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# **Sex, age, and family structure influence dispersal away from social group after a forced migration**

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Pro gradu -tutkielma

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Dispersal is movement of an individual away from its point of origin to a new social group or settlement habitat where it usually reproduces. In social species dispersal is not only moving from one environment to another but also shifting from one social group to another. Factors such as an individual's sex and age, along with number of relatives and their presence in a habitat, might influence individual's propensity to disperse. Their influence has been long studied in birds and mammals but only few behavioural ecology studies have focused on humans. Human studies that focus on the influence of individual characteristics affecting dispersal decisions are rare, and more research is needed to know how features such as sex, age, and family relations influence individual's dispersal propensity.

During the World War II people were evacuated from Karelia to new areas in western Finland; the evacuations were made in a way that individuals could live with others from the same Karelian municipality in the new areas as well, yet not everyone stayed in their designated area but left elsewhere. In this study I use a unique dataset of recorded movements and life histories of the evacuated Karelian population to test how individual characteristics such as sex, age, number of siblings, and being firstborn or laterborn, influence an individual's dispersal away from their own social group. I only focused on farmers in the data to have a cohesive study group, and the individual's birth municipality in Karelia functions as their social group. I found that young women dispersed more than young men and that the difference decreases with age, also firstborn individuals dispersed more than non-firstborns as the number of younger brothers grew. However, sisters did not have the same effect as brothers. The results suggest that young men might benefit more from staying and farming near a familiar social group, and therefore gather more resources, whereas young women could benefit more from moving elsewhere to find work or possibly spouses. The result also indicate that the increasing number of younger brothers might pressure firstborn individuals into moving elsewhere in order to lessen competition with or leave more resources to brothers. Sisters on the other hand, seem to have no influence on dispersal probability, possibly because they are less of a competition for resources. Overall, the results show that individual characteristics are important in understanding dispersal behaviour but environmental properties such as social structure might change the outcomes.

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**Keywords:** dispersal, human study, sex, age, siblings, birth order, social group

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# 1. Introduction

## 1.1 Dispersal

Dispersal is movement of an individual away from its point of origin to a new social group or settlement habitat where it usually reproduces (Greenwood 1980, Clobert et al. 2001). It has consequences on individual fitness, population dynamics and genetic structures, as well as species' distributions (Greenwood 1980, Clobert et al. 2001, Bowler & Benton 2005, Bonte et al. 2012), and it is the main reason for gene flow between populations (Greenwood 1980). Dispersal is a key interest in many subfields of biology such as ecology, evolutionary biology, microbiology, and molecular biology, all trying to explain its part in many ecological and evolutionary processes from different perspectives. Studies on these topics have demonstrated great variation in dispersal patterns between individuals, organisms, and environments (Bowler & Benton 2009). Dispersal is studied in multiple other research fields as well e.g. in mathematics, agricultural sciences, engineering, geography, anthropology, history, economics, and sociology (Nathan 2001).

Dispersal is often classified into two types: breeding dispersal is movement of individuals between successive reproduction sites or social groups, and natal dispersal is movement from birth site to first potential breeding site (Greenwood 1980, Clobert et al. 2001). Distinguishing between these two is important because their evolution seems to be driven by different selective pressures (Danchin et al. 2008). However, since the exact location of birth or reproduction might be difficult to define, other terms, such as home-range, habitat patch, or a social group, might be used to represent the sites instead (Clobert et al. 2012). Dispersal can be expressed through a complex interaction of an individual with its environment, and therefore it is also likely to be driven by a combination of environmental effects and individual characteristics (Clobert et al. 2012). Propensity to disperse among individuals can vary according to different individual characteristics such as age and sex (Bowler & Benton 2009). Another important term in dispersal studies is philopatry which describes organisms that have a tendency to stay in a particular area.

It is important to note that the decision to disperse might not be "intentional" (Starrfelt & Kokko 2012); it might be voluntary or enforced, environmentally determined or innate (Greenwood 1980). For instance, juvenile guanacos (*Lama guanicoe*) are often forced to disperse by territorial males (Sarno et al. 2003); or groups of males or females

of banded mongooses (*Mungos mungo*) are sometimes evicted from their natal groups by more aggressive (dominant) members (Cant et al. 2001). Hence, an individual's decision to disperse may not be a conscious choice but rather the act of choosing between two or more alternative options, trying to maximize its own fitness (Danchin et al. 2008).

The terms dispersal and migration may cause confusion because they are often similarly used as they both represent the act of movement of individuals or groups, and because they are used differently across disciplines (Roff & Fairbairn 2001, Clobert et al. 2001, Mascie-Taylor & Lasker 2009, Dingle 2014). Geneticists often use migration to explain gene flow between populations, whereas ecologists describe it as seasonal or repetitive movement between habitats (Danchin et al. 2008), while anthropological literatures often use migration as a synonym to dispersal (Koenig 1989).

### **1.1.1 Multicausality**

There are multiple causes affecting an individual's decision to disperse or not disperse, for example population density or a decrease in food availability might increase the propensity of dispersal (Bowler & Benton 2005). The interactions between dispersing individuals and the environment are often complex (Clobert et al. 2012). The factors causing dispersal and dispersal patterns (e.g. dispersal distance or tendency to disperse) vary among and within different species due to their way of interacting with the environment, their life history traits, or their family systems (Greenwood 1980, Bowler & Benton 2005, Matthysen 2012). The main ultimate causes of dispersal are: quality of the habitat that varies through space and time; competition within and between age and sex groups in a population and among genetically related individuals (between kin or between parents and offspring); and inbreeding avoidance (Danchin et al. 2008). These ultimate reasons for dispersal have comprehensive literature but proximate factors have had less attention (see review Bowler & Benton 2005).

Studying the proximate causes of dispersal and philopatry might be indicative of the ultimate causes of dispersal (Starrfelt & Kokko 2012). An individual's decision to disperse or stay often depends on the environment it experiences itself (Bowler & Benton 2005). Availability of resources (e.g. food, mates, or territories) and breeding sites, and avoidance of predators and parasites are all components that might affect an individual's dispersal decision (Danchin et al. 2008). Other proximate causes can include population density, sex ratio of population, competition with a parent or other

kin, patch size or simply an individual is forced to disperse. Each of these factors are interrelated and may influence dispersal in different ways and simultaneously shape the dispersal process (Bonte et al. 2012).

Just as the factors causing dispersal are expected to differ across and within species (Bowler & Benton 2005), the several possible consequences differ as well (Clobert et al. 2012). Different aspects of environment and individual characteristics alter together the costs and benefits of movement for the individual. Since the consequences vary between different individuals, their responses to cues from the environment and their own state are different as well (Clobert et al. 2012). Variation in individual tendency to disperse can be understood by contemplating variation in the benefits and costs of dispersal to different individuals (Bowler & Benton 2005).

### **1.1.2 Benefits and costs**

Dispersal is only thought to be the favoured strategy when benefits outweigh the costs (Bowler & Benton 2005, Clobert et al. 2012, Creel & Creel 2015). Dispersal allows individuals to escape unfavourable conditions and to move to more favourable conditions (Clobert et al. 2012). Dispersing individuals lose the possible benefits of the original environment but those may be compensated with benefits from dispersal, and accordingly the costs of philopatry are erased when the costs associated with dispersal are incurred (Bonte et al. 2012). Thus, individuals might have to make decisions on which benefits to gain and what costs to pay. Benefits of dispersal can include inbreeding avoidance, increased access to resources, and better mating opportunities (Greenwood 1980). However, although inbreeding avoidance has, at least theoretically, influenced the evolution of dispersal, it can also be achieved by recognition of genetic kin which allows individuals to live together while avoiding inbreeding (Danchin et al. 2008). By dispersing away from a social group, individuals may have a major benefit to avoid competition with kin (Clobert et al. 2012). For example, if a parent dies and offspring are left to compete with each other for a single breeding space left by the parent, one option for offspring is to disperse elsewhere. It is less costly for individuals to compete with nonkin rather than competing with siblings for limited resources (Bowler & Benton 2005), which indirectly increases an individual's fitness (Hamilton 1964). If there is no inclusive fitness benefit related to staying in a habitat with kin and gain indirect fitness benefits, then dispersal might be a better option.

The costs of dispersal are many and diverse, and they can happen during any state (pre-departure, departure, transfer, or settlement) of dispersal (Clobert et al. 2009, Creel & Creel 2015), and they can incur immediately or later on in life (Bonte et al. 2012). Bonte and others (2012) have classified the costs of dispersal to four types: energy costs, risk costs, time costs (the time invested in dispersal is away from other activities), and opportunity cost (surrendering advantages obtained from familiarity and prior residence, for instance the loss of benefits from nepotistic alarm calls for predators (Griesser and Ekman 2004)). Cost is often measured by changes in reproductive rates or survival by comparing fitness-related parameters between dispersing and philopatric individuals (Bonte et al. 2012, Martinig et al. 2020). For example, in North American red squirrels (*Tamiasciurus hudsonicus*), immigrated females had fewer offspring over their lifetime than those that had been philopatric in the area (Martinig et al. 2020).

## **1.2 Social groups and dispersal**

In social species dispersal is not only moving from one environment to another but also shifting from one social group to another. Accordingly, groups of relatives might even disperse together in coalitions (Packer and Pusey 1993, Koenig et al. 2000, Sharp et al. 2008). Social behaviour exists to improve an individual's ability to gain resources and get alliances which should help it reproduce and survive (Dickinson & Koenig 2018). Interactions in stable social groups tend to be altruistic which allows members of groups to perform cooperative behaviour. The evolution of cooperative behaviour is the result of inclusive fitness when an individual can indirectly increase its fitness through supporting survival and reproduction of members of kin (Hamilton 1964). This kin-selection is the key element in the evolution of social behaviour (Hamilton 1964, Maynard Smith 1964). Genetically related members of a group often have tendency to favour relatives over non-relatives, for example siblings might form alliances or parents favour their own offspring (Dickinson & Koenig 2018).

Dispersal decisions can be linked to cooperative behaviour. For example, among cooperatively breeding species, living alone and lack of mates or territories might limit dispersal and therefore staying with natal group is more beneficial even if own reproduction is delayed (Koenig et al. 1992, Kingma et al. 2016, Kingma 2018, Nelson-Flower et al. 2018). Alternatively, social species can be extremely competitive and aggressive, and dispersing individuals arriving into a new social group might have to

face unfamiliar competitors and encounter elevation in aggression in need to establish a permanent residency and dominance rank (Teichroeb et al. 2011, Ydenberg et al. 1988).

Social animals often prefer to form groups if it provides benefits to the members. Group-living might provide an individual increased access to food, and it might provide cooperative defence against non-group members and predators. However, close contact with the same species increases risk of parasitism and catching diseases, as well as competition for resources (Rubenstein & Kealey 2010). Benefits might be diluted by the costs that they come with, for example individuals sharing food resources might decrease the amount of food they each have. However, individuals are most often not equal in groups, there are dominant individuals that monopolize group's resources (Dickinson & Koenig 2018). Thus, individuals must weigh the cost-benefit ratio of living alone or in a group.

Among humans, social group usually entails the members being in some sort of interrelation and they may share common characteristics such as shared interest, values, ethnic or social background, or kinship ties (e.g. marriage, common ancestry, adoption) (Reicher 1982, Britannica 2010, Macionis & Geber 2010). In-group is a social group that an individual psychologically identifies as being a member to, which can help the person to achieve individual psychological needs (Crawford & Salaman 2012), and can have support through difficult circumstances (Bougie et al. 2011). The feeling of belonging to an in-group usually stems from feeling similar to other members of the group and having something in common with them. In-group members often share similar opinions, beliefs, values, and traits (Strangor et al. 2014). Accordingly, the group members usually have frequent interaction and communication with each other (Johnson & Johnson 2013). An individual's definition of in-group can change through circumstances, for example it can vary from family or kin to own city or municipality, even to country or continent. Individuals usually favour their own in-group as opposed to outgroup. For example, nepotism, where an individual favours own relatives or kin instead of non-kin, could be thought of as a form of in-group favouritism. As dispersal can be movement from one social group to another, individuals might have to take their in-group's benefits and costs into account while making movement decisions.

### **1.3 Individual characteristics that influence dispersal**

Individuals that disperse are not a random subset of a population (Clobert et al. 2001), therefore studying how individual characteristics and its environment differ between



dispersing and philopatric individuals might help explain variability of dispersal. Factors such as an individual's sex and age, along with number of relatives and their presence in a habitat, might influence individual's propensity to disperse (Bowler & Benton 2009, Kisdi et al. 2012). Their influence has been long studied in birds and mammals (e.g. Greenwood 1980, Cant et al. 2001, Ekman et al. 2002, Lawson Handley & Perrin 2007, Armitage et al. 2011, Nelson-Flower et al. 2018) yet there are challenges and limitations in these dispersal studies. Accurately tracking individuals and following their movement patterns in animal populations can prove difficult, and knowing what happened to missing individuals is never certain; they can be either dead or dispersed to somewhere unknown i.e. out of the reach of the study populations (Nathan 2001, Tesson and Edelaar 2013).

Even though dispersal has been under the interest of behavioural ecologists for a long time, only few behavioural ecology studies have focused on humans (Clarke & Low 1992, Clarke 1993, Voland & Dunbar 1997, Towner 2002, Beise & Voland 2008, Nitsch et al. 2016). The main goal of human behavioural ecology is to study what traits or behavioural strategies affect an individual's success to pass on its genes to the following generations, in particular social and ecological environments (Lummaa 2013). Among some disciplines, humans are often set apart from other animals, but there is no reason to consider that humans completely escape the influence of their biological nature (Briga et al. 2017). Therefore, human dispersal patterns may also be studied using the general evolutionary approaches and in the context of behavioural ecology, similarly to any other animal (Danchin et al. 2008). Indeed, Strassmann and Clarke (1998) argue that the ecological constraint model of dispersal and reproduction can be extended to humans, thus illustrating the possibilities of applying similar methods for both other animals and humans.

Empirical study settings with animals are not easy to create, and sometimes data is unavailable particularly about kin or social ties. Human studies offer an opportunity to face the challenges and limitations of dispersal studies because human life histories are well known and often better recorded than those of other species; especially social information about humans is more readily available and easier to gather than of other animals. This creates an opportunity to study dispersal behaviour in detail with humans. For example, because sibling relationships of humans are often well known, studying the influence of sibling interaction on dispersal is easier than with other animals (Nitsch et al. 2016). Thus, human studies can provide opportunities to study dispersal from

perspectives that are complicated to study with other animals. Moreover, studies of dispersal in humans - or migration studies in some cases - are not only crucial to understanding behaviour from an evolutionary point of view but also to better understand the behaviour in the contemporary world. Large scale migrations happen for numerous economic, environmental, social, or political reasons such as wars and other conflicts, environmental events, and natural disasters (e.g. floods, droughts, sea level rise) (Science for Environment policy 2015). As humans inhabit an exceptionally wide range of social and ecological environments (Clarke & Low 1992), it is reasonable to assume that the proximate reasons for dispersal change throughout life history and that dispersal is very context dependent and influenced by multiple factors together (d'Errico et al. 2012). However, some patterns of dispersal ought to be visible if individuals with the same characteristics often express the same dispersal behaviour. Overall, there are very few human studies that focus on the influence of individual characteristics affecting dispersal decisions, particularly associated to a social group, and more research is needed to know how individuals disperse based on features such as sex, age, and family relations.

### **1.3.1 Sex and age**

In general, dispersal is often sex biased in mammals and usually males seem to disperse more frequently and farther than females (Greenwood 1980). However, there are exceptions and in some mammals dispersal is more common for females than males, and in some species both sexes are known to disperse (Greenwood 1980). For example, in brown bears (*Ursus arctos*) males are more likely to disperse (Shirane et al. 2019), in chimpanzees (*Pan troglodytes*) females disperse (Greenwood 1980), and in yellow-bellied marmots (*Marmota flaviviridis*) both sexes are known to disperse equally (e.g. Van Vuren and Armitage 1994, Blumstein et al. 2009) Yet, complete sex-bias, where all individuals of one sex disperse and those of the other sex remain completely philopatric, is rare and some dispersal also occurs in the more philopatric sex as well (Lawson Handley & Perrin 2007). Usually, both sexes of a species emigrate when the same ecological and social variables strongly influence the reproductive success of both sexes, and therefore both sexes often disperse in solitary mammals and among monogamous or cooperatively breeding mammals (Smale et al. 1997). Previous studies of human dispersal, with a 19th century Swedish population, found that women had higher probability of dispersal and males were more philopatric (Clarke & Low 1992) and similarly, the proportion of dispersers in the United States and Northwest Germany

in 18th and 19th century was somewhat higher among women than men (Towner 2001, Beise & Volland 2008).

Some general potential explanations have been proposed to explain why there might be sexual dimorphism in dispersal and which of the sexes actually disperses. However, these ultimate mechanisms explaining the evolution of sex bias have also been debated (Lambin et al. 2001, Trochet et al. 2016). The first proposed evolutionary explanation, although its role is controversial (Lambin et al. 2001, Li & Kokko 2018), is inbreeding avoidance (Greenwood 1980). It usually applies to natal dispersal of organisms in which inbreeding cannot be avoided by other ways such as kin recognition (Lambin et al. 2001). Therefore, to successfully avoid inbreeding it is useful if only one sex disperses (Li & Kokko 2018). The second explanation is sexual asymmetries in competition for resources (Greenwood 1980), which is linked to mating system type and defensibility of resources where the more territorial gender defending resources should be more philopatric (Greenwood 1989, Trochet et al. 2016). Finally, competition for local mates might promote sex-biased dispersal (Dobson 1982, Perrin & Mazalov 2000, Trochet et al. 2016), because intrasexual competition should promote the sex that suffers more from it to disperse (Dobson 1982, Trochet et al. 2016). However, all of these mechanisms can interact together, and it might be difficult to separate the amounts of variation accounted for by each of these mechanisms; the dispersing individual should benefit both from decreased intrasexual competition and from better access to unrelated mates (Lambin et al. 2001). In other words when the evolutionary forces acting on dispersal are unbalanced between the sexes, dispersal becomes sex-biased (Perrin & Goudet 2001).

In many mammals, dispersal occurs often shortly after behavioural independence from the parents, and therefore it is often related to specific ages (Clobert et al. 2012). There might be different constraints or pressures to disperse at different ages, and therefore the propensity to disperse differs as well (Bowler & Benton 2005). Pressure to establish own territory might drive individuals to disperse at young age (Mayer et al. 2017). Alternatively, an individual might disperse at older ages if waiting could prove beneficial. For example, in Eurasian beavers (*Castor fiber*) if individuals had an older parent of the same sex in the natal territory, individuals dispersed at older ages compared to individuals with younger parents, most likely in the hopes of becoming the dominant one of the natal territory (Mayer et al. 2017). Studies of how age affects dispersal are however rare, especially in human studies. A few studies have found that

human dispersal rates vary with age, for example, in one study dispersal peaked at ages between 20 to 24 years (Clarke & Low 1992). Also, it is most common for young individuals to leave their parental home for different opportunities such as work, education, or social advancements (marriage, relationship) at the ages 20 to 30 years in Europe (Angelini et al. 2011), which can therefore result as dispersal away from birth area. However, all age groups are found to disperse because dispersal depends on multiple other conditions too.

### **1.3.2 Kin interactions**

Presence of parents and other kin such as siblings are important components affecting dispersal patterns especially in social species (Clobert et al. 2012). Kin interactions can be thought of as beneficial or costly; dispersal can decrease kin competition for limited resources and mates but staying with kin can provide benefits to an individual through cooperation with relatives (Lambin et al. 2001). Accordingly, social interactions are part of the theoretical framework explaining an individual's motivation for dispersal (Clobert et al. 2001). Typically, in social species, social factors such as aggression intensity individuals might receive and their need for alliances with relatives affect the decision to leave or stay (Clutton-Brock & Lukas 2012). For example, in yellow-bellied marmots, mother presence made yearling females more likely to be philopatric and if mothers were absent they were more likely to disperse, indicating that kin cooperation influenced dispersal rather than kin competition (Armitage et al. 2011). However, the influence of opposite-sex parent might promote dispersal to avoid inbreeding, for example in species of deer mice (*Peromyscus*) (Wolff 1992). Philopatry for males is often linked to benefits of kin cooperation of resource defence (Pusey and Schroepfer-Walker 2013), for example chimpanzee males cooperatively defend territories together (Goodall 1986).

The opportunity to inherit parental territory can be a factor that might affect an individual's dispersal decision (Danchin et al. 2008), and therefore staying in their original territory might be more beneficial than dispersing. In species that occupy territories year-round, territory acquisitions are initiated shortly after independence (Lambin et al. 2001). Inheriting territory can depend on the life expectancy of the parents; individuals with older parents should be more philopatric than those with younger parents (Danchin et al. 2008). In humans, in addition to inheritance practises, wealth and social standing of an individual's parents may shape dispersal but also the parent's investment behaviour should cause variation in dispersal behaviour across

children (Clarke & Low 1992, Volland & Dunbar 1997, Towner 2001). According to Clarke and Low (1992), birth order influence dispersal among males, since the youngest of a large family had the least likelihood to inherit resources and therefore were most likely to disperse in comparison to those born earlier or to smaller families.

Same-sex siblings are thought to be an important contributing factor to dispersal (Lambin et al. 2001). Nitsch et al. (2016) study on humans shows that the probability of dispersal increases when same-sex elder siblings were present in their natal area. In the study, inheriting land seems to make firstborn males more philopatric than their younger siblings, and female dispersal increased with the number of elder sisters regardless of their social status. Beise and Volland (2008) have also focused on how number of siblings and their sex influence dispersal for sex and economic group; for sons of farmers having more brothers increased their odds of dispersal compared to those with less than two brothers but not for sons of workers, and for daughters of workers two or more sisters increased the dispersal probability but not for daughter of farmers. Thus, in humans, sibling interactions seem to be one key factor driving individual's decision to disperse, at least in certain situations and societies.

#### **1.4 This study**

In this study I use a well-documented and unique dataset of recorded movements and life histories of a Karelian population which were evacuated during the World War II (Loehr et al. 2017), to test how individual characteristics such as sex, age, number of siblings, and being firstborn or laterborn, influence an individual's dispersal away from their own in-group. In this study it is defined as individual's village community (also in this thesis referred to as birth municipality) before the war, which were also kept together after the evacuation. Since the life histories, movements, and occupations of Karelians were extremely well recorded after the war, it provides a unique opportunity to study human dispersal behaviour away from their familiar social environment. Data of this magnitude about movements, characteristics and kin networks have never been available in humans before. In particular, the dataset provides an "experimental" system to study dispersal motivations not usually available in humans. During World War II, Karelians were displaced due to loss of territory and resettled elsewhere in a 'natural experiment' manner, some individually, and others with the resettlement of entire evacuated villages to new areas, thus maintaining old social bonds. Here, the choice of dispersal or relocation are not the product of previous individual conditions that may

affect health, sociality, and fitness, but predisposed by the war events and government decisions. The design also circumvents problems with heterogeneity in potential trauma before the relocation that could interact with integration behaviour after settlement and confound results, because everyone was exposed to the same trauma and were forced to leave Karelia regardless of any desire to migrate. Thus, with its comprehensive information the dataset provides a valuable opportunity to investigate individuals' dispersal behaviour under forced migration and during the aftermath of it.

### **1.4.1 Predictions**

I predict that (1) dispersal is more common among women than among men, but both sexes have both stayers and leavers similarly to findings of previous studies (Clarke & Low 1992, Towner 2002, Nitsch et al. 2016). Dispersal (2) ought to be most common for individuals at the ages of 20 to 30 years for both sexes (similarly to findings of Clarke and Low 1992), and because it is most common for young adults to move away from home and parents between these ages (Angelini et al. 2011), and therefore younger individuals might have more of a reason to disperse away from the social group as well. However, all ages should show both staying and dispersal because of different pressures individuals face at different ages. Brothers and sisters might (3) increase the propensity of individual dispersal, especially of young individuals who have multiple same sex elder siblings, possibly in order to reduce competition for parental resources. However, the advantages of siblings are kin cooperation and support so that might motivate individuals to stay. Firstborn (4) individuals might be less keen to disperse i.e. they should stay more with their in-group since they might be first in order to inherit the farm from parents and gather resources that way, and they also might have most pressure into staying and helping the family.

## **2. Material and methods**

During World War II, Finland lost a portion of Karelia to the Soviet Union and 420,000 Karelians needed to be evacuated and relocated into western Finland. It was very important for Karelians to record the history and memories of Karelians into journals, and therefore lives, movements, memories and histories of Karelian evacuees were collected into a book series called "Siirtokarjalaisten tie" (Anon.) published in 1970. These records have subsequently created an excellent basis for studying humans from

multiple different perspectives (Loehr et al. 2017, Lynch et al. 2019a, 2019b, Lynch et al. 2020, Pettay et al. 2021).

## **2.1 Historic background of the data**

In November 1939 the Winter War started when the Soviet Union invaded Finland, and some evacuations in Karelia were necessary. This was thought to be only a temporary military procedure and that people would soon be able to return back to Karelia. However, the Moscow Peace Treaty, signed by Finland and Soviet Union in 1940, forced Finland to cede areas of Karelia to Soviet Union. Everyone from the Karelian areas lost were evacuated to the west, and over 420,000 Karelians lost their homes. This evacuation (hereafter referred to as the first evacuation) followed plans of the Prompt Settlement Act of 1940 (pika-asutuslaki in Finnish) and the evacuated people were moved to designated placement areas; with each municipality of Karelia assigned its own placement municipality. These plans were not well executed, and multiple people were moved several times to new places by the Finnish government. The Continuation War started in June 1941, and Finland regained the territories of Karelia lost in the Winter War. This meant that Karelians were able to return to their home areas already in 1941, and by the spring of 1944 over 65% of Karelians had returned. When the overall war situation started to worsen for Finland in 1944, the second evacuation plan started to take place. In June 1944, evacuations started once more when Karelia was reoccupied by the Soviet Union. This time the evacuations were more organized. This evacuation was final and because returning to Karelia was not an option, the evacuees needed to settle permanently in western Finland and the evacuees needed to gradually integrate into society in the new locations (Waris et al. 1952). Overall, multiple Karelian parishes, cities and boroughs were lost partly or completely, and they are hereafter in this thesis all called municipalities for clarity.

After the evacuations and the ending of the Continuation War, the Finnish government tried to help evacuees to settle into new municipalities, as well as reimburse a proportion of their lost possessions. A land acquisition act in 1945 (Maanhankintalaki 1945 in Finnish) was created in order for war veterans (rintamamies in Finnish), relatives of the fallen soldiers, and evacuees to be able to get new land and homes after the war. These lands were called resettlement plots (asutustila in Finnish). Out of 250,000 people who got resettlement plots, 50,000 were evacuees. The act provided that Karelians received land that had similar soil and climate to areas of their homes in

Karelia. For evacuees, placement plans were made by the Finnish government as a part of the act, which tried to place and settle farmers into western Finland according to their original municipalities. The placement plans had a goal to place the farmers to areas similar to their old living areas in natural conditions, transport and communications, and economic conditions. Another purpose was to keep old neighbouring relationships intact to preserve social networks, and keep old Karelian municipalities united in culture and language. Thus, the placement plans supported the idea to keep social groups together (Waris et al. 1952 p. 66). However, the farmlands established were, on average, smaller and poorer in agricultural land than the original farms in Karelia (Paukkunen 1989).

The society of Finland changed considerably from the late 19<sup>th</sup> century to mid-20<sup>th</sup> century. It started to transform from an agricultural to non-agricultural and more modernized society (Sarvimäki et al. 2020), and growth of the industrial production was vital to the economic growth of the country especially after World War II (Statistics Finland 2007). Also, women's status in the society was gradually getting better from the early 20<sup>th</sup> century onwards; for example, women got better education rights, the right to vote, and own property independently from their husbands. These changes had impact on agricultural traditions as well. Traditionally (at least until late 19th century Finland) sons, especially firstborn sons, were usually favoured and they were the first to inherit farm and land from parents. However, sometimes all sons got an equal share of capital, cattle, or personal property and daughters got half a share, and if daughters inherited the family their husband became the head of the farm at marriage. If the firstborns inherited most of the property, then they were obligated to pay their siblings their due, which was lower in value in comparison to the value of the farm and land. (Moring 1993, Faurie et al. 2009, Moring 2003, Silvasti 2010). It is important to notice that as the society changed these inheritance practises also slowly started to shift to more modern practises (more equal share in inheritance practises). However, even if at the time of the study these inheritance practises were not followed as strictly and children inherited resources more equally than described, the patriarchal history of the society might still have influenced individual behaviour.

## **2.2 Data**

The information about movements of the evacuees was collected through interviews in 1970 into a book series called "Siirtokarjalaisten tie" and this was afterwards digitized to create a life history database called Migrant Karelia (MiKARELIA) by Loehr et al.



2017. Using these historical registers of Karelian evacuees, and the placement plans made for them, I was able to investigate how individuals disperse or stay with their in-groups after such events.

“Siirtokarjalaisten tie” is a four volume book series about experiences of Karelian evacuees who lost their homes during the Winter War and Continuation War (Anon. 1970). Systematically recorded interviews, conducted by around 300 trained interviewers, took place between 1968 and 1970 to register entries for approximately 420,000 evacuees. For each person there is an entry that lists their full name (and possible maiden name), sex, date of birth, birthplace, profession, year of marriage, records of children (name, sex, birth date), record of membership in various organizations, and of all movements from birth to the date of the interview. If the person was married, the entries also lists the name, sex, date of birth, birthplace, and occupation of their spouse. These books were scanned, and a software (Kaira Core and Natural Language Processing (NLP) software designed for use with the Finnish language) was developed to extract and digitize the records as a database called MiKARELIA (Loehr et al. 2017). Later additional information about family size and composition, individual’s number of birth order, brothers and sisters, has been added (Lynch et al. 2019b). This was done by extracting the information of siblings from records in a digitized database (Karjala-tietokanta database, n.d., recorded by the Finnish Lutheran and Orthodox Churches) and linking individuals between the databases by their name and exact day of birth. Each person has been given their own ID number. Individuals were also marked as “primary person” if they were the interviewed one of a married couple. For a more detailed description of how the data was extracted and constructed see Loehr et al. (2017), and Lynch et al. (2019b). Overall, the data consist of 250,000 individuals, including primary individuals, spouses, and children. From this previously compiled database, I extracted data of individuals’ sex, year of birth, birth municipality, municipality in 1950, occupation, record of whether they returned to Karelia after Winter War, number of brothers and sisters, and birth order (firstborns and laterborns).

The information about the placement plans have been gathered in a book called ‘Siirtokarjalaiset Nyky-Suomessa’ (Paukkunen 1989) which has small reports containing general overview of, and information about evacuations and placement plans for all Karelian municipalities that were lost in the war. From these reports I have extracted the placement municipalities in Finland for each Karelian municipality as

instructed in the land acquisition act of 1945 after the second evacuation. For example, for people from Hiitola, Karelia, the placement municipalities were Pori, Ulvila, Honkajoki, Karvia, Ahlainen, Merikarvia, Luvia, Nakkila, Siikainen, Kankaanpää, Kullaa, Pomarkku and Noormarkku in Finland according to the placement plans and land acquisition act (Paukkunen 1989).

Connecting the known records of an individual's current parish in 1950 and the placement plans, I was able to construct a variable for dispersal by 1950 for each evacuee in the dataset. Evacuees that lived in 1950 in one of the municipalities that had been assigned to their own Karelian municipality (birth municipality) in the placement plans would represent the people who stayed with their original in-group (dispersal = 0), and if they lived somewhere else, they had left their in-group (dispersal = 1). Those who had dispersed away had moved between the years 1944 and 1950. I chose the year 1950 because the settlement movement had ceased, and it was considered that the evacuees had found their permanent areas to settle by then (Waris et al. 1952). An individual's original birth municipality represented here the in-group because overall Karelians had their own culture, dialect, religion, and other customs which often set them apart from the rest of Finns, and therefore it could be argued that Karelians felt more connected to their original community. These cultural differences might have even occasionally caused some conflict between Karelians and western Finns (Waris et al. 1952).

I focused only on the interviewed individuals in the original records, excluding individuals in the database that were spouses of the person interviewed, because their information was incomplete (e.g. movements after evacuation are not listed) and they could not be considered as statistically independent observations from their partners. All individuals that I focused on were farmers because the placement plans were made with them in mind, and therefore the analyses will be more accurate for the research, as the individuals form more cohesive group. To be included in the analysis the subjects needed to be 18 years or older in 1950, as these individuals were old enough to move independently from their families. People aged older than 60 years were coded as 60 years old due to limited sample size of ages older than 60. Data were also subset only to those who returned to Karelia after the lost Karelian areas were recaptured during the Continuation War and returning was possible. The second evacuation plans in 1944 were more relevant to those that had to be evacuated again and were under the pressure of finding new home yet again (those who did not return might have already settled following previous plans and therefore had not been as influenced by the newer

placement plans). In other words, I focused on those who had to be evacuated the second time in 1944.

## **2.3 Statistics**

All analyses were conducted with SAS Enterprise guide software (SAS Institute Inc., version 8.2.1, 2019), and graphs were done with RStudio 1.2.5 (RStudio Team 2019). Due to limited information of all explanatory variables together, two separate models were conducted. Both analyses were done using generalized linear mixed models (GLIMMIX in SAS), with binomial distribution and logit link function. In both models dispersal (binary; 1 = individual had dispersed, and 0 = individual stayed) was the response variable, and birth municipality was set as a random factor. The explanatory variables were selected differently for each model; two models were conducted in order to have enough individuals of all ages in the analyses, as information about individuals' number of siblings was not available for individuals younger than 27 years. The models are described below. Statistical significance is defined at the level of  $\alpha = 0.05$ .

### **2.3.1 Influence of sex and age**

I conducted one model to analyse the possible effects of individual's sex and age on dispersal behaviour (n =12,526). The explanatory variables for this model were sex (women n = 4347, men n = 8179), age as a continuous variable, and their interaction. All individuals were between 18 to 60 years old (individuals over 60 years were considered as 60-year-old because there were only few people over the age of 60), and they were from 48 different Karelian municipalities (Table A1). Altogether there were 6552 individuals who dispersed (2629 women, 3923 men) and 5974 individuals who stayed (1718 women, 4256 men). The aim is to find if men and women differ in dispersal behaviour; is there difference between men and women i.e. one sex disperses more than the other, and to see if dispersal is age related, and if there is difference between men and women of different ages.

### **2.3.2 Influence of brothers, sisters, and birth order**

A second analysis was conducted in order to separately focus on siblings and birth order, due to more limited data (n= 4862) available of siblings. Here the explanatory variables were sex (women = 1492, men = 3370), age, number of brothers and sisters (both as continuous variable), whether or not individual was firstborn (1 = yes, 0 = no), which are also referred to as firstborns and laterborns, and interaction between firstborn

variable and number of brothers. Non-significant interaction between number of sisters and firstborn variable was removed. In this analysis the subset's most limiting factors were information of the number of brothers and sisters (this information was missing for 61 % of the individuals in the data used in the first described model). The ages in this data subset varied from 27 to over 60 years old, because information about family size and composition was available only for individuals born before 1926. If an individual had more than five brothers or sisters, the variable's value was recoded as five (5) due to a small sample size of firstborn individuals with more than five siblings (less than 10 individuals). In this subset individuals were from 42 different Karelian municipalities (Table A2). The aim is to understand if number of brothers or sisters influence dispersal decisions of individuals, and if firstborn and laterborn individuals behave differently. Also, to recognize if firstborns and laterborns behave differently regarding how many brothers and sisters they have.

### **3. Results**

#### **3.1 Influence of sex and age**

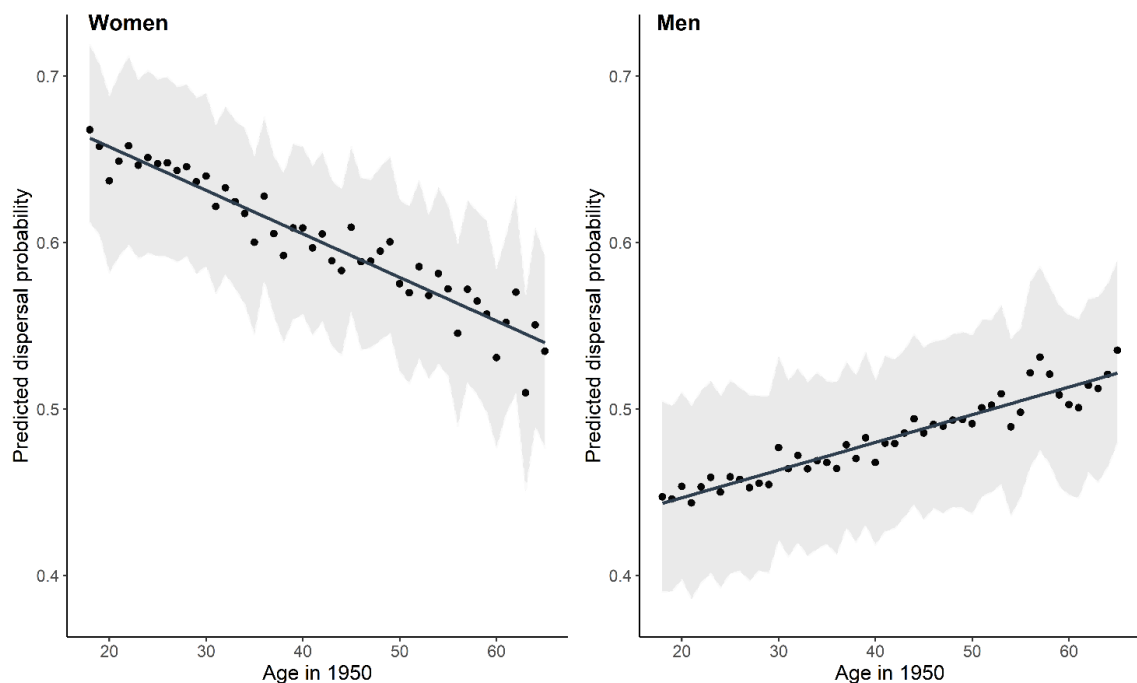
Descriptive statistics of the data ( $n = 12,526$ ) show that both sexes had both dispersers and those who stayed with their in-group in their designated placement areas. However, on average women ( $n = 4347$ ) had more dispersers (60.5%) than stayers (39.5%), whereas men ( $n = 8179$ ) had on average more stayers (52%) than dispersers (48%). Descriptive statistics also show that the mean age of women who stayed in with their in-group (dispersal = 0) was 41.7 years and that of those who left their in-group (dispersal = 1) was 40 years, whereas men who stayed were on average 39.6 years old (dispersal = 0) and those who dispersed were 40.4 years (dispersal = 1) in 1950. Descriptive statistics of the sibling subset of the data ( $n = 4862$ ) show that women had on average 2.7 brothers and 2.6 sisters, and men had 2.8 brothers and 2.7 sisters. There were 999 (women = 350, men = 649) firstborns and 3863 (women = 1142, men = 2721) laterborn individuals in the data.

The results of the analysis show that women had higher dispersal probability than men but the propensity to disperse was dependent on age ( $F_{1, 12522} = 29.57$ ,  $p < 0.0001$ , Table 1). The younger the women were, the more they dispersed, whereas men were more likely to stay with their in-group the younger they were. The model predicts that for

women a one unit increase of age (e.g. from 30 to 31 years) decreased the odds of dispersal by 1% (OR = 0.990 [0.985 – 0.995], Figure 1), while for men these odds increased 0.7% (OR = 1.007 [1.003- 1.011], Figure 1). For example, at the age of 25 the average predicted probability of dispersal for women is 29% higher than for men, but at the age of 50 the difference is only 15%.

**Table 1.** Effects of sex and age on dispersal using a generalized linear mixed model (binary distribution, logit link function, n = 12,526). Reference level for sex is “men”

Fixed effects	Estimate	Standard error	F value	P
Intercept	-0.1890	0.1133		
Sex (Women)	1.2434	0.1378	81.39	<.0001
Age	0.007215	0.002015	0.99	0.3197
Age x Sex (Women)	-0.01771	0.003257	29.57	<.0001
Random effects				
Birth municipality	0.2482	0.06660		



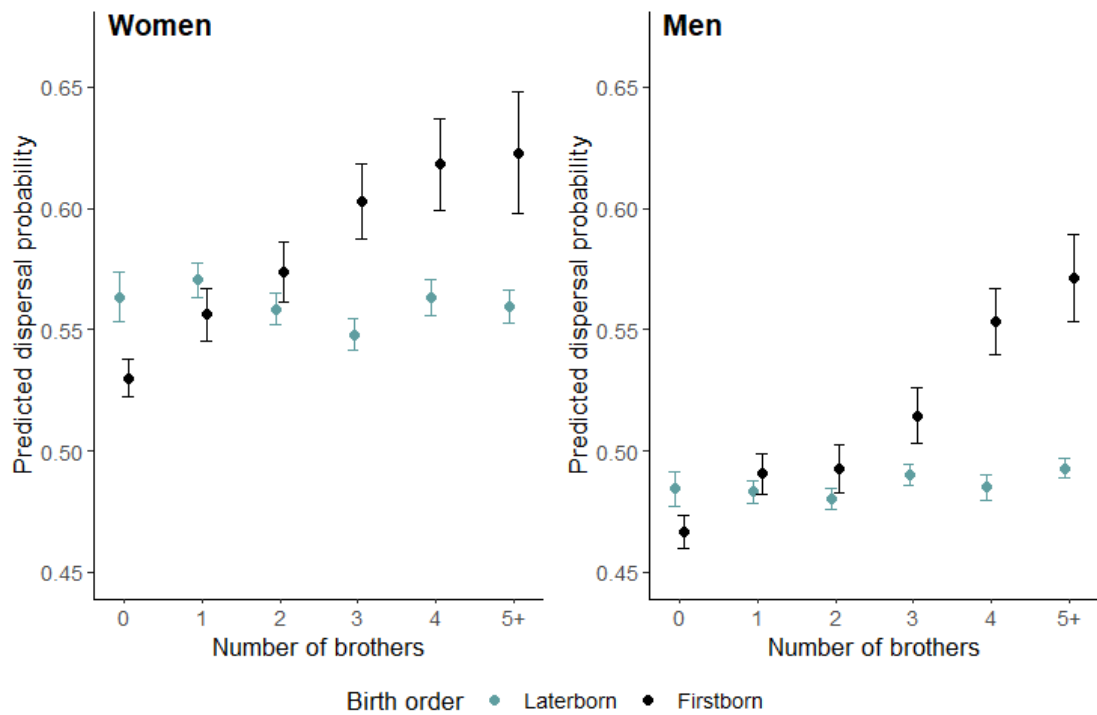
**Figure 1.** Average predicted probabilities of dispersal for men and women by age in 1950 (dots). Blue line is linear regression line for means, and grey areas are average confidence intervals.

### 3.2 Influence of brothers, sisters, and birth order

Result of the analysis also show that order of birth (firstborn or laterborn) did not have a significant effect on dispersal ( $F_{1, 4854} = 1.32, p = 0.2508$ , Table 2), however firstborns are more likely to disperse away from the in-group than laterborns when the number of brothers increases for both men and women similarly ( $F_{1, 4854} = 3.87, p=0.0492$ , Table 2). The model predicts that for firstborns a one unit increase in number of brothers (e.g. from 3 to 4) increases the odds of dispersing by 11% (OR = 1.110 [1.019, 1.209], Figure 2), while for laterborns the odds of dispersing increase by 1.1% (OR = 1.011 [0.970,1.054], Figure 2). The number of sisters did not have a significant effect on dispersal probability ( $F_{1,4654} = 2.28, p=0.1314$ , Table 2).

**Table 2.** Effects of siblings and birth order on dispersal using generalized linear mixed model (binary distribution, logit link function,  $n = 4862$ ). Reference level for sex is “men” and firstborn is “firstborn”.

Fixed Effects	Estimate	Standard error	<i>F</i> value	<i>P</i>
Intercept	-0.1305	0.2333		
Sex (Women)	1.0996	0.3313	11.02	0.0009
Age	0.003893	0.004493	1.60	0.2057
Sisters	-0.02984	0.01978	2.28	0.1314
Brothers	0.1044	0.04362	5.39	0.0203
Firstborn (Laterborn)	0.1365	0.1188	1.32	0.2508
Brothers x Firstborn (Laterborn)	-0.09327	0.04741	3.87	0.0492
Sex × Age (Women)	-0.01747	0.007024	6.18	0.0129
Random effects				
Birth municipality	0.2537	0.07751		



**Figure 2.** Average dispersal predictions for firstborns (black dots) and laterborns (light blue dots) by number of brothers, for both women and men. Each dot has its own error bars. Number of brothers that are marked as “5+” are a group of all individuals with five or more brothers.

## 4. Discussion

The results of my study provide insight into how individual characteristics influence dispersal decisions under a forced migration event. As dispersal is a complex and multidimensional concept which is affected by multiple different environmental, social and situational factors, explained from variable different perspectives, and having countless consequences, studies from all perspectives are needed to explain this complicated behaviour (Clobert et al. 2001). The resettlement of a large population of Karelians during the World War II into new environments has created a rare natural experiment to test how individuals’ dispersal behaviour might differ depending on their sex, age, birth order and sibling relations. Studies like these provide important information about human movement behaviour for multiple disciplines. I found support for the prediction (1) of female biased dispersal, yet both men and women had dispersed away and stayed in their designated areas. However, even though there was a higher proportion of women dispersing than men, the difference was greatest at younger ages. This was slightly against my prediction (2) because while women did disperse mostly at younger ages, men did not. For women the dispersal probability decreases with age and

for men it increases and therefore the difference of dispersal probability evens out at older ages. This could be due to different pressures for men and women who are at the beginning of independence from parents, and who could still for example be in search for spouses or work. A recent study using the same database tested how sex ratios were associated with dispersal behaviour of women in urban and rural areas and found that women had higher probability of dispersing from less female-biased sex ratios, especially from rural areas than towns (Pettay et al. 2021), and they concluded that the decisions of (single) women moving were not motivated by finding mates but rather work in urban areas. However, my data only focused on farmers which could lead to differing interpretations between these studies, and therefore in this case I would not exclude the possibility of finding a spouse as a motivation for moving.

Multiple previous studies of patriarchal (or societies closer to patriarchal than matriarchal, or those that have patriarchal history) have also found a greater proportion of women dispersing (Koenig 1989, Clarke & Low 1992, Towner 2002, Beise and Voland 2008) which indicates that there is a common trend that women are often the more dispersing sex in humans. However, some studies have found male-biased dispersal in humans (matriarchal society), or no difference between dispersal tendencies between sexes, indicating that the bias might be connected to society's structure (He et al. 2016). Female biased dispersal is most common in patrilocal societies where males inherit land from their parents and women tend to follow marriages (Koenig 1989) and this similar dispersal sex bias is also usual with other mammals in which males defend resources, territories, or partners (Greenwood 1980). Men's resource gathering should also be a driving force for female biased dispersal because then both sexes do not have to attain resources; women have been found to disperse more in association with marriage (Kok & Bras 2008). Therefore, resources could realistically explain some part of this female biased dispersal of the Karelian population. However, previous studies have found that both men and women behave similarly at different ages; the peak age at dispersal at the ages of 20 to 24 years old for both sexes (Clarke & Low 1992, Nitsch et al. 2016), and in this study, especially young men's decisions to stay or leave might be more connected to resource availability and access to them, than the decision of young women. Historically in Finland, men owned land more than women, and (firstborn) sons inherited family farms more often than daughters (Faurie et al. 2009). Therefore, it makes sense that young men in this situation would be more inclined to grasp the



opportunity of getting farming land where it is provided near familiar social environment, possibly for support and help.

The benefits of staying with an in-group might have been greater, and costs less for young men than for women in this study setting. It is also possible that the need for an own in-group varies between ages and possibly that is why the dispersal probability gets closer to 50% for both sexes as individuals age. In this case, younger women might more easily integrate to new social environments and/or have greater overall pressure to find a spouse or work, while older women have already established their social groups and have spouses, integrating into new societies might be less necessary. Findings of a previous study with the same database (Lynch et al. 2019a) is complementary to this assumption because it found that women were overall more likely to marry someone outside their in-group (non-Karelian Finns) and the same is true for younger individuals of both sexes. Therefore, there could be a link between these two outcomes; if young women are most likely to disperse away from their in-group then it could of course result in overall greater intermarriage rates.

I predicted that having brothers would increase dispersal probability (3) yet I found that the number of brothers only had an effect on dispersal decisions for firstborn individuals of both sexes. Contrary to predictions (4), firstborns did not stay in their in-groups more than laterborns but I found that the dispersal probability of firstborn individuals increases when the number of brothers increases. Interestingly, this finding was in contrast to previous discoveries where firstborns have been considered to stay more than laterborns, possibly because of inheritance practises. Especially eldest brothers should increase the dispersal probability of their younger brothers, in order to gain resources and avoid competition with close kin (Nitsch et al. 2016). However, there have been mixed results of how siblings and birth order affect dispersal. In some studies birth order has had no effect on the likelihood of dispersal (Beise 2001, Towner 2001) but other studies found linkage with these variables (Clarke & Low 1992, Voland & Dunbar 1995, Nitsch et al. 2016). The mixed results could indicate a case sensitive issue in sibling and birth order effects on dispersal, especially if inheritance practises are not influencing, or if siblings are neither beneficial nor costly in a population. In cases where older siblings are the inheritors of the property over younger siblings, the laterborn individuals are more likely to disperse (Nitsch et al. 2016).

It is possible that in this unique situation, where the new farming lands given to Karelians after the war are not old family farms but are rather poorer quality lands as

compared to those the farmers had before evacuations, the firstborns are not favoured as inheritors but might have more pressure to find a living elsewhere, perhaps it left more resources to younger siblings and reduced competition with brothers. In addition, as there were many societal changes happening at the time of the study, it is possible that the dynamics of sibling interactions shifted as well, and younger brothers had become more of a pushing than pulling force for dispersal. Another study has also found similar results in a German population of the 18<sup>th</sup> and 19<sup>th</sup> century, that having three or more brothers influence dispersal odds in sons of farmers, however this was true to all men in the family not just firstborns (Beise & Voland 2008). As I found no indication that the dispersal probability is different within the laterborn individuals (Figure 2) as the number of brothers were greater, it could indicate that a greater number of younger brothers is a driving force for dispersal only for firstborn individuals, at least in this study case.

Contrary to predictions (3), sisters did not influence dispersal probability, not even as an interaction with firstborn variable, like brothers did. Therefore, for firstborn women the increase of numbers of siblings of the opposite sex increased dispersal, while the same was true for firstborn men with same sex siblings. Some studies have found sisters to be useful and promote staying (Beise & Voland 2008), and sometimes elder sisters promote women's dispersal propensity (Nitsch et al. 2016). Perhaps, in this study sisters do not influence dispersal because they might not encounter as intense competition from other siblings, and they were anyway more likely to disperse away because they are women, or they were not as intensely influenced by the inheritance practises which create less competition. However, sisters are not a pulling force for staying either, indicating there was no cooperative benefits from sisters. Therefore, sisters seem to be a neutral factor in this case.

The dataset holds great potential for future studies on dispersal and other aspects. One aspect of future studies could be the distance which these dispersing individuals moved from their in-group and how it changes between men and women, because the factors that affect staying or leaving a social group might differ from those that affect the distance they move (Beise and Voland 2008). Here, I only focused on farmers but focusing on how other occupations are linked to dispersal is another potential direction for future studies as the need for social ties could greatly differ between occupations. More studies are also needed to better associate the influence of resources to men, which could be done by comparing the habitat qualities of different municipalities for

example their land sizes or soil qualities, and dispersal rates. This would also bring light to some of the dispersing individuals if certain parishes had higher dispersal rates than others. Marital status would have been another interesting variable to study here, as other studies have shown that women move more often to their spouse's birthplace than men (Nitsch et al. 2016), if there would have been more individual records of it.

In conclusion, young women and men move differently under the pressure of finding a place to live, firstborn individuals are influenced by their younger brothers to move away from their old social groups but not by their younger sisters. Overall, some individual characteristics are influencing dispersal probabilities in this population, yet there are various different aspects of dispersal that are yet to be discovered.

## 5. Acknowledgements

I want to thank the Karjala-tietokantasäätiö, and everyone involved, for the opportunity to use their data, as recording the Karelian history and memories into a chronicle shows an amazing devotion to Karelians and Finland, and it has provided extremely important knowledge about the Karelians to society and science. I am also very grateful to my supervisors John Loehr, Virpi Lummaa and Simon Chapman, as well as Jenni Pettay and Robert Lynch who all supported and guided me throughout this thesis.

## 6. References

Angelini V., Laferrère A. & Pasini G. (2011) Nest Leaving in Europe. pp. 67-80 in *The Individual and the Welfare State: Life Histories in Europe*, edited by Börsch-Supan A., Brandt M., Karsten H. & Schröder M., Berlin; Heidelberg; New York: Springer

Anonymous (1970) *Siirtokarjalaisten Tie*. Turku, Finland: Nyky-Karjala.

Armitage K.B., Van Vuren D.H., Ozgul A. & Oli M.K. (2011) Proximate causes of natal dispersal in female yellow-bellied marmots, *Marmota flaviventris*. *Ecology*, 92: 218–227

Beise J. & Volland E. (2008) Intrafamilial resource competition and mate competition shaped social-group-specific natal dispersal in the 18th and 19th century Krummhörn population. *American Journal of Human Biology*, 20(3): 325–336

Beise J. (2001) Verhaltensökologie menschlichen Abwanderungsverhaltens – am Beispiel der historischen Bevölkerung der Krummhörn (Ostfriesland, 18. und 19. Jahrhundert). Doctoral thesis, University of Giessen

- Blumstein D.T., Wey T.W. & Tang K. (2009) A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proceedings of the Royal Society B: Biological Sciences*, 276: 3007–3012
- Bonte D., Van Dyck H., Bullock J.M., Coulon A., Delgado M., Gibbs M., Lehouck V., Matthysen E., Mustin K., Saastamoinen M., Schtickzelle N., Stevens V.M., Vandewoestijne S., Baguette M., Barton K., Benton T.G., Chaput-Bardy A., Clobert J., Dytham C., Hovestadt T., Meier C.M., Palmer S.C.F., Turlure C. & Travis J.M.J. (2012) Costs of dispersal. *Biological Reviews*, 87: 290–312
- Bougie E., Osborne E., de la Sablonnière R. & Taylor D.M. (2011) The cultural narratives of Francophone and Anglophones Quebecers: Using a historical perspective to explore the relationships among collective relative deprivation, in-group entitativity, and collective esteem. *British Journal Of Social Psychology*, 50(4): 726–746
- Bowler D.E. & Benton T.G. (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews of the Cambridge Philosophical Society*, 80: 205–225
- Bowler D.E. & Benton T.G. (2009) Variation in dispersal mortality and dispersal propensity among individuals: the effects of age, sex and resource availability. *Journal of Animal Ecology*, 78: 1234–1241
- Britannica (2010) Editors of Encyclopaedia, *social group*. *Encyclopedia Britannica*, <<https://www.britannica.com/topic/social-group>> [Accessed: 3.2.2022]
- Cant M.A., Oтали E. & Mwanguhya F. (2001) Eviction and dispersal in co-operatively breeding banded mongooses (*Mungos mungo*). *Journal of Zoology*, 254: 155–162
- Clarke A.L. & Low B.S. (1992) Ecological correlates of human dispersal in 19th century Sweden. *Animal Behaviour*, 44: 677–693
- Clarke A.L. (1993) Women, resources, and dispersal in nineteenth-century Sweden. *Human Nature*, 4: 109–135
- Clobert J., Baguette M., Benton T.G., Bullock J.M. & Ducatez S. (2012) *Dispersal Ecology and Evolution*. Oxford University Press, Incorporated, Oxford.
- Clobert J., Danchin E., Dhondt A.A. & Nichols J.D. (2001) *Dispersal*. Oxford University Press, New York
- Clobert J., Le Galliard J.F., Cote J., Meylan S. & Massot M. (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, 12: 197–209
- Clutton-Brock T.H. & Lukas D. (2012) The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology*, 21: 472–492
- Crawford M. T. & Salaman L. (2012) Entitativity, identity, and the fulfilment of psychological needs. *Journal Of Experimental Social Psychology*, 48(3): 726-730
- Creel S. & Creel N.M. (2015) Opposing Effects of Group Size on Reproduction and Survival in African Wild Dogs. *Behavioral ecology*, 26(5): 1414–1422
- Danchin E., Giraldeau L.-A. & Cézilly F. (2008) *Behavioural Ecology*. Oxford University Press, Oxford

- Dickinson J. & Koenig W. (2018) *Animal social behaviour*. *Encyclopedia Britannica*, 7/2018. <<https://www.britannica.com/topic/animal-social-behaviour>> [Accessed 9.7.2021]
- Dingle H. (2014) *Migration: The Biology of Life on the Move* – Second edition. Oxford University Press, Oxford
- Dobson F.S. (1982) Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, 30:1183–1192
- Ekman J., Eggers S. & Griesser M. (2002) Fighting to stay: The role of sibling rivalry for delayed dispersal. *Animal Behaviour* 64(3): 453–459
- Faurie C., Russell A. F. & Lummaa V. (2009) Middleborns disadvantaged? Testing birth-order effects on fitness in pre-industrial Finns. *PLoS ONE* 4(5): e5680
- Goodall J. (1986) *Chimpanzees of Gombe*. Cambridge, MA: Belknap Press
- Greenwood P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, 28: 1140–1162
- Griesser M. & Ekman J. (2004) Nepotistic alarm calling in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour*, 67(5): 933–939
- Hamilton W. (1964) The genetical evolution of social behaviour I. *Journal of Theoretical Biology*, 7: 1–16
- He Q-Q., Wu J-J., Ji T., Tao Y. & Mace R. (2016) Not leaving home: grandmothers and male dispersal in a duoloccal human society. *Behavioral Ecology*, 27(5): 1343–1352
- Johnson D.W. & Johnson F.P. (2013) *Joining Together – Group Theory and Group Skills*. (11th ed). Boston: Pearson.
- Kingma S.A. (2018) Food, friends or family: What drives delayed dispersal in group-living animals? *The Journal of Animal Ecology*, 87: 1205-1208
- Kingma S.A., Bebbington K., Hammers M., Richardson D.S. & Komdeur J. (2016) Delayed dispersal and the costs and benefits of different routes to independent breeding in a cooperatively breeding bird. *Evolution*, 70: 2595–2610.
- Kisdi E., Utz M. & Gyllenberg M. (2012) Evolution of condition-dependent dispersal. pp. 139-151 in *Dispersal Ecology and Evolution*, edited by Clobert J., Baguette M., Benton T.G., Bullock J.M. & Ducatez S. (2012) Oxford University Press, Incorporated, Oxford
- Koenig W.D, Hooge P.N, Stanback M.T & Haydock J. (2000) Natal dispersal in the cooperatively breeding acorn woodpecker. *The Condor (Los Angeles, Calif.)*, 102(3): 492–502
- Koenig W.D. (1989) Sex-biased dispersal in the contemporary United States. *Ethology and Sociobiology*, 10(4): 263–277
- Kok J. & Bras H. (2008) Clustering and Dispersal of Siblings in the North-Holland Countryside. *Historical Social Research*, 33(3): 278-300
- Lambin X., Aars J. and Pieltet S.B. (2001) Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. in *Dispersal*, edited by Clobert J., Danchin E., Dhondt A.A. & Nichols J.D., Oxford University Press, New York

- Lawson Handley L. & Perrin N. (2007) Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology*, 16: 1559–1578
- Li X.Y. & Kokko H. (2019) Sex-biased dispersal: a review of the theory. *Biological Reviews*, 94(2): 721–736
- Loehr J., Lynch R., Mappes J., Salmi T., Pettay J. & Lummaa V. (2017) Newly Digitized Database Reveals the Lives and Families of Forced Migrants from Finnish Karelia. *Finnish Yearbook of Population Research*, 52: 59-70
- Lynch R., Lummaa V. & Loehr J. (2019b) Self sacrifice and kin psychology in war: threats to family predict decisions to volunteer for a women's paramilitary organization. *Evolution and Human Behavior*, 40(6): 543–550
- Lynch R., Lummaa V., Briga M., Chapman S. & Loehr J. (2020) Child volunteers in a women's paramilitary organization in World War II have accelerated reproductive schedules. *Nature Communications*, 11(1): 2377–10
- Lynch R., Lummaa V., Middleton K.M., Panchanathan K., Rotkirch A., O'Brien D., Danielsbacka M. & Loehr J. (2019a) Integration involves a trade-off between fertility and status for World War II evacuees. *Nature Human Behaviour*, 3: 337-345
- Macionis J. & Gerber L. (2010) *Sociology - 7th Canadian Ed.* Toronto, Ontario: Pearson Canada Inc.
- Martinig A.R., McAdam A.G., Dantzer B., Lane J.E., Coltman D.W., Boutin S. & Coulson T. (2020) The new kid on the block: immigrant males win big whereas females pay fitness cost after dispersal. *Ecology Letters*, 23(3): 430–438
- Mascie-Taylor C.G.N. & Lasker G.W. (2009) *Biological aspects of human migration.* Cambridge University Press, New York.
- Matthysen E. (2012) Multicausality of dispersal: A review. in *Dispersal Ecology and Evolution*, edited by Clobert J., Baguette M., Benton T.G. & Bullock J.M. (2012) Oxford University Press, Incorporated, Oxford.
- Mayer M., Zedrosser A. & Rosell F. (2017) When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. *Animal Behaviour*, 123: 375–382
- Maynard Smith J. (1964) Group Selection and Kin Selection. *Nature*, 201: 1145–1147
- Moring B. (1993) Household and family in Finnish coastal societies 1635-1895. *Journal of Family History*, 18(4): 395–414
- Moring B. (2003) Nordic family patterns and the north-west European household system. *Continuity and Change*, 18(1): 77–109
- Nathan R. 2001. The challenges of studying dispersal. *Trends in Ecology & Evolution (Amsterdam)*, 16(9): 481–483
- Nelson-Flower M.J., Wiley E.M., Flower T.P & Ridley A.R. (2018) Individual dispersal delays in a cooperative breeder: Ecological constraints, the benefits of philopatry and the social queue for dominance. *Journal of Animal Ecology*, 87: 1227–1238
- Nitsch A., Lummaa V. & Faurie C. (2016) Sibship effects on dispersal behaviour in a pre-industrial human population. *Journal of Evolutionary Biology*, 29: 1986–1998

- Packer C. & Pusey A. (1993) Dispersal, kinship and inbreeding in African lions. in *The natural history of inbreeding and outbreeding*, edited by Thornhill N.W., University of Chicago Press; Chicago, pp. 375–391
- Paukkunen L. (1989) *Siirtokarjalaiset nyky-Suomessa*. Jyväskylä: Jyväskylän yliopisto
- Perrin N. & Goudet J. (2001) Inbreeding, kinship, and the evolution of natal dispersal. pp. 123–142, in *Dispersal*, edited by Clobert J., Danchin E., Dhondt A.A. & Nichols J.D., Oxford (United Kingdom), Oxford University press.
- Perrin N. & Mazalov V. (2000) Local competition, inbreeding, and the evolution of sex-biased dispersal. *American Naturalist* 155:116–127
- Pettay J.E., Lummaa V., Lynch R. & Loehr, J. (2021) Female-biased sex ratios in urban centers create a “fertility trap” in post-war Finland. *Behavioral Ecology*, 32(4): 590–598
- Pusey A.E. & Schroepfer-Walker K. (2013) Female competition in chimpanzees. *Philosophical Transactions of The Royal Society B*, 368: 20130077
- Reicher S.D. (1982) The determination of collective behaviour. Pp. 41–83 in *Social identity and intergroup relations*, edited by Tajfel H. Cambridge: Cambridge University Press
- Roff D.A. & Fairbairn D.J. (2001) The genetic basis of dispersal and migration, and its consequences for the evolution of correlated traits. pp. 191–202 in *Dispersal*, edited by Clobert J., Danchin E., Dhondt A.A. & Nichols J.D., Oxford University Press, New York
- RStudio Team (2019). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL <http://www.rstudio.com/>.
- Rubenstein D. & Kealey J. (2010) Cooperation, Conflict, and the Evolution of Complex Animal Societies. *Nature Education Knowledge*, 3(10):78
- Sarno R., Bank M., Stern H. & Franklin W. (2003) Forced dispersal of juvenile guanacos (*Lama guanicoe*): causes, variation, and fates of individuals dispersing at different times. *Behavioral Ecology and Sociobiology*, 54(3): 320–32
- Sarvimäki M., Uusitalo R. & Jäntti M. (2020) Habit formation and the misallocation of labor: evidence from forced migrations. Available at SSRN: <<https://ssrn.com/abstract=3361356>>
- SAS Institute Inc. 2019, Version 8.2.1 (8.2.1.1223) Cary, NC, USA.
- Science for Environment Policy (2015) *Migration in response to environmental change*. Thematic Issue 51. Issue produced for the European Commission DG Environment by the Science Communication Unit, UWE, Bristol.
- Sharp S.P., Baker M.B., Hadfield J.D., Simeoni M. & Hatchwell B.J. (2008) Natal dispersal and recruitment in a cooperatively breeding bird. *Oikos*, 117: 1371–1379
- Silvasti T. (2010) *Maatilan varjossa Rakennemuutoksen anatomiaa*. Helsinki, Helsingin yliopisto.
- Silvasti T. (2010) *Maatilan varjossa: rakennemuutoksen anatomiaa*. Helsinki, Helsingin yliopisto.
- Smale L., Nunes S. & Holekamp K. (1997) Sexually Dimorphic Dispersal in Mammals: Patterns, Causes, and Consequences. *Advances in the Study of Behavior*, 26: 181-250

- Starrfelt J. & Kokko H. (2012) The theory of dispersal under multiple influences. Oxford University Press, Oxford. in *Dispersal Ecology and Evolution*, edited by Clobert J., Baguette M., Benton T.G., Bullock J.M. & Ducatez S. (2012) Oxford University Press, Incorporated, Oxford
- Statistic Finland (2007) *The growing years of Finland's industrial production*. <[https://www.stat.fi/tup/suomi90/toukokuu\\_en.html](https://www.stat.fi/tup/suomi90/toukokuu_en.html)> [Accessed: 17.8.2021]
- Strangor C., Jhangiani R. & Tarry H. (2014) *Principles of Social Psychology: 1st International Edition* (Edition 1). BCcampus Open Education.
- Strassmann B.I. & Clarke A.L. (1998) Ecological Constraints on Marriage in Rural Ireland. *Evolution and Human Behavior*, 19: 33–55
- Teichroeb J. A., Wikberg E. C. & Sicotte P. (2011) Dispersal in male ursine colobus monkeys (*Colobus vellerosus*): Influence of age, rank and contact with other groups on dispersal decisions. *Behaviour*, 148(7): 765–793
- Tesson S.V. & Edelaar P. (2013) Dispersal in a changing world: opportunities, insights and challenges. *Movement Ecology*, 1(1): 10–10
- Towner M. (2001) Linking dispersal and resources in humans: Life history data from Oakham, Massachusetts (1750–1850). *Human Nature*, 12: 321–349
- Towner M. (2002) Linking dispersal and marriage in humans: Life history data from Oakham, Massachusetts, USA (1750–1850). *Evolution and Human Behavior*, 23: 337–357
- Trochet A., Courtois E.A., Stevens V.M., Baguette M., Chaine A., Schmeller D. S. & Clobert J. (2016) Evolution of Sex-Biased Dispersal. *The Quarterly Review of Biology*, 91(3): 297–320
- Van Vuren D. & Armitage K.B. (1994) Survival of Dispersing and Philopatric Yellow-Bellied Marmots: What Is the Cost of Dispersal?. *Oikos*, 69: 179–181
- Voland E. & Dunbar R.I.M. (1997) The impact of social status and migration on female age at marriage in an historical population in north-west Germany. *Journal of Biosocial Science*, 29(3): 355–360
- Waris H., Jyrkilä V., Raitasuo K. & Siipi J. (1952) *Siirtoväen Sopeutuminen Tutkimus Suomen Karjalaisen Siirtoväen Sosiaalisesta Sopeutumisesta*. Helsingissä Otava, Helsinki
- Wolff J.O. (1992) Parents suppress reproduction and stimulate dispersal in opposite-sex juvenile white-footed mice. *Nature*, 359: 409–410
- Ydenberg R. C., Giraldeau L. A. & Falls J. B. (1988) Neighbours, strangers, and the asymmetric war of attrition. *Animal Behaviour*, 36(2): 343–347



## 7. Appendices

**Table A1.** Number of women and men by their birth municipalities/place in Karelia, in data n = 12,526

Birth municipality (Karelia)	Sex	
	Women	Men
Antrea	208	453
Harlu	53	54
Heinjoki	103	208
Hiitola	144	257
Impilahti	149	259
Inkere	4	6
Jaakkima	208	454
Johannes	87	159
Jääski	92	194
Kanneljärvi	61	114
Kaukola	73	174
Kirvu	186	345
Kivennapa	89	225
Koivisto	124	238
Korpiselkä	32	65
Kuolemajärvi	133	202
Kurkijoki	180	333
Käkisalmi	66	105
Lavansaari	0	2
Lumivaara	46	92
Metsäpirtti	61	93
Muolaa	257	500
Pyhäjärvi Vpl.	148	279
Pälkjärvi	24	58
Rautjärvi	16	40
Rautu	68	123
Ruskeala	73	147
Räisälä	211	340
Sakkola	123	251
Salmi	187	341
Seiskari	3	1
Soanlahti	62	107
Sortavala	49	70
Suistamo	124	180
Suojärvi	134	205
Suursaari	2	0
Säkkijärvi	151	269
Terijoki	8	10
Uukuniemi	64	142

**Table A2.** Number of women and men by their birth municipalities/place in Karelia, in data n = 4862

Birth municipality (Karelia)	Sex	
	Women	Men
Antrea	15	24
Harlu	13	10
Heinjoki	51	133
Hiitola	69	154
Impilahti	27	64
Inkere	0	2
Jaakkima	77	196
Johannes	44	111
Jääski	51	132
Kanneljärvi	36	92
Kaukola	44	77
Kirvu	106	221
Kivennapa	49	165
Koivisto	4	8
Korpiselkä	2	3
Kuolemajärvi	84	137
Kurkijoki	76	191
Käkisalmi	18	41
Lavansaari	0	0
Lumivaara	2	10
Metsäpirtti	29	47
Muolaa	145	332
Pyhäjärvi Vpl.	64	167
Pälkjärvi	6	35
Rautjärvi	1	3
Rautu	37	51
Ruskeala	17	52
Räisälä	24	43
Sakkola	62	145
Salmi	0	0
Seiskari	0	0
Soanlahti	16	26
Sortavala	23	37
Suistamo	8	15
Suojärvi	0	0
Suursaari	0	0
Säkkijärvi	91	177
Terijoki	6	5
Uukuniemi	1	0

Uusikirkko Vpl.	167	305
Vahviala	60	113
Valkeasaari	1	2
Valkjärvi	166	352
Viipuri	50	81
Vuoksela	40	95
Vuoksenranta	32	77
Värtsilä	2	4
Äyräpää	26	55
<b>Total</b>	<b>4347</b>	<b>8179</b>

Uusikirkko Vpl.	85	189
Vahviala	17	56
Valkeasaari	0	0
Valkjärvi	60	161
Viipuri	15	30
Vuoksela	4	9
Vuoksenranta	0	0
Värtsilä	0	1
Äyräpää	13	18
<b>Total</b>	<b>1492</b>	<b>3370</b>