investigated the consequences of female-female reproductive competition in humans by determining offspring survival when 2 or more women in the household gave birth closely to one another. Our results provided evidence for the presence of reproductive conflict between peer women living in patrilocal extended joint-families in pre-industrial Finland. This conflict was manifested as a 23% higher risk of death to age 15 for offspring when co-resident women, typically sisters-in-law, reproduced within 2 years of another, as compared with each woman being the sole reproducer in the house at the time. This finding advances our understanding of factors promoting the evolution of reproductive scheduling, dispersal patterns, and menopause—life history traits that may help women avoid costly resource competition with other females. Our findings also add to an increasing literature showing that the benefits of group living across species should be balanced against the costs of competition, including intrafemale competition over reproductive timing.

Although both theoretical studies (Hamilton 1964; Sterck et al. 1997a; West et al. 2002; Cant 2006) and empirical evidence from group living animals (Clutton-Brock and Huchard 2013; Pusey and Schroepfer-Walker 2013) predict reproductive conflict among females to appear in a range of family types, the effect of female allies and rivals on child outcomes has to date received scant attention in evolutionary anthropology (Cant et al. 2009; Lahdenperä et al. 2012; Mace 2013). The joint-families in our study typically consisted of brothers, their parents and their wives (Moring 1999; Sirén 1999; Waris 1999; Partanen 2004). Women of reproductive age were unlikely to be closely genetically related and therefore their primary evolutionary interest would have concerned ensuring resources for their own offspring, even at the expense of the offspring of their sisters-in-law. Such resources included both material provision and care: in addition to basic needs such as food and rest, the children may have competed over grandparental

investment from the same paternal grandparents (Lahdenperä et al. 2004). In Karelian joint families, resources were divided evenly among co-residing brothers and their wives (Moring 1999; Waris 1999). Larger household size overall raised the productivity in our study population: slash-and-burning agriculture is labor intensive and each family member was likely to increase the net resources of the house, rather than reduce the available resources per individual, as is the case in some other socio-ecologies (Moring 1999). Our evidence of reproductive competition between wives shows that the possible benefits of larger households for successful agriculture could not completely mitigate the costs of co-breeding. In pre-industrial Finland reproductive success was higher in wealthier individuals who owned land (Pettay et al. 2007), and this was also the case in our study, with almost all joint-families being landowning households. The fact that such a clear cost from reproductive overlap was detected in a comparatively resource-rich household type renders it particularly noteworthy. Our findings also reflect fraternal reproductive competition in patrilocal societies, although the intensity of reproductive competition is smaller among men due to their genetic relatedness.

Studying the evolution of cooperative breeding and group living requires simultaneous quantification of both helping benefits and competitive costs within groups. Whilst the role of relatives in affecting reproductive success in human societies is quite well-explored (e.g., Sear and Mace 2008; Tanskanen and Rotkirch 2014; He et al. 2016), only a few studies have specifically quantified the costs of simultaneous co-breeding for reproductive women, and none have previously done so for women of the same generation (Lahdenperä et al. 2012; Mace and Alvergne 2012; Snopkowski et al. 2014). Reproductive conflict between unrelated peer women may be common also in other types of families than the one investigated here. These conflicts have previously been studied mainly in polygynous populations, in which marriage is often associated with competition between co-wives for investment from the same husband. Such competition can be manifested as poorer overall health of polygynous women (Bove et al. 2014), reduced fertility (Mace and Alvergne 2012), and lower general survival of children (Strassmann 1997), although such negative effects can also be offset when polygyny within a local population is associated with greater wealth (Lawson et al. 2015). In sororal polygyny, when genetic sisters are co-wives, polygyny can be beneficial as measured by the number of births and children surviving to age 5 (Chisholm and Burbank 1991). These previous studies have not, however, distinguished between the potential, negative or positive effects of household size, child survival, maternal mortality, and the direct costs of reproductive competition (simultaneous timing of births) on female reproductive success. Whether it is direct reproductive competition or overall reduced resource access that drives these findings from polygynous societies are therefore currently unknown.

One caveat is that our data is gathered from church book records, in which household composition is based on house numbers recorded in the books. In some cases these numbers may refer to a small compound of households, rather than households in which members ate at the same table. This inaccuracy is, however, likely to affect our results conservatively, so that the actual effects of within-household competition would be even larger if it had been studied only within households that strictly lived together, rather than including also some larger compounds. We stress that collection of residence data can be a valuable addition to the understudied field of reproductive conflict in various human cultures and residency types.

It is likely that during human evolution, women and men were frequently competing with non-relatives for resources and breeding opportunities, leading to reproductive conflict as well as coalitionary relationships between unrelated individuals (Stockley and Campbell 2013; Ji et al. 2014). The assumption of frequent patrilocality in prehistoric humans is supported by genetic (Seielstad et al. 1998) and anthropological (Fortunato 2011) data. The type of joint-family with several breeding pairs investigated in our study population of pre-industrial Eastern Finns has been common across Eastern Europe and Asia for centuries, making such study systems a valuable comparison point (e.g., Fortunato 2011). Compared with this patrilocal population, matrilocal residence patterns have a different structure of relatedness, with ensuing differences in intrafemale competition and selection (Ji et al. 2013; Wu et al. 2013). This is because, as predicted by kin selection theory, genetic relationships between family members play a major role in both cooperation and conflict (Hamilton 1964). Competition between closely related family members is especially marked within the same generation (West et al. 2002), as shown by studies on the matrilocal communally living Mosuo, where the number of co-resident sisters and cousins were associated with reduced reproductive success (Ji et al. 2013). Therefore, similarly to studies of cooperative breeding in other species (Young and Bennett 2013), competition for shared resources can reduce female reproductive success even when competitors are close relatives. Overall, the presence of both kin and non-kin is likely to affect reproductive strategies of women, but such effects may be complex and depend on additional factors. For example, Mace and Alvergne (2012) found that in rural, patrilocal Gambia, the effects of female–female competition depend on age—young women suffer costs to their fertility from having more unrelated reproductive-aged women in their compound, whereas older reproductive-age women appear to benefit, at least in terms of number of offspring born. Future studies are needed to establish the extent and circumstances under which conflict among women in a household arises, for example, among related and unrelated co-wives of the same husband, co-resident reproductive women as in our study, and women of different generations such as mothers-in-law and daughters-in-law. In addition to its effects on fecundity, intrafemale competition may employ strategies that influence not only the number but also the quality of offspring; longitudinal data is therefore needed to estimate the fitness effects of competition among females (Stockley and Bro-Jorgensen 2011).

Our results are also interesting in the light of recent hypotheses for the evolution of menopause, which predict that a reproductive conflict between unrelated pairs of females in human households (mother-in-law – daughter-in-law) favored the evolution of menopause among the older generation in order to resolve this conflict (Cant and Johnstone 2008). Due to the current evolved separation of reproduction between generations, only a few studies have so far been able to test this hypothesis (Lahdenperä et al. 2012; Mace and Alvergne 2012; Skjaervo and Roskaft 2013; Snopkowski et al. 2014). Research like ours sheds light on the evolution of menopause, demonstrating fitness costs of simultaneous reproduction of non-kin women that do not share a husband (Cant et al. 2009).

Importantly, the cost associated with the presence of reproductive females was confined to close birth spacing, because we did not find that the overall presence of unrelated mothers in the house affected child survival. These findings corroborate a similar result from a Gambian population, in which the mere presence of unrelated women in the compound did not alter child survival (Mace and Alvergne 2012). Whether the detected reproductive conflict between women then leads to strategies to avoid the conflict, such as altered birth scheduling, would be a fruitful future research avenue. Conflicts over reproduction in social species typically appear to be resolved without overt aggression, but much remains to be learnt about the mechanisms involved (Young and Bennett 2013). In humans, studies have highlighted several proximate mediators of female aggression, including hormonal, neurobiological and cultural influences, which facilitate flexible responses to rapidly changing social environments (Stockley and Campbell 2013; Krems et al. 2015). How these mechanisms underlie the type of conflicts and outcomes highlighted in our study is yet unknown, but would significantly improve the cross-disciplinary understanding of female competition.

In conclusion, living in groups intensifies competition for limited resources and favors traits that enhance competitive ability. Our results suggest that the various benefits of human group living and cooperative breeding (Hrdy 2009) combine with costs arising from reproductive timing. The extent and manifestations of these costs is a research area that should be investigated in different cultures and ecologies.

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