Pedigree reconstruction reveals large scale movement patterns and population dynamics of wolverines (Gulo gulo) across Fennoscandia

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Abstract

Dispersal is a biological imperative for many species, facilitating gene flow and influencing population dynamics. Modern landscapes are increasingly fragmented, leaving species that rely on dispersal trapped in ever shrinking areas. Measuring connectivity at the population level is difficult using traditional tracking methods, especially for species that are rare or cryptic, but important for both theoretical and applied questions relating to animal movement.

Using genetic monitoring data collected from 2004 to 2018, SNP (single nucleotide polymorphism) genotyping was used to reconstruct pedigrees of wolverines from the whole of Sweden, Norway, and Finland. The resulting pedigree contained over 900 individuals, and six generations. These family triads were then used to identify patterns of natal dispersal for offspring, and breeding related movement between known mated pairs. The results reveal a metapopulation of several reproductive cores spread over three countries, with animals moving across borders in order to breed and disperse. Patterns of movement on this scale identify sources and sinks across the entire range, with little ambiguity due to sample size or study site. To achieve favourable conservation status, management scales should reflect the scales at which populations function.

Keywords: wolverine, pedigree, dispersal, genomics, connectivity

Contents

1 Introduction

1.1 Animal Movement

Movement is a vital mechanism for many species worldwide, allowing animals to meet their nutritional needs, seek protection from changing seasons, find mates, raise young, and breed. Increasingly, anthropogenic landscape changes have severely diminished the ability of animals to move, reducing their likelihood of survival (Tucker *et al.* 2018). Understanding how animals move across their ranges and between subpopulations is crucial for answering questions about ecology and conservation (Morales *et al.* 2010) as well as ensuring management decisions are well informed and effective in a rapidly changing environment.

Modern wildlife management often limits populations based on administrative boundaries rather than natural barriers. Many species are monitored on a much smaller scale than that of their population processes (Trouwborst 2010). To fully understand population dynamics and movement patterns of a species, it needs to be studied at the scale at which it functions. Large scale, transboundary cooperation is therefore required in order to best manage the population.

1.2 Dispersal

Dispersal is the movement of an organism away from their natal range to establish breeding territory (Matthysen 2012). It is an important driver effecting how populations respond to landscape-scale changes (Cayuela *et al.* 2018), and is a vital mechanism facilitating gene flow, population growth, and contributing to species survival (Lowe & Allendorf 2010). Limited or non-dispersal is referred to as philopatry, and the combination of dispersal and philopatry heavily impact the demography of a population (Weaver *et al.* 1996). There are multiple reasons for this trait to be selected for, including inbreeding avoidance, kin selection, bet hedging, and plasticity (Matthysen 2012). For species that rely on dispersal in their life history, landscape connectivity is an integral part of their ecology and crucial to their long term persistence. Dispersal ensures adequate gene flow in species that live in low densities or isolated patches (Brown & Kodric-Brown 1977).

In mammals, dispersal is often sex-biased, with one sex remaining philopatric, and the opposite sex dispersing, sometimes for extremely long distances (Trakhtenbrot *et al.* 2005). This strategy is thought to have evolved due to either inbreeding avoidance or intra-sexual competition (Pusey 1987). Competition driven dispersal is based on occupancy; if the natal home range is occupied, only then will there be dispersal to the first suitable unoccupied territory (Pusey 1987). Dispersal distance and rate are both reliant on turnover rate of territories (Pusey 1987). Density has been known to affect sex-biased dispersal, with lower densities resulting in lower competition and less tendency for males to disperse (Costello *et al.* 2008).

Dispersal is a crucial aspect of life history for many species, but can be difficult to study through traditional methods (Spong & Creel 2001). Genetic methods are increasingly used to answer important ecological questions about evolutionary processes such as dispersal, plasticity, fitness, selection, and demography (Bérénos *et al.* 2014).

1.3 Pedigree Reconstruction

Molecular techniques are gaining in popularity, providing new insights into evolution, behaviour, ecology, and conservation. Genetic information from a population can reveal barriers to gene flow (Manier & Arnold 2005; Coulon *et al.* 2004), levels of inbreeding (Keller *et al.* 2002; Bulmer 1973), migration patterns (Northrup *et al.* 2014), mating patterns (Sleater-Squires 2016), individual reproductive success (Mainguy *et al.* 2009), and kin relationships (Kitchen *et al.* 2005). Genetic techniques also allow novel ways of monitoring populations and individuals over time (Brøseth *et al.* 2010; Lucchini *et al.* 2002).

Direct observations and traditional tracking methods are often unable to provide sufficient data for meaningful analysis (Spong & Creel 2001). Further, disturbance to the animals and abnormal behaviour due to capture, handling, and tagging can create bias in the data (Ibáñez-Álamo *et al.* 2012). Pedigree reconstruction as a tool for dispersal inference is still fairly uncommon, but has been shown to be more accurate than traditional mark-recapture methods (Telfer *et al.* 2003).

Microsatellites (non-coding, repetitive fragments of DNA) have given way to SNPs (single nucleotide polymorphisms) as the marker of choice for molecular ecologists conducting parentage analysis (Flanagan & Jones 2018). In comparisons between the two, SNPs consistently show equal or better power than microsatellites (Flanagan & Jones 2018). SNPs are the most common marker used in modern sequencing, but are only emerging in regards to parentage analysis (Flanagan & Jones 2018). SNPs provide a more reliable and finer scale of relative differentiation (Huisman 2017). In a comparison between microsatellites (11) and SNPs (80) during kinship analysis in a population of sockeye salmon (*Oncorhynchus nerka*), SNPs provided higher assignment success, especially in analysis of parentage (Hauser *et al.* 2011). High resolution SNP data can improve accuracy of pedigree reconstruction by having a more clear differentiation between types of relatedness. However, SNPs require more markers in order to have the same accuracy as microsatellites (Huisman 2017).

Pedigree studies have their roots in captive and domestic populations, but are not as widely used to study wild populations (Haig & Ballou 2002). However, they provide the opportunity to gain unique and novel insights into individual life-history traits over generations, allowing fine-scale understanding of populations (Pemberton 2008). Determining levels of inbreeding, heterozygosity, and kinship, can help us understand the current health of the population, and also it's potential for future viability (Haig & Ballou 2002; Keller *et al.* 2002). Parentage assignment can be used in management to assess solutions to gene flow barriers, such as wildlife crossings (Sawaya *et al.* 2014), and has also been used to manage genetic diversity and reintroduction of endangered species (McLennan *et al.* 2018). Population dynamics such as sources and sinks have also been detected using parentage assignment (Peery *et al.* 2008).

Pedigree reconstruction has been used to determine relatedness and dispersal patterns in solitary carnivores (Biek *et al.* 2006; Zedrosser *et al.* 2007; Norman & Spong 2015). Modern research on solitary carnivores has revealed more sociality than previously thought (Elbroch

2017), but their structure and behaviour are exceedingly difficult to document with observation alone, and often remain unclear without employing genetic methods. However, new insights can be gained from in depth pedigree analysis for these species. Pedigree analysis has been used to analyze the relationship between dispersal and harvest pressure in black bears (Moore *et al.* 2014), and pedigree reconstruction led to the first evidence of monozygotic twins in polar bears (*Ursus maritimus*) (Malenfant *et al.* 2016).

Reconstructing pedigrees of wild populations provides information on successful reproductions, individual fitness, survival, and dispersal (Kopatz *et al.* 2017). This is especially novel information for species such as the wolverine, that are difficult to observe in the wild, and where sample sizes for tracking studies have been small due to low density and capture effort limitations. Genetic sampling has been used to infer spatial behaviour in wolverines, resulting in very similar home range patterns to traditional telemetry studies (Bischof *et al.* 2016).

1.4 Wolverine
1.4.1 Biology

Wolverines occupy tundra, montane, and boreal habitats across circumpolar regions of North America and Eurasia (Banci 1994). Highly territorial, they occupy large home ranges, which vary in size depending on region, resource abundance, and mate availability (Sandell 1989). Wolverine home ranges are variable (Copeland 1996; Banci & Harestad 1990; Hornocker & Hash 1981), and in Fennoscandia can be anywhere from 25km² to 1,246 km^2, with males averaging 669km², and females averaging 170km² (Persson *et al.* 2010). They are long distance dispersers, with previous genetic studies showing they are capable of dispersing more than 500km (Flagstad *et al.* 2004).

Due to their large home ranges and territoriality, wolverines live in low densities across their range (Aubry *et al.* 2007) which presents an ongoing challenge for monitoring their populations. In Fennoscandia, densities are approximately one per 500km² (Pasitchniak-Arts

& Lariviere 1995). Most populations are small and isolated (Ruggiero *et al.* 2007) and habitat connectivity is required for adequate gene flow between populations.

Wolverines have slow life history traits, with a low average annual reproduction (Persson 2005). Females reach sexual maturity at 15 months old, but very few females under the age of three years old were found to reproduce (Persson *et al.* 2006). Wolverines display high pregnancy rates but low reproduction (Persson 2005); a high percentage of adult females in studies of wild populations have been found to be pregnant, however few of these pregnancies resulted in births (Banci & Harestad 1988). This suggests that the energetic costs of reproduction are high for this species (Persson 2005). Mustelids with delayed implantation, such as wolverines, likely experience higher reproductive costs than other mammals (Harlow 1994). Reabsorbing fetuses is a feature associated with many mustelid species, and is thought to be related to nutritional requirements (Copeland 1996; Mead *et al.* 1993).

When pregnancy does lead to live births, kit mortality rate is conservatively one third (Banci 1994). The average female has an interval of >1 years between births, and 2 or more years is common in some populations (Weaver *et al.* 1996). The result of this is 0.6 to 1 offspring per female per year (Magoun 1985), indicating very low reproductive success of wolverines, but high rates of adult survival at approximately 0.85 annually (Weaver *et al.* 1996). Females are not likely to survive or reproduce past eight years (Hash 1987), resulting in the average female producing only two new females in her lifetime (Weaver *et al.* 1996). These traits mean that wolverines are very sensitive to adult mortality factors such as overharvesting.

1.4.2 Genetic Structure and Variation

Studies on genetic structure of isolated populations in Montana and Idaho showed evidence of significant structuring across the landscape (Kyle & Strobeck 2002; Cegelski *et al.* 2003). However, similar studies done on larger, more connected populations in Alaska and Canada did not detect such evidence of subpopulations (Kyle & Strobeck 2001, 2002). This suggests wolverines are sensitive to habitat fragmentation and human disturbance, and without

adequate connectivity are prone to population segregation. Though wolverines do not appear to treat natural landscape features as dispersal barriers (Kyle & Strobeck 2001), they do, however, appear to be affected by human development and disturbance (Banci 1994; Rowland *et al.* 2003).

In a recent study, Ekblom *et al.* (2018) sequenced the whole genome of 10 Fennoscandian wolverines, finding that their genetic diversity is one of the lowest of any species listed with the IUCN, and significantly lower than many other highly threatened carnivore species. Wolverines, like other large carnivores in Fennoscandia, were nearly extirpated in the nineteenth century, shrinking their range to only the most remote mountains on the border between Norway and Sweden (Walker *et al.* 2001). This caused a population bottleneck, and despite legal protections put in place in the 1970's, too few individuals remained to maintain genetic diversity (Ekblom *et al.* 2018). Genetic variation is therefore considerably lower than the North American wolverine population (Walker *et al.* 2001).

DNA-based research is not limited to studies on genetics. Genotyping is increasingly used as a tool for answering broader ecological questions unrelated to the field of genetics, shedding light on population dynamics, spatial ecology, and fitness (Lamb *et al.* 2019).

1.4.3 Dispersal in Wolverines
1.4.3.1 Natal Dispersal

Wolverines follow a typical solitary carnivore space use and dispersal pattern (Sandell 1989). They have the capacity to disperse across large distances; the longest recorded dispersal event recorded in wolverines is 1,342km by a male animal from Montana to North Dakota (Packila *et al.* 2017). Sex biased dispersal is generally accepted to occur in wolverines, with males being the main dispersers and females being largely philopatric (Banci 1994).

In a Canadian study, male biased dispersal and female philopatry was detected using mtDNA and allozyme analysis (Wilson *et al.* 2000). Dalerum *et al.* (2007) found a high level of dispersal in their study population of wolverines in Alaska, however there was no evidence of sex biased dispersal. This could be due to the study population being part of a larger

metapopulation, making it difficult to detect dispersers within the population (Dalerum *et al.* 2007).

In a Fennoscandian study, there was no significant difference between male and female dispersal, in either likelihood or distance (Vangen *et al.* 2001). Males dispersed 100% of the time while females dispersed 69% of the time, and females were actually found to disperse longer distances (60km) than males (51km) (Vangen *et al.* 2001). This was thought to be due to heavy control measures on wolverines in the Norwegian study area (Troms), and illegal hunting in the Swedish area (Sarek National Park) impacting the spatial dynamics of the study animals (Vangen *et al.* 2001). In wolverine populations with high harvest pressure, female territories are frequently left vacant, resulting in higher home range turnover and promoting lower rates of female dispersal (Vangen *et al.* 2001). If areas of high mortality are located near areas of low mortality, this will also influence movement dynamics (Gervasi *et al.* 2015). This could have implications for transboundary population health of wolverines in Fennoscandia, as lack of dispersing females will result in slower population recovery (Vangen *et al.* 2001). A more recent study of the Swedish population indicated high site fidelity among females (Aronsson & Persson 2018).

Previous studies have often failed to detect sex-biased dispersal due to small study areas (Vangen *et al.* 2001; Dalerum *et al.* 2007). The scale of movement in this species would indicate much larger scales are needed to adequately infer dispersal patterns.

1.4.3.2 Breeding Related Movement

Little is known about wolverine mating systems, or movement unrelated to natal dispersal. Males can mate with multiple females in a year, and these females are usually holding territories within the larger male territory (Hedmark *et al.* 2007). Energetic needs and reproductive success are the key aspects of female home range size in carnivores (Lindstedt *et al.* 1986). For solitary carnivores, the home range size of females is negatively correlated with population density (Sandell 1989). Female territories rely on resource availability, while male territories rely on the number of females in the area (Sandell 1989). In Fennoscandia,

home range size of wolverines tends to be larger than those in North America, resulting in lower densities (Persson *et al.* 2010). There are likely multiple reasons for this, including differences in prey (Lofroth *et al.* 2007; Koskela *et al.* 2013), carnivore community (Van Dijk *et al.* 2008), anthropogenic disturbance (Scrafford *et al.* 2018), habitat quality (Lofroth & Krebs 2007), and human caused mortality (Persson *et al.* 2009).

Aronsson & Persson (2018) have documented some cases of breeding dispersal in wolverines, which is exceedingly rare in large mammals. They hypothesize that the high density of animals in the study area could have led to high competition for space and resources, forcing females to abandon their territories for less saturated areas.

Harvest pressure in Norway has been implicated as a cause of decreased movement of females as territory turnover is higher (Vangen *et al.* 2001; Gervasi *et al.* 2015). The imbalance of adult mortality on either side of the Swedish/Norwegian border could have impacts on population dynamics and movement of wolverines (Gervasi *et al.* 2019).

1.5 Research Aims

Wolverines have been well studied in specific areas of their range (Landa & Skogland 1995; Walker *et al.* 2001; Vangen *et al.* 2001; Sæther *et al.* 2005; Hedmark *et al.* 2007; Persson *et al.* 2010), but the species has not been studied at the population level, and much remains unknown about landscape-scale patterns across their range. Transboundary population level studies are increasingly important for understanding ecological questions and implementing successful large scale management issues. Understanding the mechanisms of movement in a highly vagile species as it relates to political borders is important for successful management. This study aims to use DNA to reconstruct a pedigree for the entire Fennoscandian population, and to use this to determine dispersal patterns and population dynamics across the whole population.

Many wolverine studies have had small sample sizes due to their life history traits, cryptic nature, and general rarity across their range (Wilson *et al.* 2000; Vangen et al 2001; Sæther

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et al. 2005). Mark-recapture and telemetry based tracking of wolverines has proven exceedingly difficult, and generally has resulted in small sample sizes (Copeland 1996; Wilson *et al.* 2000). For rare and cryptic species, genetic methods offer the best option for both routine monitoring and novel research (Norman & Spong 2015; Lamb *et al.* 2019). Pedigree reconstruction has previously been used successfully to determine dispersal distances (Hudy *et al.* 2010; Cope *et al.* 2015; Norman & Spong 2015). For species that live at low densities and are capable of ranging long distances, a larger scale of sampling will produce more accurate results, ensuring the majority of dispersal events have been captured in the data. By using a large sample size and large geographical area, patterns of dispersal are likely to indicate important spatial dynamics on a scale not previously studied, including sources, sinks, and connectivity in relation to political boundaries.

Using genetic data collected over fourteen years, this research aims to investigate the use of pedigrees to further understand dispersal patterns and population dynamics of the Fennoscandian wolverine population. For wide ranging and cryptic species that are notoriously difficult to study using traditional methods, molecular techniques allow us to gather more information with far less time, cost, effort and disturbance to the animals.

2 Methods

2.1 Sampling and Location

Fennoscandia is made up of Norway, Sweden, and Finland, and is bordered to the east by Russia. The area is mostly boreal forest, alpine, and tundra biomes, and today contains the entirety of the European wolverine population (Linnell 2014).

A total of 1711 individuals (789 males and 922 females) were sampled between 2004 and 2018 through government monitoring of the species in Norway, Sweden, and Finland. By using long term data collected from Fennoscandia, we are able to get the most complete picture of the entire remaining wolverine population in Europe. This has resulted in the largest sample size of wolverines recorded in the literature: n = 632 (Landa & Skogland 1995) n = 671 (Kyle & Strobeck 2002) n = 901 (Aubry *et al.* 2007).

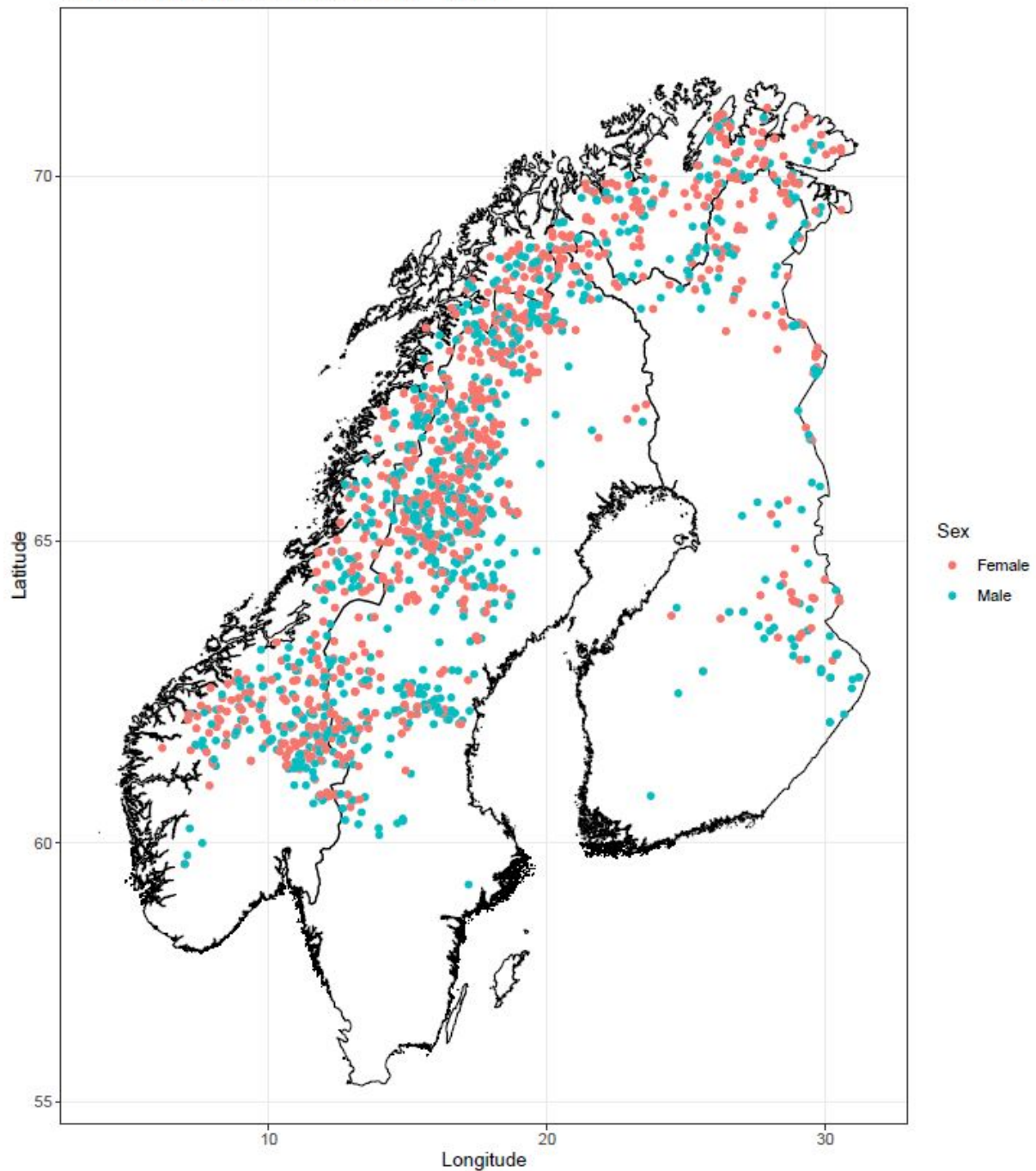*Figure 1*: Locations of male and female samples across Fennoscandia from
2004-2018 produced with R package ggmap (Kahle & Wickham 2013).

2.1.1 Norway

In Norway, carnivores are monitored by the Norwegian Environment Agency (Miljø-

Direktoratet), and the Norwegian Institute for Nature Research (NINA). Norway maintains

strict controls over population numbers of its carnivores, and the target for wolverines is 39

reproductions per year (Norwegian Environment Agency 2017). Individuals are culled to manage both population numbers as well as reduce livestock depredations, and as such both scat and carcasses were available for DNA analysis. A total of 708 individuals were sampled in Norway, 396 females and 312 males, between 2004 and 2018.

2.1.2 Sweden

Carnivores in Sweden are closely monitored by the Swedish Environmental Protection Agency (Naturvårdsverket) through the Swedish County Administration Boards (Länsstyrelsen) by recording tracks, scats, scent markings, sightings, and livestock depredations. All animals killed under special licenses, or animals found dead, are sent to Länsstyrelsen for examination and sampling. This extensive monitoring effort provides a detailed, longterm dataset with information on a large proportion of the Swedish wolverine population.

Samples from 821 individuals were collected between 2004 and 2018, consisting of 388 males and 433 females. Samples were collected by the County Administrative Boards in the counties of Västerbotten, Norrbotten, Västernorrland, Jämtland, Värmland, Södermanland, Gävleborg, and Dalarna counties. DNA was extracted from scat and tissue samples.

2.1.3 Finland

The Finnish Ministry of the Environment is responsible for carnivore monitoring in Finland. Natural Resources Institute Finland (Luonnonverkeskus) conducts research and the Finnish Forest and Park Service (Metsähallitus) conducts routine population monitoring. A total of 182 individuals were sampled in Finland, 89 males and 93 females, between 2004 and 2018.

2.2 Laboratory Methods
2.2.1 DNA Extraction and SNP Genotyping

DNA was extracted from tissue samples using DNeasy Blood and Tissue Kit (Qiagen Inc., Hilden, Germany) and from lower quality scat and scent marking samples using Maxwell 16 MDx Instrument (Promega, Madison).

PCR (polymerase chain reaction) was performed on the Finnish, Norwegian, and some Swedish samples at NINA (Norwegian Institute of Nature) while most of the Swedish samples were analyzed at SLU Umeå (Swedish University of Agricultural Sciences). For quality control and to determine error rates, 104 samples were analyzed in duplicate in both laboratories.

Specific Target Amplification primer (STA) and Locus Specific Primer (LSP) were used as pre-amplification for the SNP (single nucleotide polymorphism) regions (Norman & Spong 2015). Genotyping was done using 96 SNPs in a 96 sample x 96 marker chip (Fluidigm, San Francisco, CA). This set of markers has previously been found to reliably identify animals to the individual level (Kleven *et al.* 2019).

2.3 Analysis
2.3.1 Population Assignment

Spatial Analysis of Principal Components (sPCA), multidimensional scaling analysis (IBS Distance), and T-Distributed Stochastic Neighbour Embedding (t-SNE) were done in R using packages adegenet (Jombart 2008) and SNPRelate (Zheng *et al.* 2012).

2.3.2 Pedigree Reconstruction

Parentage assignment was done using FRANz (Riester *et al.* 2009). Total population (Nmax 3000) was estimated using the last three years of sampling and the most recent census data indicating a total Fennoscandian population of 1230 animals (Linnell 2014; Gervasi *et al.* 2015; Natural Resources Institute Finland 2016). This indicated that approximately 58% of the total wolverine population had been sampled. Maximum number of possible males (Nmmax 1370) and females (Nfmax 1630) were set using the sex ratio of the sample and applied to the maximum population size. Only triads were used in pedigree construction, as dyads do not adequately identify the direction of generations. Pedigree visualization was done using R package kinship2 (Sinnwell *et al.* 2014).

2.3.3 Relatedness Estimation

Identity by Descent (IBD) was calculated using Maximum Likelihood Estimation (MLE) in the R package SNPRelate (Zheng *et al.* 2012).

2.3.4 Dispersal and Movement

Dispersal and mating distances were estimated using the parent-offspring triads acquired from the pedigree analysis. Dyads were not used in dispersal analysis since the direction of the relationship cannot be determined without both parents. While dispersal distance can be gleaned from dyads, population dynamics would not be evident without directionality.

Distances between parents with confirmed offspring, and between each mother and each offspring were measured using the pointDistance function in the R package raster (Hijmans *et al.* 2015). 15 offspring had been recorded at the same location as their mother during sampling, indicating they were too young to have dispersed, and were removed from further analysis.

Mean distances between male and female offspring were compared using an independent two group t-test in R and visualized in a density plot using the package ggplot2 (Kahle & Wickham 2013).

3 Results
3.1 SNP Genotyping

Of 1711 individual samples genotyped, 1704 were used in the analysis. Despite the data being previously filtered for duplicates, IBD revealed 7 comparisons where r = >0.9, containing <8 mismatches. These were treated as likely to be the same individuals.

The error rate among duplicates (n = 104) was found to be <0.014. Minor Allele Frequency (MAF) was calculated as 0.4146 using harmonious mean. The lowest recorded MAF was 0.2376.
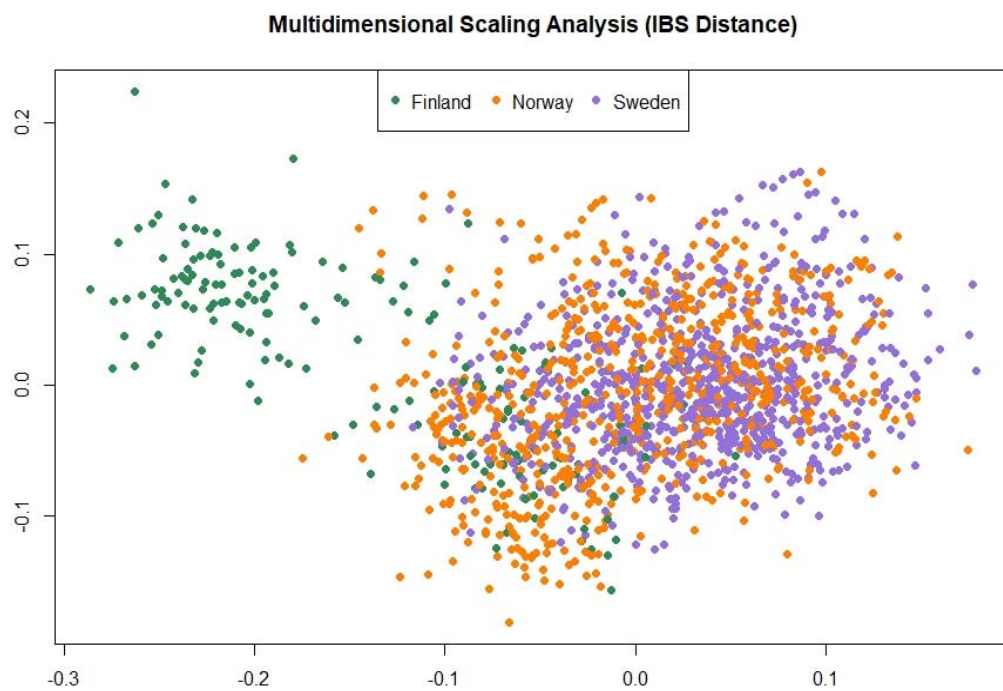
3.2 Population Assignment

Figure 2: Multidimensional scaling analysis
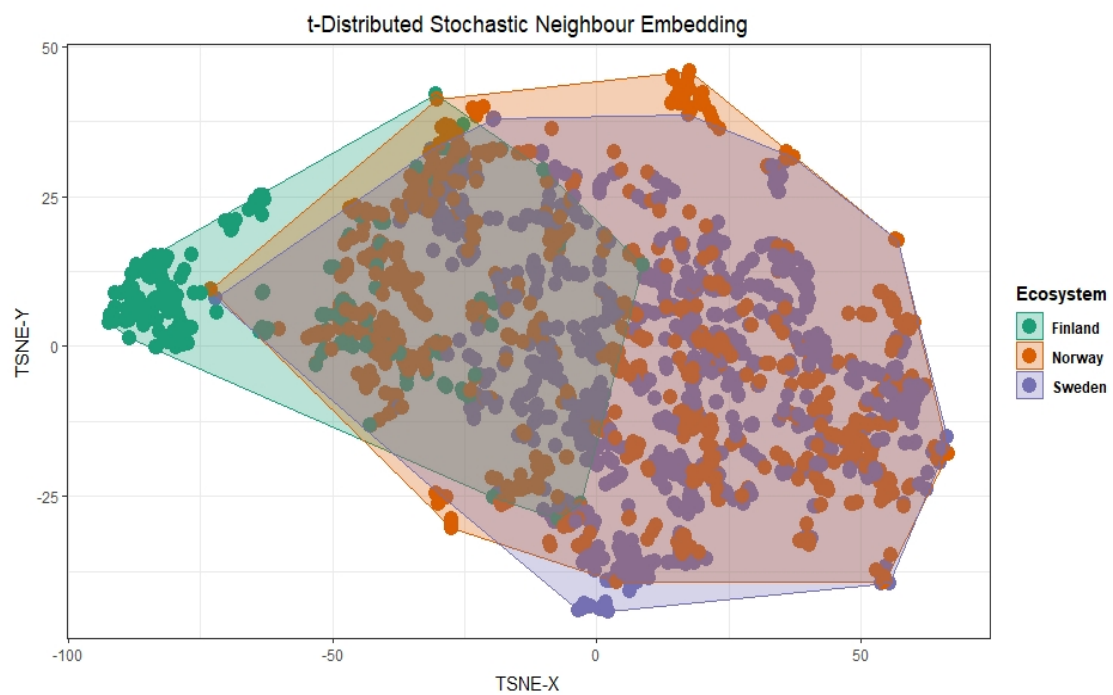
Figure 3: T-Distributed Stochastic Neighbour Embedding

Identity by state (IBS) and t-distributed stochastic neighbour embedding (tSNE) analysis

indicates that the Norwegian and Swedish animals have a lot of genetic overlap, while most

of the Finnish animals are separate. The few Finnish data points mixed in with the Norwegian

population are part of the northern Finnish population, while the cluster that is entirely

separate is the Karelian population. Few animals appear to move from Karelia to northern

Finland, and much of these dynamics could be occurring in Russia.
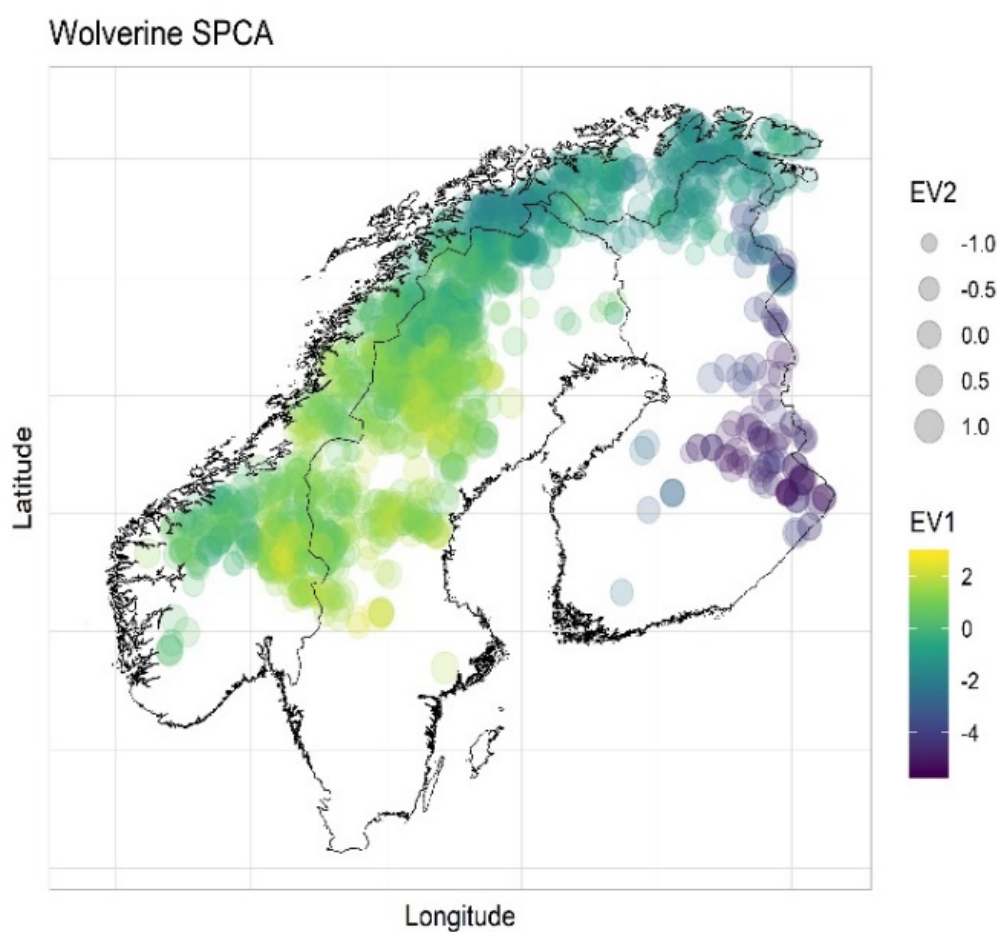
Figure 4: Spatial analysis of principal components

The sPCA shows a clear arc of historical gene flow from southern Norway and Sweden

across the arctic, and down into Finland. The Karelian population in southern Finland (seen

in purple) does not have significant connection to Fennoscandia (seen in green), however

there is some indication of Karelian animals moving north into the high arctic along the

Russian border (Figure 4). Rather than spatial structuring by country, we see the bulk of the

population in boreal Norway and Sweden (seen in yellow and green) appears to be well connected. The southern population in Norway, often thought to be separate from the main population, appears here to be well connected to the rest of Norway and Sweden. It also looks to have genetic influence from the far north. The high arctic region (seen in blue) contains animals from all three countries, and looks to maintain some distinction from both Karelia and Boreal Norway/Sweden.

3.3 Pedigree Reconstruction

Due to the error rate of the samples (<0.014), parentage inferences were discarded from analysis if mismatches were >3 and posterior probability was <0.95. This resulted in 557 triads and 513 dyads. Mean posterior probability for dyads and triads was 0.997. There was a mean number of 1.9 links per individual, while 374 individuals had no significant parentage linkages. The reconstructed pedigree contained only parent-offspring triads, as the dyads provide ambiguous information on direction of the relationship. The mean posterior probability of triads was 0.998. Pedigree plotting of known triads contained 943 unique individuals and revealed at least six generations within our sample (figure 5).

Pedigree for Wolverine in Norway, Sweden, and Finland 2004 - 2018
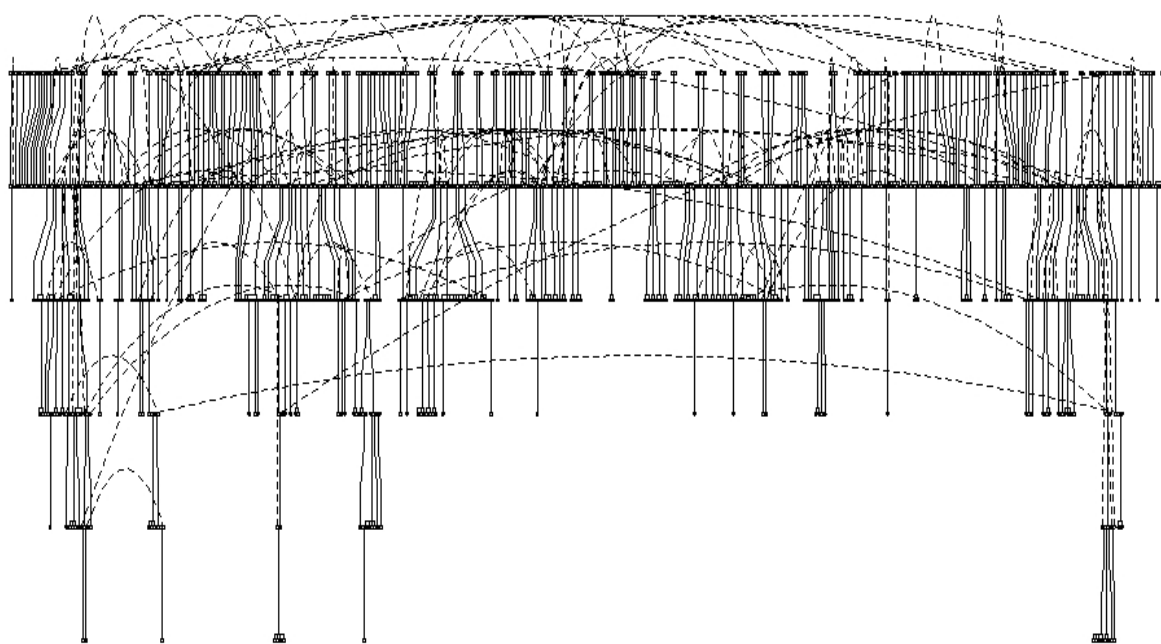
Figure 5: Pedigree plot for all triads in the wolverine population
between 2004 and 2018. Dotted lines indicate the same individual.

3.4 Relatedness Estimation

In a total of 1,454,365 pairwise comparisons, <1% (3,142) of comparisons were indicative of first order kin, with 1,833 of those with *r* values >0.5 indicating inbreeding. Approximately 3% (41,935) of comparisons were indicative of second order kin. 55% (799,620) fell between unrelated and second order kin. Approximately 40% (592,051) of pairwise comparisons were unrelated.
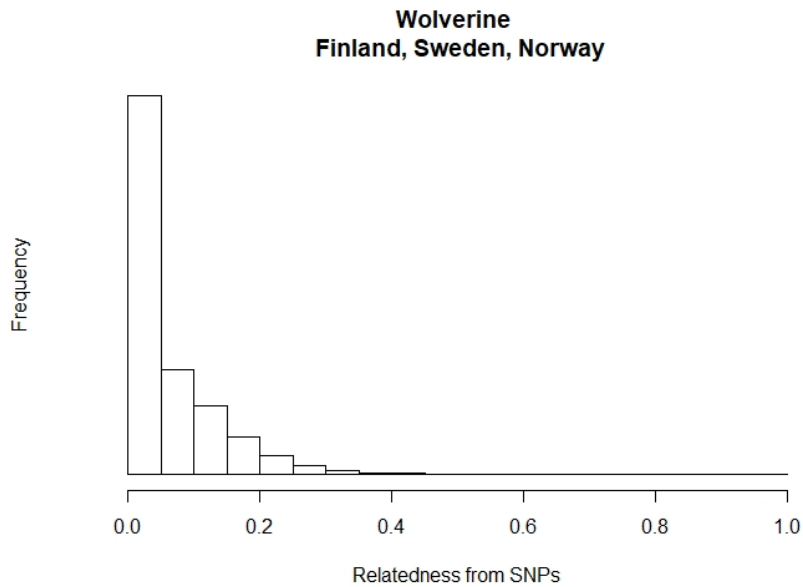
Figure 6: Frequency of coefficient of relatedness (*r*).

3.5 Breeding-Related Movement

Our data contained 557 matings (pairs of individuals that has produced confirmed offspring) apparent from the triads used in the pedigree. The distances between these mated male and female pairs was measured from 0 km to 631.3 km with a mean distance of 42.9 km between parents. In pairs with a distance of 0 km, it is likely the samples were collected at a den site, resulting in the exact same coordinate being recorded. Since details on individuals were not available for the majority of the samples, it is possible some animals were sampled as juveniles, prior to their dispersal movements (at approximately two years of age), accounting for such long distances.
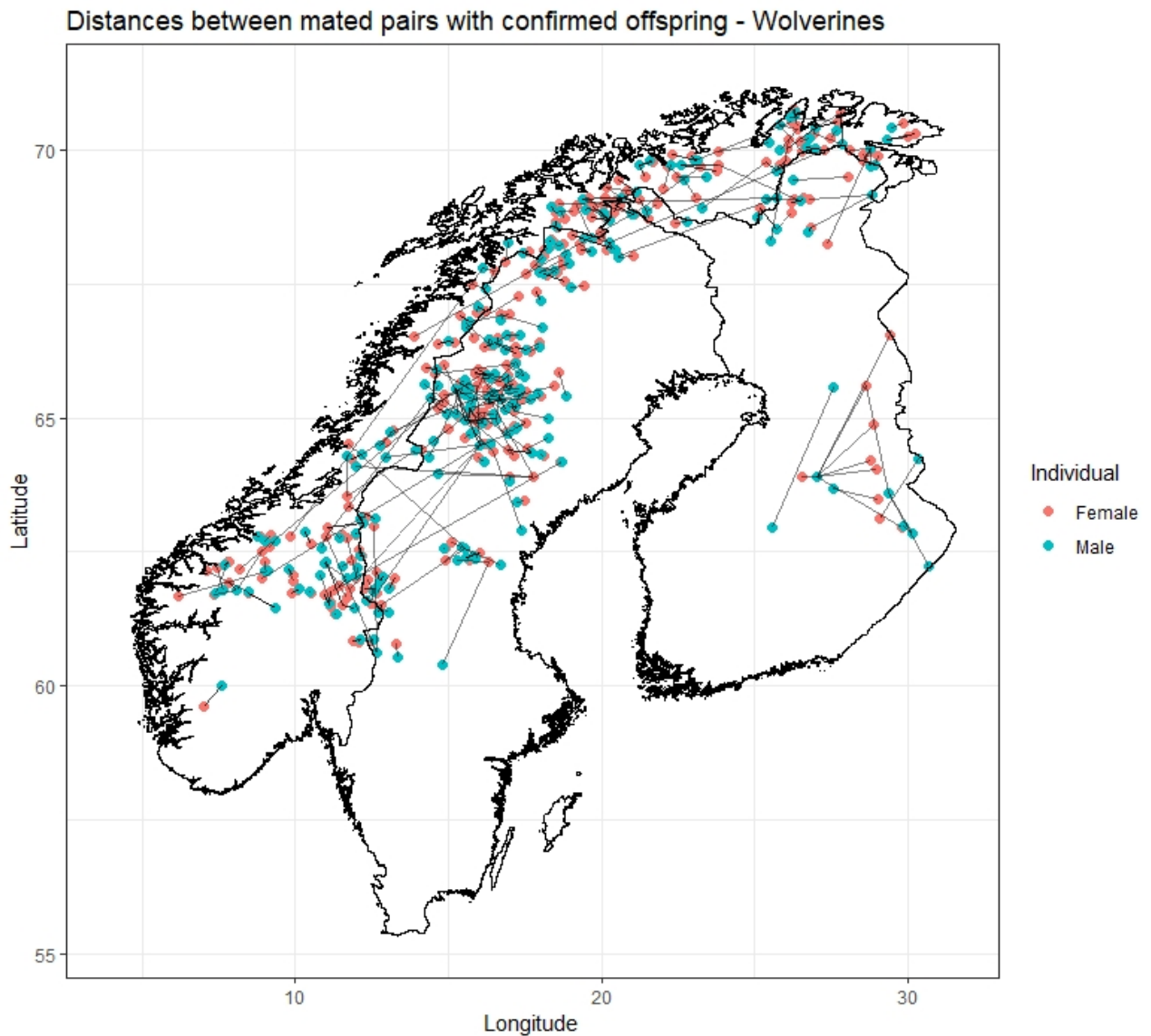
Figure 7: Distances between known mated pairs with confirmed offspring.

Of the 557 recorded matings, 101 involved transboundary movement. The majority of these movements (47.5%) were males from Sweden traveling to Norwegian females. A large portion (31.6%) were males from Norway traveling to Swedish females. Between Norway and Finland, 15.8% were males moving from Finland to Norway, with the remaining 5% consisting of males moving from Norway to Finland. There were no recorded matings between animals in Sweden and Finland.

3.6 Natal Dispersal

In total, 542 dispersal events were captured during the study period. Fifteen mother-offspring pairs were discarded in analysis as they were located at exactly the same coordinates, indicating sampling at the den location, and the offspring would then be too young to have dispersed. There was significant difference in dispersal distance between males and females (p = 0.001, 95% CI -36.77, -9.4). Mean dispersal distance was 55.6 km for females and 78.7km for males. Males ranged from 0.1 km to 548 km. Females ranged from 0.6 km to 456 km. It is possible some of the individuals with very low dispersal measurements were in fact animals that were still dependent on their mothers, however it can't be ruled out that these animals didn't take over a dead parent's territory rather than disperse further.
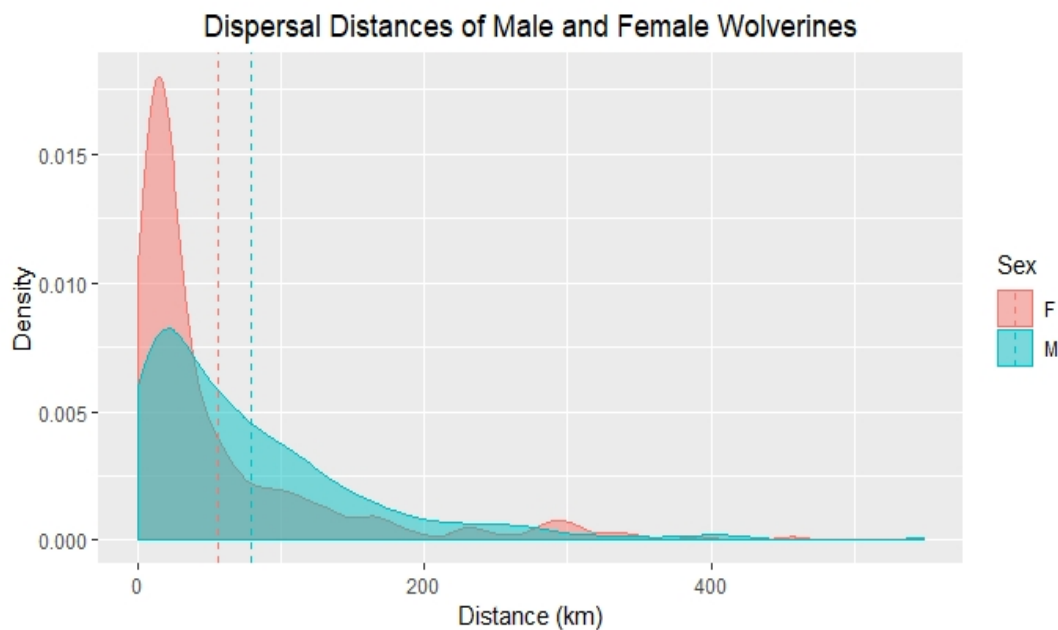
Figure 8: Difference in dispersal distances between male and females wolverines (p = 0.001).

There were 104 animals determined to have dispersed across political borders. Of these, 52 animals dispersed from Sweden to Norway, and 31 animals dispersed from Norway to Sweden. Less dispersal was seen between Norway and Finland: eight animals dispersed

from Finland to Norway and 13 animals dispersed from Norway to Finland. There were no

dispersals between Sweden and Finland captured in these data.
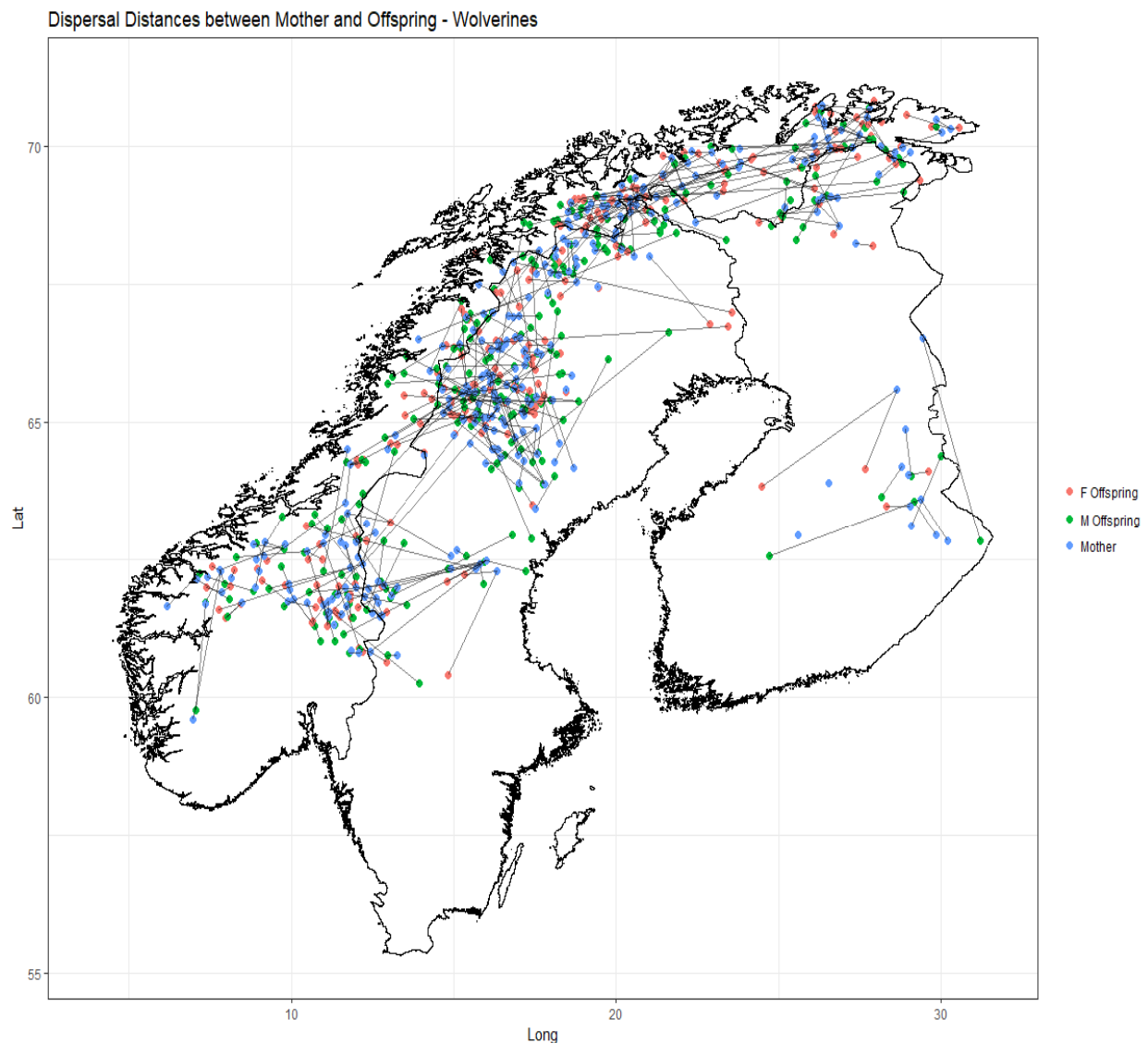
Figure 9: Dispersal distances between mothers and their offspring across Fennoscandia.

4 Discussion

4.1 Results Summary

There is evidence of gene flow throughout Fennoscandia, mostly between Sweden and

Norway, but some between Finland and Norway. First order kin did not move at all between

Sweden and Finland. Pedigree reconstruction revealed 557 triad assignments and over 500 dyad assignments. Pairwise kinship analysis resulted in approximately 3000 first order kin pairs, and approximately 40,000 second order kin pairs. Males traveled as far as 631 km to mate with a female, with a mean distance of 42.9 km between mated pairs. Nearly half (47%) of transboundary matings occurred when males moved from Sweden to Norway and 31% occurred when males moved from Norway to Sweden. Few (16%) international matings were males moving from Finland to Norway, with only 5% being males moving from Norway to Finland. There were no transboundary matings between animals from Sweden and Finland. Males dispersed significantly further than females, with the longest recorded dispersal at 548km. Transboundary dispersal showed lots of exchange between Norway and Sweden, with 50% of transboundary dispersals moving from Sweden to Norway, and 30% moving from Norway to Sweden. 13% of dispersals went from Norway to Finland, and 8% from Finland to Norway. We recorded no dispersals between Sweden and Finland. There was no movement between the Finnish Karelian population and the northern Finnish population recorded in our data.

4.2 Pedigree Reconstruction

Using the triads identified by FRANz analysis, a pedigree of 943 unique individuals was able to be reconstructed, revealing six generations in this transboundary population. This information gives a much more complete picture of many aspects of life history than traditional tracking methods. The depth of information gained from long-term genetic data is simply not possible to get from traditional observational data for most species.

Some of the pedigrees reconstructed from this sample were incredibly complete, and showed up to 6 generations (Figure 11). With this information, we can identify individuals that are especially reproductive, such as Ind2297 in Norway (Figure 10). This male fathered at least 24 kits with 7 different females. Of these, 18 were females, which are a significant contribution to the population. We can also identify individuals where inbreeding has occurred, such as Ind5133 (Figure 12), whose father is also her grandfather (r value between

Ind5133 and Ind1460 = 0.8). This information is valuable in learning about individual fitness as well as movement, and can be combined with other ecological data to answer further questions regarding land-use, movement barriers, and habitat patterns (Lamb *et al.* 2019).
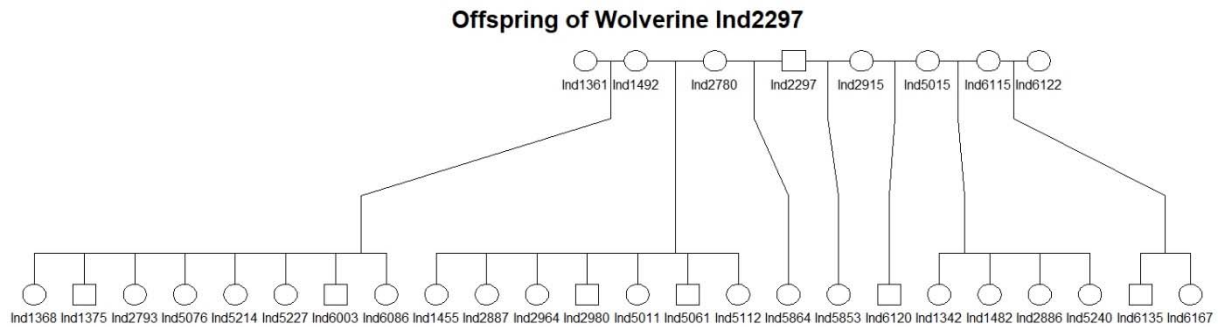
Offspring of Wolverine Ind2297

Figure 10: Isolated pedigree for Ind2297 and known offspring and mates illustrates ability to identify highly successful reproductive individuals

Pedigree for Wolverine Ind5854
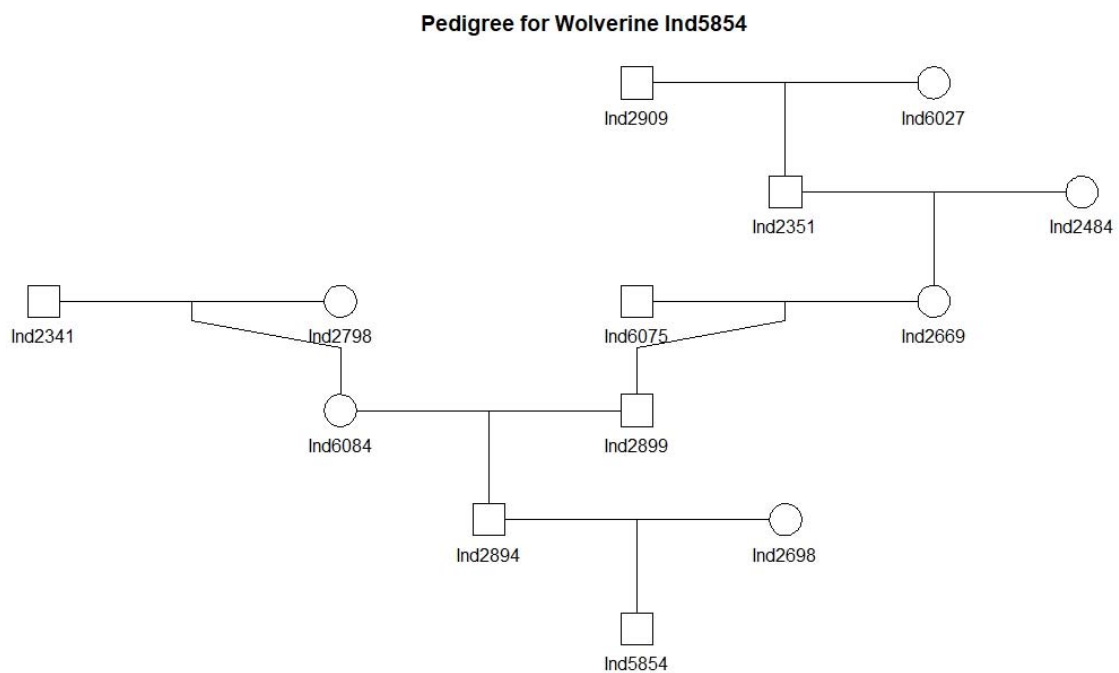
Figure 11: Isolated pedigree for Ind5854 illustrates ability to capture several generations for one individual

28
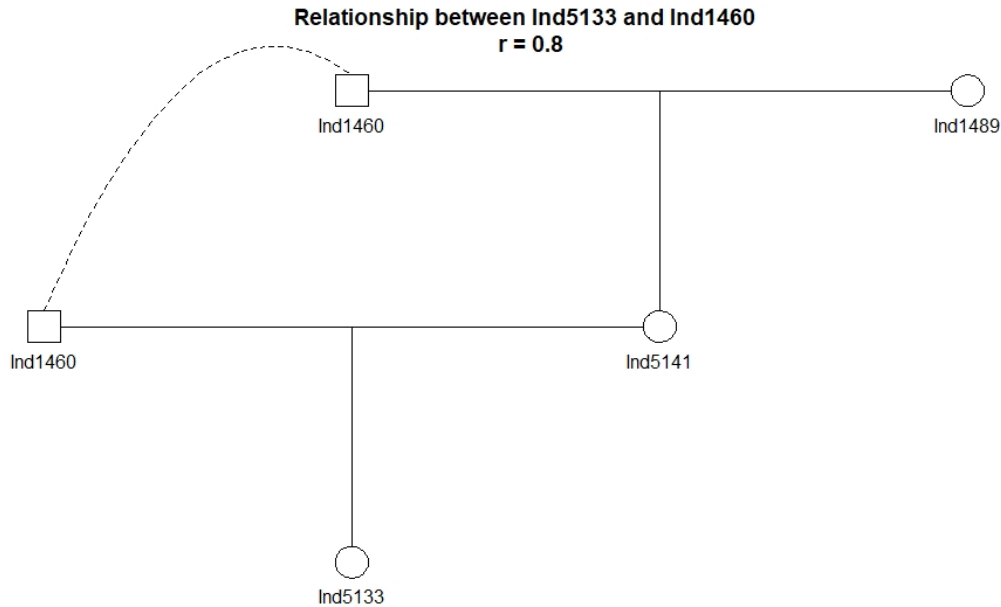
Figure 12: Isolated pedigree for Ind5133 is a visualization of inbreeding.
The father of Ind5133 is also her grandfather resulting in *r* = 0.8 between Ind1460 and Ind5133.

4.3 Breeding-Related Movement

The distances measured between mated pairs in this sample are indicative of a single sample taken at one point in an animal's lifetime, and as this is a highly vagile species, with the potential for very large territories, their locations when sampled are not absolute. Figure 7 could be illustrating multiple things at once. It could be capturing individuals before they had dispersed from their natal ranges. It could be capturing males that are nomadic, although this is not thought to occur in wolverines as they are considered extremely territorial (Persson *et al.* 2010). Overall, figure 7 clearly illustrates that males often end up mating with females a significant distance from where they were born, or even where they hold territory.

Very little research has been done on breeding-related movement in wolverines (Hedmark *et al.* 2007). Since male territories can be up to 1,246 km^2 (Persson *et al.* 2010), it would be normal for a male to travel the length of his territory to access neighbouring females. The longest breeding-related movement in our analysis was recorded at 631.3km with a mean distance of 42.9km. This suggests most males are likely mating with females in neighbouring

territories, but that some may be traveling longer distances in order to find females. Since female wolverines are unlikely to reproduce before age 3 (Persson *et al.* 2006), this could indicate low availability of females compared to males in some areas. In wolverines, male home range size and space use is dependent on female density in the area (Persson *et al.* 2010). In Fennoscandia, where home ranges are some of the largest recorded in the species (Persson *et al.* 2010), this could indicate lower densities than found in North America, leading to more breeding-related movement in order to locate suitable mates.

On the other hand, if breeding-related movement is carried out by the female, it could be due to high rather than low densities (Aronsson & Persson 2018). Female densities tend to be based on resource availability, so higher competition for resources in a certain area could lead females to abandon their territories and seek out less competitive areas (Aronsson & Persson 2018).

In solitary carnivores, spatial distribution of males and females can change throughout the year, with males moving towards females during the mating season (Sandell 1989). In brown bears, male territories on the edges of the population were larger than in core areas (Krofel *et al.* 2010). This is likely due to lower competition with conspecifics (Dahle & Swenson 2003). There tend to be more males on the periphery of populations in species with male-biased dispersal (Kojola *et al.* 2003). Male bears have been observed to move from the outer edge of the population into the source areas in order to have access to females (Krofel *et al.* 2010).

Figure 7 shows the connectivity of the landscape in terms of viability for reproduction. Wolverines, like many carnivores, rely on large uninterrupted spaces to allow them to meet their nutritional needs, hold territory, and find mates. In the absence of this, corridors enable them to move from one space to another in order to enable these important processes. While dispersal is an important mechanism for inbreeding avoidance and population expansion, long distance dispersal can also lead to reduced reproductive success as males on the expansion front have less access to females (Krofel *et al.* 2010).

4.4 Natal Dispersal

Vangen *et al.* (2001) found no significant difference in dispersal distances between males and females, and in that study females actually dispersed further than males (60km and 51km, respectively). However, they used a sample size of 24 individuals from two sites in what are identified in our results as the core reproductive areas in northern Sweden and Norway. The results from Vangen *et al.* (2001) may be representative of the trends in these areas, but the same overall pattern is not indicated in our results from the rest of the population.

The results of both the natal dispersal movements and breeding-related movements show population-wide patterns of genetic exchange. The only entirely isolated population is the Karelian population in Finland, which had no connections with northern Finland or Sweden in either natal dispersal or breeding related movement. While the northern Finnish wolverines have some exchange with Norway, there was no record of any animals moving between Sweden and Finland in our data, despite a dense cluster of reproduction where the three countries meet (Figures 7 & 9). We had some samples along the border between central Finland and Russia, but this areas is clearly not facilitating connectivity. The future of the Karelian population must rely on the influx of Russian animals, and efforts to maintain connectivity across that border will likely be important to their continued viability.

Harvest pressure has been strongly linked to dispersal behaviour (Moore *et al.* 2014). In wolverine populations with high harvest pressure such as in Norway, female territories are frequently left vacant, and females disperse less as nearby territories become available more frequently (Vangen *et al.* 2001). Female wolverines generally show high site fidelity, but factors may lead them to disperse later in life, a rare behaviour in large mammals (Aronsson & Persson 2018).

The evolutionary drivers of dispersal can prove risky in a modern world where anthropogenic factors are quickly transforming the landscape (Kokko & López-Sepulcre 2006). For wolverines, dispersal is an important aspect of their life history, preventing inbreeding and

high densities, which negatively impact their survival (Brøseth *et al.* 2010), and could be an important factor in allowing them to adapt to a warming climate (Kokko & López-Sepulcre 2006). Although this trait has led to recolonization of areas where they had previously been extirpated, it also puts them at risk as they move into areas where conflict with humans makes them unwelcome. Colonization of new areas, and recolonization of previously occupied areas, relies on dispersal, but mortality rates for dispersers can be up to 50% (Krott 1982), making the process of population expansion a slow one (Ebenhard 1991).

Over half of adult wolverine mortality in Fennoscandia is caused by humans, with 60% of deaths attributed to poaching, and 10% due to culling (Persson *et al.* 2009). Cryptic poaching has a significant impact, with 37% of human caused mortalities assumed to be due to undocumented poaching (Persson *et al.* 2009). Anthropogenic mortality is clearly a significant driver of wolverine population dynamics in Fennoscandia, with implications for transboundary population health (Gervasi *et al.* 2015). Most poaching occurs during the dispersal phase (Persson *et al.* 2009), further increasing the likelihood of mortality at this already risky stage of life (Blankenship *et al.* 2006). It is important to target dispersal areas for conservation planning, as these are the areas most likely to experience cryptic poaching, and are also vital to the connectivity of wolverines.

4.5 Metapopulation Dynamics

Previous studies indicate the population in southern Norway was genetically isolated (Walker *et al.* 2001), and describe the species range as occurring primarily in the north of Fennoscandia (Landa *et al.* 2000). The sampling locations in this study, however, show their range as having expanded significantly to the south (Figure 1). Flagstad *et al.* (2004) found evidence that the southern Norwegian population was founded by animals from the north, and still continues to receive immigrants from the north. This is in line with our results (Figure 4), which indicate that the southern population is an admixture of animals from the north of Norway (blue shading) and Sweden (yellow shading). The results of natal dispersal analysis (figure 9) show no long distance dispersers from the north to the southern area, and very few

dispersers coming from the northern population clusters at all. There was evidence of more breeding-related movement from other areas, however, including one of the longest movements recorded in our results from northern Norway to southern Norway (Figure 7).

While the map of sample locations (Figure 1) show an apparent continuous population, analysis of movement gained from the pedigree reconstruction indicates a metapopulation with varying degrees of connectivity. The core populations are where the breeding individuals are located and are sources, while the areas between and around them represent sinks or dispersal corridors. There is significant connectivity between the three core areas in northern Sweden and northern Norway, with limited connectivity between the southern cluster and the rest of the population. A small cluster has formed in central Sweden that appears to be the start of an expansion front, with most disperses coming from the southern cluster. There were several reproductions here, so this is not likely a sink, but as an area of expansion, these individuals are at higher risk than those in the core areas (Krofel *et al.* 2010).

There is less connectivity between the southern cluster and the rest of the population than anticipated, especially on the Swedish side. The sPCA (Figure 4) indicates there is gene flow throughout these areas, but that could point to historical connectivity rather than current movement. Our data only captured 2 dispersal events crossing this void within Sweden, with more in Norway (Figure 9). There was more activity when looking at mated pairs between the two clusters, but still a noticeable gap is present within the county of Jämtland (Figure 7). Similar population patterns are seen in Fennoscandian brown bears, where a significant gap in density occurs in central Jämtland (Kindberg *et al.* 2011).

The movement maps (Figures 7 and 9) show some clear clusters of movement, indicating core reproductive areas. A large productive area in northwest Sweden appears to be a large cluster, with offspring migrating into Norway, but most of the mothers are located in Sweden, suggesting a population sink on the Norwegian side. Another large cluster is located at the northern tip of Sweden where the three countries meet. This one appears to have mothers in all three countries. The area towards the coast and the Finnish border in northern Sweden

looks to be a sink, with three female and two male dispersers but no reproduction. The southern Norway population, once thought to be isolated (Walker *et al.* 2001) appears well connected with the southern Swedish population. The Karelian population in southern Finland, already thought to be disconnected from the rest of Fennoscandia, has a significant gap in dispersal, and must rely on connectivity with Russia to maintain its numbers.

The southern Norwegian population appears to be functioning well and expanding, with good connectivity on the Norwegian side. While it's important to be aware of the potential barrier existing on the Swedish side in Jämtland County, some individuals are clearly still able to move between these areas and maintain gene flow.

4.6 Connectivity

By the early 1900's wolverines had been extirpated in much of their historic range, with populations remaining in the high arctic and along the border with Norway and Sweden (Ekblom *et al.* 2018). Studies from the early 2000's map the population as a narrow strip down the mountain range, with separate areas in southwest Norway and eastern Sweden (Landa *et al.* 2000). This population bottleneck has resulted in very low levels of genetic diversity (Ekblom *et al.* 2018). Today, it is apparent that wolverines are expanding into previously held territory, similar to other large carnivores in Europe following legal protections (Trouwborst 2010). It is clear from our data that wolverines are expanding back into their historical range, with our southernmost animal (a road mortality) recorded just outside Stockholm (Figure 1). Maintaining genetic diversity moving forward will rely on understanding movement patterns and identifying sources, sinks, and barriers to connectivity.

Lowe and Allendorf (2010) divide connectivity into three categories: ecological connectivity, conservation connectivity, and harvest connectivity. Ecological connectivity requires only enough immigration to maintain the population growth rate. Conservation connectivity requires enough dispersal events to maintain population viability, and elimination of this results in an increase in extinction probability. Harvest connectivity requires the most

immigration, as it needs to maintain population viability and growth rate despite harvest pressure. Wolverines are subject to heavy harvest pressure in Scandinavia, through both legal hunting and illegal poaching. Due to this pressure, prioritizing population connectivity at its highest level is important to maintain favourable conservation status of this species. Areas with apparent barriers to movement should be prioritized for future management in order to promote a better connected metapopulation.

While some long extirpated species are now recolonizing previous territories (Milanesi *et al.* 2017), more are under severe pressure from loss of habitat and population connectivity vital to their long-term survival (Boakes *et al.* 2019). Identifying and maintaining these corridors is important for the survival of many far ranging species in an increasingly anthropogenic world.

4.7 Transboundary Management

Significant movement between Norway and Sweden was expected, with the majority of these movements originating in Sweden. Still, there were many animals originating in Norway but moving into Sweden, indicating Norway is not entirely a population sink. Management in Norway differs drastically from Sweden and Finland, with extensive lethal control and licence hunting to keep the population low and address sheep and reindeer depredations (Gervasi *et al.* 2015).

Despite a large reproductive cluster in the north where the three countries meet, our data didn't record a single movement of first order kin between Sweden and Finland. Within our sample, only 32 individuals were detected as part of triads in Finland, with a distinctive gap between north and south clusters, indicating barriers to connectivity within Finland. Finland's wolverine population is much smaller than those in Sweden or Norway, with only an estimated 200-250 individuals (Natural Resources Institute Finland 2019). In Finland, wolverines are estimated to cause more damage than wolves, lynx, and bears combined (Natural Resources Institute Finland 2019), creating severe conflict within reindeer husbandry areas. This conflict could be leading to cryptic poaching, and preventing movement of animals between northern Finland and the Karelian cluster.

Wolverines are already known to move exceptionally long distances (Packila *et al.* 2017). Our research shows that both natal dispersal and breeding related movement are occurring in all directions, across hundreds of kilometers, and across international borders. Favourable conservation status of the wolverine in Europe, and indeed many large mammals, relies on management scales that are often larger than political boundaries.

It has been suggested that the high lethal management in Norway results in spatial behaviour that is not usual for wolverines (Vangen *et al.* 2001; Gervasi *et al.* 2015). A significant driver of dispersal, especially among females, is adult mortality resulting in territory turnover (Vangen *et al.* 2001). Males will always disperse form their natal territory, but females may remain or disperse based on a number of variables – resource availability, population density, or territory vacancy (Vangen *et al.* 2001). The high harvest on the Norwegian side of the border encourages a much higher than normal territory turnover rate, decreasing female dispersal and slowing population growth rate (Vangen *et al.* 2001; Gervasi *et al.* 2015).

In other solitary carnivore species, heavy hunting pressure in some areas increases immigration into those areas (Robinson *et al.* 2008). Not only does this act a population sink, it doesn't solve the initial conflicts that increases harvest was implemented to manage. It also promotes maturity and dispersal at a younger age (Robinson *et al.* 2008). The high harvest rates in Norway impact the dynamics of the whole Fennoscandian wolverine population by constantly opening territories to male dispersers, who are then more likely to be harvested rather than establish breeding tenures (Gervasi *et al.* 2019). Hunting and management has a significant impact on population dynamics in wolverines (Persson *et al.* 2009). When there is high mortality in some areas and not others, this will impact dispersal into and out of those areas.

Low reproductive potential, low density, and low natural mortality in adults are characteristics that make wolverines especially sensitive to additive mortality (Weaver *et al.* 1996). Despite

their generalist diet, they do not have the life history traits to easily adapt to changes in their adult survival rates due to climate change, hunting, or human disturbance.

5 Conclusions

5.1 Applications of Pedigree Analysis

The wolverine is a perfect species to demonstrate the value of long term genetic monitoring data. Their low densities, rugged habitat preferences, and solitary nature make them exceptionally difficult to study without molecular methods, and as such they are not well studied on large scales. Small scale studies are prone to limitations and bias, and often do not describe population level patterns adequately. Our results cover the movements of animals in the entire population over fourteen years, and leave little room for spatial or temporal anomalies. Genetic data is increasingly used for routine monitoring as it becomes more cost and time efficient. Future applications using long term genetic monitoring of this scale could include investigating adaptations to a warming climate (Brommer *et al.* 2008; Visser 2008), a significant concern for cold-dependent northern species.

Genetic information can be used to answer important questions about population ecology. A study in Norway revealed density-dependent adult mortality and identified harvest rates as additive mortality in wolverines (Brøseth *et al.* 2010). In northern Canada, a genetic study recently indicated a severe population decline previously missed by traditional census methods (Efford & Boulanger 2018).

Recent advances in the field of genomics are bridging the gap between population genetics and applied ecology. Studying pedigrees on a large spatial scale is allowing new questions to be answered regarding dispersal and distribution that were previously beyond the scope of population genetics (Bradburd & Ralph 2019). Spatial population genetics is an emerging combination of traditional population genetics and landscape ecology (Bradburd & Ralph 2019). Reconstructing pedigrees in wild populations is becoming more and more feasible, and has important future implications for ecology and management.

6 Acknowledgements

7 List of References

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