

Sibship effects on dispersal behaviour in a pre-industrial human population

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Abstract

Understanding dispersal behaviour and its determinants is critical for studies on life-history maximizing strategies. Although many studies have investigated the causes of dispersal, few have focused on the importance of sibship, despite that sibling interactions are predicted to lead to intrafamilial differences in dispersal patterns. Using a large demographic data set from pre-industrial Finland ($n = 9000$), we tested whether the sex-specific probability of dispersal depended on the presence of same-sex or opposite-sex elder siblings who can both compete and cooperate in the family. Overall, following our predictions, the presence of same-sex elder siblings increased the probability of dispersal from natal population for both sexes, whereas the number of opposite-sex siblings had less influence. Among males, dispersal was strongly linked to access to land resources. Female dispersal was mainly associated with competition over availability of mates but likely mediated by competition over access to wealthy mates rather than mate availability *per se*. Besides ecological constraints, sibling interactions are strongly linked with dispersal decisions and need to be better considered in the studies on the evolution of family dynamics and fitness maximizing strategies in humans and other species.

Introduction

Natal dispersal, the behaviour by which an individual leaves its natal environment, is an important life-history trait influencing family living, population dynamics and population genetic structure (Greenwood, 1980; Emlen, 1995; Bowler & Benton, 2005; Hatchwell, 2009). There are three nonmutually exclusive benefits of dispersal: an increased access to mating opportunities, an increased access to resources and inbreeding avoidance (Greenwood, 1980; Dobson, 1982; Dobson & Jones, 1985). However, dispersal is a risky behaviour involving many costs (Bonte *et al.*, 2012), whereas philopatry may provide many benefits, for example through familiarity with the natal environment (Anderson, 1989). Therefore, dispersal is expected to be the

favoured strategy only when its potential benefits outweigh its costs (Clobert *et al.*, 2012).

Dispersal patterns (e.g. dispersal distance, propensity of dispersal or age at dispersal) vary drastically between species, populations and individuals (Clobert *et al.*, 2012). Family systems, life-history traits or the quality of the natal territory are some factors explaining this variability (Greenwood, 1980; Dobson, 1982; Bowler & Benton, 2005; Hatchwell, 2009; Clobert *et al.*, 2012), as they modify the overall fitness outcome of dispersal and philopatry. Among those factors, kin have been found to be of particular importance. Indeed, in addition to direct benefits, inclusive fitness theory predicts that a given dispersal strategy can benefit an individual's fitness indirectly, via the effects on kin, for instance by decreasing kin competition for limited resources or mates (Hamilton, 1964; Lambin *et al.*, 2001; Clobert *et al.*, 2012). Thus, dispersal could be the expected strategy if the fitness benefits for the philopatric kin outweigh the dispersal costs, even if dispersal is

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not associated with an increase in the own reproductive success of the dispersers themselves (Hamilton & May, 1977). This idea has been supported by analytical models (Hamilton & May, 1977; Crespi & Taylor, 1990; Rodrigues & Gardner, 2015) and field studies in various taxa (Jacquot & Vessey, 1995; for a review see Lambin *et al.*, 2001; Ekman *et al.*, 2002; Davis, 2012). For instance, recent analytical models from Kisdi (2004) suggested that the Evolutionarily Stable Strategy would be a threshold strategy: individuals will leave the natal territory once a minimal number of offspring is reached. However, other studies suggest that in social species, because of the importance of kin interactions, kin presence instead promotes philopatry (Lambin *et al.*, 2001; Bowers *et al.*, 2013; Hoogland, 2013). Consequently, dispersal patterns are closely related to family dynamics and conflicts, as they can be simultaneously viewed as an outcome of kin interactions and as a strong determinant of the future family dynamics. Moreover, sibling interactions can lead to intrafamilial differences in dispersal patterns that have been related to parental favouritism (Ekman *et al.*, 2001; Ragheb & Walters, 2011), competitive asymmetries between siblings (Strickland, 1991; Ekman *et al.*, 1999; Ellsworth & Belthoff, 1999), different family sizes (Kisdi, 2004) or the existence of territorial bequeath (Jacquot & Vessey, 1995; Ragsdale, 1999). Although these variables are likely to strongly interact with each other in modifying dispersal patterns, their influence have rarely been investigated together (for exceptions see Pasinelli & Walters, 2002; Scandolaro *et al.*, 2014b; Johnson *et al.*, 2015). However, such multivariate analysis is essential for a comprehensive understanding of dispersal and its determinants in family-living species. Previous studies on the effects of kin structure on dispersal have rarely addressed these questions against predictions derived from the effects of kin on other life-history traits, although at least in some species, the effects of kin on traits such as breeding probability and reproductive success can be sex-specific (Nitsch *et al.*, 2013; Scandolaro *et al.*, 2014a) or vary across different life-history stages (Sparkman *et al.*, 2011; Nitsch *et al.*, 2013; Berger *et al.*, 2015). Therefore, it is likely that dispersal decisions are most fruitfully examined with an integrative approach that considers effects on all such traits simultaneously.

Humans offer interesting opportunities to study in details how sibling interactions affect dispersal patterns against potential effects on other life-history traits, as they combine characteristics that are relevant for such studies: several different-aged offspring are raised simultaneously, who both cooperate and compete within the natal family (Sear & Mace, 2008), unusually accurate data exist on their dispersal events (e.g. Clarke & Low, 1992; Towner, 2001), and most of the family members can be followed throughout life. In humans, few studies have investigated the individual determinants of dispersal, and even fewer have focused on

sibling interactions, although their importance is strongly suggested by the literature. First, previous studies have emphasized the influence of sibship configuration on several other key life-history traits, such as survival or reproductive success (Boone, 1987; Borg-erhoff Mulder, 1998; Nitsch *et al.*, 2013). Second, other studies from historians have pointed out the importance of siblings on dispersal decision (Kesztenbaum, 2008; Kok & Bras, 2008). However, the lack of an evolutionary approach in these latter studies precludes understanding of the causes of dispersal, namely whether dispersal was influenced preferentially by competition over mating opportunities, resources or by the risk of inbreeding. These studies did not consider intra-sex birth order (e.g. Clarke & Low, 1992; Beise & Volland, 2008) or the interaction with the family socio-economic status (SES), although more recent studies have shown the importance of considering those latter factors in studies on sibling interactions (Faurie *et al.*, 2009; Nitsch *et al.*, 2013). Therefore, similarly to non-human species, studies investigating in detail the determinants of variation of dispersal patterns between siblings are lacking, thereby preventing the emergence of a comprehensive picture of the interplay between sibling interactions, dispersal behaviour and other potentially confounding factors.

In this study, we investigate the detailed effect of co-resident siblings on dispersal behaviour in a pre-industrial human population from Finland. More specifically, using time event survival analysis, we tested whether the probability of dispersal depended on the number of co-resident siblings alive at each age, while controlling for the effects of several potentially confounding factors, such as family SES and parental age. This data set is suited to investigate the effect of sibling interactions on dispersal behaviour for several reasons: (1) accurate data exists on the dispersal status, age, dispersal destination of individuals, their siblings and on other life-history traits (e.g. marital status), enabling a comprehensive investigation of the determinants of dispersal; (2) the effect of the presence of siblings on other fitness outcomes (survival to sexual maturity and reproductive success) has already been investigated previously in this population (Nitsch *et al.*, 2013), revealing a strong sex-specific negative effect of elder siblings on reproductive success. However, this study did not investigate differences in dispersal patterns potentially existing between siblings. In this study, the negative effect of the presence of elder brothers on reproductive success was mainly mediated by a competition over inheritable land resources with the eldest son inheriting most of the parental resources and subsequently having increased marriage probability and reproductive success. On the contrary among females, competition between sisters was mainly mediated by competition over mating opportunities with elder sisters having a higher marriage probability and reproductive success than their

younger sisters (Nitsch *et al.*, 2013). This latter effect was strongly mediated by younger sisters marrying men of lower social class and at a later age than their elder sisters. More generally variation in fitness among sisters was likely to be driven by an unequal distribution of sex-specific resources necessary for marrying (e.g. parental resources or mating opportunities). Therefore, we predicted that dispersal patterns should follow the outcome of sibling interactions on other life-history traits. Specifically, (1) dispersal propensity should increase with the number of same-sex elder siblings present; (2) for males, dispersal pattern should strongly depend on resources and inheritance patterns, with nonheirs being more likely to disperse; and (3) for females, dispersal pattern should reflect an intrasex conflict for mating opportunities, females with more elder sisters being unable to find a suitable mate in their birth parish. We focused on the effect of siblings on dispersal probability and age of dispersal, as previous studies enable to make clear predictions on these outcomes. On the contrary, potential kin effects on dispersal destination (e.g. distance of dispersal or location) could depend on a range of other factors (such as economical or ecological features of dispersal location, kin residence in other parishes, the availability of information from kin or nonkin) (Matthysen *et al.*, 2005; Epstein & Gang, 2006; Kesler & Walters, 2012) which have been overlooked in humans (Glover & Towner, 2009) and was therefore out of the scope of this study.

We found that, for both sexes, the presence of same-sex elder siblings increased the probability of dispersal from natal population, whereas the number of opposite-sex siblings had less influence. Overall, these results show that sibling interactions are an important driver of an individual's dispersal decision, in addition to other ecological constraints (e.g. population density) and social environment. Consequently, simultaneously considering the type of resources of the population and detailed sibship (birth order and sex) is necessary for the investigation of dispersal patterns.

Materials and methods

Study population

We used a large demographic data set from historical Finnish populations to investigate the effect of sibling interactions on natal dispersal. This data set was compiled from records of the Lutheran church which was obliged by law to document all births, marriages, deaths and movements between parishes in the whole country since 1749 (Pitkänen, 1977; Luther, 1993). The records provide accurate information on the survival, reproductive histories and movement of all individuals in the country. We limited our study period to individuals born before 1880, that is before the spread of industrialism and more modern methods of birth control

(Soininen, 1974), and before the transition to reduced birth and mortality rates (Liu *et al.*, 2012; Bolund *et al.*, 2015), changes in kin networks (Sear & Coall, 2011) and development of the Finnish railway (Martí-Henneberg, 2013).

Individuals included in our analysis were born in 116 geographically distinct parishes located in mainland or in south-western coastal areas of Finland. These local populations mostly depended on farming for their livelihood and were supplemented with fishing in the coastal areas. Overall, the standard of living was low with both famines and diseases common (Turpeinen, 1978; Hayward *et al.*, 2015b). We categorized all individuals into three family SES groups (treated as a three-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. landowners) (Pettay *et al.*, 2007). By law, inheritance of the farm was only directed towards one sibling, whereas the other siblings received other types of goods (e.g. cattle) (Moring, 2003). Inheritance customs usually favoured the eldest son (primogeniture) and inheritance generally occurred when the eldest son was getting married (Moring, 1993). Daughters could inherit in the absence of any male heir (Moring, 2003). The mating system was monogamous, divorce was forbidden, and females usually moved to their husband's family at the time of marriage (Sundin, 1992).

Like the general European pattern at the time (Moring, 2008), the average age at first marriage in our sample was 24 years for women (range 15–53) and 26 for men (range 16–64), the mean age at first reproduction was 25 for women (range 15–45) and 27 for men (range 17–69), and 88% of offspring married if they survived to sexual maturity (defined here as 15 years of age, the age of the youngest known reproducer in our population). Parents often recommended potential mates, and marriages required agreement from spouses and parents (Heikinmäki, 1981). Daughters received a dowry which was seen as part of their inheritance in the form of money, cattle or household goods and a trousseau consisting of garments and linen that the bride sewed herself (Heikinmäki, 1981; Moring, 1998).

We limited the study to the first movement of an individual out of his/her birth parish (i.e. intraparish movements were considered as nondispersal). Thus, philopatry refers both to individuals who never left their parental household and to those settling in their birth parish but outside the parental household. Younger siblings (both males and females) usually moved away from their parental household in their early twenties to work in other farms (Moring, 1993). Offspring resident at their parents were working at the farm or performing household tasks (Moring, 2003). However, no effect of the resident nonreproducing siblings on survival of other children residing in the same

parish was detected in a previous study (Nitsch *et al.*, 2014). Therefore, the predominant household was composed of the eldest son, his wife, their children, his parents and one or more unmarried siblings (Moring, 2003). Children under 15 were also taking care of different tasks in the household (Moring, 1993). Individuals dispersing during childhood (before age 15) as family members were excluded from the data set (< 1% of the overall sample). Using the geographical coordinates of the parishes, we calculated the distances of dispersal for individuals staying in Finland (i.e. not those going abroad, 6% of dispersing individuals). Because of the variation in the geographical size of the parishes, considering only whether an individual disperses during lifetime might overestimate dispersal in small parishes and underestimate it in larger parishes. To minimize this bias, individuals dispersing to a parish located < 10 km from the birth parish were considered as nondispersing (Fig. S1). Similarly to other historical human populations, about 20% of individuals dispersed from their natal parish (e.g. see Clarke & Low, 1992).

The study sample was restricted to individuals who survived to age 15, for whom all the variables controlled for in our statistical analysis were available, and whose mother's full reproductive life was recorded, in order to have accurate information on sibship configuration. Twins were excluded from the study because they have the same number of elder brothers and sisters and should be considered as a special study design, but in our data set, their numbers were too few (4% of the overall sample). The final study sample contained 4881 focal males and 4737 focal females born between 1720 and 1880 to 3877 mothers.

Event history analysis

We examined the consequences of sibling presence on dispersal probability at different ages, depending on the number of brothers and sisters residing in the same parish (see details below on how the presence of brothers and sisters was fitted). As the focus of the study was the effect of sibling competition on dispersal patterns, we only tested the hypothesis that these potential effects could be mediated by competition over mating opportunities or over resources. Thus, the investigation of the importance of inbreeding avoidance in dispersal patterns is beyond the scope of this study and would require very different methods (e.g. see Nelson-Flower *et al.*, 2012). Specifically, we used discrete event history analysis to study the dispersal chance of the focal individual during each observation interval from age 15 to age 40 (the age at which 95% of individuals dispersing had already left was 40.3 and 39.6 for men and women, respectively), as a function of the presence of brothers and sisters residing in the same parish at the beginning of each time unit (Singer & Willett, 2003). We specified 4 'age categories' (or 'observation

intervals') for dispersal events (15–20, 20–25, 25–30 and 30–40 years) to provide accurate information on individual dispersal status and family structure without compromising the model fit by overparametrization. Dispersal status of the focal individual at each observation interval was scored as a binary response (0 = did not disperse, 1 = dispersed) and analysed using Generalized Linear Mixed Models (GLMMs) with a binomial error structure and a logit link function. This method has several important advantages. First, it enables us to investigate simultaneously the effect of time-independent (e.g. the family SES) and time-varying variables (e.g. the number of brothers and sisters alive and present at the beginning of each observation interval) (Singer & Willett, 2003). 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 towards individuals that either died young or whose exact date of death was known. All analyses were conducted separately for each sex, because dispersal patterns, life histories and sibling competition can differ between males and females (Sear & Mace, 2008; Bolund *et al.*, 2013; Nitsch *et al.*, 2013; Pettay *et al.*, 2014). All models included the mother's identity, the birth parish and the birth cohort (divided into 20 years birth intervals) as random factors to take into account the dependency between individuals of the same family, the same geographical area and its characteristics (e.g. demographic or environmental conditions), or born in the same time period.

Multimodel inference

We focused on the effect of same-sex elder siblings because a previous study on this population showed a significant negative effect of their presence on reproductive success (Nitsch *et al.*, 2013). Thus, we calculated for each individual the number of elder brothers and sisters alive and living in the same parish at the beginning of each observation interval. The effect of same-sex elder siblings can be included as a linear variable (i.e. the more same-sex elder siblings an individual has, the more important the competition), or as a categorical variable. Because of the primogeniture inheritance system of this population, competition between brothers could be summarized as being the inheritor of the wealth of the family or not (as already shown for reproductive success (Nitsch *et al.*, 2013)). Even if sisters could only inherit the wealth of the family in the absence of a male heir, investigating the hypothesis that the eldest sister had a different dispersal behaviour from her younger sisters is important in the light that the eldest daughter could be favoured (e.g. through a higher dowry) (Moring, 1998). To determine which approach best explained our data, we used a linear variable, but we also transformed the number of same-sex elder siblings into a two-category variable (referred

to later as *Heir*), indicating whether the focal individual had at least one same-sex elder sibling alive and residing in the same parish at the start of each observation interval (*Heir* if the focal individual had no same-sex elder sibling, and *Nonheir* otherwise). We then used model averaging techniques to investigate whether the data were better fitted by including the effect of same-sex elder siblings as a linear or a categorical variable. Multimodel selection techniques allow estimating the relative importance of each variable in a model. We used an *a priori* model set corresponding to the different hypothesis (see details below). These models were ranked according to their goodness of fit to the data based on the Akaike information criterion (AIC) (Burnham & Anderson, 2002). The difference in AIC (Δ_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*. 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 (Burnham & Anderson, 2002). Following Burnham & Anderson (2002), we only considered models with Δ_i values up to 2. We computed model-averaged parameters and error estimates for each variable (Burnham & Anderson, 2002). We also calculated the odds ratios (OR) 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 dispersing during the 'age category'). Conversely, when the 95% CI includes one, it indicates that the variable studied is not systematically associated with higher or lower dispersal chances, and therefore, its effect in our analyses is not found to be strong. All the analyses were conducted with the statistical software Rv2.15.3 (R Development Core Team, 2012), the packages *lme4* (Bates *et al.*, 2013) and *AICcmodavg* (Mazerolle, 2013).

Candidate model set

For each sex, we considered a set of 10 different models to investigate the effect of same-sex elder siblings on the probability of dispersal. In each case, we considered: (1) a null model, controlling only for the age category (*Age Cat*) and the random terms (see details above); (2) a control model C, containing the *Age Cat*, the random terms, and the confounding factors (see details below); (3) a model to test for a linear effect of elder same-sex siblings (continuous variable *Cont*): C + *Cont*; (4) a model to investigate whether being the first offspring of the particular sex additionally influenced dispersal probability (binary variable *Heir*): C + *Heir*. Then we investigated the importance of the interaction between family SES and the presence of same-sex elder siblings, measured both as a continuous variable (5) C + *Cont* +

Cont x *Family SES*; and as a binary variable (6) C + *Heir* + *Heir* x *Family SES*; we also examined the interactions between the age category and the two different measures of presence of same-sex elder siblings: (7) C + *Cont* + *Cont* x *Age Cat*; (8) C + *Heir* + *Heir* x *Age Cat*. Finally, we examined two different models which included both interactions simultaneously, one using the continuous variables, (9) C + *Cont* + *Cont* x *Age Cat* + *Cont* x *Family SES*; the other using the binary categorization, (10) C + *Heir* + *Heir* x *Age Cat* + *Heir* x *Family SES*.

Confounding variables

The models controlled for the following confounding fixed factors: the mother's and father's age at an individual's birth (Gillespie *et al.*, 2013; Hayward *et al.*, 2015a) and the family SES. We also included as continuous variables the number of opposite-sex elder siblings, younger brothers and sisters alive and residing in the same parish at the start of each observation interval, to control for the potential overall intrafamilial competition for resources (Gillespie *et al.*, 2008). The numbers of siblings of all categories above four were pooled to avoid an excessive influence of extreme numbers.

Dispersal and marital status

We further investigated whether competition over mating opportunities (i.e. individuals disperse to find a mate) was a strong driver of dispersal decisions. First, we quantified whether those individuals who dispersed did so before or after finding a spouse and marrying. Following Towner (2002), the marital status at dispersal was coded as a three-level categorical variable which indicated whether dispersal occurred 'before' (> 1 year before), 'after' (> 1 year after) or 'coincided' with marriage (dispersal occurred within 1 year of marriage). We predicted that if competition occurred mainly for mating opportunities, dispersing individuals were more likely to be unmarried. Conversely, in the case of dispersal being due to competition over resources, marital status should be less strongly linked to dispersal probability.

Second, we also tested the hypothesis that dispersal is related to competition over mating opportunities by investigating whether dispersers are more likely marrying a nonlocal partner than nondispersers, as would be predicted if dispersers are those individuals who are not marrying locally. Specifically, the effect of same-sex elder siblings on dispersal probability could be mediated by their negative effect on the probability of marrying locally. To investigate this hypothesis, we fitted a model on the probability for an individual to marry someone from the same parish. This latter variable was analysed using GLMMs with a binomial error structure and a

logit link function. The sample was restricted to individuals who married and whose spouse's birth parish was known (3159 males and 3240 females). Like the models on the probability of dispersal, we used model averaging techniques and considered a set of four models: (1) a null model, controlling only for the random terms; (2) a control model C, containing the random terms and the confounding factors; (3) a complete model, C + the variable indicating the number of same-sex elder siblings; and (4) a model investigating the importance of the interactions between the family SES and the presence of same-sex elder siblings. The fixed and random effects included were the same as in the time event analysis, apart from the variables on siblings, which represented the number of siblings of each category alive at age 15. The effect of same-sex elder siblings was fitted as a categorical or a continuous variable, according to the results of the model selection on the probability of dispersal.

Results

Overall, our results provide evidence for a strong positive effect of the presence of same-sex elder siblings on dispersal.

Male dispersal

Of males who survived to age 15, ($n = 4881$), 19.6% dispersed before age 40, defined as moving out of their birth parish (see Methods for details). The mean age of dispersal was 24.5 years old (± 0.3 SE). The mean distance of dispersal was 68.1 km (± 2.4), and 30.5% of dispersers were going to their spouse's birthplace. The mean age of males leaving before getting married (29% of dispersers) was 19.8 (± 0.4), whereas men leaving after getting married (35%) or synchronously with the marriage (36%) were 36.8 (± 1.1) and 25.3 (± 0.3), respectively. In total, 41.9% of males surviving to sexual maturity had at least one elder brother alive and living in the same parish at the age 15 and 40.7% had at least one elder sister alive.

The decision to disperse was strongly linked to sibling presence, with elder brothers increasing the probability that younger brothers dispersed. Results of the model selection indicate that the positive effect of elder brothers on dispersal probability is better represented by the inheritance status (heir vs. nonheir) than as a linear variable (i.e. number of elder brothers): the best model includes the effect of elder brothers summarized as the inheritance status (Table S3a). It suggests that the effect of elder brothers was mainly driven by competition over inheritable resources.

Further, the best model contained both the interaction between the age category and the inheritance status and the interaction between the family SES and the inheritance status; thus, both of these interactions were

important to take into account. As this model received a strong support ($w_i = 0.92$), it indicates that the effect of inheritance status on dispersal probability varied according to family SES and age category (Figs 1a and 2a, Table S3a). First, the effect of the inheritance status on male dispersal probability was slightly stronger during ages 20–25 (OR = 3.23, 95% CI = 2.32–4.50) and 25–30 (OR = 3.69, 95% CI = 2.56–5.32) than during ages 15–20 (OR = 2.03, 95% CI = 1.40–2.94), meaning that nonheirs dispersed more frequently than heirs particularly after reaching their 20s. Individuals from families with a middle (OR = 3.08, 95% CI = 2.38–4.01) or low SES (OR = 4.38, 95% CI = 3.18–4.01) were more likely to disperse compared to individuals from high SES families. Among high SES families, being a later-born was associated with a 2.03 times (95% CI = 1.40–2.94) higher probability of dispersal compared to inheritors. Conversely, among families of middle and low SES, the odd ratio and confidence intervals of the effect of inheritance status included 1 (OR = 1.30, 95% CI = 0.87–1.30, OR = 0.99, 95% CI = 0.62–1.57 for middle and low family SES, respectively) suggesting that firstborns and laterborns did not differ in their probabilities of dispersing. Moreover, the number of elder sisters, younger brothers and sisters were found to have a small negative effect on the probability of dispersal (Table S4a). These results were not confounded by other factors such as paternal or maternal age, which were controlled for.

Additionally, we investigated whether the effect of elder brothers on male dispersal probability was mediated by their negative effect on the younger brothers' probability of finding a mate in the natal parish through competition over mating opportunities. We found that 34% of males married a woman born in another parish. However, the best model concerning the probability of marrying locally was the null model (Table S5a), suggesting that the effect of elder brothers on the probability of dispersal was not strongly mediated by the probability of not marrying locally.

Female dispersal

Of females who survived to age 15 ($n = 4737$), 22.6% dispersed away from their birth parish before age 40. The mean age of dispersal was 23.6 years (± 0.3 SE), and the mean dispersal distance was 64.6 km (± 1.8). 50.2% of dispersing females went to their spouse's birthplace. Dispersal coincided with marriage for 57% of females dispersing (mean age at marriage: 23.8 (± 0.3)), indicating that dispersal was tightly linked to marriage timing for females. The mean age at marriage of females dispersing before (25% of dispersers) or after getting married (18% of dispersers) was 19.2 (± 0.4) and 39.2 (± 1.6), respectively. In total, 41.1% of women who reached sexual maturity had at least one elder brother alive and living in the same parish

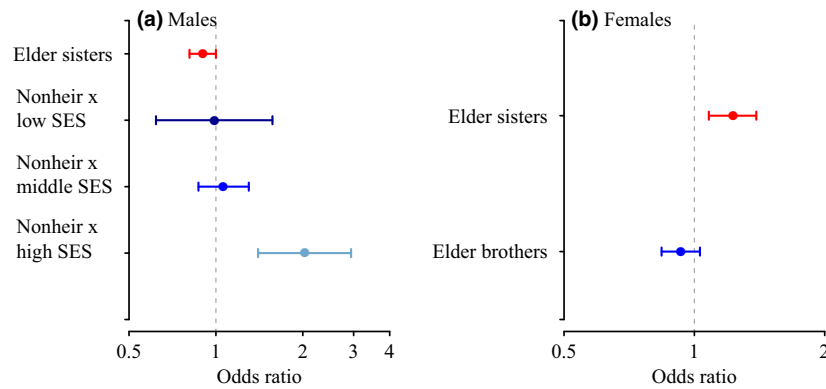


Fig. 1 Probability of dispersing for (a) males ($n = 4881$) and (b) females ($n = 4737$) by socio-economic status (SES). Figures represent the relative odds (\log_{10} -transformed) and their 95% confidence interval (error bars) of the estimate (1) for males and females with an increment of 1 for the effect of elder sisters (red line), (2) for males compared to the reference category 'Heir' for the effect of elder brothers for each family SES (blue lines) and (3) for females with an increment of 1 for the effect of elder brothers (blue line). The odds ratios are calculated from the model average estimates (Table S4a, b).

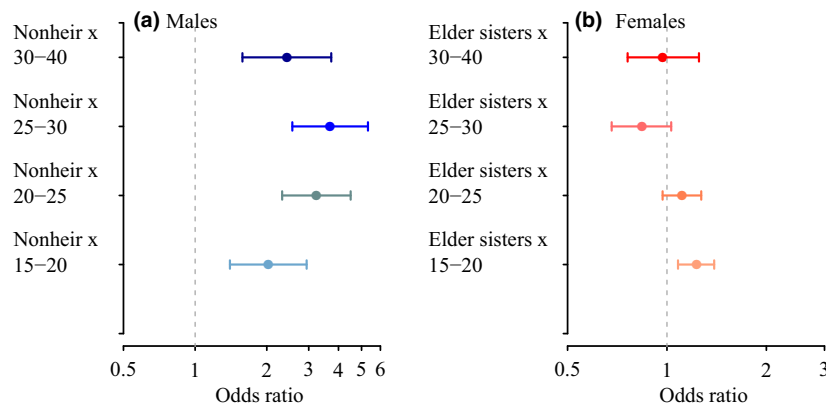


Fig. 2 Probability of dispersing for (a) males ($n = 4881$) and (b) females ($n = 4737$) by age category. Figures represent the relative odds (\log_{10} -transformed) and their 95% confidence interval (error bars) of the estimate (1) for males compared to the reference category 'Heir' for the effect of elder brothers for each age interval compared to the reference age interval 15–20 (blue lines) and (2) for females with an increment of 1 for the effect of elder sisters for each age interval compared to the reference age interval 15–20 (red lines). The odds ratios are calculated from the model average estimates (Table S4a, b).

at the age 15 and 43.0% had at least one elder sister alive.

Overall, we found evidence that the presence of elder sisters was positively linked with dispersal propensity (Fig. 1b, Tables S3b and S4b). The two best models from the candidate set fitted the effect of elder sisters as a continuous variable rather than according to the inheritance status. Each additional elder sister present was associated with a 1.23 times (95% CI = 1.08–1.38) increase in the probability of dispersing. These models did not include an interaction between the family SES and the presence of elder sisters, thereby indicating that the effect of same-sex elder siblings did not differ strongly between family SES groups as it did for males.

Thus, it is unlikely that the competition between sisters was driven mainly by competition over land resources. Moreover, the overall best model contained the interaction between age category and the number of elder sisters, which suggests that their effect on the probability of dispersal changed with age (Fig. 2b). The model estimates indicate that the effect of elder sisters was slightly stronger at ages 15–20 and 20–25 than later (Table S4b). However, the effect of elder sisters was not strongly varying between age categories, given that the best model only received a support of 0.39, whereas the second best model, not including the interaction between the number of elder sisters and age interval, received a support of 0.37 (Table S3b). Finally, the

number of younger brothers was found to have a small negative effect on the probability of dispersal (Table S4b). These findings were not confounded by other factors like paternal or maternal age, the effect of other siblings (elder brothers or younger sisters), which were all controlled for in our models.

Finally, we again investigated whether the effect of elder sisters on female dispersal probability was mediated by their negative effect on the younger sisters' probability of finding a mate in the natal parish. For 35% of females, the spouse came from a different parish. However, contrary to our predictions, the model selection on the probability of marrying locally did not support the hypothesis that elder sisters were more likely to marry locally than their laterborn sisters as the best model did not contain the number of elder sisters and the odd ratio of the effect of elder sisters included 1 (OR = 0.99, 95% CI = 0.89–1.10) (Tables S5b and S6b). This suggests that the effect of elder sisters on the probability of dispersal was not mediated by an increase of the probability of not being able to marry locally.

Discussion

Investigating the importance of siblings' interactions on dispersal patterns is important for the understanding of the evolution of family dynamics and dispersal. However, detailed studies are still scarce, thereby limiting the understanding of the variability existing across family systems and populations in both humans and non-human species. Moreover, the design of these previous studies precluded investigating in detail the effect of sibling presence on dispersal patterns, and how this compares against the known effects of siblings on other life-history traits. For example, previous studies in humans investigating the influence of siblings on dispersal have provided mixed results: no effect (Towner, 2001, 2002), positive effect of same-sex siblings (Strassmann & Clarke, 1998; Beise & Volland, 2008) or general birth order effect (Clarke & Low, 1992). In general, studies investigating in detail the determinants of variation of dispersal patterns between siblings are lacking thereby preventing the emergence of a comprehensive picture of the interplay between sibling interactions, dispersal behaviour and other factors.

Using a large demographic Finnish data set from the pre-industrial period, we tested whether an adult's probability of dispersing at each age depended on their co-resident siblings. Our results show (1) an increase in the probability of dispersal when more same-sex co-resident elder siblings were present; (2) among males, that heirs were more likely to stay than laterborn sons among landowning families, whereas no effect of birth order was detected in landless families (middle and low SES families); and (3) among females, an increase in the probability of dispersal with the number of co-resident elder sisters across families of all SES. Moreover,

the presence of other co-resident siblings (younger and opposite-sex elder siblings) decreased the likelihood of dispersal for males, whereas only the presence of younger brothers had such an effect for females. These results are not likely to be confounded by parental age, the family SES or birth parish, as these effects were all controlled for in our analysis. The effect of same-sex elder siblings on dispersal changed through time for both males and females, with a greater effect of same-sex elder siblings at younger ages (before 30 and before 25 for males and females, respectively). Overall, these results show that sibling interactions are an important driver of an individual's dispersal decision, in addition to other ecological constraints (e.g. population density) and social environment and that considering simultaneously the type of resources of the population as well as detailed sibship (birth order and sex) is necessary to the investigation of dispersal patterns. Furthermore, our study is among the few to study the effects of sibship configuration on dispersal patterns alongside known sex-specific effects on other important life-history traits, and our results suggest that the consequences of sibling interactions are not limited to fitness outcomes such as reproductive success or survival among the co-resident family members but also affect dispersal decisions. Therefore, a full understanding of family dynamics requires simultaneous consideration of all such outcomes.

The effects of sibling competition on dispersal patterns can be driven by two main mechanisms: competition over mating opportunities or over resources. The strong interconnection between these processes can lead to similar dispersal patterns in our study, as access to resources was important for marriage both for males and females (through inheritance for males or dowry for females). For instance, individuals dispersing before marrying could disperse either because of competition over mating opportunities or over resources. However, our results allow distinguishing to some extent whether competition over access to resources or over marriage opportunities was likely to be the most important driver explaining our findings, for males and for females.

Our results for males support the hypothesis that the effect of elder brothers was driven mainly by competition over land resources. Indeed, being the heir of the family was associated with a lower probability of dispersal among landowning families. Moreover, siblings did not have a strong effect on the probability of marrying locally vs. finding a spouse from another parish, which suggests that competition over mating opportunities was not a strong driver of dispersal decision. These results add to findings from other populations (Clarke & Low, 1992; Strassmann & Clarke, 1998; Towner, 2001; Beise & Volland, 2008), which also found that being the heir of the family was associated with lower dispersal. In contrast, in landless families, the presence of brothers had almost no effect on dispersal

probability. Dispersal rates were generally higher among landless families, so our results also suggest that dispersal was a favoured strategy equally for firstborns and laterborns in such families.

In contrast to males, the effect of siblings on female dispersal was unlikely to be strongly linked to competition over family resources, as no interaction between the effect of siblings and the effect of the family SES was found. A previous study on this population showed a lower probability of marrying among those women who had more elder sisters (Nitsch *et al.*, 2013), so we predicted that dispersal would be mainly driven by competition over mating opportunities; thus, we expected laterborn daughters to be more likely to marry outside the birth parish. Our results did not support this prediction, thereby suggesting that the higher dispersal probability of laterborn daughters was not driven by a limitation of potential mates locally (e.g. in the case of population of small density or biased sex ratios). However, females having few or no elder sisters were more likely to marry a landowner (Nitsch *et al.*, 2013), which is likely to be associated with a lower probability of dispersing out of the birth parish after marriage. Conversely, laterborn sisters were more likely to marry a landless man (middle or high SES), which is likely to be associated with a higher probability of dispersing after marriage. Therefore, it is likely that our results might reflect a competition between sisters over the quality of the marriage instead of competition over access to mates. This effect could be driven either by a difference in the amount or quality of dowry between sisters or by a difference in the marriage order in the family. Therefore, although the patterns of dispersal are not strongly linked to local marriages, we argue that dispersal patterns of females were probably driven by competition over mating opportunities between sisters. This differs from previous studies which found that dispersal and local marriages were strongly linked in historical Germany and in Massachusetts (USA) (Towner, 2002; Beise & Voland, 2008) and could potentially be explained by different costs of dispersal or differences in the availability of suitable mates in the birth parish.

Our results also highlighted the effects of opposite-sex and younger siblings on male and female dispersal patterns. The negative effect of the presence of others siblings (i.e. elder sisters and younger siblings) on males' dispersal probability is likely to reflect the fact that heirs had a legal obligation to take care of their siblings until their independence (i.e. unmarried siblings or minors) (Moring, 2003). Therefore, earlier-borns having younger siblings would have to stay in their parental household with their other siblings and therefore would disperse less often than earlier-borns with fewer siblings. Similarly, the negative effect of the presence of younger brothers on female dispersal might be due to the potential obligation for those women to

take care of their younger brothers and therefore might be retained by their parents (Moring, 2003).

The effect of sibling competition on reproductive success and dispersal patterns are likely to be strongly interconnected. A previous study on this population showed that heirs had a higher reproductive success than nonheirs across all SES (Nitsch *et al.*, 2013). Although our results on dispersal patterns are similar to those on reproductive success among high SES families for males and among females, several disparities exist. Indeed, a strong effect of inheritance status on reproductive success was detected in males from low SES families, but was not present for dispersal patterns. These differences can be explained by the fact that the presence of heritable goods (e.g. territory or social position) has a critical role in shaping family dynamics and fitness maximizing strategies (Ragsdale, 1999). For instance, Ragsdale (1999) showed that due to increased future benefits of philopatry, dispersal probability was lower in family systems with heritable goods. Our results of different dispersal patterns between SES groups are consistent with this finding. However, although several models currently enable to investigate the effect of kin competition on dispersal (e.g. Crespi & Taylor, 1990; Ragsdale, 1999; Kisdi, 2004; Rodrigues & Gardner, 2015), they do not enable clear predictions concerning the potential outcomes of intrafamilial dynamics on different life-history traits. Therefore, studying dispersal outcomes alongside other life-history outcomes is particularly helpful as it may improve our understanding of how dispersal patterns and fitness maximizing strategies are connected and lead to the evolution of different family systems.

The importance of sibling interactions in determining dispersal decisions is likely to depend on the resource gathering system, the family system (e.g. extended families vs. joint families), the system of inheritance (Gibson & Gurmu, 2011) or the ecological conditions of the study population. However, lack of detailed studies on sibship dispersal patterns and fitness outcomes in other types of families or resource gathering systems currently limits the generalization of our results as well as the understanding of how dispersal behaviour might have evolved with other aspects of human family systems and local conditions. The increasing number of databases allowing detailed analysis of human life-history in different socio-ecological and environmental contexts should fuel such future studies (Lummaa, 2013).

More generally, our results show that the drivers of sex-specific dispersal strategies can be very different between sexes and can ultimately be highly taxon-specific depending on the biology of the species. The nature of our data collection and presentation allows model selection to disentangle the principle correlates of dispersal and thus complements previous work on vertebrates (often correlative) and invertebrates (often

experimental) (Uller, 2006; De Meester & Bonte, 2010; Sparkman *et al.*, 2012; Scandolara *et al.*, 2014b). For instance in spiders (*Erigone atra*), resource competition was found to be the strongest driver in female dispersal (investment in reproduction), whereas competition over mating opportunities was more important among males (De Meester & Bonte, 2010). Such sex-specific effects of sibship on dispersal could vary across different life-history stages as previously documented for other life-history traits (Sparkman *et al.*, 2011; Nitsch *et al.*, 2013; Berger *et al.*, 2015). We therefore stress the importance of studying dispersal decisions with an integrative approach that considers kin effects on dispersal within each sex against known effects on other life-history traits.

Finally, a broader understanding of our results requires placing them in the framework of fitness maximizing strategies. At the individual level, an individual should disperse depending on the ratio of the costs and benefits of dispersal. The underlying mechanisms could depend on fitness maximizing strategies that can differ between siblings (e.g. driven by personality differences (Cote *et al.*, 2013), or different access to resources). For instance, our results among males from high SES families suggest that benefits of staying might be higher for heirs than nonheirs. Costs of dispersal have been documented in several species, but studies on intrafamilial differences of dispersal costs are still scarce (Bonte *et al.*, 2012). However, in the context of family conflicts, dispersal does not necessarily involve direct fitness benefits for an individual and could instead benefit mainly other family members (Hamilton & May, 1977). From a parental perspective, forcing some of their offspring to disperse could benefit their own fitness, for example by lowering the level of sibling competition. It has for instance been shown in the western slaty-antshrrike, *Thamnophilus atrinucha*, that parents forced the dispersal of their offspring before starting another breeding season (Tarwater & Brawn, 2010). Studies on some other nonhuman species have also found that dispersal probability or timing depends strongly on sibling dominance (Strickland, 1991; Ekman *et al.*, 2002) and could involve dispersal forced by siblings (Ellsworth & Belthoff, 1999; Pasinelli & Walters, 2002). More generally, control of dispersal decision is likely to be a key parameter in the understanding of dispersal decision. For instance, Rodrigues & Gardner (2015) obtained different predictions concerning the number of philopatric offspring depending on the relatedness (kin vs. nonkin) and the identity of individuals (mother vs. offspring) exerting control over the dispersal decision. However, in most family-living species, including humans, benefits of dispersal for different family members remain unclear as (1) few data on behavioural mechanisms preceding dispersal exist and (2) contrasting results on fitness consequences of dispersal for the remaining family have been found. For instance, in the case of human

families, a study on an Irish population suggested that philopatric siblings increased the overall amount of resources of the family, thereby benefitting the whole family (Strassmann & Clarke, 1998). In contrast, another study showed that the presence of nondispersed individuals in the family did not enhance the survival of their nephews and nieces (Nitsch *et al.*, 2014). In our population, unmarried siblings could remain in the family household until marriage (Moring, 1998), which suggests that dispersal decisions might be under individual rather than parental control. Furthermore, studies on differences in parental investment between birth ranks and the variability of inheritance systems support the idea that parents might be the main beneficiaries of differential fitness maximizing strategies among siblings (Boone, 1987; Hrdy & Judge, 1993). However, these studies did not investigate the importance of dispersal strategies for fitness maximizing strategies, which stresses the fact that more studies on the fitness consequences of dispersal are needed to understand the interplay between family dynamics and dispersal patterns.

In summary, our results show a complex effect of sibling competition on dispersal, which was influenced simultaneously by sex, birth order and the type of family resources. Furthermore, these patterns differed from the effect of sibling competition on other fitness outcomes. Overall, our study implies that more studies considering the influence of kin on dispersal decisions are needed for an accurate understanding of dispersal. More importantly, it stresses the importance of studying the effects of sibship configuration on dispersal patterns alongside known sex-specific effects on other important life-history traits.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1 Descriptive statistics and details of the results.

Figure S1 Histogram of dispersal distances of (a) males ($n = 1029$) and (b) females ($n = 1129$) dispersing.

Table S1 Descriptive statistics of the categories of siblings for the overall sample ($n = 9618$).

Table S2 Descriptive statistics on the proportion of (a) males ($n = 4881$) and (b) females ($n = 4737$) dispersing according to SES and the presence (referred as 'Non Heir') or absence (referred as 'Heir') of same-sex elder siblings.

Table S3 Summary of the best a priori models on the probability of dispersal with a difference in a range of $\Delta_i = 2$ for (a) males and (b) females, including the total number of estimable parameters (K), the log-likelihood (LogLik), AIC differences relative to the minimum value in the set (dAIC), and the Akaike weight (w_i).

Table S4 Probability of dispersal: odd ratio and 95% confidence intervals from the averaged estimates of the best models for (a) males ($n = 4881$) and (b) females ($n = 4737$).

Table S5 Local marriage.

Table S6 Probability of marrying locally: odd ratio and 95% confidence intervals from the averaged estimates of the best models for (a) males ($n = 3159$) and (b) females ($n = 3240$).

Data deposited at Dryad: doi: 10.5061/dryad.jt03g

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