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Potential consequences for disease transmission

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Master's thesis in Biology
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Abstract

Animal movement patterns influence many ecological processes, ultimately affecting individual fitness. In addition to the spatial scale of individual movement, e.g. measured by seasonal and annual home range size, consistency in space use and overlap with other individuals can have important fitness consequences such as impacts on disease susceptibility. Whereas causes and consequences of individual home range patterns are much studied in a range of taxa, how consistent individual movement is over time, i.e. the level of site fidelity, and the spatial interactions between individuals are less studied. Spatial behavioural patterns may thus be important for the understanding of disease transmission dynamics, which can be essential for control and management of diseases in a population.

The wild alpine reindeer (*Rangifer tarandus tarandus*) is a migratory cervid living in social herds. Herd size and composition vary throughout the year, and males and females predominantly stay in separate groups except during the rut. Males, being larger than the females, are due to larger metabolic requirements expected to have larger home ranges than the females. However, females often form larger groups, counteracting the effect of body size on home range size. Recently, the fatal Chronic wasting disease (CWD) was found in a herd of alpine reindeer in Norway. Studies of this and other infected cervid populations in North America show a higher CWD prevalence in males than females. Differences in space use patterns are suggested as potential causal factors, as CWD transmits both through direct animal-to-animal contact, and indirectly through the environment. The scale of individual space use and how they overlap with other individuals in space and time can thus be important for the rate of CWD transmission in a population. Accordingly, I used GPS data to study annual and seasonal space use patterns in alpine reindeer from three populations in Norway.

In all populations, both annual and seasonal home ranges were larger for females than for males, except during the rut. The fidelity to seasonal areas across years was similar for both sexes. However, between seasons within the same year the site fidelity was larger for females in two out of three populations. Seasonal home range overlap was larger between same-sex individuals, except during the rut where both the male – female overlap and male – male overlap increased. These patterns suggest that the rut season may be of high importance for disease transmission in a population. The results of this study reveal a consistent pattern of sexual differentiation in reindeer space use, manifested in sex-specific home range sizes and overlap, and to some degree site fidelity. These differences in space use may thus be of importance for the disease transmission patterns in a population.

Sammendrag

Dyrs bevegelsesmønstre påvirker mange økologiske prosesser, som til syvende og sist påvirker individets fitness. I tillegg til den romlige skalaen av individets bevegelser, for eksempel målt i størrelsen på sesongmessige eller årlige hjemmeområder, vil et individs romlige bruksmønster og overlapp med andre individer ha store fitnesskonsekvenser, og blant annet påvirke dets mottagelighet for sykdommer. Mens årsaker og konsekvenser av individuelle mønstre i områdebruk er godt studert i en rekke artsgrupper, vet vi mindre om hvor konsistente individuelle bevegelsesmønstre er over tid, det vil si dets grad av stedstrohet, samt individers romlige interaksjonsmønstre. Romlige bevegelsesmønstre kan dermed være viktige for forståelsen av smittespredningsdynamikk, som kan være essensielt for kontroll og forvaltning av sykdommer i en populasjon.

Villrein (*Rangifer tarandus tarandus*) er et migrerende hjortedyr som lever i sosiale flokker. Flokkstørrelse og -sammensetning varierer gjennom året, og bukker og simler er stort sett i separate grupper unntatt under brunsten. Bukkene, som er større enn simlene, er grunnet høyere metabolske behov forventet å ha større hjemmeområdestørrelse enn simlene. Men simlene danner imidlertid større flokker, som motvirker effekten av bukkenes større kroppsstørrelse på hjemmeområdestørrelse. Nylig ble den fatale sykdommen skrantesjuke (Chronic wasting disease, CWD) påvist i en villreinpopulasjon i Norge. Studier av denne og andre smittede hjortedyrpopulasjoner i Nord-Amerika viser til en høyere CWD-prevalens hos bukker sammenliknet med simler. Forskjeller i områdebruk har blitt foreslått som potensiell årsaksfaktor, da CWD smitter både gjennom direkte kontakt og indirekte gjennom miljøet. Skalaen av individuell områdebruk og hvordan de overlapper med andre individer i tid og rom er dermed viktig for hastigheten av CWD-smitte i en populasjon. Følgelig brukte jeg GPS-data til å studere mønstre i villreinens områdebruk i tre populasjoner i Norge.

I alle populasjoner var både årlig og sesongmessig hjemmeområdestørrelse større hos simlene enn bukkene, unntatt i brunsten. Mellom-års stedstrohet var lik for begge kjønn. Innen-års stedstrohet var imidlertid større for simler i to av tre populasjoner. Overlapp i sesonghjemmeområde var større mellom individer av samme kjønn sammenliknet med individer av motsatt kjønn, unntatt under brunsten hvor overlappen mellom både bukk – simle og bukk – bukk økte. Disse mønstrene indikerer at brunstsesongen er viktig for smittespredning i en populasjon. Resultatene fra dette studiet viser konsistente mønstre av seksuell differensiering i områdebruk hos villrein, vist gjennom kjønnsspesifikke hjemmeområdestørrelser og -overlapp, og til en viss grad stedstrohet. Disse forskjellene i områdebruk kan dermed være viktig for smittespredningsmønstre i en populasjon.

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List of Abbreviations

CWD   Chronic wasting disease

GLMM   Generalised linear mixed-effect model

KDE   Kernel density estimation

LMM   Linear mixed-effect model

m.a.s.l.   Metres above sea level

MCP   Minimum convex polygon

NINA   Norwegian Institute for Nature Research

NTNU   Norwegian University of Science and Technology

SD   Standard deviation

SE   Standard error

TSE   Transmissible spongiform encephalopathy

UD   Utilisation distribution

w_i   Akaike weight

1 Introduction

1.1 Space use and home range size

The movement of animals has consequences for many ecological processes. An individual's movements can influence what it can eat (Patterson and Messier, 2001, Herfindal et al., 2009), its mating opportunities (Komers and Brotherton, 1997, Spritzer et al., 2005), mortality risk (Bergerud et al., 1984, Lewis and Murray, 1993, Dussault et al., 2005, van Beest et al., 2013), and disease susceptibility (Merkle et al., 2018), thereby affecting its overall fitness. The increased focus on wildlife diseases with potential negative effects also for humans demands a better understanding of ecological mechanisms that may affect the transmission of such diseases. As diseases may be transmitted both directly between animals, and also via the environment, the spatial scale of individual movement, and the prevalence to visit the same area or areas visited by conspecifics, may be important factors influencing potential outbreaks and transmission patterns of wildlife diseases.

An individual's home range is a frequently used term to describe individual space use, and has been a central ecological concept ever since Darwin (1861) pointed out that animals restrict their movements to certain home ranges. Burt (1943) defined home ranges as "that area traversed by an individual in its normal activities of food gathering, mating, and caring for young". Today, home range is often quantitatively defined in terms of the utilisation distribution (UD, the probability distribution of an animal's position in the plane), and a frequently used definition is the smallest area associated with a given (often 95 %) probability of finding the animal (White and Garrott, 1990).

Many factors influence the size of an individual's home range. Whereas a larger home range has more resources in the form of for instance foraging and mating opportunities, it also becomes increasingly costly to uphold as more movement is needed to cover the entire area. The size of a mammal's home range is largely determined by their metabolic requirements (McNab, 1963), where larger individuals must utilise a larger area to cover its increased demand for energy (Kelt and Van Vuren, 2001, Mysterud et al., 2001, Jetz et al., 2004, Ofstad et al., 2016). Habitat type has also been shown to cause variation in home range size in ungulates (Ofstad et al., 2016, Ofstad et al., 2019). Individuals living in covered habitats have smaller home ranges than individuals of the same size living in open habitats (Ofstad et al., 2019), and individuals in mixed habitats tend to have even smaller home ranges (Saïd and Servanty, 2005, Laundré and Loxterman, 2007).

Animals in open habitats often form groups (Caro et al., 2004), to increase vigilance and lower predation risks (Fitzgibbon, 1990). The home range of a group must cover an area that has enough resources for the entire group (Skogland, 1994). Increased scramble competition leads to an expected relationship between group size and home range size similar to that of body mass (Lindstedt et al., 1986). Consequently, for group-living animals, the group becomes the functional unit in measuring space use (Makarieva et al., 2005), and group size may thus be a better predictor for the scale of space use than body mass.

Males and females often exhibit different space use patterns. Such sexual segregation is common among large herbivores outside the rutting season (Ruckstuhl and Neuhaus, 2002), but the causes of such patterns are widely discussed. Sex-specific differences in activity budget and predation risk have been supported as ecological mechanisms affecting the sexual segregation in ungulates (e.g. Conradt and Roper, 2000, Ruckstuhl and

Neuhaus, 2002, Loe et al., 2006, Main, 2008). In sexually size dimorphic species, the females are less efficient in digesting forage due to their smaller body size. Accordingly, they must compensate by foraging for longer while males can spend more time lying or ruminating. This mechanism consequently predicts differences in activity budgets, causing social segregation between the sexes (Ruckstuhl and Neuhaus, 2002). Subsequently, these differences could imply differences in home range size, as the females are expected to move around more.

Differences in predation risks between males and females may also influence sex-specific patterns of space use (Linnell et al., 1995, Ruckstuhl and Neuhaus, 2002). Females, especially when they are with offspring, often choose more predator safe habitats to maximise the offspring's survival, rather than habitats with better forage quality (Main, 2008, Bjørneraas et al., 2012). However, these mechanisms are not mutually exclusive, and several different factor may be in play (Ruckstuhl and Neuhaus, 2002, Mooring et al., 2003, Bonenfant et al., 2004, Mooring and Rominger, 2004, Loe et al., 2006, Main, 2008). In addition, sex-specific space use patterns may simply be a result of males being larger than females, and thus needing larger home ranges to fulfil their energetic needs. Indeed, two reviews of home range size in mammals found no effect of sex on home range size after accounting for body size (Mysterud et al., 2001, Ofstad et al., 2016).

Causes and consequences of individual home range patterns are widely studied in a range of taxa, but less is known about how consistent individual movement patterns are over time, or if individuals have overlapping use of areas in a given time scale. Animals adapt their movements to their environment (Switzer, 1993), mediated by a number of trade-offs to optimise foraging and resource use (Charnov, 1976). If resources are spatially and temporally predictable, returning to areas with previous successes in resource use may thus be favourable. Site fidelity is a term used to define an animal's tendency to return to a previously visited place (White and Garrott, 1990), and is a common feature in animal communities (Piper, 2011). Site fidelity can have a number of fitness enhancing effects, such as optimising use of resources (Van Moorter et al., 2009) and lowering predation risk (Forrester et al., 2015, Gehr et al., 2020). Many animals show site fidelity to at least some part of their occupied area, although to which degree differ extensively (White and Garrott, 1990). The level of site fidelity often vary between seasons (Morrison et al., 2021). Higher site fidelity has been observed in several species particularly in seasons prior to the green-up period, where the spatial distribution of foraging patches may be predictable across years (Morrison et al., 2021), and during parturition and breeding (Greenwood, 1980, Tremblay et al., 2007). An animal's site fidelity tendency is important for management and conservation of the species, and can influence the disease transmission and susceptibility rates in a population as diseases may sustain in the environment for a longer time.

1.2 Wild alpine reindeer

The wild alpine reindeer (*Rangifer tarandus tarandus*) is a mixed feeder (Mathiesen et al., 2000) mostly inhabiting open habitats within the alpine tundra ecotone (Andersen and Hustad, 2004). Norway is the only European country with wild populations of the subspecies *Rangifer t. tarandus*, and thus have a special international responsibility for its persistence (Andersen and Hustad, 2004). The Norwegian alpine reindeer herds are today managed within 24 more or less separated populations in the Southern-Norway, with a total of approximately 30 000 - 35 000 animals (Gunn, 2016, Reimers, 2018). The populations are to a large extent isolated from each other by natural and human made

barriers (Skogland, 1994, Andersen and Hustad, 2004). Many of the populations are to some level descended from or have some genetic influx from reindeer of domestic or mixed origin (Andersen and Hustad, 2004, Kvie et al., 2019). The alpine reindeer traditionally conduct long distance migrations between seasonal ranges, increasing the size of their annual home ranges compared to populations of sedentary individuals. This migratory behaviour is a strategy to exploit the seasonal abundance of forage (Klein, 1970, Skogland, 1984, Klein, 1992, Heard et al., 1996), or to avoid excessive predation during the calving period (Bergerud, 1988, Bergerud, 1996, Heard et al., 1996).

The alpine reindeer is, as most ungulates, sexually size dimorphic, with adult males being approximately 60 % larger than females (Melnycky et al., 2013). Consequently, by considering metabolic requirements alone, one could expect males to have larger home ranges than females. However, unlike many boreal cervids such as moose (*Alces alces*), red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), reindeer live in large social herds (Andersen and Hustad, 2004). Their migrating lifestyle and herd living are thus expected to increase the reindeer's home range compared to other boreal cervids (Andersen and Hustad, 2004). The alpine reindeer mainly form three types of herds: females with calves (fostering groups), male herds, and rutting herds. The calves follow the females throughout the suckling period (around 100 days). Male calves then gradually start following the older males, while the female calves stay with the mother throughout their whole first year.

The size and composition of a reindeer herd vary throughout the year (Bevanger and Jordhøy, 2004, Holand and Punsvik, 2016, Reimers, 2018). In the rutting season, both sexes and all age classes can be found in the same group (Reimers, 2018). After the rut, the largest males split up from the females, calves and yearlings (Holand and Punsvik, 2016, Reimers, 2018). As the social life in a reindeer herd is strongly hierarchical, the males, losing their social status after the rut, tend to stay in smaller grazing herds to avoid too many superiors (Skogland, 1994, Bevanger and Jordhøy, 2004). The larger female groups may, depending on food availability, split up in smaller groups throughout winter (Holand and Punsvik, 2016, Reimers, 2018). After the calving, the females gather in large fostering groups to provide protection against predators (Bevanger and Jordhøy, 2004). Later in summer when forage is highly available, the fostering groups may split up into smaller groups (Holand and Punsvik, 2016). However, harassment from insects increases the need to stay together in larger herds (Bevanger and Jordhøy, 2004, Holand and Punsvik, 2016). The herds may group themselves in small areas (Skogland, 1990) such as on top of snow patches or windy hilltops (Toupin et al., 1996, Hagemoen and Reimers, 2002, Holand and Punsvik, 2016), or spend long periods of the day running up and down hills to seek refuge from the insects (Hagemoen and Reimers, 2002). During the hunting season the herds grow bigger with increasing hunting intensity (Bevanger and Jordhøy, 2004, Reimers, 2018).

The temporal variation in movement patterns caused by a multitude of factors indicates that there may be complex mechanisms affecting the rate of disease transmission in wild alpine reindeer. A better understanding of these factors may thus be important to minimise and control the spread of wildlife diseases in the populations.

1.3 Disease transmission and Chronic wasting disease

Parasites and pathogens are fundamental driving forces for the ecology and evolution of mammalian populations (Barber and Dingemanse, 2010, Tompkins et al., 2011, Dunn et al., 2012). Understanding the mechanisms and routes of disease transmission is critical for population and species management in the face of increased disease rates. Two main hypotheses regarding the mechanisms for disease spread have been broadly discussed in the literature, namely density-dependent and frequency-dependent transmission. Density-dependent transmission assumes that the rate of infection of susceptible hosts is directly related to the population density. With frequency-dependent transmission however, the rate of transmission is independent of density, and the disease prevalence and rate of interactions between individuals instead affect the transmission rate (McCallum et al., 2001, Begon et al., 2002). Type of transmission mechanism along with the host's space use patterns may be important considerations for disease management strategies, as the host's spatiotemporal patterns can strongly influence the level of interaction and contact rates between individuals.

Chronic wasting disease (CWD) is a transmissible spongiform encephalopathy (TSE), a neurodegenerative prion disease solely affecting cervids (Gilch et al., 2011). CWD is fatal to all infected individuals (Gilch et al., 2011, Benestad et al., 2016), and is unique amongst the TSE's in that it affects both farmed and wild-living animals (Gilch et al., 2011). An individual affected with CWD will follow a slow progressively clinical course, and the duration of the infection is very variable (Gilch et al., 2011).

CWD was first detected in captive mule deer in Colorado, US, in the 1960s. It has only been found in North America, as well as in South Korea due to import from Canada, until 2016 (Gilch et al., 2011). The mechanisms of CWD transmission are not fully understood. A prominent feature of CWD is however its pronounced ability to spread horizontally (Miller et al., 2004). CWD is transmittable both directly by animal-to-animal contact, but also indirectly through the environment (Miller et al., 2004, Mathiason et al., 2006, Gilch et al., 2011). Saliva, blood, urine, faeces and decomposing carcasses can be sources of disease contamination in the environment (Miller et al., 2004), and the prions can bind to soil particles and remain infectious (Johnson et al., 2006).

In 2016, the first case of CWD was detected in Europe in a female wild alpine reindeer in the Nordfjella range in Norway (Benestad et al., 2016). In an attempt to eradicate the disease, the whole population in the northernmost part of the range was culled in the fall and winter of 2017-2018. A strong male bias was found of the infected reindeer in the Nordfjella population; males were 2.7 times more likely to test positive for CWD than females (Mysterud et al., 2019). Similar results have been found in both mule deer (Miller and Conner, 2005) and white-tailed deer (Heisey et al., 2010, Jennelle et al., 2014) in North America. As other prion diseases, CWD does not trigger an adaptive immune response (Prusiner, 1998). Behavioural differences in for instance space use or sociality have therefore been suggested as a possible reason for the differences in disease prevalence in males and females (Miller and Conner, 2005, Smyth and Drea, 2016, Silk et al., 2018).

1.4 Study aims

The aim of this study is to investigate sex-specific space use patterns in the wild alpine reindeer. I will first investigate seasonal and annual variation in home range size for males and females. The size of an individual's home range is important considering disease susceptibility and exposure, as a larger home range potentially will expose the individual to more sources of infection, both indirectly through the environment, and potentially also directly by increasing contact rate between individuals.

Second, I will investigate the level of individual site fidelity both between seasons (intra-annual site fidelity), and across years (inter-annual site fidelity). The individuals' site fidelity patterns will uncover differences in indirect disease susceptibility by differences in exposure to contaminated environments. I expect the intra-annual overlap between successive seasons to be larger than between non-successive seasons, due to natural constraints such as time and logical space and movement patterns, and the inter-annual site fidelity to be larger in seasons around the green-up and parturition.

Third, I will investigate the home range overlap between individuals in different seasons and investigate differences in same-sex and different-sex overlaps. This may reveal patterns of interaction frequencies between individuals, which may influence disease transmission rates in a population. I expect the overlap between males and females to be largest during the rutting season, and to be lower in the other seasons due to social and spatial segregation. Moreover, I expect the males' overlap to vary across the year, with an increase during the rut due to male – male fights, and the females to show less variation in seasonal overlap patterns due to their more stable group structure. I will do these analyses in three populations of wild alpine reindeer and assess whether there are population-specific movement and space use patterns. This may uncover potential differences that can affect the disease transmission patterns in the populations.

2 Materials and methods

2.1 Study area and populations

The three study populations are located in the wild alpine reindeer areas Nordfjella, Snøhetta and Setesdal Ryfylke in Southern Norway (Figure 1). The Nordfjella and Setesdal Ryfylke populations have some influx of animals descended from domestic reindeers, while the Snøhetta population is one of the few populations of alpine reindeer with minor influence from domestic reindeer activities (Andersen and Hustad, 2004, Reimers, 2007, Kvie et al., 2019).

The Nordfjella population (Figure 1B) covers an area of approximately 2800 km^2 and is separated into two zones (zone 1; around 2000 km^2, and zone 2; around 800 km^2) by a state highway (Strand et al., 2011a). The population size in winter, after the hunt, was on average 1600 animals in zone 1 and 550 in zone 2 across the study period (0.80 and 0.69 animals per km^2 in zone 1 and 2, respectively, G. R. Rauset, unpublished data). There are large areas at >1500 metres above sea level (m.a.s.l.), with peaks up to 1900 m.a.s.l. and deep valleys and glaciers sculpturing the landscape (Strand et al., 2011a). There is little exchange of individuals between the subpopulations (Strand et al., 2011a), but there are however records of some individuals crossing from zone 2 to zone 1 in the winter of 2007-2008. There are also some exchange of animals between zone 2 and the Hardangervidda population in the south (Strand et al., 2011a). Zone 1 is now uninhabited by reindeer after the culling in 2017-2018 as a management strategy to eliminate CWD and prohibit the spread to other populations (The Norwegian Food Safety Authority and The Norwegian Environment Agency, 2017).

The Snøhetta area (Figure 1A) comprises a total of 3300 km^2, partly separated into an eastern and a western area (2100 km^2 and 1200 km^2, respectively). The total winter population size in Snøhetta was on average 2750 individuals across the study period, with an approximate density of 0.82 animals per km^2 (G. R. Rauset, unpublished data). There is little to no exchange of animals between the Snøhetta population and other populations. The landscape in the Snøhetta area is varied, with gentle formations in the east and increasingly rugged alpine landscapes in the west (Jordhøy et al., 2012).

The Setesdal Ryfylke population (Figure 1C) is the southernmost population of wild alpine reindeer in Europe. The population utilises an area of around 6000 km^2, and is thereby the second largest alpine reindeer area in Norway (Strand et al., 2011b). The total winter population size was 2200 individuals across the study period (0.37 animals per km^2, G. R. Rauset, unpublished data). Setesdal Ryfylke is bounded by highways in the north and south, Setesdalen valley in the east and the Ryfylke fjords in the west. The population have some exchange of animals with two other areas, Hardangervidda in the north, and Setesdal Austhei in the east. The area covers altitudes from above 1400 to below 500 m.a.s.l. (Norsk villreinsenter, 2020).
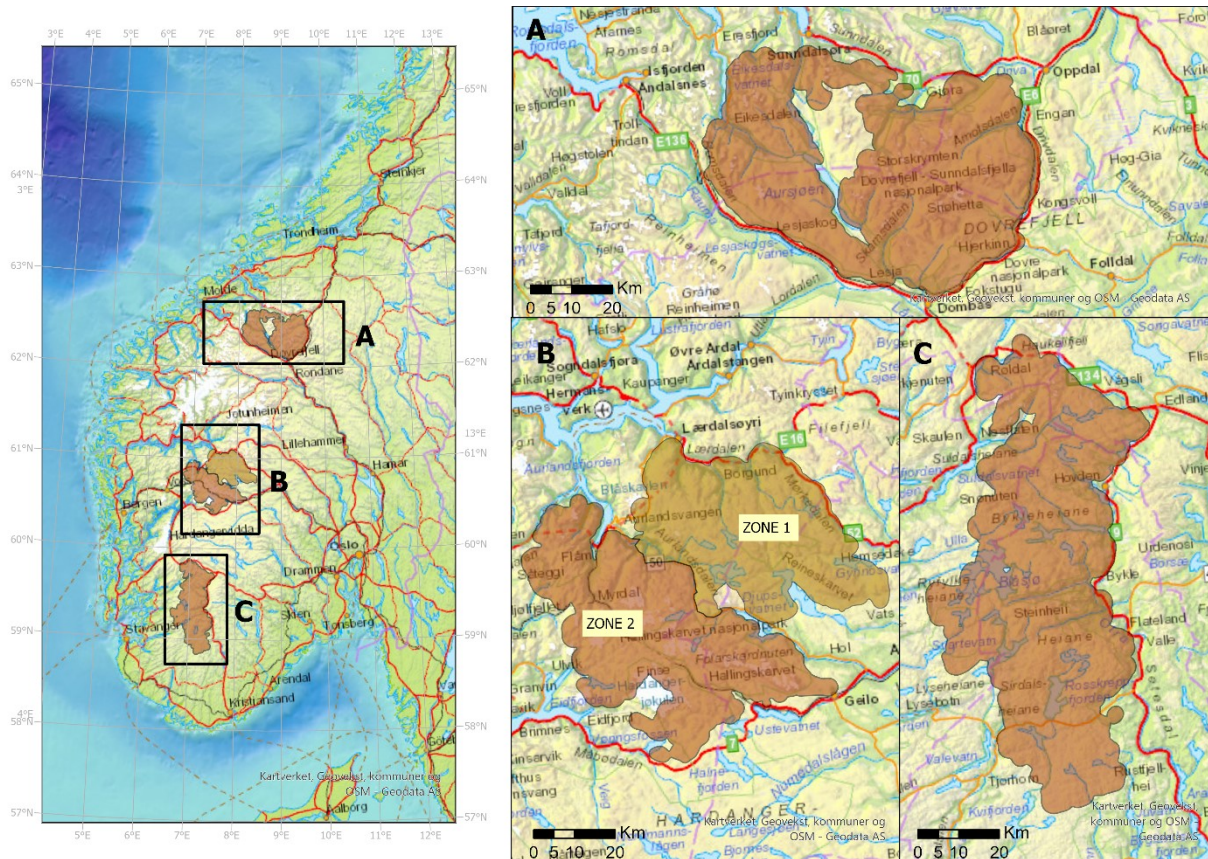
Figure 1: The study areas of three populations of wild alpine reindeer (*Rangifer tarandus tarandus*) in Southern Norway. The leftmost map presents an overview of Southern Norway and the location of the three study areas. Map A further shows a detailed map of the Snøhetta area, map B of the Nordfjella areas (zone 1 and zone 2), and map C of the Setesdal Ryfylke area. Areas are based on kernel density estimated home ranges from GPS point location data (see section 2.2 and 2.3).

2.2 Data collection and processing

Global positioning system (GPS) data was gathered from individuals in the three study populations Nordfjella, Snøhetta and Setesdal Ryfylke as part of a long-time study on reindeer ecology and management. Animals were darted from helicopter during the winter and equipped with GPS collars. The individuals chosen for tracking were considered representative for the spatial distribution given the sex category they comprised. Data was available from 2007 to 2020 from the Nordfjella population, from 2009 to 2018 from Snøhetta and from 2006 to 2019 from the Setesdal Ryfylke population. The data was provided by the Norwegian Institute for Nature Research (NINA). Animal capturing and handling followed standard procedures and was approved by the Norwegian Environment Agency and the Norwegian Animal Research Authority. Some data from Nordfjella zone 2 was also provided by the Norwegian Environment Agency, collected for management purposes (i.e. monitoring the remaining subpopulation and making sure it did not enter zone 1 as part of the CWD disease eradication plan). The data collected was subsampled to a standard scheme of one location every three hours, and screened for errors and outliers following Bjørneraas et al. (2010) before analyses.

The data was divided into six different ecological seasons: a calving season, summer, hunt, rut, early winter and winter season. The ecological seasons were chosen to highlight the different aspects of the reindeer's phenology, such as the calving, hunt and rut, in addition

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to more climatic changes such as the summer, early winter and winter (Table 1). As the reindeer do not necessarily follow our set calendar year, a "home range year" was also defined. This home range year was defined as to start in April, so that the calving season would be the first and the winter season the last season in the year.

The individuals in the dataset were tracked for a variable amount of time (18-2674 days, median = 605 days for all three populations combined). To exclude individuals tracked for only a small part of a season, only individuals that were tracked for at least 50 % of a season were included in the dataset and used for further analyses. As the home range sizes *per se* are not the main goal of this study, but rather the differences in home range sizes between groups, this threshold was a way of balancing the trade-off between larger sample sizes and accurate home range estimates. The minimum number of days tracked per season is given in Table 1, as well as the number of days tracked per season for each population. For the annual home ranges, investigations of the data indicated that at least 300 days with observations was required for accurate estimations (Table S1, Table S2 and Figure S1 in the Supplementary material for justification of this threshold). There is an underrepresentation of males in the data for all three populations (Table 2).

In 2017, the hunting season was extended in Nordfjella due to the planned outtake of the entire population to stop the CWD spread. During the last part of the extended hunting season in 2017 (October 2017), the reindeer showed markedly greater daytime movements compared to what is normal for that time of year (Mysterud et al., 2020). Consequently, all data collected in zone 1 after the ordinary hunting season (from 21st of September) was removed from the dataset. In addition, two individuals in Nordfjella were excluded from the analysis, as their ranging behaviour were not representative for the population. The first individual was excluded completely due to sickness and abnormal behaviour, and the second got stuck in a steep mountainside without being able to get up (O. Strand, pers. comm., November 2020).

Table 1: Start and end dates of each ecological season, the minimum number (#) of days tracked per individual per season (50 % of the total length) and the mean number of days tracked (standard deviation, SD, in parentheses) for all individuals in each population.

Season	Start and end dates of season	Min. tracking length (# days)	Nordfjella Mean # days (SD)	Snøhetta Mean # days (SD)	Setesdal Ryfylke Mean # days (SD)
Calving	1st May – 15th June	23	45.25 (2.99)	45.18 (3.22)	45.23 (2.73)
Summer	1st July – 19th August	25	49.32 (3.14)	49.20 (3.34)	49.32 (2.91)
Hunt	20th August – 20th September	16	31.57 (2.08)	31.64 (1.77)	31.47 (2.12)
Rut	21st September – 20th October	15	29.92 (0.87)	29.79 (1.16)	29.53 (2.04)
Early winter	15th November – 31st January	29	76.58 (6.07)	77.17 (4.33)	76.12 (6.41)
Winter	1st February – 15th March	22	40.59 (5.33)	42.34 (3.06)	41.91 (3.44)

Table 2: The number of males (M) and females (F) and total (Tot) number of individuals tracked in the three study populations (Nordfjella, Snøhetta and Setesdal Ryfylke). Sample sizes are provided for both the seasonal and annual home range estimations. The number of individuals refers to the number of unique individuals having been tracked, whereas the number per season is the given sample size for the particular season. The number of annual home ranges is the sample size for the annual home ranges. Individuals can appear more than once in the seasonal and annual home ranges if they are tracked for multiple years. Hence, these numbers are larger than the total number of individuals.

		Nordfjella			Snøhetta			Setesdal Ryfylke		
		F	M	Tot	F	M	Tot	F	M	Tot
Seasonal home ranges	**#Individuals**	48	15	63	35	4	39	32	15	47
	Calving	98	17	115	88	8	96	90	19	109
	Summer	94	16	110	88	7	95	84	18	102
	Hunt	89	13	103	82	6	88	80	17	97
	Rut	76	8	84	73	6	79	77	16	93
	Early winter	6	2	69	69	5	74	69	8	77
	Winter	75	12	87	63	4	67	63	8	71
Annual home ranges	**#Individuals**	33	2	35	29	3	32	26	6	32
	#Annual home ranges	61	2	63	61	5	66	64	7	71

2.3 Spatial analyses

2.3.1 Calculation of home ranges

I used 95 % fixed kernel density estimation (KDE, Worton, 1989) to calculate seasonal and annual home ranges. KDEs are known for being somewhat more accurate in the estimation of home ranges than for instance the method minimum convex polygon (MCP), and is currently the prevalent method to calculate home ranges in wild animals (Laver and Kelly, 2008). While MCPs derive home range estimations directly from the point observations gathered by e.g. GPS tracking, KDE is derived from an individual's UD (i.e. the probability distribution of an animal's position in the plane). Thus, the estimates used in the further analyses are obtained using the KDE method. However, for comparison with other studies and to assess the robustness of my results with respect to the choice of home range estimator, I also included home range estimates by MCP in the Supplementary material (Table S3).

Estimation of seasonal and annual home ranges was done using the statistical software R version 4.0.4. To estimate home range sizes using KDE, the functions `kernelUD` and `getverticeshr` in the package `adehabitatHR` was used. A limitation to KDE is its sensitivity to what smoothing parameter ("*h*", also called bandwidth) is used in the estimations. The

smoothing parameter controls the amount of variation in each component of the estimate (Worton, 1989). Hence, if a small smoothing parameter is used, you can observe fine detail of the data, while a large smoothing parameter will only provide the most prominent features. A variety of methods are available to objectively select the smoothing parameter. In these analyses, I used a fixed smoothing parameter. Consequently, the home range estimations for the individuals in all three populations have the same smoothing parameter, regardless of the concentration of data points. Since comparison among home ranges rather than accurate estimates was the focus of this study, a fixed smoothing parameter seemed an appropriate choice (Worton, 1989). To find the smoothing parameter that would best fit all three areas, the mean of all reference smoothing parameters per population was calculated. Then the mean of these means was calculated again, resulting in a smoothing parameter of 1965.64 metres. This way, the three populations would have the same leverage for the now fixed common smoothing parameter.

A visual comparison of the spatial distribution of the original GPS locations and the KDE estimated using the mean reference smoothing parameter suggested overestimation of the home ranges by the model. This is a common feature of the reference smoothing parameter when animals use several centres of activity, often resulting in too large home range estimations (Silverman, 1986). To limit the overestimation, I then followed an approach proposed by Kie (2013), where the smoothing parameter was sequentially reduced with 0.1 increments (0.9*h, 0.8*h etc.) until the estimated home ranges more closely fitted the original GPS locations. The general rule followed for assessing the fit was that the estimated home range would not smooth the edges far outside the GPS locations, but also not split the home range into many polygons unless there was a clear division in the GPS locations as well. By following this procedure, the chosen value for multiplying with the smoothing parameter was 0.5.

In the calculation of the seasonal home ranges, some individuals had to be removed from the analyses, as the estimation of home range with the set statistical tools and settings was not possible for those individuals. The likely reason for this in exceptionally small home ranges in the given season. The individuals removed were one male in Nordfjella (hunt 2019) and one female in Setesdal Ryfylke (summer 2007, hunt 2007, and hunt 2008).

2.3.2 Site fidelity and overlap between individual home ranges

For calculation of the level of site fidelity and overlap between individual home ranges, I estimated the overlap in home ranges using the function `kerneloverlaphr` in the package `adehabitatHR` in R. For the site fidelity calculations, the overlap was calculated between home ranges of the same individual, but either different seasons or years, and for the overlap between individuals, the overlap was calculated between home ranges of different individuals in the same season and year. I used the method Bhattacharyya's affinity (BA, Bhattacharyya, 1943) after suggestions from Fieberg and Kochanny (2005). The BA statistic ranges from zero to 1, where zero equals no overlap and 1 equals complete overlap and similar UD's. For the estimation of intra-annual site fidelity, I calculated the overlap for the same individual between the different seasons within the same year. For the inter-annual site fidelity, I calculated the overlap between the same season across different years. Finally, for the overlap between individuals, I calculated the overlap of each individual to all other individuals in the population (excluding itself), for the same season and year.

2.4 Statistical analyses

I used linear mixed-effect models (LMMs) and generalised LMMs (GLMMs) with the R package `lme4` (Bates et al., 2015) to analyse variation in home range size, site fidelity and overlap between individual home ranges. (G)LMMs were chosen as there is non-independence in the data due to repeated observations from the same individual over seasons and years, and from the grouping of individuals within study areas. Therefore, individual and year was included as random effects in all models. In addition, mixed-effect models account for the differences in sample size between the groups.

Model selection was used to find the most parsimonious model given the set of candidate models (Johnson and Omland, 2004). This was done by ranking the *a priori* defined random intercept candidate models according to Akaike's Information Criterion adjusted for sample size (AICc). The confidence intervals (CI's) of the model estimates were all based on parametric bootstrapping using the function `bootMer` in the `lme4` package.

2.4.1 Home range sizes

Seasonal home range size was analysed with sex, season and population (study area) as explanatory variables. To examine whether sexual differences in home range size varied among seasons, I included the interaction between sex and season in the model. However, this sex-specific temporal pattern in home range size could also vary among populations. Hence, I also included the interactions between sex and season with population, as well as a three-way interaction between sex, season and population. Annual home range size was analysed in a second model, with sex and population as explanatory variables. I also included an interaction between sex and population, as there could be variation in the sex-specific annual home range patterns between the populations. Home range size was in both models log transformed to reduce the heteroscedasticity.

2.4.2 Site fidelity

Level of both intra- and inter-annual site fidelity was estimated with LMM's with sex and population as explanatory variables. Although the inter-annual site fidelity includes two years (to which the site fidelity is calculated), only the first year was included as a random effect as the other year-variable did not explain any more of the variation in the data. As the level of site fidelity could vary with sex, and that there could be variation in this sex-specific temporal pattern between the seasons, an interaction between sex and population was also included in the models. I chose not to include season as an explanatory variable in the models, as I was not interested in how the different seasons *per se* affect the level of site fidelity, but rather the effect of sex and population.

2.4.3 Overlap between individual home ranges

For investigations of probability of overlap between individuals, overlaps ≥ 0.1 counted as presence of overlap and overlaps < 0.1 as absence of overlap. A logistic GLMM with the binomial presence/absence of overlap as a response variable was fitted. Explanatory variables included were season, population, and pairs of individuals (i.e. male – male, male – female and female – female). An interaction between pair type and season was also included, as the degree to which individuals overlap may vary with the different pairs in the different seasons. Population was however kept as a solely additive effect, as this temporal pattern were thought not to vary between populations.

For the between-individual home range overlaps that were ≥ 0.1 (and thereby counted as presence of overlap in the logistic model), a LMM was fitted to investigate the differences in degree of overlap given that there actually was presence of overlap. The explanatory variables and random effects were the same as for the logistic model. Additionally, as these analyses included data from two individuals, both individuals were included as random effects in the two models investigating between-individual overlap, in addition to the given year of the overlap.

3 Results

3.1 Annual home range size

The average annual home range size for all individuals in the three populations was 599.22 km^2 (SD = 144.68), 449.35 km^2 (SD = 145.58) for males, and 610.50 km^2 (SD = 138.56) for females (Table S4 in the Supplementary material). According to the AICc-based model ranking, annual home range size varied both with sex and population, and the effect of sex differed between populations (the Akaike weight, w_i, of the most parsimonious model was 0.780, Table S5 in the Supplementary material). The second-most parsimonious model, not including the interaction between sex and population, had a ΔAICc value of 2.56 (w_i = 0.220, Table S5 in the Supplementary material). I therefore retained the more complex model.

The results from the most parsimonious model show that in all populations, females had larger annual home ranges than males (Figure 2, Table S7 in the Supplementary material). The Snøhetta population had the largest annual home ranges and Nordfjella the smallest for both sexes. Nordfjella had the greatest difference between the two sexes, with a 2.16 times larger annual home range for females than males. In Snøhetta and Setesdal Ryfylke, females had 1.32 and 1.25 times larger annual home ranges than the males, respectively (Figure 2).
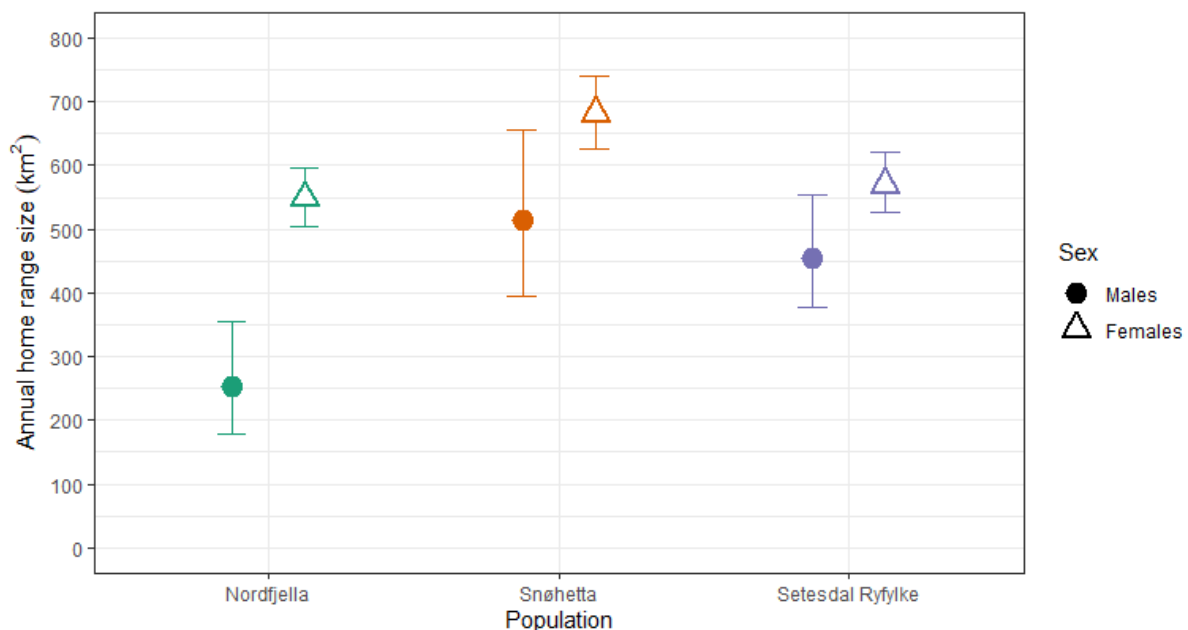
Figure 2: Annual home range size for males and females of *Rangifer t. tarandus* in the three populations Nordfjella, Snøhetta and Setesdal Ryfylke, based on the highest-ranking model (Table S5 in the Supplementary material). Error bars show the 95 % confidence intervals.

3.2 Seasonal home range size

There were large variations in seasonal home range sizes. The largest male home ranges across all populations were in the rut season (207.47 km^2, SD = 134.23), whereas the largest female home ranges were in the summer season (256.49 km^2, SD = 87.39). The highest ranked model suggested that seasonal home range size was influenced by both

sex, population and season, and the effect of these variables were dependent on each other. Hence, the most parsimonious model was the most complex, including the three-way and all two-way interactions of the explanatory variables. ΔAICc to the second-best model was 25.70 (Table S6 in the Supplementary material). The large ΔAICc of the second most parsimonious model and the fact that the w_i of the most complex model was > 0.999, gave high support to this model.

The females in all populations had larger home ranges than the males in most seasons (Figure 3). The Snøhetta and Setesdal Ryfylke populations displayed relatively similar sex-specific space use patterns in most seasons (Figure 3, Table S8 in the Supplementary material), while Nordfjella stood out from the two other populations in the calving and winter season. In the calving season, the Nordfjella females had 1.13 times larger home ranges than the males, whereas in Snøhetta and Setesdal Ryfylke, the males had larger home ranges with respectively 1.17 and 1.15 times that of females. In winter, the Nordfjella males had 1.44 times larger home ranges than the females, whereas in Snøhetta and Setesdal Ryfylke, females had larger winter home ranges (2.10 and 1.84 that of males, respectively, Figure 3).

In the remaining seasons (summer, hunt, rut and early winter), the three populations displayed similar patterns (Figure 3). Although the females for the most part had larger home ranges, the rutting season stood out with larger male home ranges in all three populations. The summer season also stood out with particularly large differences between the sexes, with females having 4.12 times larger estimated home ranges than males, averaged across the three populations. The males in Snøhetta also showed a much greater space use in the hunt and rut season, both compared to the males in the two other populations, and compared to themselves in successive seasons.
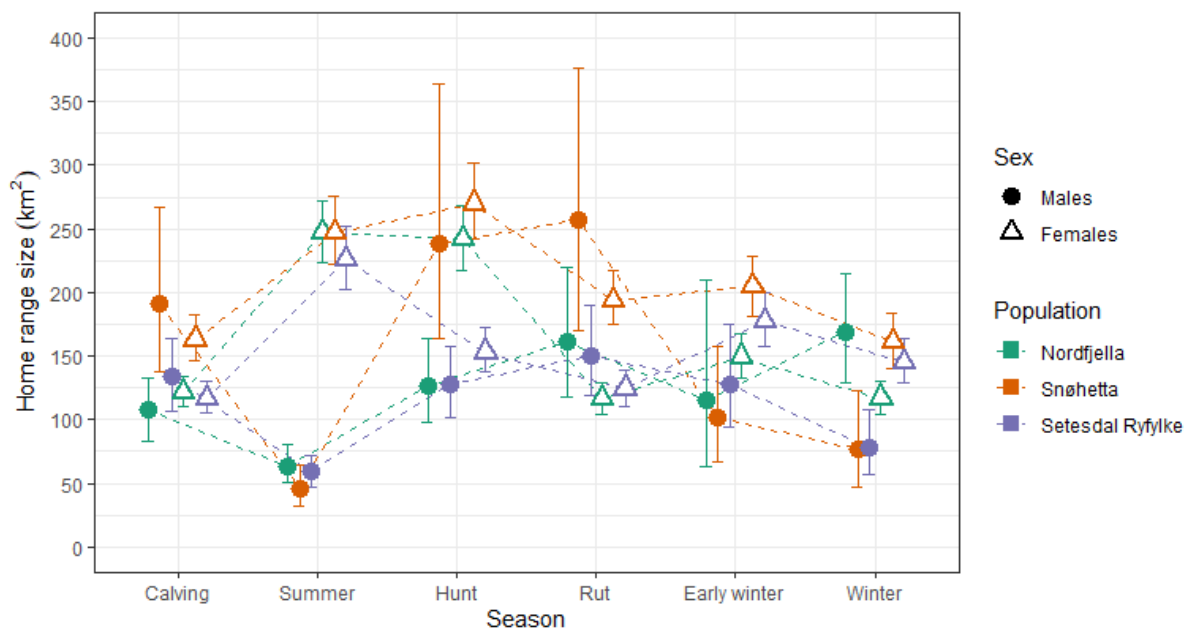

Figure 3: Seasonal home range sizes for male and female *Rangifer t. tarandus* in the three populations Nordfjella, Snøhetta and Setesdal Ryfylke. Error bars show the 95 % confidence interval. Estimates are based on the highest-ranking model (Table S6 in the Supplementary material).

3.3 Intra-annual site fidelity

The intra-annual site fidelity pattern, i.e. the overlap between seasons within the same year, was somewhat similar across the three populations. Higher intra-annual site fidelity was observed between successive seasons, particularly between the early winter and winter season, and between the summer and hunting season (Figure 4, in upper triangles). The results from the model selection showed that the intra-annual site fidelity varied with both sex and population, and the effect of sex varied with population. The second-most parsimonious model with only population as explanatory variable had a ΔAICc of 14.43 (w_i = 0.001, Table S10 in the Supplementary material). Consequently, I saw the most complex model as best at explaining the intra-annual fidelity patterns. In Nordfjella, the males had 1.48 times greater site fidelity than the females, while in Snøhetta and Setesdal Ryfylke, the females had respectively 1.53 and 1.19 times greater intra-annual site fidelity than the males in the same population (Figure 5A and Table S12 in the Supplementary material). The males in Nordfjella had the largest intra-annual site fidelity across both sexes and all three populations (Figure 5A).

A) Nordfjella

	Calving	Summer	Hunt	Rut	Early winter	Winter	
Calving	0.379	0.307	0.222	0.155	0.081	0.141	F
	0.351	0.396	0.336	0.233	0.099	0.067	M
Summer		0.476	0.408	0.246	0.095	0.103	F
		0.045	0.539	0.133	0.107	0.145	M
Hunt			0.329	0.267	0.077	0.088	F
			0.089	0.223	0.099	0.175	M
Rut				0.189	0.091	0.097	F
				0.345	0.000	0.082	M
Early winter					0.233	0.426	F
					NA	0.686	M
Winter						0.160	F
						0.373	M

B) Snøhetta

	Calving	Summer	Hunt	Rut	Early winter	Winter	
Calving	0.394	0.323	0.186	0.134	0.071	0.060	F
	0.433	0.247	0.150	0.073	0.207	0.152	M
Summer		0.538	0.360	0.218	0.134	0.151	F
		0.859	0.485	0.000	0.000	0.000	M
Hunt			0.303	0.300	0.168	0.172	F
			0.382	0.155	0.018	0.000	M
Rut				0.213	0.253	0.181	F
				0.298	0.099	0.039	M
Early winter					0.524	0.431	F
					0.323	0.576	M
Winter						0.280	F
						0.387	M

C) Setesdal Ryfylke

	Calving	Summer	Hunt	Rut	Early winter	Winter	
Calving	0.441	0.254	0.316	0.135	0.017	0.021	F
	0.176	0.191	0.156	0.041	0.196	0.060	M
Summer		0.434	0.369	0.220	0.123	0.129	F
		0.589	0.490	0.063	0.084	0.007	M
Hunt			0.440	0.273	0.050	0.067	F
			0.410	0.148	0.092	0.021	M
Rut				0.266	0.139	0.104	F
				0.096	0.108	0.055	M
Early winter					0.384	0.402	F
					0.000	0.427	M
Winter						0.184	F
						0.000	M

Figure 4: Average site fidelity for *Rangifer t. tarandus* in Nordfjella (A), Snøhetta (B) and Setesdal Ryfylke (C), calculated from GPS locations from the tracked individuals. Inter-annual site fidelity values are presented on the diagonal, and intra-annual in the upper triangle. Values for females are shown in shades of red, and blue for males. The darker the shade, the higher the level of site fidelity.
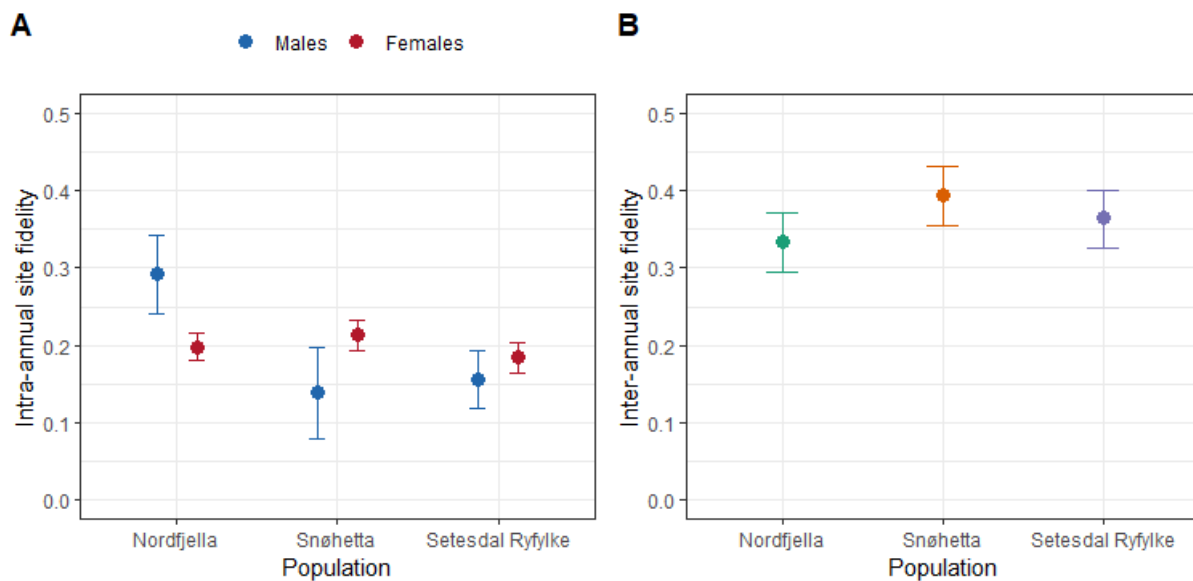
Figure 5: Estimates and 95 % confidence intervals of the most parsimonious model explaining the variation in A) intra-annual site fidelity (Table S10 in the Supplementary material), and B) inter-annual site fidelity (Table S11 in the Supplementary material) of the three *Rangifer t. tarandus* populations Nordfjella, Snøhetta and Setesdal Ryfylke.

3.4 Inter-annual site fidelity

The inter-annual site fidelity, i.e. the home range overlap in the same season across different years, showed some variation between sexes and populations (Figure 4, in diagonals). The females displayed fairly similar patterns with higher levels of site fidelity in particularly the summer season and also to some degree the calving and hunt season in all populations. For the males however, the inter-annual site fidelity varied a lot, and was likely affected by low male sample sizes (Table S9 in the Supplementary material). However, males in two out of three populations showed higher site fidelity levels in the summer season as well.

The results from the model selection showed that only population influenced the variation in inter-annual site fidelity (w_i = 0.350 for the most parsimonious model, Table S11 in the Supplementary material). Consequently, sex did not seem to explain the observed variation. The null model was the second-most parsimonious (ΔAICc = 0.58 and w_i = 0.263, Table S11 in the Supplementary material). According to the highest ranked model, the inter-annual site fidelity in Snøhetta was greater than in the two other populations, with a predicted site fidelity of 0.395 in Snøhetta versus 0.364 and 0.335 in Setesdal Ryfylke and Nordfjella, respectively (Figure 5B and Table S13 in the Supplementary material).

3.5 Overlap between individual home ranges

Home range overlap between individuals varied both with population, season and type of pair the overlap was calculated between. The effect of pair type also varied with season. This was supported by both the most parsimonious model explaining variation in the probability of overlap, and the most parsimonious model explaining variation in degree of

overlap (Table S15 and Table S16 in the Supplementary material). For the probability of overlap, the w_i for the most parsimonious model was 0.627 compared to 0.373 for the second-most parsimonious model (ΔAICc = 1.03, not including population as explanatory variable, Table S15 in the Supplementary material). For the degree of overlap between pairs with overlaps ≥ 0.1, the w_i for the most parsimonious model was > 0.999 (ΔAICc = 26.03 for the second-most parsimonious model, not including population as explanatory variable, Table S16 in the Supplementary material). I retained the most complex model in both cases.

The results from the two models showed similar patterns. Same-sex individuals (male – male and female – female) had a higher probability of overlap than different-sex individuals (male – female, Figure 6), and that given that there was overlap between the home ranges, the degree of it was larger between same-sex individuals than different-sex individuals (Figure 7). In addition, the different-sex overlap showed a clear increase towards the rutting season, while the female – female overlaps seemed to be stable throughout the year. The male – male overlap varied more between seasons, being lowest during summer, before gradually increasing towards the rut and early winter season. Moreover, the degree of overlap between all three pair types in Nordfjella was larger than in the two other populations. The spatial distribution of the home ranges of the GPS tracked individuals in the three study populations are presented in Figure 8 (annual home ranges) and Figure 9 (seasonal home ranges), displaying the variation in location and overlap between home ranges.
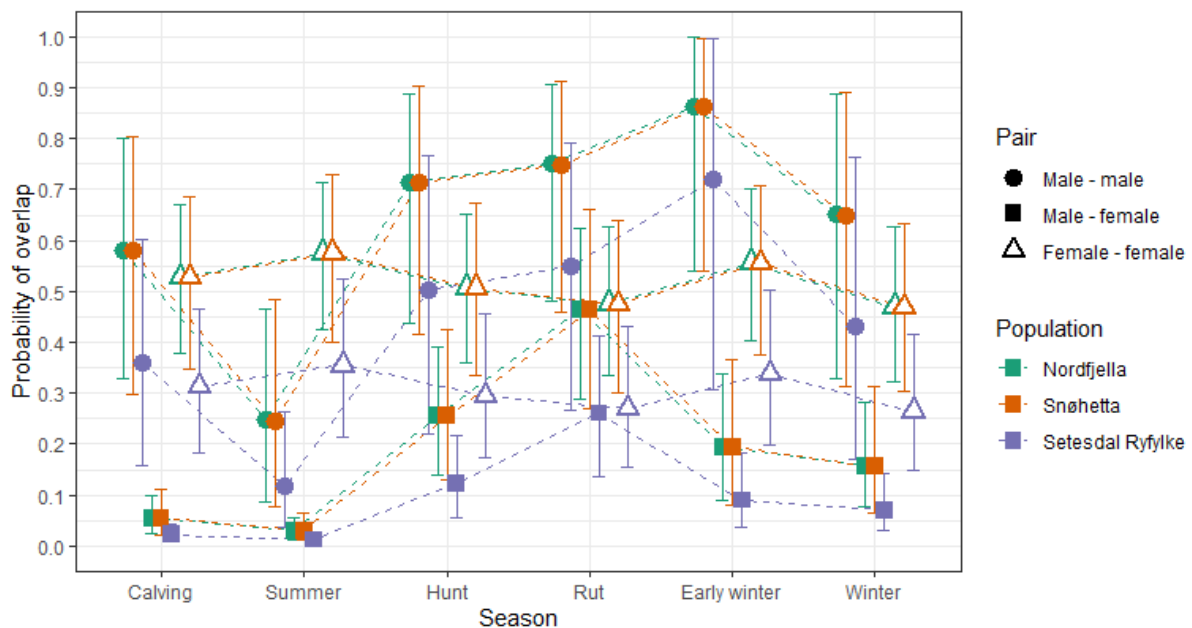
Figure 6: Probability of home range overlap between same-sex individuals (male – male and female – female) and different-sex individuals (male – female) of *Rangifer t. tarandus* in the populations Nordfjella, Snøhetta and Setesdal Ryfylke. The probability of overlap is estimated using the most parsimonious logistic model (Table S15 in the Supplementary material). Estimates are on logit scale. A home range overlap was counted as overlap if the home ranges had an overlap of ≥ 0.1.
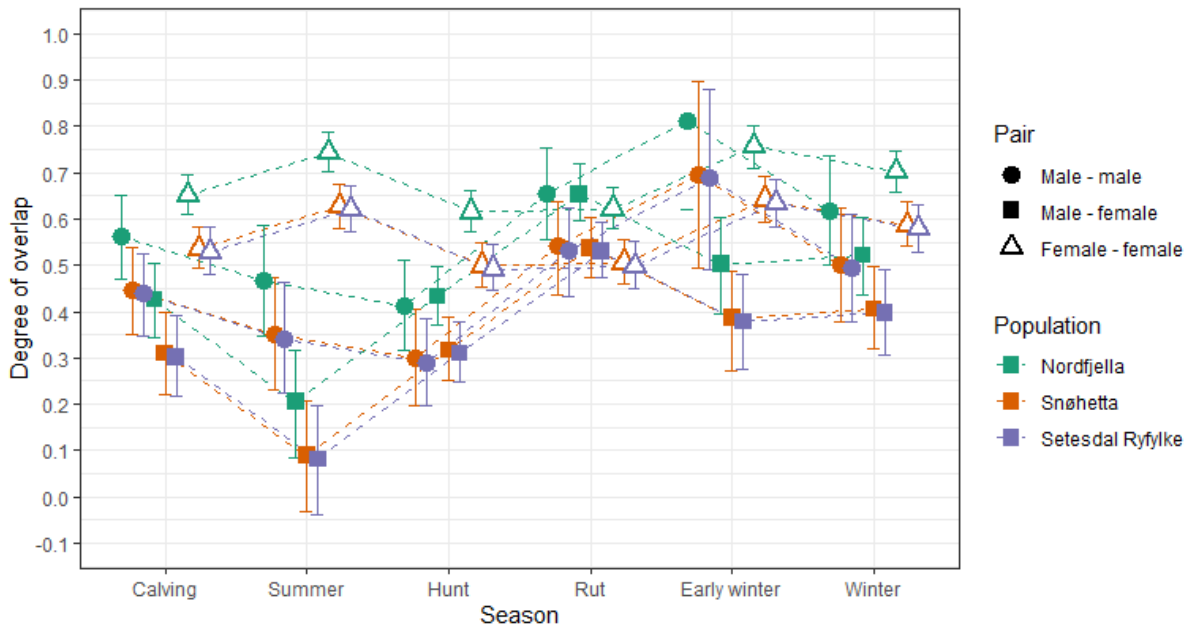
Figure 7: Degree of home range overlap given that there was overlap (overlap ≥ 0.1), for *Rangifer t. tarandus* in the populations Nordfjella, Snøhetta and Setesdal Ryfylke. Estimates are based on the most parsimonious model (Table S16 in the Supplementary material).
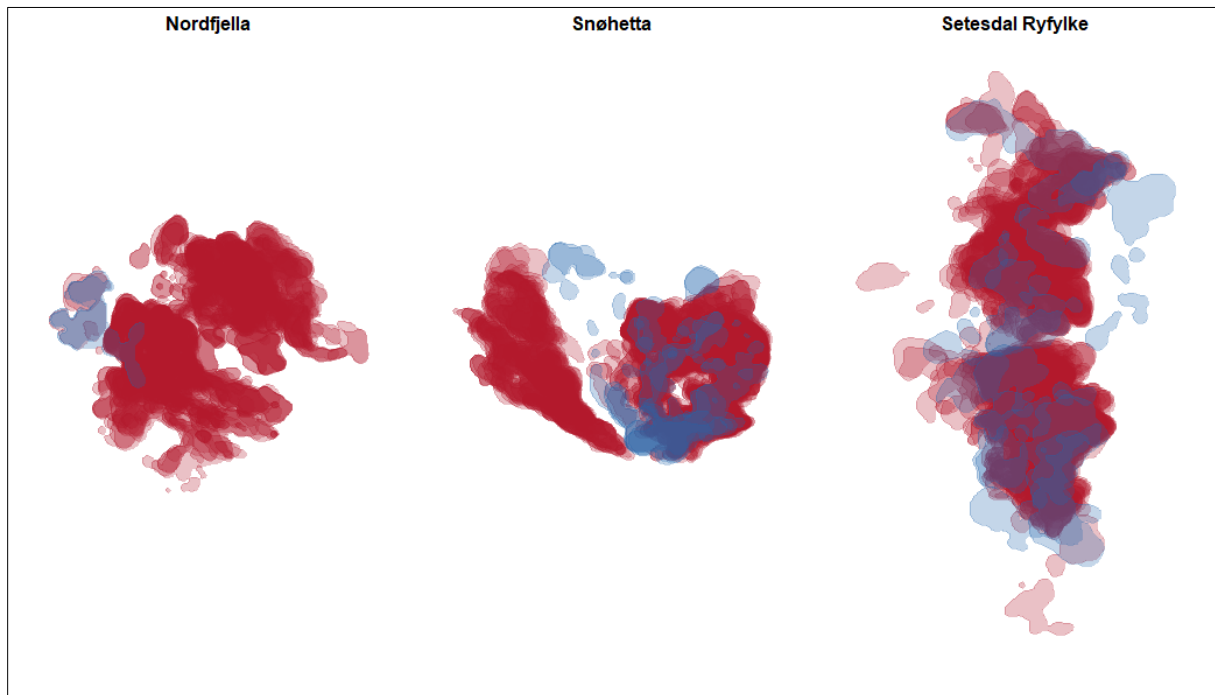
Figure 8: Annual home ranges for *Rangifer t. tarandus* in the three populations Nordfjella, Snøhetta and Setesdal Ryfylke. The home ranges are estimated from the GPS locations of the tracked individuals with kernel density estimation. The home ranges are shown in blue for males, and red for females.

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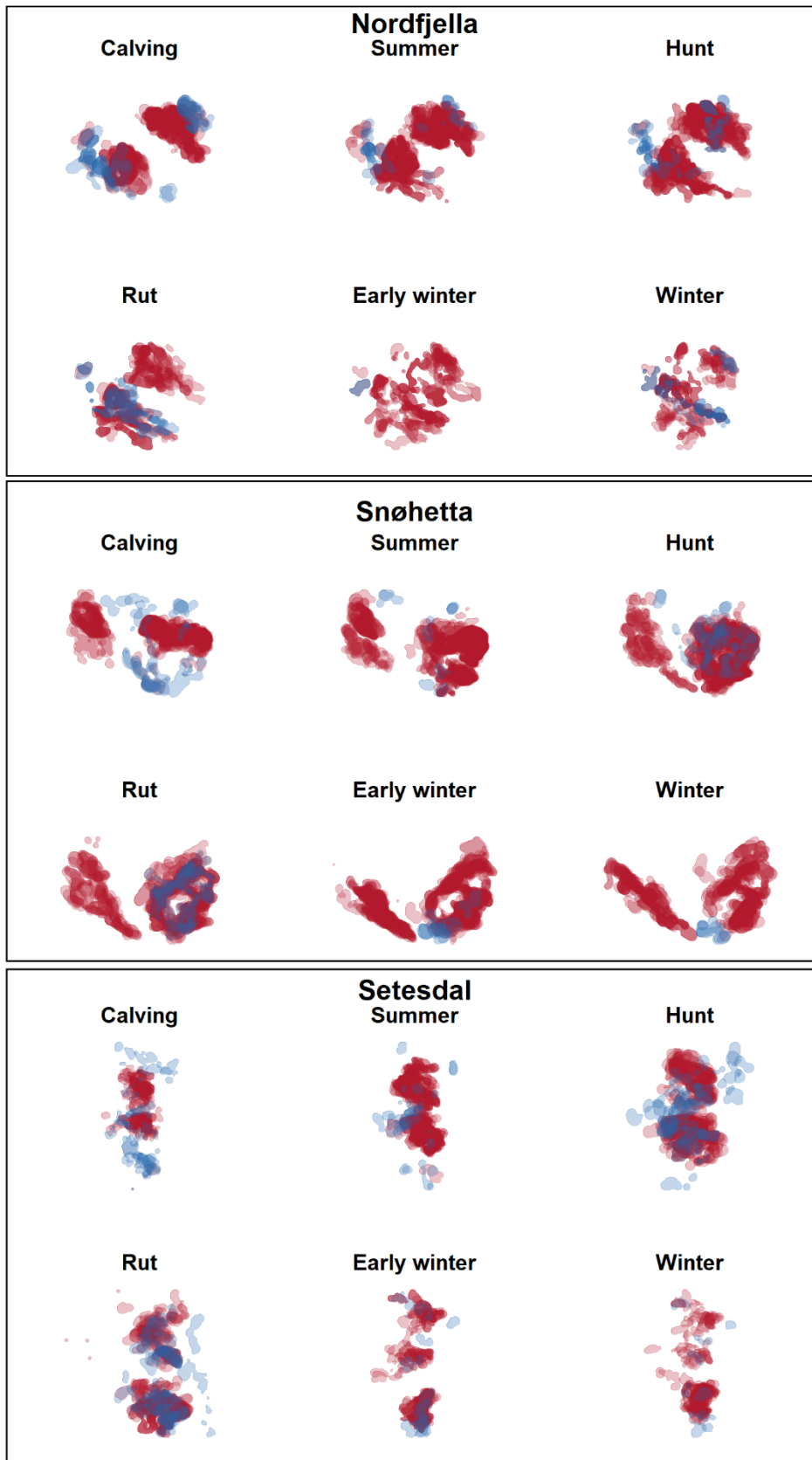
Figure 9: Seasonal home ranges for *Rangifer t. tarandus* in the populations Nordfjella, Snøhetta and Setesdal Ryfylke. The home ranges are estimated from the GPS locations from the tracked individuals with kernel density estimation. The home ranges are shown in blue for males, and red for females.

4 Discussion

My results suggest that individual space use patterns vary both with sex, population and season for the wild alpine reindeer. There is a consistent pattern of sexual differentiation in reindeer space use, manifested in sex-specific home range sizes and overlap, and to some degree site fidelity. These results point to important differences in how male and female alpine reindeer utilise space in compliance with their environment and with conspecifics, which may have consequences for disease exposure and transmission rates in a population. However, a note of caution for the male space use analyses is that some of the findings are based on few individuals and have large uncertainties in the parameter estimates. Thus, the results might not be fully representative for males overall, and should be interpreted with this in mind.

4.1 Seasonal and sex-specific patterns of space use

Females had, with few exceptions, larger home ranges than males both on a seasonal and annual basis. The smaller male home ranges can be explained by sex-specific differences in activity budget, where males need move over smaller areas due to their higher digestion rate as a result of a larger body size (Ruckstuhl and Neuhaus, 2002, Loe et al., 2006). The sex-specific differences in home range size can also be caused by the reindeer's grouping behaviour, where the smaller male groups need to cover a smaller area than the larger female groups to fulfil the group's total demand for resources (Skogland, 1994, Bevanger and Jordhøy, 2004). Differences in activity budget can also explain the results from the between-individual overlap analyses. Home range overlap between same-sex individuals was higher than the overlap between different-sex individuals in most seasons. This suggests that there is a consistent pattern of social and sexual segregation, where reindeer stay in single-sex groupings most of the year.

Despite the generally smaller male home ranges, the rutting season stood out as an exception in both the between-individual overlap and home range size analyses. The results showed a clear increase in the male – female and male – male overlaps, as well as larger male home ranges. A larger overlap between males and females, and between males themselves, are expected patterns in the rutting season as males and females gather to reproduce and males compete with each other for mates. Additionally, the larger male home ranges during the rut may be caused by the males' tendency to form harems, herding females and chasing after them if they start roaming away from the harem (Espmark, 1964).

The sexual differentiation in home range size was largest in the summer season for all three populations, with females having more than four times larger home ranges than the males across all three study populations. The male – female overlap was also at its lowest, suggesting a high social and spatial segregation during summer. The large female home ranges can be a result of females with calves choosing foraging areas with lower predation risk, but in turn offer less optimal forage (Ruckstuhl and Neuhaus, 2002, Main, 2008, Bjørneraas et al., 2012). Consequently, these patterns support that sex-specific differences in predation risk (Linnell et al., 1995, Ruckstuhl and Neuhaus, 2002) may cause sexual segregation particularly in the period successive to calving, as the females need to move over larger areas to get the same foraging output as the males that can choose more optimal, high-quality forage patches. In addition, lactating females also need to account

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for the subsequent additional nutritional requirements (Clutton-Brock et al., 1989), reinforcing the need for more forage.

In summer, insect harassment can increase the reindeer's movements and have a large effect on their activity budgets as a result of less time spent feeding (Hagemoen and Reimers, 2002). Reindeer are seen to utilise proportionally more habitats at high elevations when the insect harassment is high due to lower temperatures and stronger winds providing relief from the insects (Vistnes et al., 2008). The need for such areas may sometimes override the need to avoid human disturbances (Skarin et al., 2004), although some studies still report low reindeer activity near areas with high human activity (Nellemann et al., 2000, Vistnes et al., 2008). Male reindeer have been shown to have a higher tolerance to human activity than female reindeer (Nellemann et al., 2000, Vistnes et al., 2008). Many hiking trails and cabins in Norway are at high elevation locations, and the males may thus utilise more of these areas than the females. Consequently, the males' need for running and moving to seek refuge from the insects may be lower than the females', further increasing the sexual differentiation in space use during summer.

My site fidelity analyses showed similar intra-annual site fidelity levels for the females in the three populations. The males had a more variable pattern, with lower site fidelity in Snøhetta and Setesdal Ryfylke and larger in Nordfjella compared to the females. Hence, for the two former populations, the males appear to compensate for their smaller home ranges by switching between locations more often than the females. The Nordfjella males on the other hand, had both the largest intra-annual site fidelity across both sexes in all three populations, as well as the smallest annual home ranges. Consequently, the Nordfjella males do not seem to compensate for their small home ranges by varying their home range locations like the males in the two other populations.

For the inter-annual site fidelity, sex did not seem to have an effect. The low male sample sizes in these analyses (Table S9) may have affected these results, leading to no detectable sexual differentiation in site fidelity across years. However, the results show a higher inter-annual site fidelity than intra-annual, inferring that the reindeer may to a larger degree return to an area occupied in the same season last year, than in another season in the same year. The descriptive calculations for intra-annual site fidelity showed patterns of higher site fidelity between successive seasons for both males and females. An explanation for this pattern is that the seasons in this study were discretely defined, whereas the assumed phenological behaviour setting the limits for them are not. Consequently, the continuous behaviour of the individuals, as well as variation between individuals and years affecting the timing of seasonal onset, may therefore have led to a higher site fidelity between successive seasons. Indications of seasonal differences in inter-annual site fidelity could also be seen in the descriptive calculations, with tendencies of higher site fidelity in the summer, calving and hunt season for the females. Calving and summer are seasons in which other species also tend to show higher site fidelity (Greenwood, 1980, Tremblay et al., 2007, Morrison et al., 2021). However, further investigations with statistical assessments of seasonal site fidelity patterns are needed before proposing real differences on this subject.

The level of genetic similarity to semi-domestic reindeer have been shown to affect the level of vigilance, alert and flight responses of wild reindeer to humans, with an increase in these responses with increasing genetic distance from domestic reindeer (Reimers et al., 2012, Reimers et al., 2014). Of the three study populations, Nordfjella and Setesdal Ryfylke are both to some extent influenced by influx from domestic reindeer, while the Snøhetta population is of wild origin (Andersen and Hustad, 2004, Reimers, 2007, Kvie et

al., 2019). Hence, the Snøhetta population is expected to show greater vigilance and alert and flight responses to humans. The results from my analyses show that Snøhetta stands out from the two other populations with larger home ranges both annually and seasonally. The expectedly greater alert and flight responses can be a causal factor for this pattern.

4.2 Implications for disease transmission

Differences in space use and social behaviour has been pointed out as potential factors affecting the transmission patterns of CWD in a population, as it does not trigger an adaptive immune response in the infected individuals (Prusiner, 1998). One of the main motivations for this study on sex-specific space use patterns in the Norwegian alpine reindeer was the sexual differences in CWD prevalence pattern found in several studied cervid populations (Miller and Conner, 2005, Heisey et al., 2010, Jennelle et al., 2014, Mysterud et al., 2019). Although this study does not include data on CWD infection rates, it is still interesting to discuss my findings in light of the highly relevant disease.

A leading hypothesis regarding the mechanism for CWD transmission is the frequency-dependent hypothesis (Gross and Miller, 2001, McCallum et al., 2001, Begon et al., 2002, Schauber and Woolf, 2003, Potapov et al., 2013, Jennelle et al., 2014), suggesting that the rate of interactions between animals is positively related to the rate of disease transmission, and that the rate of transmission is not affected by density. By living in herds, the reindeer therefore may facilitate the transmission of CWD, and larger home ranges may lead to a higher probability of infection through the environment as the potential contact with infected areas increases with the size. However, the results from my analyses show that male reindeer, although having a higher CWD prevalence, have smaller home ranges than the females. Consequently, the observed prevalence patterns cannot be explained by a higher infection risk due to the home range size alone. The smaller home ranges may even make them less susceptible for CWD infection through the environment than the females.

On the other hand, the males' larger home ranges during the rut, as well as a larger overlap both between males, and between males and females, indicate that seasonal behavioural patterns might have a larger explanatory value for disease transmission patterns. The increased male – female and male – male overlap during the rut suggest that this season may be of high importance for disease transmission in a population, and thus could be a point for further investigations on the subject. Other non-spatial rutting behaviour can also increase the potential disease transmission rate between animals. During the rut, male reindeer display behaviour such as male – male fights and ingestion of bodily fluids from various females by sniffing and licking their anogenital area during courtship (Müller-Schwarze et al., 1979). Such behaviour influences the rate of disease transmission both within and between sexes. Consequently, knowledge about both social and spatial patterns in the rutting season can be crucial for the understanding of disease transmission in populations of alpine reindeer, and potentially also in other cervid species displaying similar behavioural patterns.

A point of remark regarding my overlap analyses is that although a higher home range overlap indicates a higher probability of interaction between the individuals, it does not necessarily mean that the individuals have interacted directly, as the overlap analyses only examines whether the home ranges overlap within a seasonal time interval. Future investigations would ideally analyse direct transmission rates with models for encounters

between individuals, to get a more precise estimate on the sexual and seasonal differences in social interactions. Such analyses however require both a higher GPS data resolution and larger sample sizes, particularly for males, than what I had available for these analyses.

For understanding the pattern of disease transmission in a population and how it relates to space use, it is important to consider in what stage the epidemic is in. In an early epidemic stage where only few individuals are infected, direct disease transmission by animal-to-animal contact will likely be a more prominent transmission route rather than through the environment, which will be more important in a later epidemic stage. As there is no current vaccine or treatment for CWD, hunting or culling is a common management strategy for disease control. In addition, as distinguishing between infected and uninfected individuals is difficult in the earlier stages of the disease progression, nonselective harvesting is often the most chosen strategy. Although the causes for the higher CWD prevalence in males are not yet fully understood, several infected populations still exhibit this prevalence pattern (Miller and Conner, 2005, Heisey et al., 2010, Jennelle et al., 2014, Mysterud et al., 2019). Harvesting a proportionally larger number of adult males rather than females could thus be a management action to consider rather than harvesting nonselectively (Jennelle et al., 2014). Other strategies, such as reducing the number of high-density meeting spots, for example salt licks and feeding stations (VKM et al., 2018), could also reduce the contact rate and thus disease spread.

If a population is in a later stage in the epidemic course, actions to reduce further spread by transmission through the environment might then be more prominent. Patterns of site fidelity can then become important for disease management, and forced reduction of site fidelity behaviour could be a potential management action by deliberately moving animals and restrict movement to areas with potential high environmental disease prevalence.

As humans are increasingly altering natural habitats, large-scale animal movements have become gradually more restricted (Tucker et al., 2018). The alpine reindeer's need of large areas makes them greatly affected by habitat loss and fragmentation from infrastructure and cabin building in their natural ranges (Panzacchi et al., 2013). Restricting their habitats force the reindeer to make use of much smaller areas compared to their historically larger ranges (Skogland, 1986), and may thus lead to increasing site fidelity. As CWD can sustain in the environment for years (Miller et al., 2004) and infect susceptible individuals, populations restricted to smaller areas with correspondingly higher levels of site fidelity may thus have a higher risk of infection through the environment by increased encounter rates of infected sites. Consequently, humans further fragmenting and restricting the natural ranges and movement patterns of animals may be in disfavour of managing and eradicating diseases such as CWD. Reducing the anthropogenic impact on natural habitats can therefore be highly important in future management of wild populations and new and emergent wildlife diseases.

4.3 Conclusions

This study has shown that a multitude of factors can influence an individual's space use. My analyses revealed consistent sexual differences in space use patterns, varying between seasons and across populations. The findings in this study show that female alpine reindeer, with few exceptions, have a larger space use than males, both annually and seasonally. The results also support that reindeer often stay within single-sex groups large parts of the year, and that largest home range overlap between males and females are found during the rut. Although the drivers of the sex-specific differences in CWD prevalence is still not known, my findings have contributed to rule out some potential causes in the alpine reindeer. I have also uncovered space use patterns in need of further investigations to aid in the management and understanding of CWD transmission patterns.

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6 Supplementary material

Samples sizes and estimates of annual home ranges with varying threshold for tracking length

Home range size based on minimum convex polygon estimates (MCP)

Home range size based on kernel density estimates (KDE)

Model selection for home range size models

Parameter estimates of home range size models

Sample sizes in site fidelity calculations

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Sample sizes in between-individual overlap calculations

Model selection for between-individual overlap models

Parameter estimates of between-individual overlap models

Sample sizes and estimates of annual home ranges with varying threshold for tracking length

To find a threshold for the number of days with observations needed for the annual home range estimations, comparisons of estimates of linear mixed-effect models set with different thresholds (a variation from 200 to 365 days, Table S2) was made. Sample size was also taken into account. The sample sizes particularly for males decreased drastically with increasing threshold (Table S1). With the threshold set to ≥300 days, i.e., that individuals with observations from at least 300 days per year were included in the dataset, 85 % of these (173 out of 203 individuals) were tracked for 350 or more days. 65 % (131 individuals) were tracked for the full year.

Table S1: Sample size in three *Rangifer t. tarandus* populations (NF = Nordfjella, SH = Snøhetta, and SR = Setesdal Ryfylke) in total (Tot) and for males (M) and females (F) separately, with different criteria set for number of days tracked. The sample size provided are the number of individuals per year, with the overall number of individuals given in parentheses.

	Days tracked ≥ 200			Days tracked ≥ 250			Days tracked ≥ 300			Days tracked ≥ 347			Days tracked ≥ 365		
	Tot	**M**	**F**	**Tot**	**M**	**F**	**Tot**	**M**	**F**	**Tot**	**M**	**F**	**Tot**	**M**	**F**
NF	85 (47)	8 (6)	77 (41)	74 (43)	4 (4)	70 (39)	63 (35)	2 (2)	61 (33)	55 (32)	2 (2)	53 (30)	46 (29)	2 (2)	44 (27)
SH	79 (34)	6 (3)	73 (31)	71 (33)	5 (3)	66 (30)	66 (32)	5 (3)	61 (29)	58 (30)	4 (2)	54 (28)	44 (27)	4 (2)	40 (25)
SR	87 (37)	11 (9)	76 (28)	77 (34)	7 (6)	70 (28)	71 (32)	7 (6)	64 (26)	61 (31)	5 (5)	56 (26)	41 (24)	1 (1)	40 (23)
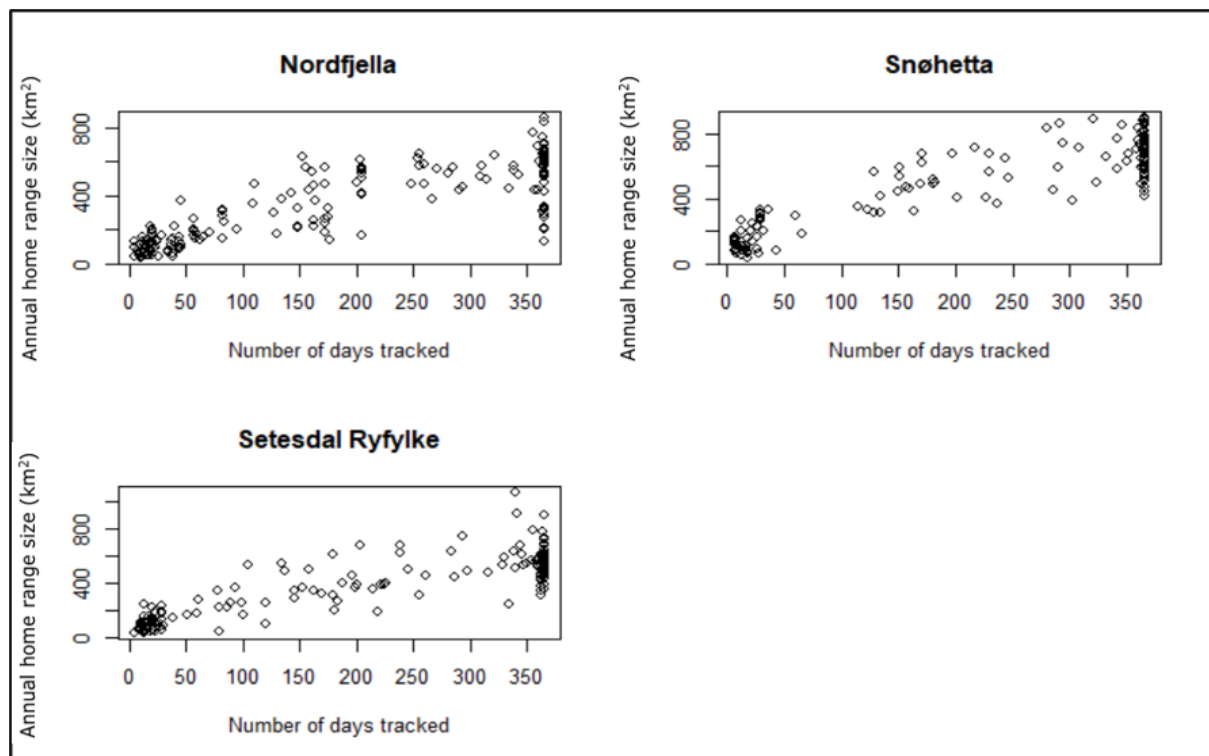
Figure S1: Annual home range size in km^2 for *Rangifer t. tarandus* plotted against number of days tracked for the three populations Nordfjella, Snøhetta and Setesdal Ryfylke.

Table S2: Estimates on log scale and standard error (SE) of annual home ranges for *Rangifer t. tarandus* with a varying threshold of number (#) of days tracked. The intercept is the estimate and SE given for males in the Nordfjella population. Estimates for females in all populations and for males in the two other populations (SH = Snøhetta, SR = Setesdal Ryfylke) are provided as the difference from the given intercept. Interactions between parameters are denoted by colon (:).

# Days tracked		Estimate	SE
≥ 200	Intercept	5.957	0.066
	Females	0.335	0.063
	SH	0.218	0.052
	SR	0.055	0.051
≥ 250	Intercept	5.971	0.068
	Females	0.319	0.066
	SH	0.233	0.051
	SR	0.071	0.050
≥ 300	Intercept	5.541	0.180
	Females	0.770	0.184
	SH	0.707	0.222
	SR	0.581	0.206
	Females:SH	-0.491	0.228
	Females:SR	-0.543	0.213
≥ 347	Intercept	5.545	0.181
	Females	0.763	0.185
	SH	0.809	0.234
	SR	0.623	0.214
	Females:SH	-0.599	0.239
	Females:SR	-0.599	0.221
≥ 365	Intercept	5.541	0.186
	Females	0.756	0.190
	SH	0.805	0.243
	SR	0.842	0.315
	Females:SH	-0.593	0.249
	Females:SR	-0.800	0.320

Home range size based on minimum convex polygon estimates (MCP)

Table S3: Mean home range sizes (and standard deviations (SD)) for both sexes (M = males, F = females) separately and together (= Tot) for *Rangifer t. tarandus* in the three populations Nordfjella, Snøhetta and Setesdal Ryfylke, calculated using the method minimum convex polygon (MCP).

Season	Nordfjella			Snøhetta			Setesdal Ryfylke		
	Tot	F	M	Tot	F	M	Tot	F	M
Annual	219.36 (169.76)	223.70 (169.82)	87.04 (104.58)	1272.19 (809.50)	1302.72 (816.53)	1404.81 (916.38)	1207.62 (854.66)	1209.41 (722.99)	1298.74 (1044.18)
Calving	113.93 (75.63)	113.57 (68.66)	116.00 (110.30)	207.27 (131.27)	186.10 (89.85)	440.17 (256.70)	128.53 (98.88)	119.26 (92.00)	172.44 (119.78)
Summer	242.21 (151.83)	275.25 (137.60)	48.08 (55.58)	288.33 (172.19)	308.82 (161.74)	30.73 (40.48)	219.74 (132.94)	250.92 (115.13)	74.24 (114.28)
Hunt	271.54 (140.54)	293.73 (132.79)	119.62 (91.01)	436.67 (254.16)	434.06 (254.79)	472.30 (265.86)	159.63 (94.14)	158.30 (83.01)	165.91 (138.20)
Rut	132.90 (140.17)	114.22 (74.39)	310.39 (365.91)	273.09 (147.28)	264.83 (147.56)	373.53 (108.49)	129.22 (84.79)	116.90 (66.18)	188.49 (123.79)
Early winter	170.35 (120.87)	173.94 (120.84)	50.39 (0.13)	235.01 (110.65)	245.06 (105.83)	82.43 (42.53)	188.89 (122.85)	194.81 (124.93)	137.83 (94.47)
Winter	155.13 (136.17)	154.16 (138.69)	219.06 (138.69)	178.80 (104.98)	187.10 (102.75)	48.10 (6.12)	149.98 (105.46)	160.59 (105.33)	66.45 (63.02)

Home range size based on kernel density estimates (KDE)

Table S4: Means and standard deviations (SD, in parentheses) of home range*s* for both sexes (Tot) and per sex (M = males, F = females) in the three populations Nordfjella, Snøhetta and Setesdal Ryfylke. Both annual and seasonal home ranges are given. The home range sizes are calculated with kernel density estimation.

Season	Nordfjella			Snøhetta			Setesdal Ryfylke		
	Tot	F	M	Tot	F	M	Tot	F	M
Annual	556.49 (149.51)	566.27 (141.12)	258.23 (85.08)	676.30 (123.67)	688.90 (116.99)	522.61 (106.11)	570.72 (133.27)	583.30 (126.92)	455.76 (144.79)
Calving	128.96 (53.98)	131.61 (53.41)	113.66 (56.35)	176.88 (56.36)	175.16 (56.58)	195.74 (53.69)	131.81 (59.18)	129.29 (60.49)	143.77 (52.77)
Summer	233.65 (112.70)	263.41 (94.88)	65.68 (28.96)	253.29 (109.37)	269.21 (96.76)	53.24 (34.83)	203.91 (86.88)	234.92 (60.84)	62.65 (23.52)
Hunt	246.79 (98.37)	262.57 (91.96)	129.74 (57.97)	318.84 (155.62)	322.69 (155.64)	266.30 (159.44)	162.60 (65.08)	167.34 (65.63)	140.57 (59.36)
Rut	140.37 (91.10)	129.54 (55.39)	243.31 (228.36)	211.41 (73.88)	207.71 (73.60)	256.34 (62.27)	140.05 (55.72)	133.57 (48.35)	171.22 (77.13)
Early winter	159.27 (69.48)	161.53 (69.25)	83.71 (0.0024)	210.48 (67.73)	218.39 (62.82)	101.32 (25.68)	180.75 (58.35)	185.31 (56.27)	141.46 (65.04)
Winter	138.35 (73.58)	133.49 (74.42)	168.74 (62.48)	167.84 (64.15)	173.65 (61.64)	76.46 (12.84)	148.17 (58.76)	156.25 (55.95)	84.49 (39.79)

Model selection for home range size models

Table S5: Model selection for LMM's explaining variation in annual home range sizes in *Rangifer t. tarandus*. HR = home range size, P = population, S = sex. The models are ranked with decreasing ΔAICc value. K = the number of parameters in the model, i.e. the number of explanatory variables, plus the intercept, the random effects and the residual error, and w_i = Akaike weights. Interactions between explanatory variables are denoted by colon (:). All models were fitted with maximum likelihood and random intercept for home range year and individual.

Model	K	ΔAICc	w_i
HR = P+S + P:S	7	0.00	0.780
HR = P+S	6	2.53	0.220
HR = S	5	16.04	<0.001
HR = P	5	18.39	<0.001
HR = Only intercept	4	29.64	<0.001

Table S6: Model selection for LMM's explaining variation in seasonal home range sizes in *Rangifer t. tarandus*. HR = home range size, P = population, SE = season, S = sex. The models are ranked with decreasing ΔAICc value. K = the number of parameters in the model, i.e. the number of explanatory variables, plus the number of random effects, the intercept and the residual error. w_i = Akaike weights. Interaction between explanatory variables is denoted by colon (:). All models were fitted with maximum likelihood and random intercept for home range year and individual.

Model	K	ΔAICc	w_i
HR = P+SE+S+P:SE+P:S+SE:S+P:SE:S	11	0.00	>0.999
HR = P+SE+S+P:SE+SE:S	9	25.70	<0.001
HR = P+SE+S+P:SE+P:S+SE:S	10	29.20	<0.001
HR = P+SE+S+SE:S	8	99.12	<0.001
HR = P+SE+S+P:S+SE:S	9	102.60	<0.001
HR = SE+S+SE:S	7	127.95	<0.001
HR = P+SE+S+P:SE	8	302.46	<0.001
HR = P+SE+S+P:SE+P:S	9	305.73	<0.001
HR = P+SE+P:SE	7	346.76	<0.001
HR = P+SE+S	7	348.32	<0.001
HR = P+SE+S+P:S	8	351.83	<0.001
HR = SE+S	6	377.42	<0.001
HR = P+SE	6	394.06	<0.001
HR = SE	5	424.18	<0.001
HR = P+S	6	562.99	<0.001
HR = P+S+P:S	7	566.28	<0.001
HR = S	5	593.57	<0.001
HR = P	5	608.52	<0.001
HR = Only intercept	4	639.50	<0.001

Parameter estimates of home range size models

Table S7: Estimates and 95 % confidence intervals (CI's) of the most parsimonious model explaining variation in annual home range sizes for *Rangifer t. tarandus* (Table S5). Estimates are back transformed from log to original scale, and CI's are based on parametric bootstrapping. Standard deviations (σ) of the random effects are also provided.

Population	Sex	Estimate (km^2)	95 % confidence interval	
			Lower	Upper
Nordfjella	M	253.94	178.49	358.29
	F	548.88	507.43	594.89
Snøhetta	M	514.24	393.42	657.72
	F	681.40	630.02	742.05
Setesdal Ryfylke	M	453.83	370.50	545.83
	F	570.18	524.08	621.23
$\sigma_{individual}$		0.164		
σ_{year}		0.051		
$\sigma_{residuals}$		0.184		

Table S8: Estimates and 95 % confidence intervals (CI's) of the most parsimonious model explaining variation in seasonal home range sizes for *Rangifer t. tarandus* (Table S6). Estimates and CI's are back transformed from log to original scale. Standard deviations (σ) of the random effects are also provided. M = males, F = females.

Season	Population	Sex	Estimate (km²)	95 % confidence interval	
				Lower	Upper
Calving	Nordfjella	M	107.49	83.60	132.64
		F	121.84	110.38	134.06
	Snøhetta	M	190.61	137.80	266.76
		F	163.13	146.58	182.49
	Setesdal Ryfylke	M	134.44	107.23	163.45
		F	116.61	105.80	130.69
Summer	Nordfjella	M	63.69	51.27	81.01
		F	246.89	223.86	272.51
	Snøhetta	M	45.67	32.53	64.60
		F	246.67	222.07	275.75
	Setesdal Ryfylke	M	59.04	47.46	72.26
		F	226.05	202.41	252.54
Hunt	Nordfjella	M	126.33	97.96	164.21
		F	241.67	216.78	268.70
	Snøhetta	M	238.48	163.48	363.86
		F	270.05	241.60	301.56
	Setesdal Ryfylke	M	127.89	102.31	157.25
		F	153.00	137.16	171.94
Rut	Nordfjella	M	161.39	117.56	219.15
		F	116.58	104.30	129.59
	Snøhetta	M	256.65	170.26	376.22
		F	193.51	174.47	216.73
	Setesdal Ryfylke	M	150.10	119.00	189.72
		F	124.57	111.02	139.23
Early winter	Nordfjella	M	115.15	63.37	209.38
		F	149.27	133.18	167.52
	Snøhetta	M	101.49	66.63	157.19
		F	204.82	181.81	228.27
	Setesdal Ryfylke	M	128.18	94.70	174.64
		F	177.32	157.92	199.78
Winter	Nordfjella	M	169.23	129.42	214.79
		F	117.22	104.24	130.27
	Snøhetta	M	76.41	47.29	122.88
		F	160.99	140.40	183.27
	Setesdal Ryfylke	M	78.33	56.99	107.43
		F	144.88	129.23	164.39
$\sigma_{individual}$			0.18		
σ_{year}			0.048		
$\sigma_{residuals}$			0.41		

Sample sizes in site fidelity calculations

Table S9: Sample sizes of *Rangifer t. tarandus* males (M) and females (F) in each pair of seasons in the calculations of inter-annual (diagonal) and intra-annual (upper triangle) site fidelity. Sample sizes are provided per population (NF = Nordfjella, SH = Snøhetta, SR = Setesdal Ryfylke).

		Calving		Summer		Hunt		Rut		Early winter		Winter	
		F	M	F	M	F	M	F	M	F	M	F	M
Calving	NF	74	2	92	16	89	12	76	8	66	2	62	3
	SH	84	6	85	7	79	6	71	6	67	5	61	4
	SR	114	6	81	17	78	15	76	14	68	8	63	8
Summer	NF			68	2	88	12	76	8	67	2	63	3
	SH			80	4	81	6	72	6	68	5	63	4
	SR			92	5	77	15	74	13	66	7	61	7
Hunt	NF					60	2	76	8	66	2	62	3
	SH					73	4	73	6	67	5	62	4
	SR					88	4	75	15	67	7	62	7
Rut	NF							48	2	66	2	62	3
	SH							59	4	66	5	61	4
	SR							84	3	68	8	63	8
Early winter	NF									39	0	63	2
	SH									52	2	62	4
	SR									67	1	63	8
Winter	NF											51	1
	SH											42	2
	SR											58	1

Model selection for site fidelity models

Table S10: Model selection for LMM's explaining the variation in intra-annual site fidelity in *Rangifer t. tarandus*. O = overlap. The models are ranked with descending ΔAICc value. K = number of parameters, i.e. the number of explanatory variables, plus the intercept, random effects and residual error. w_i = the Akaike weights. Interactions between parameters are denoted by colon (:).

Model	K	ΔAICc	w_i
O = Sex + Population + Sex:Population	7	0.00	0.999
O = Population	5	14.43	0.001
O = Sex + Population	6	16.44	<0.001
O = Only intercept	4	18.47	<0.001
O = Sex	5	20.20	<0.001

Table S11: Model selection for LMM's explaining the variation in inter-annual site fidelity in *Rangifer t. tarandus*. O = overlap. The models are ranked with descending ΔAICc value. K = number of parameters, i.e. the number of explanatory variables, plus the intercept, random effects and residual error. w_i = the Akaike weights. Interactions between parameters are denoted by colon (:).

Model	K	ΔAICc	w_i
O = Population	5	0.00	0.350
O = Only intercept	4	0.58	0.263
O = Sex + Population	6	1.33	0.180
O = Sex	5	1.98	0.130
O = Sex + Population + Sex:Population	7	3.05	0.076

Parameter estimates of site fidelity models

Table S12: Estimates and 95 % confidence intervals (CI's) of the most parsimonious model explaining the variation in intra-annual site fidelity in *Rangifer t. tarandus* (Table S10). M = males, F = females. CI's are based on parametric bootstrapping. Standard deviations (σ) of the random effects and residuals are also provided.

Population	Sex	Estimate	95 % confidence interval	
			Lower	Upper
Nordfjella	**M**	0.293	0.244	0.346
Nordfjella	**F**	0.198	0.180	0.216
Snøhetta	**M**	0.139	0.081	0.196
Snøhetta	**F**	0.213	0.195	0.232
Setesdal Ryfylke	**M**	0.155	0.118	0.194
Setesdal Ryfylke	**F**	0.184	0.165	0.204
$\sigma_{individual}$		0.029		
σ_{year}		0.018		
$\sigma_{residuals}$		0.195		

Table S13: Estimates and 95 % confidence intervals (CI's) of the most parsimonious model for explaining inter-annual site fidelity variation in *Rangifer t. tarandus* (Table S11). CI's are based on parametric bootstrapping. Standard deviations (σ) of the random effects and residuals are also provided.

Population	Estimate	95 % confidence interval	
		Lower	Upper
Nordfjella	0.335	0.296	0.373
Snøhetta	0.395	0.357	0.432
Setesdal Ryfylke	0.364	0.327	0.402
$\sigma_{individual}$	0.079		
σ_{year}	0.009		
$\sigma_{residuals}$	0.232		

Sample sizes for between-individual overlap calculations

Table S14: Sample sizes for the between-individual overlap calculations. The numbers provided are the sample sizes of each pair type with an overlap of ≥ 0.1, per season per population. Pair = pair of individuals the overlap is calculated between (with three levels: male-male, male-female, and female-female).

Season	Pair	Nordfjella	Snøhetta	Setesdal Ryfylke
Calving	**M–M**	25	3	7
	M–F	23	1	10
	F–F	143	212	135
Summer	**M–M**	14	NA	1
	M–F	15	NA	1
	F–F	141	240	116
Hunt	**M–M**	12	2	10
	M–F	23	26	27
	F–F	122	183	87
Rut	**M–M**	4	4	15
	M–F	6	48	33
	F–F	71	157	85
Early winter	**M–M**	1	4	NA
	M–F	2	6	13
	F–F	66	156	83
Winter	**M–M**	13	2	NA
	M–F	29	NA	5
	F–F	80	118	73

Model selection for between-individual overlap models

Table S15: Model selection for logistic GLMM's explaining the variation in probability of overlap between individuals of *Rangifer t. tarandus*. O = overlap, and Pair = pair of individuals the overlap is calculated between (with three levels: male-male, male-female, and female-female). The models are ranked with descending ΔAICc value. K = number of parameters, i.e. the number of explanatory variables, plus the intercept, random effects and residual error. w_i = the Akaike weights. Interactions between parameters are denoted by colon (:).

Model	K	ΔAICc	w_i
O = Pair + Season + Population + Pair:Season	9	0.00	0.626
O = Pair + Season + Pair:Season	8	1.03	0.374
O = Pair + Season	7	200.50	<0.001
O = Pair + Season + Population	8	200.78	<0.001
O = Pair	6	210.10	<0.001
O = Pair + Population	7	210.60	<0.001
O = Season + Population	7	423.89	<0.001
O = Season	6	425.97	<0.001
O = Population	6	434.16	<0.001
O = Only intercept	5	436.06	<0.001

Table S16: Model selection of LMM's explaining the degree of overlap between *Rangifer t. tarandus* individuals given that there is overlap (overlap ≥ 0.1). O = overlap, and Pair = pair of individuals the overlap is calculated between (with three levels: male-male, male-female, and female-female). The models are ranked with descending ΔAICc value. K = number of parameters, i.e. the number of explanatory variables, plus the intercept, random effects and residual error. w_i = the Akaike weights. Interactions between parameters are denoted by colon (:).

Model	K	ΔAICc	w_i
O = Pair + Season + Population + Pair:Season	9	0.00	>0.999
O = Pair + Season + Pair:Season	8	26.03	<0.001
O = Pair + Season + Population	8	97.63	<0.001
O = Pair + Season	7	129.34	<0.001
O = Season + Population	7	150.01	<0.001
O = Season	6	172.92	<0.001
O = Pair + Population	7	227.86	<0.001
O = Pair	6	251.63	<0.001
O = Population	6	296.24	<0.001
O = Only intercept	5	320.32	<0.001

Parameter estimates of between-individual hoverlap models

Table S17: Model estimates and 95 % confidence intervals (CI's) for the most parsimonious model explaining variation in the probability of overlap between *Rangifer t. tarandus* individuals (Table S15). Overlap values ≥ 0.1 was counted as overlap, while <0.1 was counted as no overlap. Pair = pair of individuals the overlap is calculated between (male-male (M-M), male-female (M-F), and female-female (F-F). Estimates are on logit scale, and CI's are based on parametric bootstrapping. Estimates of the standard deviations (σ) of the random effects are also provided.

| Season | Population | Pair | Estimate | 95 % confidence interval | |
				Lower	Upper
Calving	Nordfjella	M - M	0.580	0.329	0.800
		M - F	0.054	0.025	0.100
		F - F	0.527	0.378	0.669
	Snøhetta	M - M	0.580	0.297	0.805
		M - F	0.054	0.022	0.112
		F - F	0.527	0.346	0.686
	Setesdal Ryfylke	M - M	0.360	0.158	0.604
		M - F	0.023	0.010	0.043
		F - F	0.312	0.182	0.467
Summer	Nordfjella	M - M	0.247	0.088	0.466
		M - F	0.029	0.012	0.056
		F - F	0.576	0.426	0.714
	Snøhetta	M - M	0.246	0.076	0.484
		M - F	0.029	0.011	0.064
		F - F	0.575	0.400	0.731
	Setesdal Ryfylke	M - M	0.118	0.036	0.263
		M - F	0.012	0.005	0.025
		F - F	0.356	0.214	0.525
Hunt	Nordfjella	M - M	0.713	0.436	0.888
		M - F	0.255	0.141	0.391
		F - F	0.507	0.360	0.652
	Snøhetta	M – M	0.713	0.417	0.904
		M - F	0.255	0.129	0.424
		F - F	0.507	0.334	0.673
	Setesdal Ryfylke	M - M	0.503	0.219	0.766
		M - F	0.122	0.056	0.217
		F - F	0.295	0.173	0.455
Rut	Nordfjella	M - M	0.750	0.480	0.907
		M - F	0.464	0.288	0.623
		F - F	0.476	0.336	0.627
	Snøhetta	M - M	0.750	0.459	0.912
		M - F	0.464	0.269	0.660
		F - F	0.475	0.301	0.641
	Setesdal Ryfylke	M - M	0.550	0.266	0.791
		M - F	0.261	0.136	0.413
		F - F	0.270	0.155	0.433

Season	Population	Pair	Estimate	95 % confidence interval	
				Lower	Upper
Early winter	**Nordfjella**	**M - M**	0.864	0.541	0.998
		M - F	0.194	0.089	0.339
		F - F	0.556	0.404	0.701
	Snøhetta	**M - M**	0.864	0.539	0.998
		M - F	0.194	0.080	0.368
		F - F	0.556	0.376	0.709
	Setesdal Ryfylke	**M - M**	0.721	0.306	0.995
		M - F	0.089	0.036	0.182
		F - F	0.338	0.199	0.503
Winter	**Nordfjella**	**M - M**	0.650	0.329	0.888
		M - F	0.156	0.076	0.282
		F - F	0.469	0.323	0.627
	Snøhetta	**M - M**	0.650	0.312	0.891
		M - F	0.156	0.065	0.314
		F - F	0.469	0.304	0.633
	Setesdal Ryfylke	**M - M**	0.431	0.171	0.764
		M - F	0.070	0.030	0.141
		F - F	0.265	0.148	0.414
$\sigma_{individual\ 1}$			1.344		
$\sigma_{individual\ 2}$			1.450		
σ_{year}			0.137		

Table S18: Model estimates and 95 % confidence intervals (CI's) for the most parsimonious model explaining the variation in degree of overlap between pairs of *Rangifer t. tarandus* given that there is an overlap (Table S16). Pair = pair of individuals the overlap is calculated between (male-male (M-M), male-female (M-F), and female-female (F-F). Only pairs with an overlap value ≥ 0.1 are included in the calculations. CI's are based on parametric bootstrapping. Estimates of the standard deviations (σ) of the random effects are also provided.

| Season | Population | Pair | Estimate | 95 % confidence interval | |
				Lower	Upper
Calving	Nordfjella	M – M	0.563	0.478	0.639
		M – F	0.425	0.337	0.505
		F – F	0.651	0.609	0.690
	Snøhetta	M – M	0.447	0.366	0.531
		M – F	0.309	0.221	0.396
		F – F	0.535	0.487	0.580
	Setesdal Ryfylke	M – M	0.440	0.354	0.522
		M – F	0.302	0.217	0.382
		F – F	0.527	0.481	0.574
Summer	Nordfjella	M – M	0.465	0.351	0.590
		M – F	0.204	0.088	0.316
		F – F	0.743	0.700	0.785
	Snøhetta	M – M	0.349	0.230	0.476
		M – F	0.088	-0.026	0.204
		F – F	0.627	0.581	0.673
	Setesdal Ryfylke	M – M	0.341	0.226	0.470
		M – F	0.080	-0.033	0.195
		F – F	0.619	0.570	0.667
Hunt	Nordfjella	M – M	0.414	0.321	0.516
		M – F	0.433	0.369	0.497
		F – F	0.615	0.575	0.657
	Snøhetta	M – M	0.298	0.201	0.398
		M – F	0.317	0.251	0.380
		F – F	0.499	0.455	0.546
	Setesdal Ryfylke	M – M	0.290	0.195	0.390
		M – F	0.309	0.245	0.372
		F – F	0.492	0.444	0.541
Rut	Nordfjella	M – M	0.656	0.563	0.759
		M – F	0.653	0.589	0.711
		F – F	0.621	0.579	0.668
	Snøhetta	M – M	0.540	0.444	0.646
		M – F	0.537	0.479	0.599
		F – F	0.505	0.460	0.550
	Setesdal Ryfylke	M – M	0.532	0.435	0.635
		M – F	0.530	0.467	0.591
		F – F	0.498	0.449	0.548

Season	Population	Pair	Estimate	95 % confidence interval	
				Lower	Upper
Early winter	**Nordfjella**	**M – M**	0.811	0.625	0.993
		M – F	0.502	0.402	0.610
		F – F	0.758	0.713	0.804
	Snøhetta	**M – M**	0.695	0.512	0.879
		M – F	0.386	0.282	0.497
		F – F	0.642	0.594	0.689
	Setesdal Ryfylke	**M – M**	0.687	0.505	0.865
		M – F	0.378	0.286	0.479
		F – F	0.634	0.586	0.687
Winter	**Nordfjella**	**M – M**	0.617	0.499	0.738
		M – F	0.521	0.435	0.608
		F – F	0.702	0.658	0.747
	Snøhetta	**M – M**	0.501	0.372	0.628
		M – F	0.405	0.314	0.499
		F – F	0.586	0.540	0.633
	Setesdal Ryfylke	**M – M**	0.494	0.372	0.612
		M – F	0.397	0.308	0.490
		F – F	0.578	0.527	0.629
$\sigma_{\text{individual 1}}$			0.056		
$\sigma_{\text{individual 2}}$			0.051		
σ_{year}			0.049		
$\sigma_{\text{residuals}}$			0.202		