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Original Article

# Alloparenting in humans: fitness consequences of aunts and uncles on survival in historical Finland

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Offspring success depends on parental investment in humans, but it can also be improved by investment from other genetically related "helpers," known as "alloparents." Kin selection theory predicts that individuals with a low current reproductive value should be more likely to exhibit such helping behavior to improve their inclusive fitness. In humans, nonreproductive adult uncles and aunts are often expected to improve their nephews' and nieces' fitness, but few studies exist to test this hypothesis in detail. Using an extensive ($N$ = 4145) demographic data set from 18th- to 19th-century Finland, we investigate whether the presence of adult aunts/uncles benefitted their nieces or nephews. Specifically, we use discrete time survival analysis to assess the effect of having adult aunts/uncles residing in the same parish in a given year, on a child's risk of dying at each age from birth to 15, while controlling for the effect of other types of helpers (e.g., grandmothers and siblings). We also compare the effects of reproductive versus nonreproductive aunts/uncles and lineage (paternal vs. maternal). Overall, we show that contrary to predictions, the presence of nonreproductive uncles and aunts in the parish was not correlated with offspring survival, with only old childless uncles weakly improving their niece's survival, young childless uncles decreasing their nephew's survival, and old childless aunts decreasing their niece's survival. This study is the first to directly investigate the fitness consequences of having childless adult aunts and uncles in a human family and has implications for understanding the evolution of family dynamics and cooperative breeding strategies in humans.

*Key words*: **alloparental investment, child mortality, cooperative breeding, family, nephews/nieces.**

## INTRODUCTION

In humans, as in other species with altricial young, parental investment (Trivers 1974) has profound effects on offspring survival and reproductive success (Clutton-Brock 1991; Pavard et al. 2007; Sear and Mace 2008). However, offspring fitness can also be improved by investment received from other individuals, commonly called "helpers," who are genetically related to the offspring (but to a lesser extent than genetic parents): such behavior is known as "alloparenting" (Solomon and French 1997; Koenig and Dickinson 2004). Positive effects of alloparents on offspring fitness have been documented in various taxa (Cockburn 1998; Clutton-Brock et al. 2001; Meade and Hatchwell 2010). Kin selection theory and the ecological constraints hypothesis predict that such alloparenting behavior could be selected for its effects on inclusive fitness when costs of reproducing independently are too high (for physiological or ecological reasons) or when individuals are not able to reproduce (e.g., when they are not yet sexually mature) (Koenig et al. 1992; Hatchwell and Komdeur 2000; West et al. 2002). In cooperatively breeding species, helpers are commonly sexually mature individuals waiting for reproductive opportunities to arise, and in rare cases, individuals foregoing reproduction altogether to specialize in helping (e.g., eusocial insect societies) (Emlen 1982a, 1982b; Andersson 1984; Emlen 1995; Clutton-Brock 2006).

Humans are considered to be cooperative breeders (Hrdy 2011) because their fast birth rate coupled with a long offspring dependence period leads to several different-aged dependent offspring being raised simultaneously in a family—a task often requiring care from other adults besides the mother. In humans, the study of alloparenting has mainly concentrated on 2 potential groups of helpers, and such studies from several populations have shown that

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the presence of grandmothers (and to a far lesser extent grandfathers) (Lahdenperä et al. 2007, 2011) or older siblings can improve offspring survival (Crognier et al. 2001; Sear and Mace 2008; Lahdenperä et al. 2011; Nitsch et al. 2013). Some studies suggest that childless reproductive-aged uncles and aunts could also benefit from improving the survival of their nephews and nieces as their own current reproductive value is low (Pollet et al. 2006; Pollet and Dunbar 2008). For instance, Pollet and Dunbar (2008) showed that in contemporary Belgium populations, childless aunts above the age of 35 years had more recent contacts with their nephews and nieces than aunts having their own children. Pollet and Dunbar (2008) also showed that childless uncles and aunts were more likely to take care of their nephews and nieces than aunts and uncles with children of their own, in an American population at the beginning of the 20th century. Moreover, other studies have shown that maternal uncles and aunts invested more toward their nephews and nieces than paternal kin, which is suggested to arise from paternity uncertainty (Gaulin et al. 1997; McBurney et al. 2002; Pashos and McBurney 2008). Finally, a few studies have documented effects of uncles and aunts on the survival of children (for a review, see Sear and Mace 2008) and reported mixed results (positive, negative, or no effects of uncles or aunts). For instance, in a nomadic hunter-gatherer population of the Ache of Paraguay, Hill and Hurtado (1996) found no effect on child survival to age 5 of the presence of aunts and uncles (however, the importance of lineage or reproductive status was not investigated). Another study on a communal Mormon society of Utah, United States, reported that the presence of maternal uncles, maternal aunts, and paternal aunts was associated with higher chances of child survival during the first year of life (Heath 2003). However, none of these previous studies of fitness effects took into account simultaneously the age, the reproductive status, and the lineage of potential helping uncles and aunts. Therefore, a detailed study investigating the actual fitness consequences of potentially helping uncles and aunts, and how their effects depend on their lineage, reproductive status, and age, is necessary to improve our understanding of the extent of cooperative breeding behavior in humans.

In this study, we investigated whether the presence of childless uncles or aunts was associated with enhanced child survival in a historical Finnish population, and thus whether these kin improved their own inclusive fitness by helping their siblings to reproduce more successfully. We focused on effects on early survival because it is the most important trait affecting overall fitness variance both in hunter-gatherers (Strassmann and Gillespie 2002) and agricultural populations such as the one studied here (Courtiol et al. 2012). Therefore, improving the early survival of an individual is considered as an effective way for kin to improve their own inclusive fitness in high mortality populations and, in line with this, most previous studies on humans investigating fitness effects of other types of kin such as grandmothers or elder siblings have focused on this trait (Sear and Mace 2008; Hrdy 2009). Specifically, we investigated the effect of having no versus varying numbers of living nonreproductive sexually mature aunts or uncles, residing in the same parish at each age from birth to sexual maturity, on the focal child risk of dying at that age. We also compared the effects of the presence of childless aunts and uncles with high versus low future reproductive potential and investigated whether there were differences in the effects between paternal and maternal aunts and uncles. We determined whether any potential effects depended on the age or sex of the child, socioeconomic status (SES), or number of siblings (both indicative of the general level of competition for resources within the family). Our models controlled for the presence of other kin with potential helping effects, such as parents, grandmothers, and elder siblings.

We predicted that the presence of childless adult uncles and aunts residing in the same parish would enhance their nieces' and nephews' survival, whereas uncles and aunts with at least 1 child were expected to have a null (when they were living in a separate household from the focal child) or a negative effect (due to a bias in investment toward their own child(ren) in cases of joint residence with the focal child). Moreover, given that the expected reproductive success of younger uncles/aunts is higher than for older uncles/aunts, we also predicted that older uncles/aunts should be more beneficial for child survival than younger uncles/aunts. Finally, due to paternity uncertainty, we predicted that the maternal lineage would be more involved than the paternal lineage.

## METHODS

### Study population

We used a large demographic data set from historical Finnish populations to investigate the effects of childless aunts and uncles on their nephews' and nieces' survival. This data set was compiled from records of the Lutheran church documenting all births, marriages, deaths, and movements in the whole population since 1749 (Luther 1993). The records provide accurate information on the survival and reproductive histories of all individuals in the country and allow us to follow families across several generations (e.g., in this sample, 91% of individuals with known birth date were followed to age 15) (Courtiol et al. 2012). We limited our study period to individuals born during the 18th and 19th centuries before the spread of industrialism and more modern methods of birth control (Soininen 1974), as well as a transition to reduced birth and mortality rates (Liu et al. 2012) and change in kin network (Sear and Coall 2011). Indeed, effects of kin on child survival have only been highlighted in population with high mortality rates, whereas in postdemographic transition populations, studies on kin investment have focused on other traits (e.g., on SES) (Sear and Coall 2011).

Individuals included in our analysis were born in 29 geographically distinct parishes located either in mainland or in southwestern coastal areas. These populations mostly depended on farming for their livelihood and were supplemented with fishing in the coastal areas. We categorized all individuals into 3 SES groups (treated as 3-level categorical variable in the analyses) according to the father's occupation: low (e.g., farmless families and servants), middle (e.g., tenant farmers, smiths, and fishermen), and high (e.g., aristocrats and landowners) (Pettay et al. 2007). Overall, the standard of living was low with both famines and diseases common (Turpeinen 1978; Pitkänen et al. 1988; Helle et al. 2004; Hayward et al. 2012). Surviving offspring usually moved away from home to work from around age 15 onward (mean age at departure from the parental household = 22 years old in our study sample), but some returned home (Moring 2003a). Most siblings usually settled to live close by the parental household (i.e., in their natal parish, only 17% of individuals moved to another parish) (Moring 1993). Therefore, even in the case where uncles and aunts had moved out from their parental household, they often remained in close contact with their family with the possibility to impact the fitness of their kin.

Similarly to the general European pattern at the time, the average age at first marriage was 25 for women (range 15–67) and 27

for men (range 16–78), the mean age at first reproduction was 26 for women (range 15–45) and 28 for men (range 17–68) (Gillespie et al. 2010), and 83% of offspring married if they survived to maturity (defined here as 15 years of age, the age of the youngest known reproducer in our population). Inheritance usually favored the eldest son (primogeniture) and the predominant household was composed of the eldest son, his wife, their children, his parents, and one or more unmarried siblings (Moring 2003b). The mating system of this population was monogamous, patrilocal, and divorce was forbidden (Sundin 1992).

The study sample is restricted to individuals for whom all the variables controlled for in our statistical analysis (see below) were available. Twins (4% of the overall sample) were excluded from the study because of their lower average survival chances (Lummaa et al. 2001). To be able to take into account the uncles and aunts from both maternal and paternal sides, individuals were included in the study only if their 4 grandparents' identities were known. The final study sample contains 2151 focal males and 1994 focal females born 1750–1900 to 907 mothers. In this sample, 28.3% of individuals born did not survive until age 15.

## Event history analysis

We used discrete event history analysis to predict the survival chances of the focal child to the following year from birth to age 15, depending on the number of childless aunts and uncles residing in the same parish in that year (see below for the details on which uncles and aunts were considered as potential helpers) (Singer and Willett 1993). Year was chosen as the time unit to have precise and accurate enough information on individual life histories and the presence of uncles and aunts without compromising the model fit by overparametrization. Year, rather than a more exact date, was also the unit in which dispersal events were recorded. Survival status of the focal child at each age (15 time intervals for each child from birth to age 15 referred to later as "observation year") was scored as a binary response (0 = did not survive, 1 = survived) and analyzed using generalized linear mixed models with a binomial error structure and a logit link function. This method combines several important advantages. First, this method enables us to investigate at the same time the effect of time-independent and time-varying variables (e.g., the number of uncles and aunts alive at a particular age or the survival of the mother) (Singer and Willett 1993). Second, the method allows for inclusion of censored individuals, that is, individuals that have not been followed until the end of the study period. This avoids biasing the sample toward individuals that either died young or have complete records. Lastly, this method does not require assumptions regarding the distribution of survival through time. All analyses were conducted separately for each sex because life histories and the amount of help received from other family members can differ between males and females (Sear and Mace 2008; Faurie et al. 2009; Nitsch et al. 2013). Mother's identity, parish, and birth year were included as random factors to take into account the dependency between individuals of the same family, same geographic area, or same year. Each discrete time unit (here years) for each individual was considered as a separate observation in this analysis and within subject correlation cannot exist with this type of data; therefore, we did not include the child's id as a random term as it was unnecessary (Allison 1982; Singer and Willett 2003). We also controlled for the fixed effect of the following confounding factors: mother's and father's survival status (whether or not the mother or the father was alive at each age of the focal child), birth order (i.e., firstborn or laterborn to account for lower survival of firstborns in the study population) (Faurie et al. 2009), number of living siblings, the SES of the family (a 3-level categorical variable), and the grandmothers' survival status (whether at least one of the grandmothers was still alive at each age of the focal child). Grandfathers' survival status was not included in the model as previous studies on this population did not highlight any influence of their presence on child survival (Lahdenperä et al. 2007, 2011). Controlling for the number of living siblings included simultaneously any effects from competition for resources between siblings and the potential help provided by elder siblings (Nitsch et al. 2013).

## Uncle and aunt variables

Our aim was to investigate the potential positive effect of currently childless uncles and aunts on the survival of their nephews and nieces. Childlessness status at a given time point could nevertheless refer to different situations: 1) individuals had not begun their reproduction yet, although they went on to reproduce later in their life; 2) individuals had no child(ren) during their entire lifetime; and 3) individuals had begun to reproduce, but their children had died. These situations could imply different fitness-maximizing strategies. First, most young individuals are childless but reproduce later in their life. This category of currently childless individuals could potentially invest mainly in their future reproduction and not in their nephews' and nieces' fitness. Second, childless individuals who are older than the age at which most individuals have already started reproducing have lower chances to ever reproduce, and this could imply a higher investment toward their nephews and nieces. In order to compare the effects of these 2 categories of uncles and aunts on their niece's or nephew's survival, the childless uncles and aunts were divided into 2 groups based on the age when 75% of individuals had already started reproduction (age 28 for women and 31 for men). These 2 groups have very distinct expectations of ever reproducing (proportion of individuals who eventually managed to reproduce in their lifetime = 70.7% for individuals under 28 or 31 years referred later as "young", proportion of individuals who eventually managed to reproduce in their lifetime = 48.4%, for "old" childless individuals above 28 or 31 years) and therefore could have different fitness-maximizing strategies.

We also counted the number of uncles and aunts who had already at least 1 child at a given time and classified them into similar age categories as the childless uncles and aunts, in order to be able to distinguish whether any detected effect depended on the age classification or the reproductive status. Reproductive uncles and aunts whose child(ren) had died ($n$ = 477, 5.6% of the overall sample size of childless uncles and aunts) were categorized with the reproductive uncles and aunts because although they currently had no alive children to look after, they had already started investing in their own direct fitness and were in a situation closer to that of the reproductive uncles and aunts (married and most of the time not residing anymore at their parents) and therefore were not expected to maximize their fitness mainly by enhancing that of their nephews and nieces.

Finally, in order to test the importance of the lineage (father's vs. mother's relatives), in further analyses, we split these variables into paternal and maternal uncles/aunts. For all of these variables, only uncles and aunts sexually mature (older than 15 years), alive, and living in the same parish as the focal child in a given observation year (i.e., those born in the same parish and not dispersed or those born in another parish but moved into the parish of the focal child) were included.

### Multimodel selection and model averaging techniques

We used model averaging techniques to determine whether the presence of a particular class of uncles and aunts had an important effect on child survival. Multimodel selection techniques make it possible to estimate the relative importance of each variable in a model. From a global model, a set of all the possible combinations of models is generated and these models ranked according to their goodness-of-fit to the data based on the Akaike information criterion (AIC) (Grueber et al. 2011; Symonds and Moussalli 2011).

The difference in AIC ($\Delta i$) between the model with the lowest AIC (considered as the best model) and the other models provides a measure of how much more likely the best model is than model $i$. Following Burnham and Anderson (2002), we only considered models with $\Delta i$ values up to 4. For each model, we calculated a weight ($w_i$) as an estimation of the probability that a given model is the best approximating model among this subset of models (Symonds and Moussalli 2011). We summed the weights $w_i$ of all models containing any given variable, to estimate the relative importance of this variable. The relative importance of a variable reflects the probability that it is a component of the best model, and how it improves the model fit (Symonds and Moussalli 2011). We computed model-averaged parameters and error estimates for each variable (Anderson et al. 2001; Symonds and Moussalli 2011). We also calculated the odds ratios (ORs) of the effects and the 95% confidence interval (95% CI) for each variable. When the 95% CI excludes one, the variable studied is considered as associated with the response variable (here the probability of survival until next year). Conversely, when the 95% CI includes one, it indicates that the variable studied is not systematically associated with higher or lower survival chances and therefore that its effect in our analyses is not found to be strong.

All analyses were conducted using R 2.15.2 (R Development Core Team 2012) and the packages "*lme4*," "*MuMIn*," and "*AICcmodavg*" (Barton 2012; Bates et al. 2013; Mazerolle 2013).

As suggested in Grueber et al. (2011), we investigated a priori which interactions to include in the global model. Interactions between covariates and the niece's or nephew's age were tested, to determine whether any effects varied with individual age. Interactions between uncles' and aunts' presence and the family SES or mother's and father's survival were also tested, to determine whether SES and mother's or father's presence could influence uncles' and aunts' behavior. As these interactions were nonsignificant at the level of $\alpha = 0.05$, they were not included in the global model. We also tested for the interaction between father's survival status and the SES of the family. As this interaction was significant for males, we kept this interaction in the models on males. Our global model included the uncle and aunt variables (see above) and the potentially confounding variables. Potential confounding variables were included in all models generated: the only changes between models concerned the uncle and aunt variables. Prior to model selection and for each model, we compared the fit of the global model to that of a null model comprising only the random terms and the constant to test whether the difference in AIC was significant. This step ensured that the models were able to explain our response variable.

The test of the effect of uncles and aunts on child survival was 2-fold. In a first step, we fitted a global model with all types of uncles and aunts (young or old and childless or not), but without any specification of lineage. In a second step, we investigated whether there were differences in the effects of paternal and maternal uncles and aunts: the variables specified separately the number of maternal or paternal uncles or aunts of each category. However, for this latter analysis, we could not include simultaneously all of the uncle and aunt variables (16 different variables) because of overparameterization (see Grueber et al. 2011). Therefore, in this second step, we fitted 2 separate global models: the first one included only the younger uncle/aunt variables and the second only the older uncles/aunts. Then similarly to the overall first analysis, we used model averaging techniques to determine the estimates and the standard errors (SEs) associated with the effect of each factor.

## RESULTS

### Effect of uncles and aunts on child survival

Overall, our results provided little support for a positive effect of childless uncles and aunts on their nephews' and nieces' survival.

#### *Nephew's survival*

Mortality during the study period was high with 29% of the males included in our model dying before reaching 15 years of age. Many males had the opportunity to be aided by uncles or aunts, given that 58% of boys had nonreproductive uncle(s) and 55% nonreproductive aunt(s) present in the parish at least for part of their childhood (on average for 9 years for childless uncles or aunts). The mean age of childless young uncles and aunts was 23.9 (±0.04 SE) and 22.0 (±0.04 SE), respectively (Supplementary Table 1). However, the presence of such kin provided no benefits to the survival of the nephews. Instead, our analyses show that males with no young childless uncles present had a higher chance of survival during childhood than those with at least 1 young childless uncle (under 31), given that the 95% CI of the effect of young childless uncles excludes 1 (OR = 0.91, 95% CI [0.84; 0.99], Table 1, Figure 1c). Model selection revealed that this negative effect of the presence of young childless uncles is reasonably robust with a relative importance weight of the variable of 0.87 (Table 1). In additional analyses, we included the variable "number of young childless uncles" as a categorical variable (0, 1, 2, 3, 4, or more): a negative effect of having young childless uncles on male survival was highlighted only in cases where at least 3 uncles were present. The models including the effects of other types of childless or reproductive uncles and aunts had much lower support with relative importance ranging from 0.17 to 0.35 (Table 1) and from 0.12 to 0.24, respectively (Supplementary Table 2a), indicating weak effects of these kin.

#### *Niece's survival*

Twenty-eight percent of the females included in our model died before reaching 15 years of age. As in males, many females had the opportunity to be helped by their uncles or aunts, given that 58% of girls had nonreproductive uncle(s) and 54% nonreproductive aunt(s) present at least for part of their childhood (on average for 9 years for nonreproductive uncles or aunts) (Supplementary Table 1). The mean age of childless young uncles and aunts was 23.9 (±0.04 SE) and 21.9 (±0.04 SE), respectively. Overall, similarly to males, most categories of uncles and aunts were not positively related to niece's survival, with the exception that the presence of old childless uncles provided benefits to the survival of the nieces (Table 1 and Figure 2d). Moreover, the presence of old childless aunts was moderately negatively associated with their niece's survival (Table 1 and Figure 2b). The relative importance associated with the other categories of uncles and aunts, such as young

**Table 1**
**Effect of childless uncles and aunts on the probability of survival for males and females**

Probability of survival

| | Relative importance | OR [95% CI] | ΔAIC |
|---|---|---|---|
| Males | | | |
| Childless uncles | | | |
| <31 years | **0.87** | **0.91 [0.84; 0.99]** | **2.3** |
| >31 years | 0.19 | 1.03 [0.88; 1.22] | −1.9 |
| Childless aunts | | | |
| <28 years | 0.35 | 1.07 [0.95; 1.21] | −0.3 |
| >28 years | 0.17 | 1.04 [0.89; 1.23] | −1.8 |
| Females | | | |
| Childless uncles | | | |
| <31 years | 0.45 | 0.93 [0.84; 1.03] | 0.3 |
| >31 years | **0.97** | **1.25 [1.02; 1.52]** | **4.1** |
| Childless aunts | | | |
| <28 years | 0.50 | 1.09 [0.96; 1.26] | 0.3 |
| >28 years | 0.66 | 0.81 [0.71; 1.02] | 0.7 |

Relative importance of the variable in model selection, OR of the estimates and 95% CI for childless uncles and aunts ($n_{observation\text{-}years}$ for males = 22 998 from 2151 males; $n_{observation\text{-}years}$ for females = 21 386 from 1994 females). Categories of uncles and aunts with a relative importance > 0.7 and with a 95% CI not including 0 are highlighted in bold. The effect of removing each variable on the full model AIC is shown (ΔAIC). The full model contains the random terms and all the main fixed terms included in the model selection (i.e., the controlled factors and all the categories of uncles and aunts). Positive ΔAIC values indicate the parameter improved model fit. See Supplementary Table 2 for details of the effect of the other variables.

nonreproductive uncles and old nonreproductive aunts (or reproductive aunts or uncles) ranged from 0.16 to 0.5, therefore indicating a weak effect of these kin on the survival probabilities of females (Table 1 and Supplementary Table 2b).

## Are the effects of uncles and aunts lineage dependent?

### *Nephew's survival*

Our further analyses separately investigating the effects of paternal versus maternal relatives confirm our overall conclusion that presence of kin provided little benefits to the survival of the nephews. They also revealed that the above negative effect of the presence of young nonreproductive uncles on their nephews' survival was driven mainly by paternal uncles. Indeed, in the model selection analysis using a data set on either maternal or paternal kin, young paternal childless uncles had an importance of 0.95, whereas young maternal uncles only had an importance of 0.19. The other types of young uncles and aunts (i.e., childless aunts and reproductive uncles and aunts) exerted only a weak influence on a male chance of surviving to adulthood with relative importance of these variables ranging from 0.16 to 0.25 (Table 2 and Supplementary Table 3a).

Finally, we did not find any evidence in the model selection that the older uncles and aunts influenced male survival (range of weights: 0.13–0.28) (see Supplementary Table 4a).

### *Niece's survival*

Similarly, most lineage specific effects of uncles and aunts on niece's survival were small. For example, in model selection on young uncles and aunts, young maternal childless uncles had negative effect with a weight of 0.66, but the 95% CI of the OR overlaps 1 indicating that this variable is not strongly associated with female survival. No effect of the other categories of young uncles and aunts on their niece's survival was detected (range of weights: 0.17–0.41) (see Table 2 and Supplementary Table 3b).

In the model selection analysis including only older uncles and aunts, the moderate negative effect of the presence of older nonreproductive aunts was found to be mainly driven by paternal aunts (Table 2). Moreover, the positive effect of old childless uncles highlighted in previous models was found to be mainly driven by maternal uncles, although the association is not very strong with the 95% CI just including 1 (Table 2). The relative importance of the other categories of older uncles and aunts (range of weights: 0.15–0.44) was low, suggesting that their influence on their niece's survival was weak (Supplementary Table 4b).

## DISCUSSION

Determining the effects of childless adult uncles and aunts on child survival helps to understand the evolution of family formation and living, and the extent to which the cooperative breeding theory may apply to humans. Indeed, several studies have suggested that, similarly to other categories of kin with a low current reproductive value (such as elder siblings and grandmothers), adult uncles and aunts could also have beneficial effects on child survival with the nonreproductive ones more likely to have beneficial effects than those with children (Pollet et al. 2006; Pollet and Dunbar 2008). However, no study has yet distinguished the fitness consequences of reproductive versus childless uncles and aunts, and therefore their potential effects remain unclear. We used an extensive demographic data set from 18th- to 19th-century Finland to investigate whether the presence of nonreproductive adult aunts/uncles living in the same parish benefitted their niece's or nephew's survival to adulthood in a population with extended family system. Our results show that contrary to predictions, most childless uncles and aunts did not benefit the survival of their nephews and nieces. The only exception was that the presence of old childless uncles improved somewhat the survival of their nieces during childhood. The presence of 2 types of kin even had negative effects: young childless uncles negatively influenced the survival chances of their nephews and the presence of old childless aunts those of their nieces. These results are not likely to be confounded by SES, mother's survival, father's survival, or the presence of other kin, as these effects were all controlled for in our analyses. Moreover, because we used time event analyses, we would have detected any effect that was limited to a particular time period of childhood and that is usually not detectable with global analyses. We explored the effect of all the categories of uncles and aunts residing in the same parish in order to test the following predictions: 1) those who are childless would be beneficial, 2) those who had children would be neutral (when they were living in a separate household from the focal child) or deleterious (in cases of joint residence with the focal child), 3) those who were older would be more beneficial that those who were younger, and 4) maternal lineage would be more beneficial than paternal lineage. Despite the use of powerful techniques, a large sample size and the risk of finding false positive effects associated with multiple tests, we highlighted only small or even no effects of the presence of uncles and aunts. Therefore, our results suggest that although elder siblings in this population could be helpful toward each other in childhood (Nitsch et al. 2013), they provide little assistance in

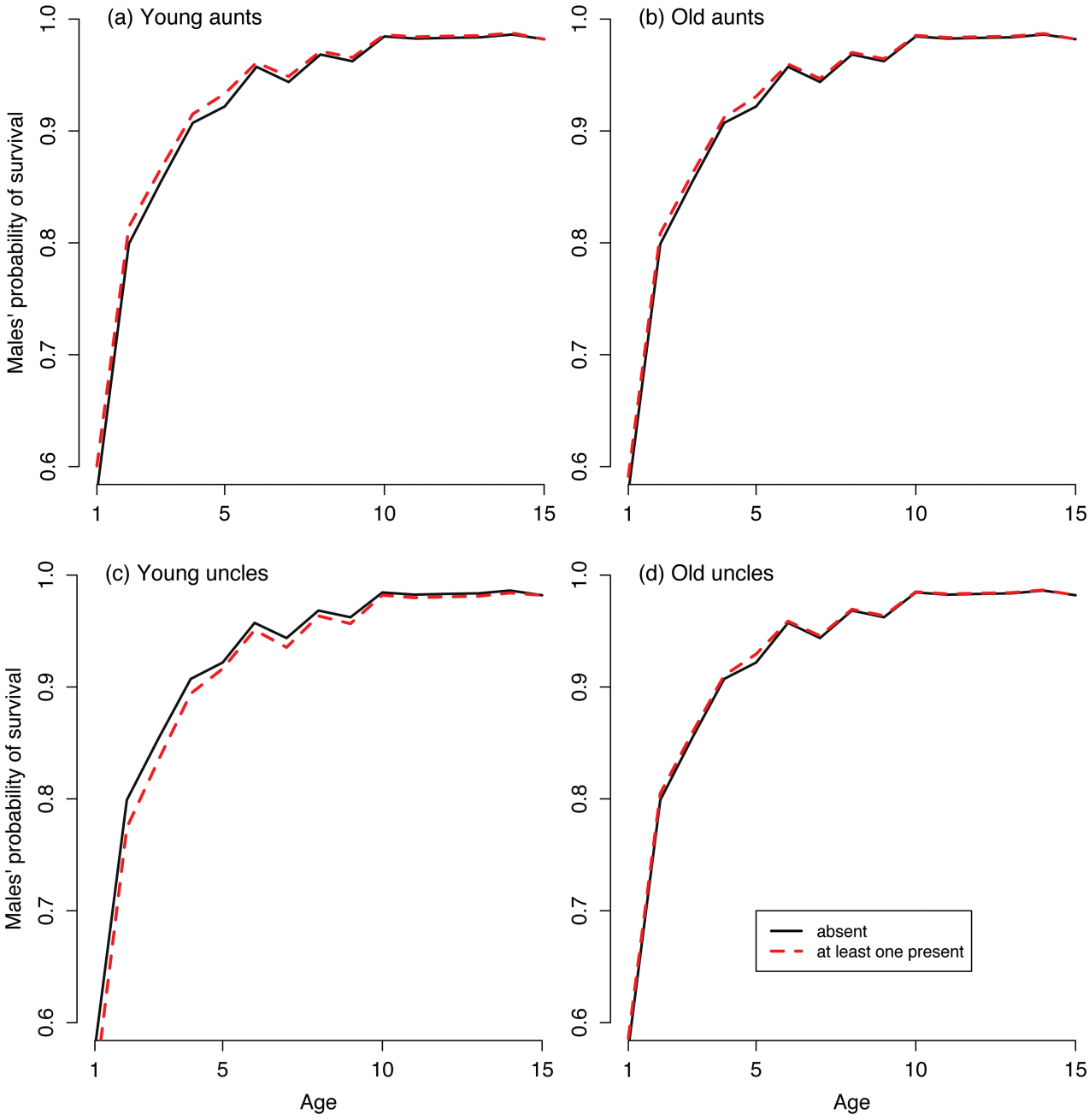


**Figure 1**
Male probability of surviving to the following year by age depending on the presence (dashed line) or absence (plain line) of (a) young childless aunt(s) whose relative importance was 0.35 in the model selection, (b) old childless aunt(s) whose relative importance was 0.17 in the model selection, (c) young childless uncle(s) whose relative importance was 0.87 in the model selection, and (d) old childless uncle(s) whose relative importance was 0.19 in the model selection. Predicted values are calculated from the model average estimates. Survival probability in the presence of childless uncle(s)/aunt(s) is calculated for the average number of this category among the study population when at least 1 uncle/aunt was present.

childrearing to their siblings in adulthood (this study) and may even reduce sibling fitness by for instance competing for marital opportunities (Nitsch et al. 2013).

In regression analyses of demographic data sets, the causal relations are difficult to establish given the lack of information on the underlying mechanisms. The historical records on the Finnish population provide us with information about the mating system, marriage locality, and inheritance system in this period, enabling insights into several potential mechanisms explaining our results. Our results can be interpreted differently for each lineage as during our study period the mating system was patrilocal, with women moving to their husband's household (Moring 2003b). Thus, childless paternal uncles and aunts were more likely to have an influence on the survival of their nephews and nieces because they often remained in the same household until they married (86% of childless young uncles or aunts were unmarried in our study sample). Therefore, unmarried aunts had the opportunity to provide direct care, and unmarried uncles could have worked and thereby

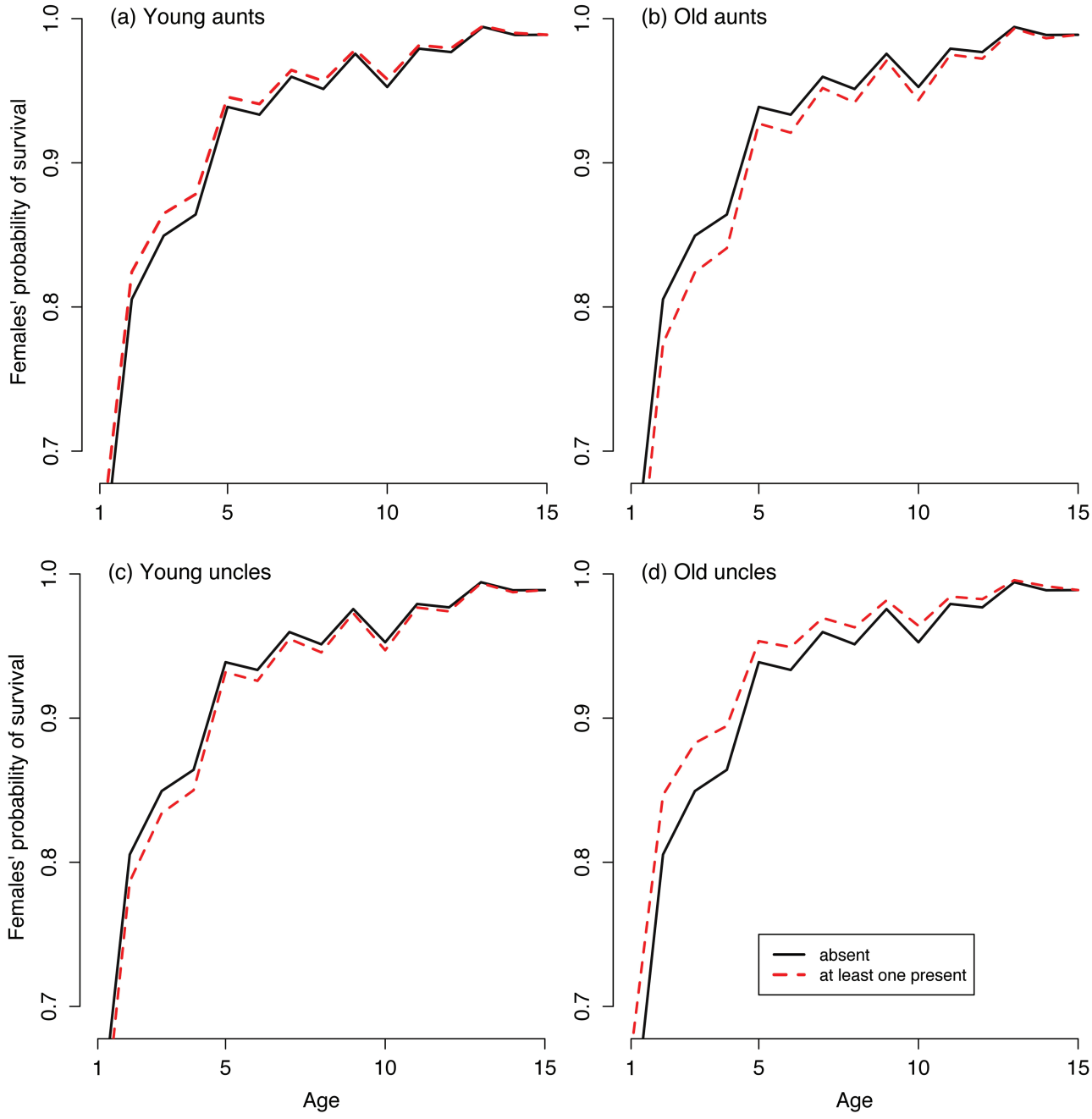


**Figure 2**
Female probability of surviving to the following year by age according to the presence (dashed line) or absence (plain line) of (a) young childless aunt(s) whose relative importance was 0.5 in the model selection, (b) old childless aunt(s) whose relative importance was 0.66 in the model selection, (c) young childless uncle(s) whose relative importance was 0.45 in the model selection, and (d) old childless uncle(s) whose relative importance was 0.97 in the model selection. Predicted values are calculated from the model average estimates. Survival probability in presence of childless uncle(s)/aunt(s) is calculated for the average number of this category among the study population when at least one of them was present.

provided additional resources to the family. However, as unmarried paternal uncles and aunts depended on the resources of the household, their work may have just counterbalanced their own consumption of resources, which could explain why their presence did not increase child survival (and even decreased it in the case of paternal younger uncles or paternal older aunts). Moreover, it may not be an advantageous strategy for a paternal uncle to improve his nephews' survival chances because they are in conflict of interest over goods and land inheritance. Our results also suggest that younger childless uncles are detrimental for child survival only in situations of high competition (e.g., for resources or mating opportunities, perhaps partly due to an investment bias of grandparents favoring their sons over their grandchildren).

On the contrary, patrilocality in this population implies that the interactions between maternal uncles or aunts and their nephews or nieces were limited (Moring 2003b), therefore reducing the potential effect of maternal uncles or aunts on their nephews and nieces, which could explain why the presence of most types of maternal

**Table 2**

**Effect of maternal and paternal childless uncles and aunts on the probability of survival for males and females**

| | | Relative importance | OR [95% CI] | ΔAIC |
|---|---|---|---|---|
| Males | | | | |
| Young childless uncles and aunts | | | | |
| Uncles | | | | |
| <31 years | Maternal | 0.19 | 0.96 [0.84; 1.09] | −1.5 |
| | Paternal | **0.95** | **0.88 [0.70; 0.99]** | **2.7** |
| Aunts | | | | |
| <28 years | Maternal | 0.18 | 1.04 [0.89; 1.22] | −1.6 |
| | Paternal | 0.25 | 1.11 [0.70; 1.32] | −0.9 |
| Old childless uncles and aunts | | | | |
| Uncles | | | | |
| >31 years | Maternal | 0.19 | 0.94 [0.74; 1.20] | −1.7 |
| | Paternal | 0.28 | 1.13 [0.90; 1.42] | −1.0 |
| Aunts | | | | |
| >28 years | Maternal | 0.13 | 0.98 [0.76; 1.25] | −1.9 |
| | Paternal | 0.23 | 1.11 [0.88; 1.39] | −1.4 |
| Females | | | | |
| Young childless uncles and aunts | | | | |
| Uncles | | | | |
| <31 years | Maternal | 0.66 | 0.88 [0.76; 1.02] | 1.6 |
| | Paternal | 0.16 | 0.99 [0.86; 1.14] | 2.0 |
| Aunts | | | | |
| <28 years | Maternal | 0.41 | 1.13 [0.93; 1.36] | −0.1 |
| | Paternal | 0.29 | 1.09 [0.90; 1.32] | −1.2 |
| Old childless uncles and aunts | | | | |
| Uncles | | | | |
| >31 years | Maternal | **0.79** | **1.34 [0.98; 1.82]** | **1.8** |
| | Paternal | 0.44 | 1.20 [0.91; 1.57] | 0.1 |
| Aunts | | | | |
| >28 years | Maternal | 0.17 | 0.97 [0.73; 1.30] | −1.9 |
| | Paternal | **0.85** | **0.79 [0.62; 0.99]** | **2.4** |

Relative importance of the variable in model selection, OR of the estimates and 95% CI for childless uncles and aunts ($n_{observation\text{-}years}$ for males = 22 988 from 2151 males; $n_{observation\text{-}years}$ for females = 21 386 from 1994 females). Categories of uncles and aunts with a relative importance > 0.7 and with a 95% CI not including 0 are highlighted in bold. The effect of removing each variable on the full model AIC is shown (ΔAIC). The full model contains the random terms and all the main fixed terms included in the model selection (i.e., the controlled factors and all the categories of uncles and aunts). Positive ΔAIC values indicate the term improved model fit. See Supplementary Tables 3 and 4 for details of the effect of the other variables.

uncles and aunts had no effect on child survival. Nevertheless, our results also highlighted a positive effect of maternal older uncles, thereby suggesting their potential care was not, as for paternal uncles, counterbalanced by the negative effect of sharing the same household. It is interesting noting that this positive effect was limited to nieces, perhaps because nephews were potential future competitors for inheritance. However, investigating the causal explanations of these effects would require detailed behavioral data and more information of the causes of childlessness.

From an evolutionary point of view, our results suggest that apart from the case of old maternal uncles, the relative costs and benefits of helping versus attempting to reproduce do not favor investment by uncles or aunts toward their nephews or nieces. The benefits of helping strongly depend on relatedness, which, in turn, is determined by 2 main factors: type of parentage and the type of lineage. First, when considering solely parentage, expected relatedness between uncles or aunts and their nephews or nieces is relatively low ($r$ = 0.25) compared with other types of kin, such as siblings (0.5). Second, due to paternity uncertainty, relatedness could vary with the type of lineage: collateral kin (e.g., uncles or aunts) may have an even lower (perceived) relatedness with their nephews or nieces, as opposed to direct kin such as maternal grandmothers (Webster et al. 2008). Similarly, relatedness between uncles and aunts and their nephew and nieces is likely to be lower for paternal than for maternal kin. This hypothesis is supported by our finding that only the presence of paternal uncles and aunts was negatively associated with child survival.

Another important parameter to take into account to understand the investment of uncles and aunts toward the offspring is the costs associated with helping. These costs are likely to be higher for nonreproductive uncles and aunts than for the other categories of helpers who are not currently able to reproduce (e.g., grandmothers). Due to the low expected indirect benefits and the high costs of helping, investing into their own reproduction might be a better strategy for childless uncles and aunts, even when the chances of ever reproducing are low, as was the case for older uncles or aunts. Our results suggest that helping may have not been an adaptive strategy in this population possibly apart from individuals having simultaneously a high lineage certainty and low cost for their own reproduction (i.e., the maternal old uncles).

The presence of other categories of kin such as grandmothers and sexually immature elder siblings has been found to benefit offspring survival in this population (Lahdenperä et al. 2004; Nitsch et al. 2013). The higher relatedness certainty and lower reproductive prospects of grandmothers compared with uncles and aunts might explain why, despite grandmothers being similarly related to their grandchildren as uncles and aunts are to their nieces and

nephews (0.25), grandmothers appear to provide beneficial care in this population (Lahdenperä et al. 2004). Conversely, the higher relatedness of sexually immature elder siblings with their siblings (0.5) and their potentially lower current costs of helping might explain why they are beneficial to their younger siblings. However, understanding the differences in helping patterns among different categories of kin would require more information on the costs and benefits of investment toward direct and indirect fitness.

Moreover, characteristics of the family system, the inheritance system, patrilocality versus matrilocality, and the availability of resources, are likely to influence these costs and benefits of helping across different human populations. For instance, in Malawi, in families where resources are owned by the women, the presence of maternal aunts was found to be detrimental to child survival, whereas in families where resources are owned by men, maternal aunts were reported to be beneficial (Sear 2007). It is also likely that in other family systems (e.g., joint families), patterns of helping and effects of childless reproductive-aged adults could be different. However, lack of studies thoroughly investigating the effects of childless uncles and aunts precludes any comparative analysis.

Finally, it is important to note that in cooperative breeding species other than humans, where most helpers are young nonreproductive individuals (Clutton-Brock 2009; Lukas and Clutton-Brock 2012), contradictory effects of helpers have also been highlighted. In some cases, helpers' presence was not associated with higher survival chances of offspring (Woodroffe and Macdonald 2000; Allainé and Theuriau 2004). Individuals might help to raise offspring that are not their own to increase their direct fitness as well as their indirect fitness (Richardson et al. 2002; Kingma et al. 2011). For instance, care of offspring could be used for helpers as a training of parental care, but as they are inexperienced they do not always improve the survival of the young (Komdeur 1996). Similarly, the help they provide might be a price to pay to be allowed to stay in the breeding group, increasing their future mating opportunities or chances of inheriting the territory, but not necessarily the survival of helped young (Cant and Field 2001; Richardson et al. 2002). A similar situation could be encountered in humans, where for young adults, sharing the parental household, or living close by and helping, could increase parental investment in their mating opportunities or chances of inheriting in cases of death of the heir. It is also possible that staying at the parental household is only beneficial for the remaining individuals and not for the parental overall fitness or their other kin. However, these hypotheses have not been thoroughly tested yet in humans. Therefore, the implications of the family structure, kin interactions, and share of households need further investigation, in order to understand the fitness-maximizing strategies of childless uncles and aunts and, more broadly, conflict and cooperation in the human family.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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