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Sex-biased dispersal in water voles (*Arvicola amphibius*) in northern Norway

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1 Abstract

Dispersal is key to the population dynamic in discrete habitats. There is variation in dispersal rate and range both between and within species, based on environmental variation and between both populations and individuals. Sex-biased dispersal is found in both birds and mammals, and earlier studies have found variation in both dispersal rate and range with both male and female bias in different rodent species. In this study, I investigated sex-specific dispersal on two different spatial scales in water voles (*Arvicola amphibius*) in island-habitats off the coast of Helgeland in northern Norway. I found a male-biased dispersal both within and between islands. Of twelve between-island dispersers seven were males, zero were female, three were probably males (subadults) and two were registered as unknown (juveniles). Males dispersed greater distances (17 ± 2 meters) than females (11 ± 1 meters) within islands. These results support the hypothesis of mating systems and inbreeding avoidance as important aspects in the multicausality of dispersal. By dispersal in one of the sexes, the possibility of mating among kin is reduced, and hence the inclusive fitness increases. As a consequence, the lack of female between-island dispersal would influence the possibility of island recolonization.

1.1 Key-words

Dispersal, sex-biased dispersal, metapopulation, water vole, *Arvicola amphibius*, capture-mark-recapture, inbreeding avoidance, mating systems.

2 Sammendrag

Spredning er avgjørende i populasjonsdynamikken i diskrete habitat. Det er variasjon i rate og distanse både mellom og innad i arter, basert på miljøvariasjon og mellom både populasjoner og individer. Kjønnbasert spredning finnes hos både fugler og pattedyr, og tidligere studier har funnet forskjellige forskyvninger mot både hanner og hunner i flere gnagerarter. For å se nærmere på disse variable resultatene undersøkte jeg spredningsdynamikk på to forskjellige romlige skalaer hos vånd (*Arvicola amphibius*) på Helgelandskysten i Nord-Norge. Av resultatene fant jeg at det dominerende kjønn i spredning er hanner, både mellom og innad på øyene. Av totalt tolv individ som spredte seg var syv hanner, null hunner, tre mest sannsynlig hanner (unge voksne) og to av ukjent kjønn (juvenile). Jeg fant også at hanner spredte seg signifikant lengre (17 ± 2 meter) enn hunner (11 ± 1 meter) innad på øyene. Disse resultatene støtter hypotesene om at parringssystem og strategi mot innavl er mulige aspektene i spredningsårsaker. Ved spredning hos kun ett kjønn reduseres mulighetene for å parre seg med nære slektninger, og dermed en økning i inklusiv fitness. Som en konsekvens påvirker manglende hunnlig spredning mellom øyene mulighetene for rekolonisering av øyer.

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5 Introduction

Dispersal is the main mechanism leading to gene flow within and between subpopulations (Matthysen, 2012) and could be described as Bowler and Benton (2005; 218) did: “*Dispersal is a strategy to increase fitness in a heterogeneous landscape by changing the environment in which an organism lives, with variability in expected fitness between different habitat patches as the driving force for the evolution of dispersal*”. Distinguishing natal dispersal (from natal patch to patch of first breeding) from breeding dispersal (from one patch of successful breeding to another) is often useful since dispersal is linked to the populations’ social structure (Clobert et al., 2001, Greenwood, 1980).

MacArthur and Wilson (1967) presented a biogeographical model that focused on the importance of immigration and extinction on insular environments (“islands”), based on the size of and distance between islands. In this model, every subpopulation had some individual probability of extinction. Levins (1969) introduced the term “metapopulation” to describe a large population consisting of several local patches, or subpopulations, that were more or less connected. Further, Hanski and Simberloff (1997) argues that these patches are spatially distinct, with local breeding and the influence of migration on the local dynamics. Runge et al. (2006) suggest that source populations are defined with self-recruitment rate greater than one, and sink populations smaller than one. Linked to MacArthur and Wilson (1967), Brown and Kodric-Brown (1977) argues that there are some source populations that adds a rescue effect to decrease the probability of recipient patch extinction (sink populations). The categorization of patches are not necessarily fixed, and which patch acting as donor or recipient may change both between and within seasons (Krebs, 2013).

Causes of dispersal could be separated in ultimate and proximate causes. Both categories of dispersal causes are also influenced by the individual variation in dispersal propensity (i.e. sex or development stage) (Bowler and Benton, 2005). However, dispersal causes may be difficult to separate in some cases. If dispersal is due to starvation, which impacts fitness directly, the motivation are both proximate and ultimate (Stenseth, 1983). The ultimate causes are discussed as kin interactions and inbreeding avoidance, while proximate causes may be habitat variability (like population dynamics and intrinsic patch quality). Based on these causes, the inclusive fitness of the individual increases since the dispersal event would also benefit the individual’s kin (Hamilton, 1963, Hamilton, 1964a, Hamilton, 1964b). The population density could also be a cause of dispersal. Density and dispersal are positively correlated when individuals disperse

from donor patches to recipient patches relative to the quality of the patch (Aars and Ims, 2000). Bowler and Benton (2005) emphasizes that plastic, condition-dependent dispersal strategies are in most cases superior to fixed strategies.

Stenseth and Lidicker (1992) categorizes three phases of dispersal; leaving, travelling and arriving (see also Bowler and Benton, 2005, Clobert et al., 2004). In addition, they separate what they call quasi-dispersal, events that are similar to the phases of dispersal, but without the same result. (1) Excursions, where individuals explore surrounding habitats, but returns to origin; (2) nomadism, where individuals fail to establish home range and ends up as everlasting dispersers; (3) shifting, where individuals do a gradually relocation of home range, but never really leave. However, given the heterogeneity of the habitat, dispersal is not necessarily long-distance. Benton and Bowler (2012) emphasizes that the idea of discrete patches is only for simplicity. As environmental stochasticity continuously influences the heterogeneity of habitats, the patches are overlapping and dispersal from one patch to another is not necessarily a great distance.

There are several factors which influence individual dispersal propensity. Developmental stage, body size/condition and sex is closely related to the benefits, costs and risks of dispersal (Bowler and Benton, 2005, Matthysen, 2012). Although there are trends within classes of animals, there is variation between as well as within species when it comes to which sex that is most prone to disperse (Dobson, 1982, Greenwood, 1980, Lambin et al., 2001, Le Galliard et al., 2012, Stenseth, 1983, Stenseth and Lidicker, 1992). Costs and benefits of dispersal differ between sexes (Matthysen, 2012). This could influence which sex that acts philopatric or disperse. In their articles, both Dobson (1982) and Greenwood (1980) found that most dispersal in birds, both natal and breeding, are female biased. However, the majority of dispersal in mammals are male biased natal dispersal. In rodents, both a bias towards males of older age are found (Krebs et al., 1976) and towards natal dispersal of juvenile males (Cockburn, 1992).

As Dobson (1982) and Greenwood (1980) emphasizes, mating systems are influencing dispersal because it contributes to the differences in costs and benefits of dispersal. Likewise, Cockburn (1992) found this coherent with the sex-bias found in birds as males are more territorial with high costs of dispersal, and most female birds benefit of dispersal by increased choice among male-defended resources (see also Lambin et al., 2001). In rodents, with mostly polygamous or promiscuous mating systems, females are often the limiting factor (Krebs, 2013), which inflict a bias towards male dispersal. Hence, the influence of male competition for mates may be the reason that predominant dispersers are juvenile males in promiscuous

systems (Dobson, 1982). As Ims and Hjernmann (2001) emphasizes, there can be expected inconsistent patterns within and among species in condition-dependent dispersal since there are opposing selecting forces acting on the same mechanism. Males in populations with polygynous mating systems should be highly mobile to interact with multiple females and with mating partners as the limiting factor.

In metapopulations it is important to consider the cost of inbreeding and the promotion of sex-biased dispersal. Inbreeding depression is likely to occur when closely related individuals breed and may cause a reduction in fitness (Charlesworth and Charlesworth, 1987), usually because of the expression of recessive deleterious alleles (Billing et al., 2012, Frankham, 2005, Whitlock, 2004). Perrin and Mazalov (2000) found that it is sufficient with one dispersing sex to avoid inbreeding. Dispersal is beneficial regarding inbreeding avoidance and presence of kin could directly influence the individual dispersal (Matthysen, 2012), no matter which sex that disperse. When including inbreeding depression, the simulations of Gros et al. (2008) found that for monogamous species differences in the costs of dispersal may lead to sex-biased dispersal, even for small differences. In the polygamous mating systems, there is expected to be significant differences in sex-specific costs of dispersal, and most often males are in favor to disperse (Perrin and Mazalov, 2000).

Stenseth and Lidicker (1992) argues that small mammal dispersers are a heterogeneous assemblage based on the multicausality of dispersal (see also Cockburn, 1992). Their review found dispersal to occur in both sexes and all age groups, although dispersal rates and distances varied with species. Aars and Ims (1999) and Lambin et al. (2004) argues that dispersal in small mammals is most common in subadults and takes place early in life as a strategy of inbreeding avoidance. Dispersal in root voles (*Microtus oeconomus*) is thought to be density-dependent for females, but not for males (Aars and Ims, 1999). In the same species, long-distance dispersal is male biased according to Gundersen and Andreassen (1998), which concluded with inbreeding avoidance as the underlying cause. However, in the common vole (*Microtus arvalis*), short-distance dispersal is found to be strongly male-biased and long-distance was more balanced between the sexes (Gauffre et al., 2009).

As the causes of dispersal often are scale dependent the definition of “patch” is pivotal (Bowler and Benton, 2005). The physical environment in the study area determines the patchiness of the metapopulation (i.e. islands surrounded by water), and hence the cost of travelling. Gauffre et al. (2009) found different dispersal patterns between sexes in relation to spatial scales with no bias in long-distance dispersal, but male-bias at short distances. As long-distance dispersal may

be to escape crowding or to colonize new territory (Lawson Handley and Perrin, 2007), dispersal would be of high value for both sexes. Moreover, short-distance dispersal to avoid inbreeding and kin competition should influence biased dispersal towards only one of the sexes. Size of suitable habitat, soils, food availability, and the presence of pathogens, parasites and predators are temporal and spatial variables that contributes to the variation of extinction rates between habitats, including the costs and benefits of dispersal at both individual and population level.

In this study, I investigated sex-specific dispersal in an insular metapopulation of water voles in cooperation with an ongoing project on PhD level. Given the patchiness of this metapopulation, the variation between habitats may have a large influence on the extinction rate of the individual subpopulation, which increases the benefits of dispersal (Begon et al., 2006, Brown and Kodric-Brown, 1977, Hanski, 1998, Hanski and Simberloff, 1997, Lambin et al., 2004, MacArthur and Wilson, 1967). As causes and consequences of dispersal may change by spatial scale, I have chosen to analyze dispersal at two different scales, long-distance dispersal in discrete habitats (between islands) and short-distance dispersal in continuous habitats (within islands). The possible differences between the sexes will be discussed and compared with earlier studies to establish possible causes of dispersal on each spatial scale at this study site.

Earlier studies on water voles in different habitats have ended up with varying results of both mating systems and dispersal patterns. In Sweden, Jeppsson (1987) found that mating systems in water voles varied from facultative monogamy in grasslands, to polygyny in marshes. This could be because of different levels of above ground cover which influences the above ground mobility, hence reducing size of home range and female overlapping. In an insular water vole population located 50-60 kilometers north of our study site, Frafjord (2016) found that water voles in island habitats had a polygamous (promiscuous) mating system, with male home range greater than female's and overlapping several female home ranges. This fits with the polygynous mating system, as males compete for access to several females, while females compete for resources and defense of offspring (Krebs, 2013). A study of water voles in Scotland found a slight female-biased dispersal in both rate and range in patchy habitats at low densities (Aars et al., 2006). Based on these various conclusions it is interesting to investigate the current dispersal dynamics in our study site.

Nevertheless, correlations to Frafjord (2016) are expected as the study systems are 50-60 kilometers apart, on the same species, and multiple factors of similarity (i.e. composition of habitats, distances between islands, environmental stochasticity). This, along with general theory of mating systems in rodents (i.e. Bowler and Benton, 2005, Dobson, 1982, Greenwood, 1980, Pusey, 1987, Stenseth, 1983), it is expected a polygamous (promiscuous) mating system in our metapopulation of water voles. A male-bias in water vole dispersal both within and between islands is predicted based on the dispersal correlation with mating systems and the overall theory of dispersal patterns in small mammals.

6 Material and methods

6.1 Study species

The northern water voles, *Arvicola amphibius* (formerly *A. terrestris*), are rodents weighing between 140-350 grams, varying in grey and brown colouration with rounded body and blunt muzzle (Strachan et al., 2011). Until the first winter, juvenile pelage is often glossier than that of adults (Stoddart, 1971). Water voles are herbivorous with the main diet of lush aerial stems and plant leaves. To survive the winter, water voles use food storage beneath ground (Strachan et al., 2011). The species are great swimmers both as dispersal and escaping strategy, however it is not typically adapted to water, i.e. no web on the feet. Water voles build tracks and tunnels in the moss, soil and grass to walk/run between different areas of habitat, such as ponds, marshes and heaths. Close to tunnel-openings it is typically found latrines and lawns who give indication of water vole presence (Strachan et al., 2011). Latrines are particular areas of feces often used as territory indication, and lawns are small areas of fresh, low-cut grass.

Nests are found below ground and, in the study site, often located beneath juniper shrubs (*Juniperus communis*) or heaths. Breeding females appear territorial in contrast to wide-ranging males who compete for female access (Strachan et al., 2011). The females produce 2-4 litters each breeding season (April-July) (Frafjord, 2016), each of 5-8 young. The biggest litters are usually observed in June (van Wijngaarden, 1954). According to Stoddart (1971) the juveniles use about 45-55 days to attain a mass of 100 grams. Most often the offspring reach sexual maturity after their first winter, but offspring from earliest litter(s) may also be able to breed in their first autumn (Stoddart, 1971). When water voles are sexually mature, one can feel the testes in the scrotum and often see the penis tip in males, while females have noticeable nipples and often a visible vaginal opening.

6.2 Study site and field methods

The study was conducted in the Skålvær archipelago located at Helgeland in northern Norway (65.885°N, 12.225°E) (Figure 1). The 13 islands in this study is part of the metapopulation of water voles in the archipelago. Marshes, mosses, reed beds and heaths made up most of the habitat of the island's inland and made great movement opportunities for the water voles (Appendix 1). In addition, ponds, trenches and rocky grounds contributed to variation in the habitat. The areas closest to the ocean, often two to five meters, were mostly rocks and were rarely inhabitable for water voles. There were different distances between the islands (Figure 1) and they were of different sizes (Appendix 2). By choosing island that were between 2000

and 13000 square meters, it would be possible to get an overview of the population sizes and dynamics, as well as trends of dispersal distances and local dispersal variation. Local predators in the study site archipelago were aerial, such as eagle owl (*Bubo bubo*), short-eared owl (*Asio flammeus*), common kestrel (*Falco tinnunculus*) and, for the juveniles, seagulls (especially *Larus canus* and *Larus marinus*). There were no terrestrial predators on the islands as far as we knew. The main study is based on capture-mark-recapture (CMR) with at least 70% recapture rate within period, however, for some islands in the pilot study (autumn 2015) this was not achieved.

Seasons of sampling were chosen to be spring (April-May), summer (June-July) and autumn (August-October). This made it possible to study dispersal dynamics between seasons. Sampling water voles in the spring provided an indication of how many individuals who survived the winter and what made the foundation before the upcoming mating season. That time of the year, the population size was usually at its smallest, and observations of extinct populations were most likely in that season. The field work in the spring were important because of natal dispersal of offspring from the previous year may have happened in the spring, along with breeding dispersal of second year adults. Because of high numbers of juveniles and limited time in the summer, we chose to sample the four islands with highest number of individuals in the spring, i.e. Geiterøya N, Gulbrandsøyen Midt N, Gulbrandsøyen Midt S and Gulbrandsøyen S (Appendix 4). Summer and autumn sampling gave valuable information about the possible natal dispersal of juveniles and subadults, in addition to the location of dispersed adults from spring season.

The positions of traps were determined with a GPS (accuracy 2-4 meters). The number of traps on each island varied between 70 and 170 depending on island size. In addition, as field work procedures have become more efficient during the study period, the number of traps used have increased (Appendix 3). All between-season movement based on GPS-locations of capturing traps were categorized as dispersal either between- or within-island to avoid confusion about the terms of movement versus dispersal.

The water voles were captured using folding traps from H.B. Sherman Traps, Inc. model XLF15 (Figure 2). The traps were loaded with about a handful of moss or hay and a chunk of both potato and carrot. Trap sites were chosen based on latrines, lawns or tunnel openings. The traps were also covered with either moss or a piece of tarpaulin in case of bad weather. For the same reason, the traps were placed away from areas which may get flooded during heavy rain.

Skålvær archipelago

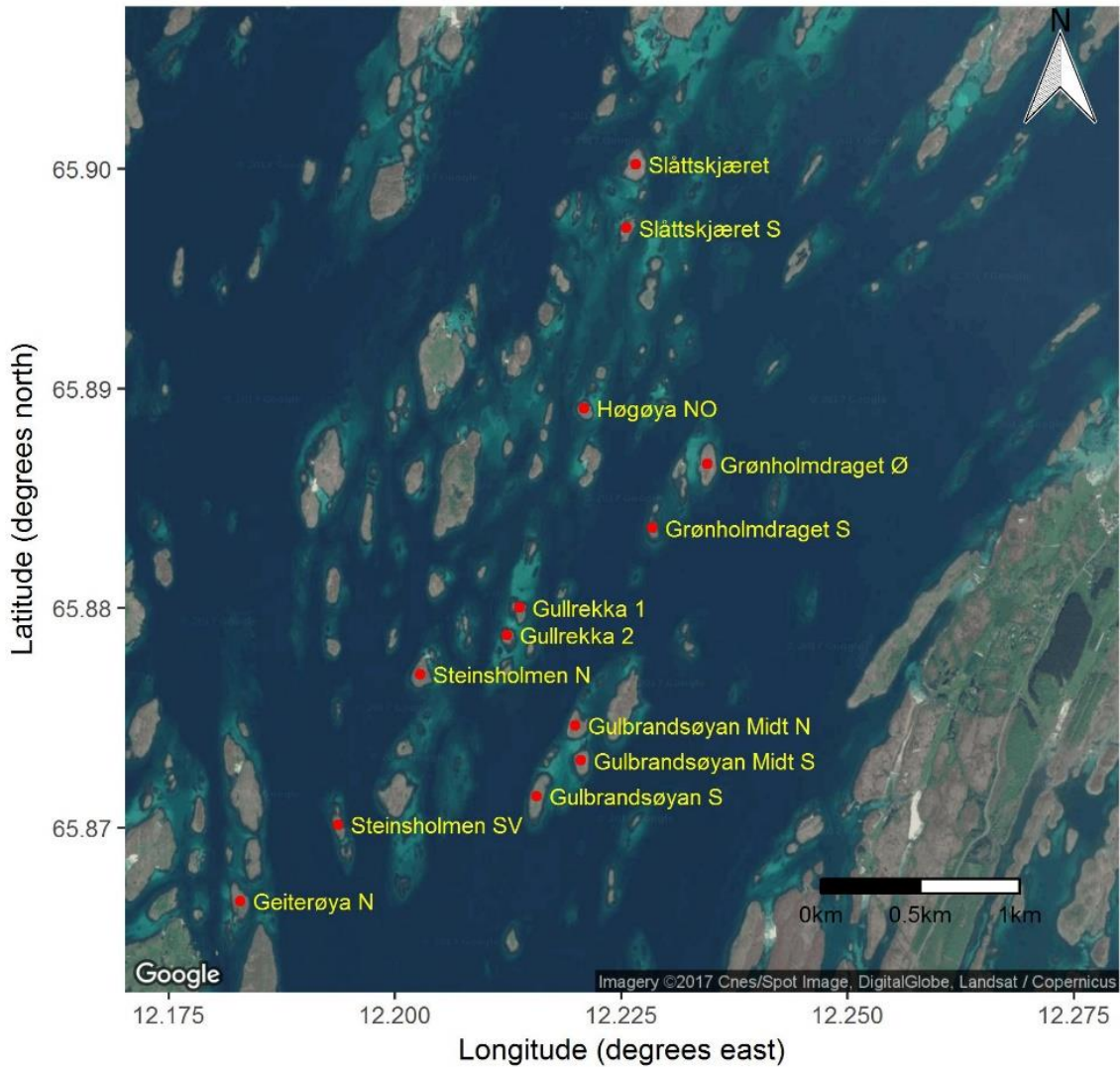


Figure 1: Map of study sight, the Skålvær archipelago at Helgeland in northern Norway (65.885°N, 12.225°E). The 13 islands are marked as red dots with corresponding names to the right in yellow. There are islands in between the islands of study that were not sampled. The islands are of different sizes and with various distances between them.



Figure 2: A picture of a Sherman trap XLF15. Traps are possible to collapse during transport, and possible to deconstruct when washing and disinfecting them.

Traps were checked every 1-1,5 hours. The water voles were handled one by one and released in the area of capture immediately after handling. We measured weight, determined sex, age, stage of reproduction, and presence/absence of ectoparasites, before we took tissue biopsy (2mm diameter) from one ear and marked each individual with a unique PIT-tag (TROVAN unique ID-100B; dimensions: length = 11.5mm., diameter = 2.12mm.) using an IM-200 syringe implanter. A mass of 45 grams was set as minimum threshold to mark with PIT-tag of both ethical and practical reasons.

To get as much information as possible when determining sex, we used five categories; male (“m”), female (“f”), probably male (“pm”), probably female (“pf”) and unknown (“u”). Adults were usually determined to “m” or “f” because of exposed genitalia (Stoddart, 1971). “pm” and “pf” were used if sexing was uncertain, mostly used on subadults. The category “u” was used for individuals that had no indication of male or female genitalia, mostly used on juveniles. Due to sexual maturity and growth of genitalia, the probability of correct sex determination is higher with older age of the individual. Therefore, the last registered sex of each individual is used throughout the dataset. Only individuals that were determined as males (“m”) or females (“f”) were used in the analysis of within-island dispersal, as there was greater uncertainty to the other categories in sex determination. We did the same thing with age with the five categories; adult (“a”), juvenile (“j”), probably adult (“pa”), probably juvenile (“pj”) and unknown (“u”). Since the oldest offspring of the year may have reached the same mass as adults, the “u”-, “pj”- and “pa”-categories were useful in the autumn and could give some additional information about the individual.

The dispersal distances were calculated as the geometric distance between traps. The distances of between-island dispersal were calculated as the shortest distance between GPS-location of the last and first trap of capture before and after dispersal event (Table 2). The within-island dispersal distances were calculated as distances between center of activity from one season to the next. The center of activity is the mean position of all captures in the given season, this is influenced by the number of captures of each individual, e.g. the more captures the more precise. Because of these calculations only individuals captured in at least twice in two different seasons or captured on at least two different islands were included in the calculations.

6.3 Data analysis

Every island in the dataset were sampled at least across two seasons (Appendix 4). “Grønholmdraget S”, “Grønholmdraget Ø”, “Gullrekka 1”, “Høgøya NO”, “Steinsholmen N” and “Steinsholmen SV” were added to the study after the pilot study of autumn 2015, and were only sampled across two seasons (spring and autumn 2016). “Geiterøya N” and “Gulbrandsøyen S” were also added after pilot study, but were sampled across three seasons (spring, summer and autumn 2016). “Gullrekka 2”, “Slåttskjæret” and “Slåttskjæret S” were in the pilot study and sampled across three seasons in total (autumn 2015, spring and autumn 2016). The remaining “Gulbrandsøyen Midt N” and “Gulbrandsøyen Midt S” were sampled all four seasons. The island “Steinsholmen” was removed from the data set as it was only sampled once (in pilot study) and no individuals from this island were later observed.

Data analysis were carried out with R version 3.3.2 (R Development Core Team, 2016) in RStudio version 1.0.136 (RStudio Team, 2016). Data preparation and tables were made with additional packages: `data.table` (Dowle and Srinivasan, 2016) and `zoo` (Zeileis and Grothendieck, 2005). Maps and figures were constructed with additional packages: `ggmap` (Kahle and Wickham, 2013) and `ggplot2` (Wickham, 2009).

Linear mixed-effects models were used to analyze the relationship between within-island dispersal and sex and seasons. To this, the additional package `lme4` (Bates et al., 2015) was used. As fixed effect, the main effect of sex and season were included in the full model. In addition, to test if an effect of sex on dispersal differed between seasons, the interaction `sex*season` was included in the model. As random factors, I included site and individuals nested in sites. The latter term was included to avoid pseudoreplication since multiple individuals were observed between multiple seasons. As there were only one observation of within-island dispersal between autumn 2015 and autumn 2016, this observation was removed from the

dataset to implement the model selection. The most parsimonious model explaining variation in dispersal distance was determined based on AICc (Burnham and Anderson, 2002). The AICc values were calculated using the package AICcmodavg (Mazerolle, 2016). The model with sex as a single fixed effect had the lowest AICc (Appendix 5). However, model with both sex and season without interaction did have some weight. As models were compared regarding selection, models were first fitted with maximum likelihood (ML) and after selection with restricted maximum likelihood (REML) to obtain parameter estimates (Burnham and Anderson, 2002). Evaluation of residual plots of best model were satisfactory and did not reveal any obvious deviations.

The analysis of between-island dispersal was planned to be done in the same way as within-island dispersal, with sex and season as fixed effects and individuals nested in sites as random effects. Unfortunately, because of few data points and no individuals determined as females there is a high risk of overfitting, hence the model may fail to identify effects that should be supported by the data (Burnham and Anderson, 2002). The estimates from the model would be of great uncertainty and it would be difficult to make any biological sense of the results even if they were statistically significant.

There are difficulties in defining what is, and what is not, short-distance dispersal as this is depending on the continuity of the habitat. In some habitats, movement of one meter in two-dimensional space pose no difference, but in other habitats one meter could represent two highly different habitats (i.e. from pond, through marsh, to heath). Based on the highly variable habitats in this study I have chosen to incorporate all within-island dispersal distances in the main model. However, to be safe I ran a model only including distances greater than five meters and ended up with the same results.

The total number of individuals captured are 1368 (males = 312, females = 362, probably males = 250, probably females = 188, unknown sex = 253, not registered = 3) in four different seasons; autumn 2015, spring-, summer- and autumn 2016. 37 individuals were not injected with PIT-tag as they were below the mass threshold (< 45 grams). Big differences of population size are registered between the seasons, with noticeable deaths through the winter and large number of juveniles during summer and autumn 2016 (see Appendix 4).

7 Results

Between-island dispersal events are observed within and between all seasons (Table 1). Most adults are observed to disperse in early seasons, and juveniles in late seasons. Distance of between-island dispersal are various, but 10/12 have dispersed 900 meters or shorter, and 8/12 shorter than 400 meters (Table 2). Longest between-island dispersal distance is 3002 meters from Gulbrandsøyen Midt S to Slåttskjæret (Figure 4).

There are twelve registered between-island dispersers. Ten out of twelve individuals are registered as males (“m”) or probably males (“pm”) (Table 2). The remaining two were too young to be determined as neither male nor female (registered as u). Thus, no females (“f”) or probable females (“pf”) were observed to disperse between islands.

Table 1: Number of between-island dispersed individuals between and among seasons. “From season” is the last season of registration at the island the individual dispersed from, and “To season” is the first season the dispersed individual is observed on the new island. Number of individuals dispersed at the given seasons are presented. Age of dispersers are given as last registered age before dispersal event, adult(a), juvenile(j), probably adult (pa) and not registered (NA).

From season	To season	No. of ind.	Age of dispersers
Autumn 2015	Spring 2016	2	pa, NA
Spring 2016	Spring 2016	3	a, a, a
Spring 2016	Summer 2016	1	a
Summer 2016	Summer 2016	1	j
Summer 2016	Autumn 2016	3	a, j, j
Autumn 2016	Autumn 2016	2	j, j

Within-island dispersal has a total of 203 observations (male = 62, female = 141) from 140 individuals with confident sex-determination (males = 46, females = 94) on 13 islands (Figure 3 and Appendix 6-9). A total of 36 female observations had dispersal distance less than five meters, opposed to the total of seven male observations. From the mixed-effect model the effect of sex is found to be statistically significant ($t = 3.003$, $p = 0.003$). Furthermore, the dispersal distance increases by nearly 55 % from 11 (± 1) metres in females to 17 (± 3) metres in males (Figure 3). That is, males disperse over greater distances than females within islands. Model including both sex and season without interaction had some weight in model

selection (Appendix 5), but did not reveal any differences of dispersal distances between seasons. Model including both sex and season as fixed effects with interaction was non-significant, the effect of season regarding dispersal distance was not different between the sexes.

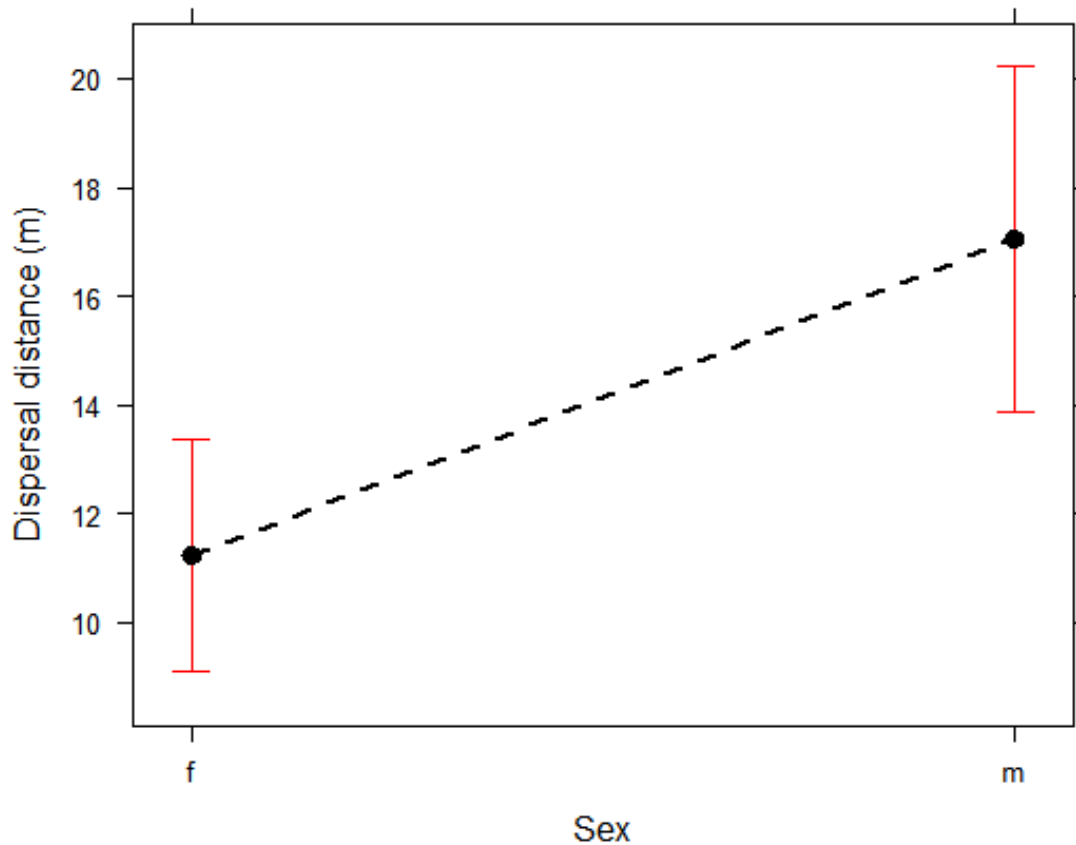


Figure 3: Plot of within-island dispersal distance in meters of both females (“f”) and males (“m”) based on the most parsimonious model explaining variation in dispersal distance. Estimated mean is marked as black dots with corresponding error bars marked as red lines. A total number of 141 female observations and 62 male observations. Dataset is based on individuals that were captured at least two seasons and determined to one of the specific sexes. Distances were calculated from center of activity (mean position) from one season to the next.

Table 2: Information about all 12 dispersed individuals before and after dispersal event. “From site” is the island the dispersed individual was last registered before dispersal event, and “To site” is the island of capture after dispersal event. “From season” and “To season” are the seasons of respectively last and first capture before and after dispersal. Age and mass are also corresponding to the last and first registered information about the individuals before and after dispersal event. Sex is presented as the last registered sex in the dataset to maximize the likelihood of correct sex determination. Distance is calculated in meters from location of last and first trap of capture, before and after dispersal

From site	To site	From season	To season	Age	To age	Mass (g)	To mass (g)	Sex (last reg.)	Distance (m)
Grønholmdraget S	Grønholmdraget Ø	Autumn 2016	Autumn 2016	j	j	165	155	pm	352
Gulbrandsøyen Midt N	Gulbrandsøyen Midt S	Spring 2016	Spring 2016	a	a	190	190	m	588
Gulbrandsøyen Midt N	Grønholmdraget Ø	Spring 2016	Spring 2016	a	a	200	205	m	172
Gulbrandsøyen Midt N	Gullrekka 1	Spring 2016	Spring 2016	a	a	190	190	m	1432
Gulbrandsøyen Midt S	Gulbrandsøyen S	Autumn 2015	Spring 2016	NA	a	NA	180	m	266
Gulbrandsøyen Midt S	Gulbrandsøyen Midt N	Spring 2016	Summer 2016	a	a	190	170	m	168
Gulbrandsøyen Midt S	Slåttskjæret	Summer 2016	Autumn 2016	j	j	90	145	pm	3002
Gulbrandsøyen Midt S	Gulbrandsøyen S	Summer 2016	Summer 2016	j	j	110	110	u	263
Gulbrandsøyen Midt S	Gulbrandsøyen S	Summer 2016	Autumn 2016	a	a	170	195	m	345
Gulbrandsøyen S	Gulbrandsøyen Midt S	Summer 2016	Autumn 2016	j	j	110	145	pm	290
Gullrekka 2	Gullrekka 1	Autumn 2015	Spring 2016	pa	a	170	235	m	124
Gullrekka 2	Gulbrandsøyen S	Autumn 2016	Autumn 2016	j	j	110	120	u	900

Between-island dispersal

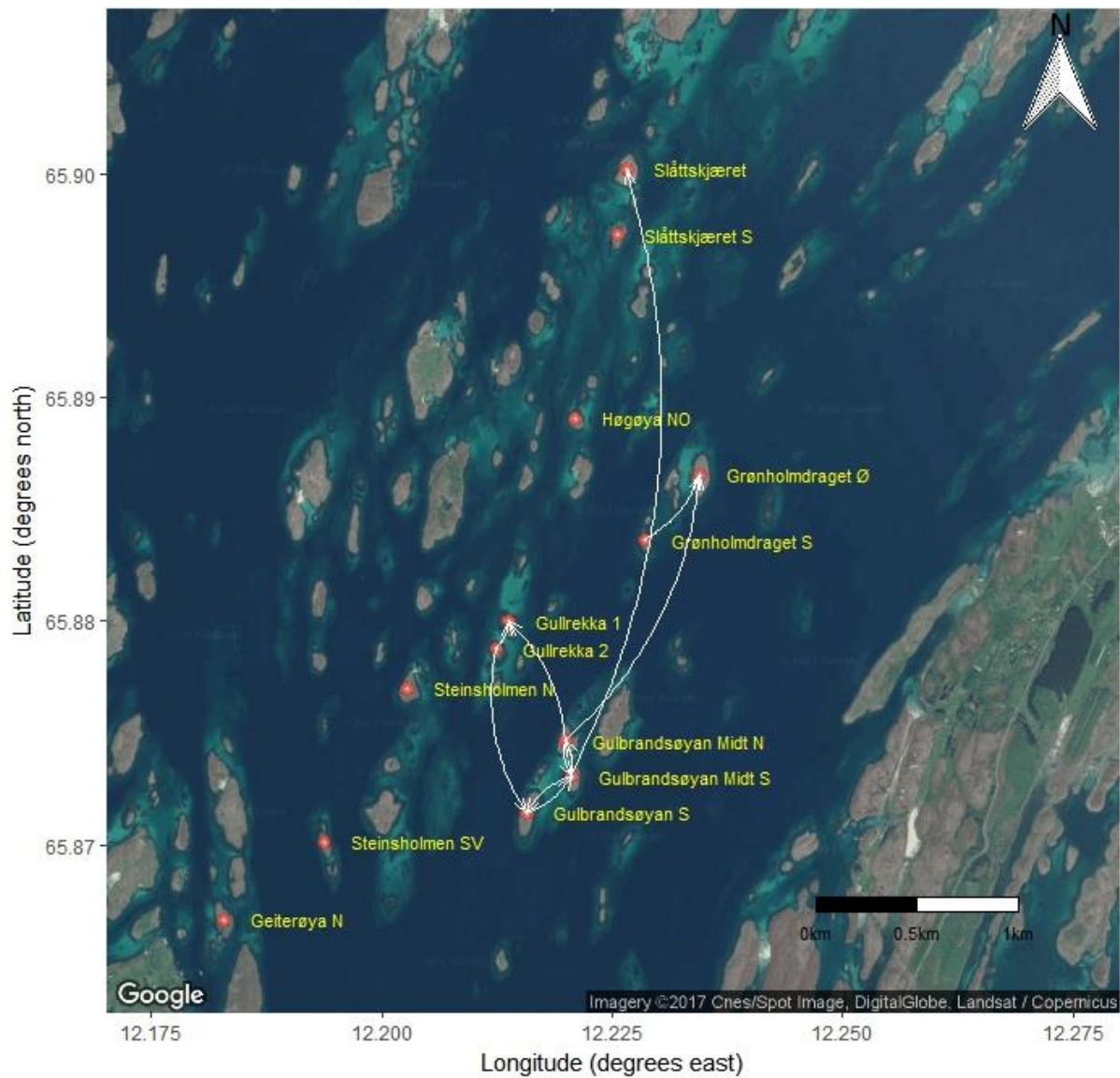


Figure 4: Geographic representation of between-island dispersal. All islands included in the study are marked as red dots with corresponding names. Right-curved, white arrows indicate observations of between-island dispersal events. The number of dispersal events between islands are not considered in this representation, i.e. arrows represent at least one dispersal event.

8 Discussion

This study found evidence of sex-biased dispersal in water voles. There is no record of any female between-island dispersal event in this study system, and at this point of time, i.e. there was no observations of dispersers determined as “F” or “pf”. Between-island dispersal are observed at all seasons, and most of the distances ($\frac{2}{3}$) are shorter than 400 meters. I found significantly longer within-island dispersal distance in males with nearly 55 % greater mean distance than females. Season had no significant main effect on within-island dispersal distance, nor any significant interaction effect with sex.

Based on Frafjord (2016), I assume a polygamous (promiscuous) mating system in our study system. From reviews of both Dobson (1982) and Greenwood (1980) male-biased dispersal is expected in mammals with polygynous or promiscuous mating systems. Stenseth (1983) argues that there is no reason to believe that small mammals of fluctuation populations (i.e. rodents) should be any different in sex-specific dispersal than other mammals. As expected when taking the mating system of the population into account, I have found male-biased between-island dispersal in the water voles of this study (Table 2). The bias towards males in long-distance dispersal is coherent with the root vole study of Gundersen and Andreassen (1998) in southeast Norway. Results of their study found female long-distance dispersal and male dispersal to be mechanisms to avoid inbreeding. In a genetic study of insular water vole populations in northern Norway, Melis et al. (2013) found high levels of genetic differentiation between populations and low inbreeding coefficients. This is expected when dispersal is sex-biased as it decreases the probability of mating with kin when mainly one sex disperse (Pusey, 1987). In addition, only about 1% of all sampled water voles were found to be population immigrants (Melis et al., 2013), which is coherent with the number of dispersers in my study (13 dispersers of 1368 individuals). Additionally, a result of the field work in spring 2017 regarding the PhD-study of Sindre L. Sommerli, is observation of additionally four between-island dispersal events, all males. These observations give more support to the results of male-biased dispersal in water voles in northern Norway.

The result of longer within-island dispersal distance in males (Figure 3 and Appendix 5) are supported by the findings of Frafjord (2016), who found promiscuous mating system and larger male home range in water voles. When males disperse longer within-island distances than females they will interact with more females, increasing the number of possible matings and offspring. This result is also consistent with conclusions for polygynous species in the review

of Le Galliard et al. (2012), who found a general trend of female arvicolines to be more philopatric than males, in both within- and between-island dispersal. However, in the same review water voles were the only species found to have female biased natal dispersal. This is in direct contrast to my findings of greater male within-island dispersal distances. It is thought that female offspring often settle close to natal nest, while male offspring often avoid kin competition and inbreeding by dispersing longer within-island distances (Gros et al., 2008, Gundersen and Andreassen, 1998). In addition, asymmetric dispersal distance between the sexes would contribute to inbreeding avoidance as possible matings among kin would be more difficult (Pusey, 1987). The contrasting results from my study and the review of Le Galliard et al. (2012) could be indicating a plastic dispersal strategy in water voles.

Small differences in sex-specific costs of dispersal influence the sex-bias in monogamous systems (Gros et al., 2008). Moreover, in polygynous and promiscuous systems it is thought to be bigger differences in sex-specific costs and hence influence an even stronger sex-bias in dispersal. Since males and females have different limiting factors, i.e. respectively mating partners and territories (with its accompanying factors), the costs of dispersal are expected to be even more asymmetric and in favor of males (Perrin and Mazalov, 2000). Additionally, eviction because of mate competition among males may result in involuntary dispersal from the patch or island (Lawson Handley and Perrin, 2007).

Both spatial scales of dispersal are found to be male biased in this study. This would indicate higher benefits or smaller costs of male dispersal both within and between islands (Le Galliard et al., 2012). Gauffre et al. (2009) argues that female long-distance dispersal is not rare in common voles, which is contradictory to this study with no observation of female between-island dispersal. However, Gauffre et al. (2009) suggests female long-distance dispersal is generally in colonization events as it is difficult for females to acquire territories in habitats already colonized by related females. The different results in long-distance dispersal of these studies could be related to habitat, as ours are of discrete island habitat and theirs are of continuous agricultural habitat. The costs of dispersal in unsuitable habitats are most likely bigger in discrete habitats. Additionally, the information about territory occupancy is most likely less costly and more accessible in a continuous habitat than in a discrete.

My findings are also in contrast with what Aars et al. (2006) found in water voles in Scotland with a slight female dispersal bias at low densities and no sex-bias at high densities. The Scottish study separated lowland and highland habitats as respectively intermediately fragmented and highly fragmented populations. These results are possibly influenced by small population size

and the high extinction probability of the Scottish highland habitats, hence a necessity of colonization and an increased level of female dispersal rate. Additionally, the unsuitable stretches of heath that separates some of the patches in Scotland may be less costly regarding travelling than the waterways exclusively separating the islands in northern Norway.

Aars and Ims (1999) found an increased female dispersal rate at high densities in root voles as an effect of habitat corridors. This could mean that short-distance female dispersal is density-dependent as in root voles (Aars and Ims, 2000), but that between-island dispersal is most often non-beneficial for females. Differences in density-dependence between males and females could be one of the reasons that only male between-island dispersal is observed in this study. However, even though dispersal influences the metapopulation persistence, female dispersal is of importance to maintain subpopulations and colonize or recolonize habitats (Lambin et al., 2001). If there is 100% female philopatry a recolonization and development to a viable population would be impossible as there would not be any females present. This implies a certain rate of female between-island dispersal that is not captured in the data, as the islands most likely would become extinct, one by one, without female between-island dispersal. Females could also be less sensitive of population density, and the reason there were no observations of female between-island dispersal was that the threshold density was not reached in our sampling periods.

Throughout the seasons variation in multiple factors could influence dispersal. However, since there was no significant trend of seasons in neither within-island nor between-island dispersal, limited food resources or population density does not seem to be causes of dispersal. Without any interaction effect of sex and season in within-island dispersal distances, the effect of sex does not seem to influence dispersal differently between seasons. If population density would be a cause of dispersal I would expect a peak of dispersing individuals at the peak of population size, but this is not the case. Looking at the number of individuals at each island throughout the seasons (Appendix 4), there are noticeable fluctuations in populations size. When there are fluctuations like this, every year some subpopulations might go extinct by chance, i.e. demographic and environmental stochasticity. To increase the population size from spring 2016 without the risk of inbreeding depression, and hence increased extinction risk, between-island dispersal of both sexes is necessary. This is especially applicable to the smallest islands since habitat size influence the extinction probability (Brown and Kodric-Brown, 1977, MacArthur and Wilson, 1967), and the lack of female between-island dispersal would cause consequences in recolonization of habitats.

Although male within-island dispersal is significantly longer than female, one should not ignore the potential female dispersal. 58 females dispersed more than five meters between seasons, this could, as Cockburn (1992) argues, be breeding dispersal as a form of parental investment at high densities. Density-dependence is also what Aars and Ims (1999) found to be influencing female dispersal. By dispersing from nest and abandoning the home range shortly after weaning, the mother provides a possible breeding site for her female offspring. Female short-distance dispersal in root voles seem to be adaptive and caused by resource competition (Gundersen and Andreassen, 1998). Considering this and the conclusion of Moorhouse and Macdonald (2005), a possible drift in female's territories could be the reason that female within-island dispersal distance are short, but distinct. This is coherent with what Stenseth and Lidicker (1992) call shifting as quasi-dispersal, and is based on the environmental stochasticity and/or territorial intrusion of other females. This territorial shift may cause males to disperse longer than without the shifting to increase their number of matings and to reduce the kin interaction. Moreover, the female breeding dispersal could also decrease the necessity of male dispersal and the associated costs, as it is sufficient with dispersal of one of the sexes to avoid inbreeding (Perrin and Mazalov, 2000).

As expected there were most observations of short-distance between-island dispersal (Figure 4 and Table 2). This is linked to the positive correlations between cost and distance of dispersal (Le Galliard et al., 2012). Waterways with strong currents and cold water are difficult and costly to handle and would increase the cost of dispersal, and because of the high travelling cost there is low probability of between-island quasi-dispersal (Stenseth and Lidicker, 1992). Strong currents could also be determining for longer distances as the season and tide could impact the speed of the current. If dispersal is random movement, the likelihood of recapturing dispersers across short distances is much higher than of long distances. In addition, reduced shelter towards predators has been shown to reduce the home range of water voles in Sweden (Jeppsson, 1987). This could also mean that longer dispersal distances without shelter would interact with the mortality risk and increase the cost of dispersing, especially dispersing more than once. This could influence populations extinction-time on distant islands, since reduced female dispersal rate on longer distances may be crucial when female between-island dispersal is initially low.

There does not seem to be any bias of between-island dispersal towards males of older age as Krebs et al. (1976) pointed out as a general trend in rodents. As many juvenile or subadult dispersers as adults are observed dispersing between islands. Two of the adults are indications

of breeding dispersal as they most likely dispersed after their first breeding season. The dispersing juveniles and subadults are most likely male natal dispersal and in accordance with other studies on small mammals (i.e. Dobson, 1982, Greenwood, 1980, Gundersen and Andreassen, 1998, Le Galliard et al., 2012, Pusey, 1987). Based on these results of both adult and juvenile dispersal it seems that both natal and breeding dispersal is present in these populations.

In conclusion, I have found my expectations to hold as dispersal is male-biased in water voles, both between and within islands. I did not observe any female between-island dispersal. The very low female between-island dispersal rate may have important consequences for the rate of recolonization of empty patches. I argue that the sex-specific dispersal pattern in the water vole is shaped by the mating system (i.e. differences in sex-specific costs and benefits) and inbreeding avoidance in this metapopulation. However, as multiple studies conclude, dispersers are a heterogenous group of individuals which may be influenced by multiple factors on which they determine to disperse or not, and therefore more research is needed.

8.1 Further research

By genetically determining sex of all individuals, one could include all juveniles and subadults in analysis of sex-biased dispersal. Genetic familiarity of dispersers and their offspring would be interesting to analyze and observe possible heritability of dispersal, which could imply some genetical relation of dispersal. Additionally, genetic analysis would make it possible to assess reproductive success.

It would be necessary to complete multiple years of study, this should give a better view of the actual dynamics involved in dispersal. Increasing the number of individuals observed as between-island dispersal would give more statistical possibilities, running simulations and models. This could give an estimate of potential population fraction of dispersal, which is closely related to the possibility of recolonizing extinct island populations. It could be of value to incorporate the population densities after multiple years of study to examine dispersal as density-dependent, both within and between sexes. Moreover, an analysis of food availability throughout the year would be interesting in regard to population density and density-dependent dispersal.

There is a possibility that within-island breeding dispersal influence some sort of nomadism for adult males. As islands are discrete habitats, a seasonal within-island dispersal would eventually make the males return to earlier visited patches. This may cause loss of observations on within-

island dispersal, as nine out of 13 islands were only visited spring and autumn, and only observations in the summer season is of the remaining four islands. Hence, there would be of best interest to gather data on all islands in all three seasons.

Another aspect regarding genetical analysis, however as of behavioral ecology, would be to compare offspring survival of dispersing and non-dispersing individuals. This could give an indication of fitness benefits of the dispersing individuals. Higher levels of testosterone and/or corticosterone could influence the aggressive behaviour as well as the determination of dispersal (Ronce and Clobert, 2012). Hence, blood samples would also be of interest to analyze the differences in hormone-levels of between-island dispersers and non-dispersers.

The vast number of water voles has created problems for farmers at Helgeland in northern Norway. IUCN reports water vole as a pest species in northern continental Europe, even though it is red listed in other areas (e.g. United Kingdom, the Netherlands and Italy) (Batsaikhan et al., 2016). I recommend further studies to know more about the present ecosystem where there might be lengthened periods of rodent fluctuations.

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10 Appendix

Appendix 1: Picture of typical island habitat. Mosses, reed beds and trenches are visible. Yellow tags are numbered trap markings.



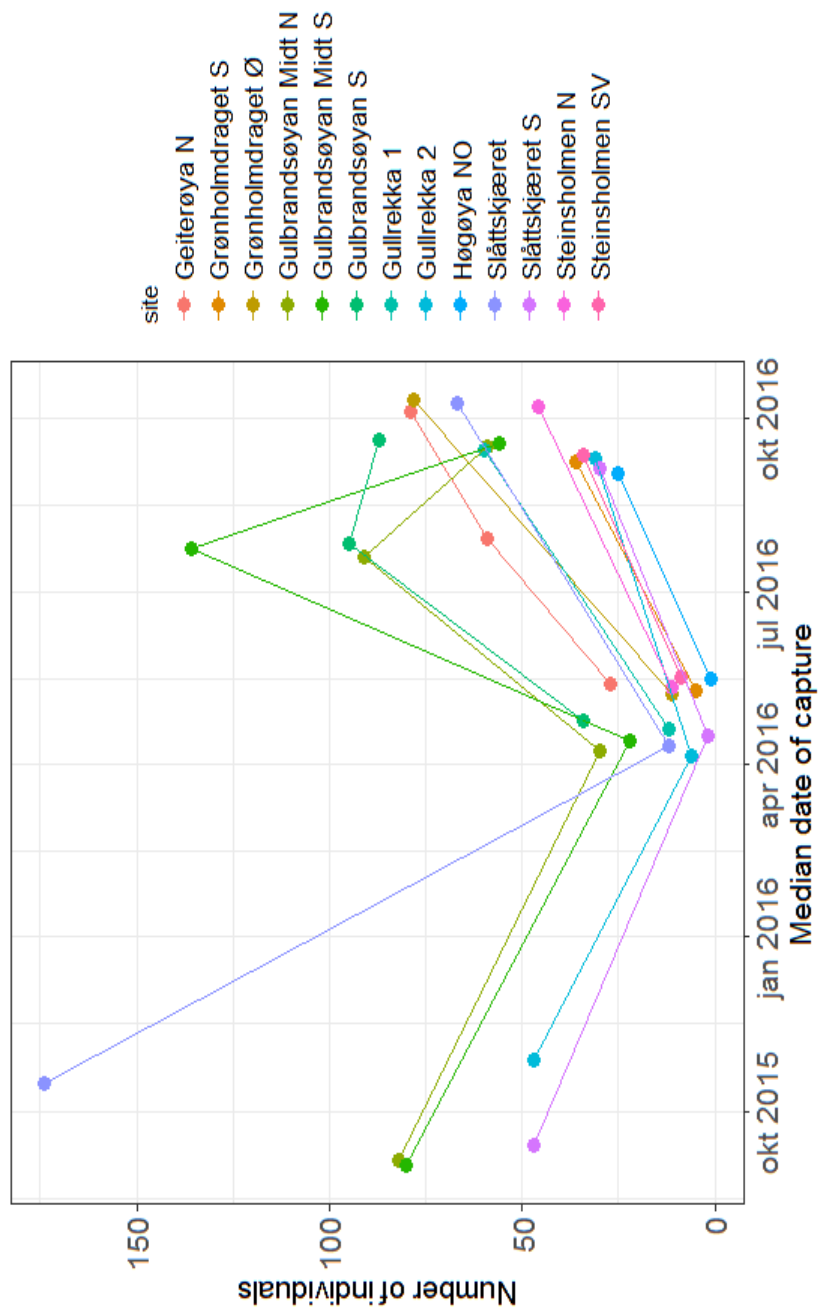
Appendix 2: Area (m²) and water vole population size on all 13 study islands. Island areas are given in square meters. Population sizes in each sampling season is given as total individuals captured on the island at the given season. Seasons without sampling on the given island is marked as “NA”.

Island	Area(m ²)	Population size			
		Autumn 2015	Spring 2016	Summer 2016	Autumn 2016
Geiterøya N	9 692	NA	27	59	79
Grønholmdraget S	2 564	NA	5	NA	36
Grønholmdraget Ø	12 862	NA	11	NA	78
Gulbrandsøyen Midt N	9 226	82	30	91	59
Gulbrandsøyen Midt S	6 568	80	22	136	56
Gulbrandsøyen S	10 980	NA	34	95	87
Gullrekka 1	4 070	NA	12	NA	60
Gullrekka 2	2 053	47	6	NA	31
Høgøya NO	4 333	NA	1	NA	25
Slåttskjæret	12 524	174	12	NA	67
Slåttskjæret S	5 357	47	2	NA	30
Steinsholmen N	9 717	NA	11	NA	46
Steinsholmen SV	4 975	NA	9	NA	34

Appendix 3: Number of traps and trap density on all 13 study islands at each sampling season. Trap density is calculated as number of traps divided by the island area times 100 to get the mean number of traps in a 10 by 10 meters' square. "NA" indicates lack of sampling in the given season at the given island.

Island	Season							
	Autumn 2015		Spring 2016		Summer 2016		Autumn 2016	
	Traps	Trap density	Traps	Trap density	Traps	Trap density	Traps	Trap density
Geiterøya N	NA	NA	130	1,3	130	1,3	170	1,8
Grønholmdraget S	NA	NA	95	3,7	NA	NA	80	3,1
Grønholmdraget Ø	NA	NA	110	0,9	NA	NA	170	1,3
Gulbrandsøyen Midt N	70	0,8	90	1,0	130	1,4	150	1,6
Gulbrandsøyen Midt S	99	1,5	100	1,5	130	2,0	150	2,3
Gulbrandsøyen S	NA	NA	110	1,0	130	1,2	150	1,4
Gullrekka 1	NA	NA	80	2,0	NA	NA	110	2,7
Gullrekka 2	75	3,7	75	3,7	NA	NA	90	4,4
Høgøya NO	NA	NA	103	2,4	NA	NA	100	2,3
Slåttskjæret	110	0,9	110	0,9	NA	NA	170	1,4
Slåttskjæret S	70	1,3	100	1,9	NA	NA	110	2,1
Steinsholmen N	NA	NA	130	1,3	NA	NA	170	1,7
Steinsholmen SV	NA	NA	110	2,2	NA	NA	110	2,2

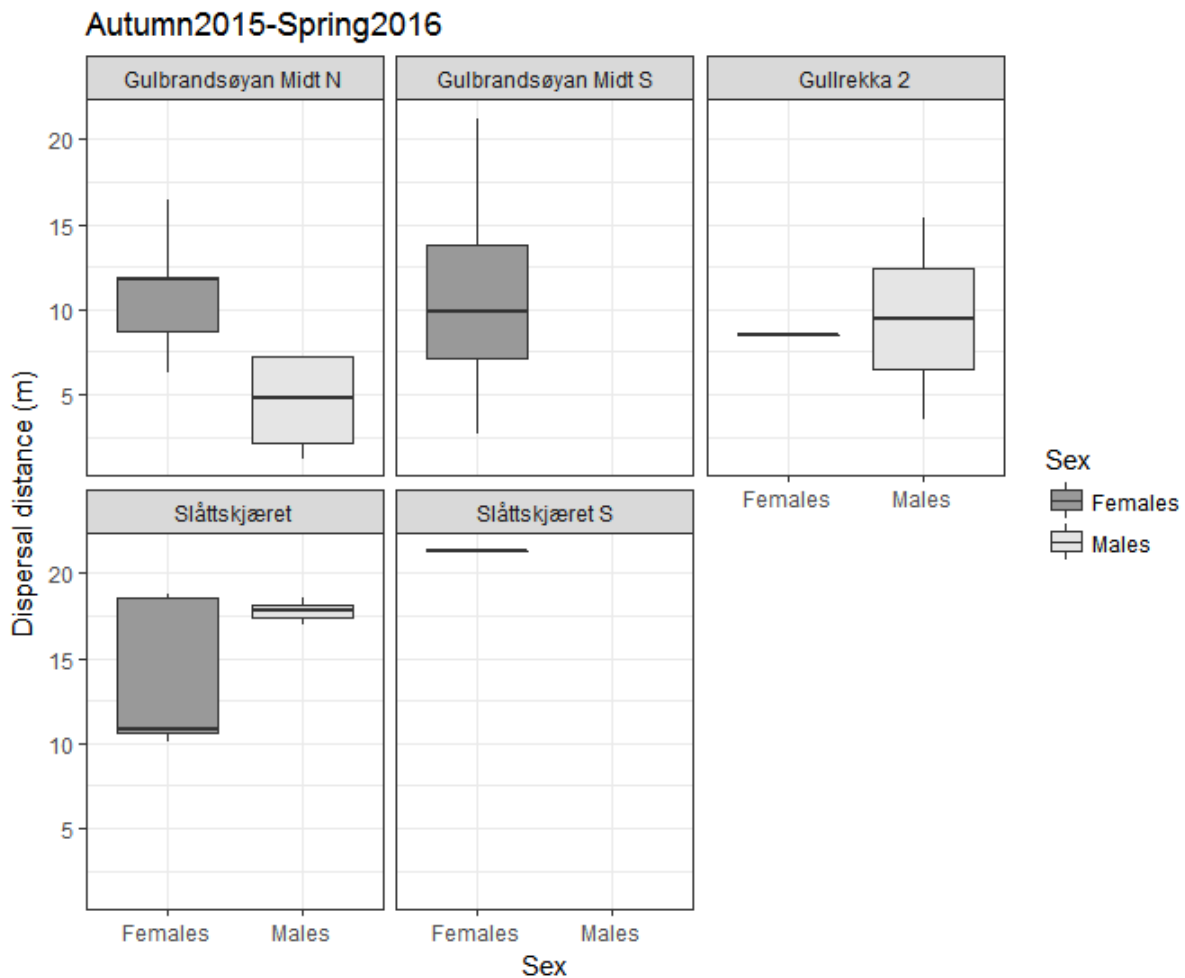
Appendix 4: Number of individuals at each sampling season at each island. All 13 islands are represented with individual colors, all with at least two sampling seasons marked as dots at median date of island sampling.



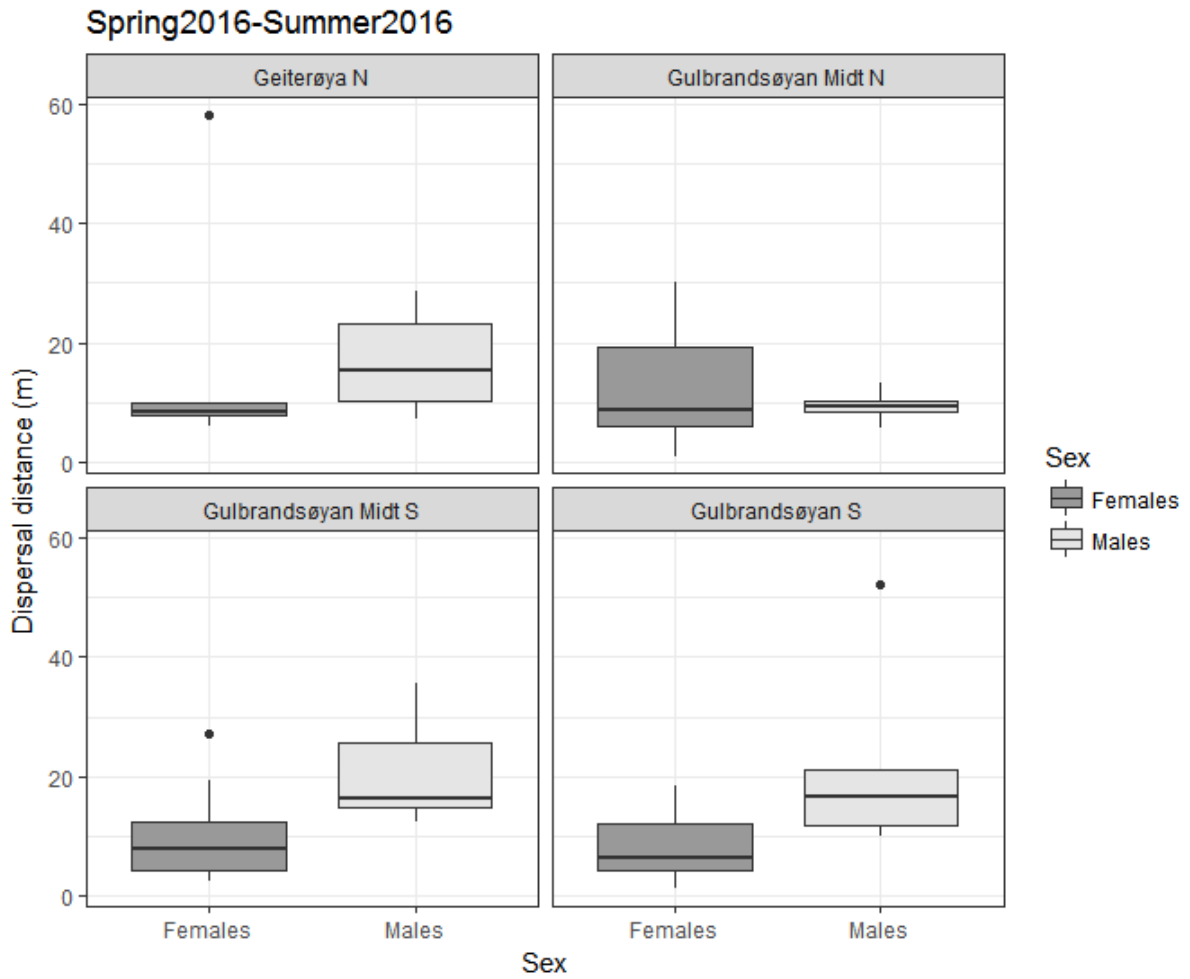
Appendix 5: Ranking of models of within-island dispersal distance based on AICc. “Terms” indicate what fixed effects the given models are based on to describe within-island dispersal distance. “K” is the number of estimated parameters for each model. “Delta AICc” are differences in the AICc values from the highest weighted model. “AICcWt” are measures indicating the level of support (i.e., weight of evidence) in favor of the given models.

Terms	K	Delta AICc	AICcWt
Sex	5	0.00	0.64
Sex + Season	8	1.68	0.28
Sex * Season	11	4.86	0.06
Intercept only	4	6.45	0.03

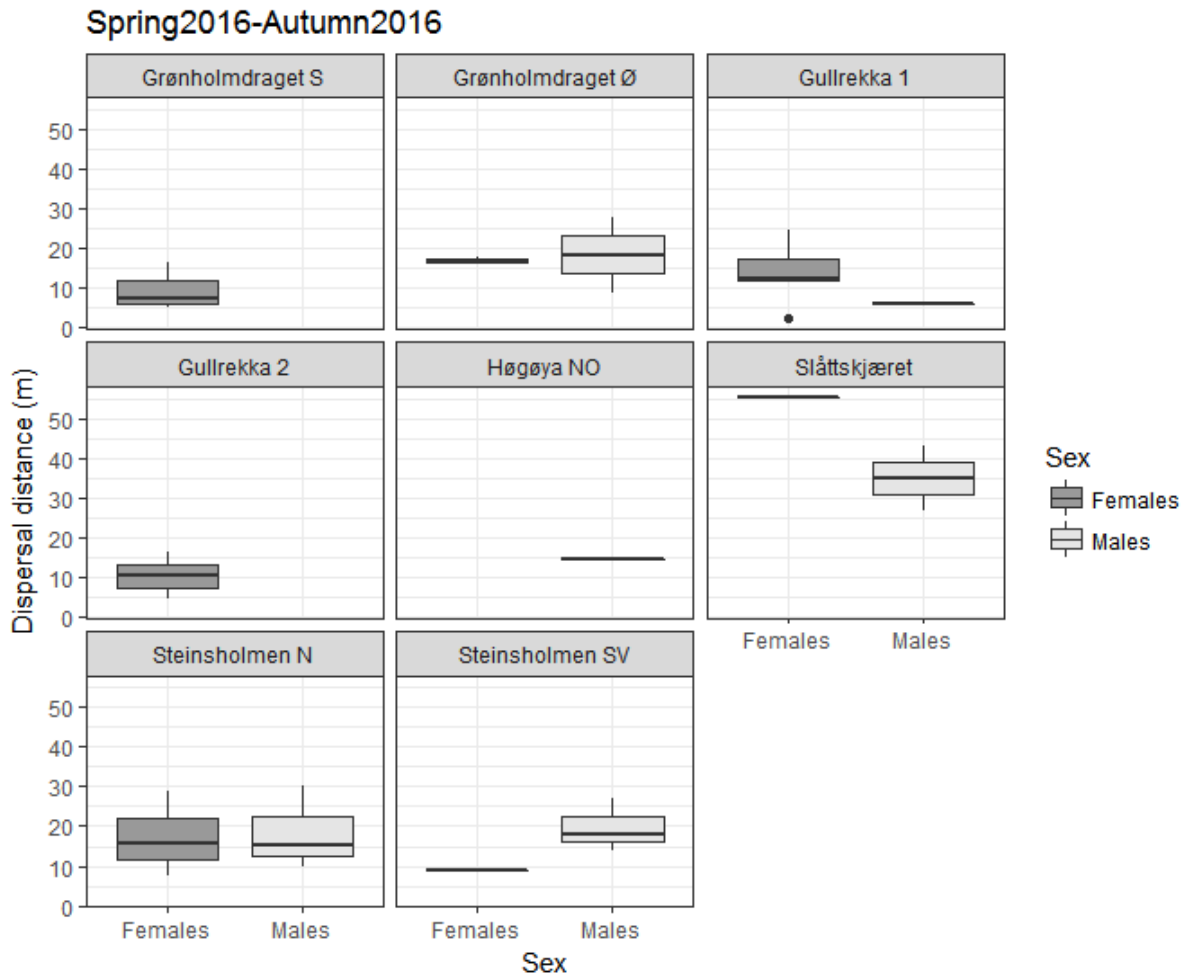
Appendix 6: Within-island dispersal distance in meters, autumn 2015 - spring 2016, separated as sex within island. Females are presented in dark grey color, and males in light grey. Only islands who have at least one observation of within-island dispersal between the current seasons are presented. Lack of within-island dispersal in one sex is presented as blank space in the current space.



Appendix 7: Within-island dispersal distance in meters, spring 2016 - summer 2016, separated as sex within island. Females are presented in dark grey color, and males in light grey. Only islands who have at least one observation of within-island dispersal between the current seasons are presented. Lack of within-island dispersal in one sex is presented as blank space in the current space.



Appendix 8: Within-island dispersal distance in meters, spring 2016 - autumn 2016, separated as sex within island. Females are presented in dark grey color, and males in light grey. Only islands who have at least one observation of within-island dispersal between the current seasons are presented. Lack of within-island dispersal in one sex is presented as blank space in the current space.



Appendix 9: Within-island dispersal distance in meters, summer 2016 - autumn 2016, separated as sex within island. Females are presented in dark grey color, and males in light grey. Only islands who have at least one observation of within-island dispersal between the current seasons are presented. Lack of within-island dispersal in one sex is presented as blank space in the current space.

