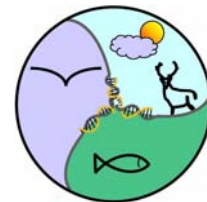


Master of Science thesis

**Seasonal home ranges and migration
of red deer (*Cervus elaphus*)
in Norway**

Kirsten Kleveland

**Centre for Evolutionary and Ecological
Synthesis
Department of Biology
University of Oslo, Norway**



CEES

Oslo, 2007



Out in the field.

Photo by Inger Maren Rivrud

Preface

Many thanks to the Sunnfjord/ Ytre Sogn deer project by Hallvard Flatjord for letting me use their GPS data and to Odd Rønningen and Harald Kjær, Knut O. Førde and Ola Jan Birkeland in Nordfjord for valuable tips and assistance as well as loan of equipment in the field.

Further thanks to my supervisors Atle Mysterud, Leif Egil Loe and Vebjørn Veiberg for guidance, corrections, help with statistical mysteries and above all: patience.

Also many thanks to:

Mum and Dad, for support in the mental, physical and economical departments (there is such a thing as a free lunch) as well as proof-reading,

Kjetil and Ingela Kleveland for the meals, coffee and company served down the street when morale was low,

Marianne Beck Heien for being a patient flat mate through the crazy times, with her seemingly unlimited faith in my capabilities,

all the loopy people (Oda Bjærke, Kim Magnus Bærum, Eirik Krogstad, Truls Næsje, Annette Taugbøl and Kristin Vesterkjær) in study room 4419 (“Næsje et al.”) for your company and general silliness,

Bess for fuzz therapy through the final frustrating days of writing and Birger Godvik for chauffeuring me around in the field when I couldn't see,

Adine. Because she asked me to.

And last but not least: plenty of cheers to Inger Maren Rivrud for being field partner, reading room crony and the general friend sitting at the other oar in our little boat as it passed through the scary, unfamiliar waters of Master Thesis.

Kirsten,

University of Oslo, August 30th 2007

Abstract

1. Many studies have dealt with home range and migratory patterns of Cervid species, but there are few explicit analyses quantifying migratory patterns and home range size as a result of habitat. Red deer is known to perform migrations between seasonal home ranges, but there is little quantitative information specifically on the Norwegian red deer, *Cervus elaphus atlanticus*. Using position data from VHF-collared and GPS-collared red deer females, this study aimed to address patterns of migration and home range size and how this can be related to habitat use in the Norwegian red deer.

2. I predict a seasonal migration pattern where animals move between winter ranges at low altitude to summer ranges at higher altitudes (H1). I expect spring migration to be slow, following the phenological development of plants (H2). As a consequence of strategies for energy conservation, and snow cover potentially restricting mobility during winter, I predict home range sizes to be smaller in winter than in summer (H3). Assuming that home range size is determined mainly by food quality, I predict that home range size will decrease as the proportion of agricultural pastures increase (H4). I also expect home range size to increase as the animals move higher, into mountainous areas (with smaller and more scattered vegetation patches) (H5). Assuming that the need for shelter is equally important for home range size as available food, an increasing proportion of forest is expected to reduce home range size (H6).

3. I found that a little more than half the animals migrated between separate summer and winter home ranges, and there was a clear selection for elevated areas in the summer. The summer ranges were larger than the winter ranges, but there was no effect of altitude on home range size in the summer. As predicted, forested areas caused a decrease and mountainous areas an increase in home range size, but contrary to predictions, the presence of pastures tended to increase home range size. Since home ranges were larger when incorporating mountainous areas, but were not affected by altitude, I suggest that altitude itself is of less importance to home range size than the accessibility of habitat types.

4. I found that the spring migration was very rapid; contradicting the prediction that migration is driven gradually by plant phenology. The cues of migration seem to differ between topographically different areas, as migration speed is faster in areas with steep hills and appear less related to the gradual green-up in the altitudinal gradient.

Table of contents

Preface	ii
Abstract	iv
1. Introduction	1
2. Materials and methods	4
2.1. Study area	4
2.2. Study animals	4
2.2.1. <i>VHF-collared animals, Nordfjord</i>	4
2.2.2. <i>GPS-collared animals, Sunnfjord</i>	6
2.3. Statistical analyses	6
2.3.1. <i>Maps</i>	6
2.3.2. <i>Migration</i>	7
2.3.3. <i>Home range</i>	8
2.3.4. <i>Habitat selection</i>	8
3. Results	9
3.1. Migration	9
3.2. Home range size	9
3.3. Habitat selection patterns	10
4. Discussion	18
4.1. Variation in movement strategies and landscape characteristics	18
4.2. Timing and speed of migration	19
4.3. Home range size and large scale habitat selection	21
5. Concluding remarks	23
6. References	24
Appendices	26
Appendix 1. Kernel and MCP home ranges of all individuals	26
Appendix 2. Numbers of tried and successful GPS fixes	28
Appendix 3. The best models for factors affecting home range size, excluding outliers	29
Appendix 4. Output from the Aebischer analyses	30
Appendix 5a. Migration information on the Nordfjord (VHF-collared animals)	31
Appendix 5b. Migration information for the Sunnfjord (GPS-collared) animals	32
Appendix 6. Annual pattern of a migratory individual	33
Appendix 7. The annual pattern of a non-migratory individual	33
Appendix 8. Julian days vs. cumulative distance from marking point	34



Curious stags.

Photo by Inger Maren Rivrud

1. Introduction

Seasonal changes lead to considerable temporal and spatial variation in available resources and force animals to develop strategies for dealing with this. Migration is one such strategy, allowing animals to take advantage of the most profitable regions available at any given time. Having the opportunity to exploit the best areas as they become available in the spring or rainy season will be an important resource refuge. The yearly migration of African ungulates is a well known example, where animals migrate hundreds of kilometres in order to follow the new vegetation sprouting after the rainy season (Baker, 1978). As Sinclair (1983) points out, long distance migration to temperate regions will be a way of finding more suitable areas for feeding and breeding, with favourable periods of superabundant food supplies at times when tropical areas may suffer from droughts.

Animals in northern areas face a situation where the probability of dying can be increased considerably by heavy snowfall and low temperatures. Finding enough food to satisfy the energetic demands through winter can be challenging. Most animals in these areas will therefore time their reproduction to give birth in the spring in order to feed the young through the summer, when food is more abundant (Langvatn et al., 2004). Despite the increased amounts of food, spatial variation in resources may still cause variation in individual fitness (Pettorelli et al., 2002). The best area to reside in will not only be affected by habitat quality, but also by the number of competitors. The ideal-free distribution predicts a distribution of animals among patches of different quality that gives equal gain to each animal, when assuming that animals have ideal knowledge about patch quality, and are free to move between them (Drickamer et al., 1996). In light of this, migration to places of lower animal density and more nutritious forage may result in a trade-off between seasonal variation in habitat quality and competition.

A lot of research has been done on the migration and habitat use of Cervid species (roe deer, *Capreolus capreolus* (Börger et al., 2006; Mysterud, 1999); moose, *Alces alces* (Cederlund, 1994; Cederlund, 1988; Edge, 1985); white-tailed deer, *Odocoileus virginianus* (Sabine et al., 2002); elk, *Cervus elaphus* (Anderson et al., 2005; Edge, 1985) European red deer, *Cervus elaphus* (Georgii, 1980; Luccarini et al., 2006; Szemethy et al., 2003). The reasons for undertaking a migration to an alternative area may be dependent on the available vegetation and topography and animal density in the area (Albon and Langvatn, 1992; Georgii and Schröder, 1983; Swenor, 1988). The earlier studies also recognise that the summer home ranges generally lie at higher altitudes than the winter ranges. The delayed snowmelt at higher

altitudes will result in a longer period of access to highly nutritious forage in the early summer (Albon and Langvatn, 1992; Mysterud et al., 2001a) which explains why deer will seek to elevated areas in search of food in these periods. Female deer with access to a more varied topographic landscape with higher altitudes have been found to be heavier than animals with access only to lowland areas (Albon and Langvatn, 1992; Langvatn and Albon, 1986). This indicates that an increased period of access to high quality food plants may validate an energy demanding migration. Seasonal cues are thought to be responsible for initiating the autumn migration back down into the lowlands (Sabine et al., 2002; Tierson et al., 1985). The lowlands tend to have a milder climate, resulting in less precipitation falling as snow (Mysterud et al., 2000), and there will be larger areas of coniferous forests which further reduce the snow depth on the ground. A more patchy snow distribution may greatly reduce both the energy costs of movement, predation risk and also difficulties in finding food through the winter months (Schmidt, 1993).

The home range of an animal, i.e. the “area traversed by the individual in its normal activities of food gathering, mating and caring for young” (Burt, 1943), will depend on the amounts of available resources within an area. Finding food of sufficient quality and abundance will be the main issue, but having access to shelter, breeding sites and conspecifics will also be important factors in deciding where to reside and where to move to (Sinclair, 1983). Such an area can be studied at different scales, depending on the variables considered. Simple spatial studies should be backed up by temporal and social factors in order to understand the underlying mechanisms deciding home range size (Börger et al., 2006). The separation of seasonal home ranges is helpful, as these are fairly stable. As seasonal changes occur and alter the composition of obtainable food, the home range sizes are expected to vary accordingly (Mysterud et al., 2001b). The size of the seasonal home ranges at an intra-specific level is believed to depend on the amount of and access to quality food, as well as on shelter used for predator avoidance (Tufto et al., 1996). Even in areas where red deer have no remaining large natural predators and the predator risk per se is negligible, the need for cover is still important for shelter and rest. Home range size has been found to increase as the number of critical resources becomes scarce and their distribution more patchy (O'Neill et al., 1988; Tufto et al., 1996) and decrease as the supply of important resources increase in an area (Anderson et al. 2005). Forage quality is known to be an important aspect of deer habitat use (Langvatn and Hanley, 1993) and access to food of sufficient quality will therefore be an important factor in the choice of habitat, the size of home range and the benefit of migration.

Like other cervids, the red deer may migrate between a winter and a summer home range (Albon and Langvatn, 1992; Georgii, 1980). Despite the importance of red deer as a game species in Norway, very little research has been done on their migration patterns and no explicit analyses of their selection of home range has been conducted. Albon and Langvatn (1992) studied the benefits of migration by comparing the body weight of females occupying lowland summer ranges and those moving to altitudes above 250 metres above sea level. Their study area in the municipality of Snillfjord, Sør-Trøndelag, has a more gradual elevation from coast to inland than is characteristic for the area where my study was carried out. It is likely that this may affect the coarse scale choices of home range and migration patterns. More research is needed in this area, especially in Sogn og Fjordane, being a central area for red deer in Norway. In this study, using information gathered from animals equipped with GPS collars and tracking of animals with VHF-collars, I aimed to address closely related issues regarding the basic patterns of migration and home range in the Norwegian red deer, *Cervus elaphus atlanticus*.

Firstly, assuming that migratory behaviour is a result of seasonal changes in resource distribution, I predict animals to have seasonal migrations between a winter range at low altitude and a summer range at higher altitudes (H1). I expect the spring migration to be slow, following the gradual green-up of vegetation as snow melts in the mountains (H2). A second migration is expected in the autumn, as snowfall force the animals back down to their winter range. I expect animals to keep to more concentrated patches in lower areas during winter, both to conserve energy when snow increases mobility resistance and because snow and bad weather reduce access to, and profitability of, certain areas. As animals move higher, I expect them to enter areas with more rock outcrops, steep and inaccessible areas and streams, where high quality forage may be more dispersed. In addition, with lactation increasing energy demands in the summer, I predict larger home range sizes in summer than in winter (H3). Assuming that home range size is determined mainly by food supply, I predict that home range size will decrease as the proportion of agricultural pastures increase (H4). This is because pastures signify patches of more easily attainable high quality forage. In the same respect, I expect home range size to increase as the animals move into mountainous and rocky areas where the distribution of high quality forage is more scattered (H5). Assuming the need for shelter is as important for home range size as available food, an increasing proportion of forest is expected to reduce home range size (H6).

2. Materials and methods

2.1. Study area

The study area covered 13 municipalities (Gloppen and Stryn: area of Nordfjord; Flora, Naustdal, Jølster, Førde, Gaular, Askvoll, Fjaler: area of Sunnfjord; Balestrand, Høyanger, Hyllestad, Solund: area of Ytre Sogn) in the county of Sogn og Fjordane, Norway (Fig. 1). The topography is characterized by steep mountain sides which slope down to sea level (fjords), lakes or narrow valleys. Common vegetation on the mountain sides include pine (*Pinus sylvestris*) and birch (*Betula spp*) woods up to the tree line with an undergrowth of heather (*Calluna vulgaris*), bilberry (*Vaccinium myrtillus*), juniper (*Juniperus communis*) and grasses and ferns, which may continue up to the bare rock of the mountains. In the valleys and lowlands, the woods have been cleared for cultivation and the land is mainly used for grazing fields and meadows for grass production, with timothy (*Phleum pratense*), as the main grass type. Patches of planted spruce (*Picea abies*) are often bordering the cultivated fields.

Temperatures generally decrease with altitude and distance to the coast. Still, temperatures may be low even close to the sea. Temperatures average -0.5 in February and 14.2 in July (Institute of Meteorology, station no 58070). Longer periods of both thaw and freeze are common. There are usually high levels of precipitation, 1260- 1630 mm/ year (Institute of Meteorology, station no 58070 and 58320) in this part of the country, which will also decline with distance to the coast. Variation in the amount of winter precipitation falling as snow is an important factor for the length of the growth season on the mountain sides. Snow depth will increase with altitude, as more precipitation falls as rain in the lowlands, and snow melting will vary from year to year, depending on snow depth in different parts of the mountains. Wetter winters, with a lot of snow in elevated areas, will give a longer period of snow melt, which in turn may give longer periods of sprouting vegetation. In drier, colder winters, snow melt will occur faster, and grazing animals will experience shorter periods of accessibility to the most nutritious feed.

2.2. Study animals

2.2.1. VHF-collared animals, Nordfjord

Of 57 animals with functioning VHF-collars in Nordfjord in 2006, 22 female red deer were radio tracked daily in the municipalities of Stryn, Gloppen and Jølster (Jølster belongs to

Sunnfjord, but for convenience we denote the VHF-animals as Nordfjord animals). The individuals were all marked with coloured ear tags (orange and yellow) and Televilt VHF collars during winter in the years 2001-2005 at locations in Nordfjord. Radio tracking was divided between me and another student for a total of 60 days in order to get information about day to day movement. One third of the tracking was done at night. The field periods were split into 30 days in February and March and 30 days during June, July and August to compare the use of habitat between seasons. To locate the animals, we used standard handheld Televilt and Telonics tracking equipment. We obtained a minimum of 3 bearings on each individual deer within a short time interval. Observer positions were taken with a handheld Garmin GPS. The animal bearings were later triangulated in order to estimate the location. We also calculated an associated error ellipse (White and Garrott, 1990) as a quality check on the accuracy of each position estimate (result not shown). Calculation of positions were conducted in the ecological software programme LOAS (Location Of A Signal, Ecological Software Solutions, USA).

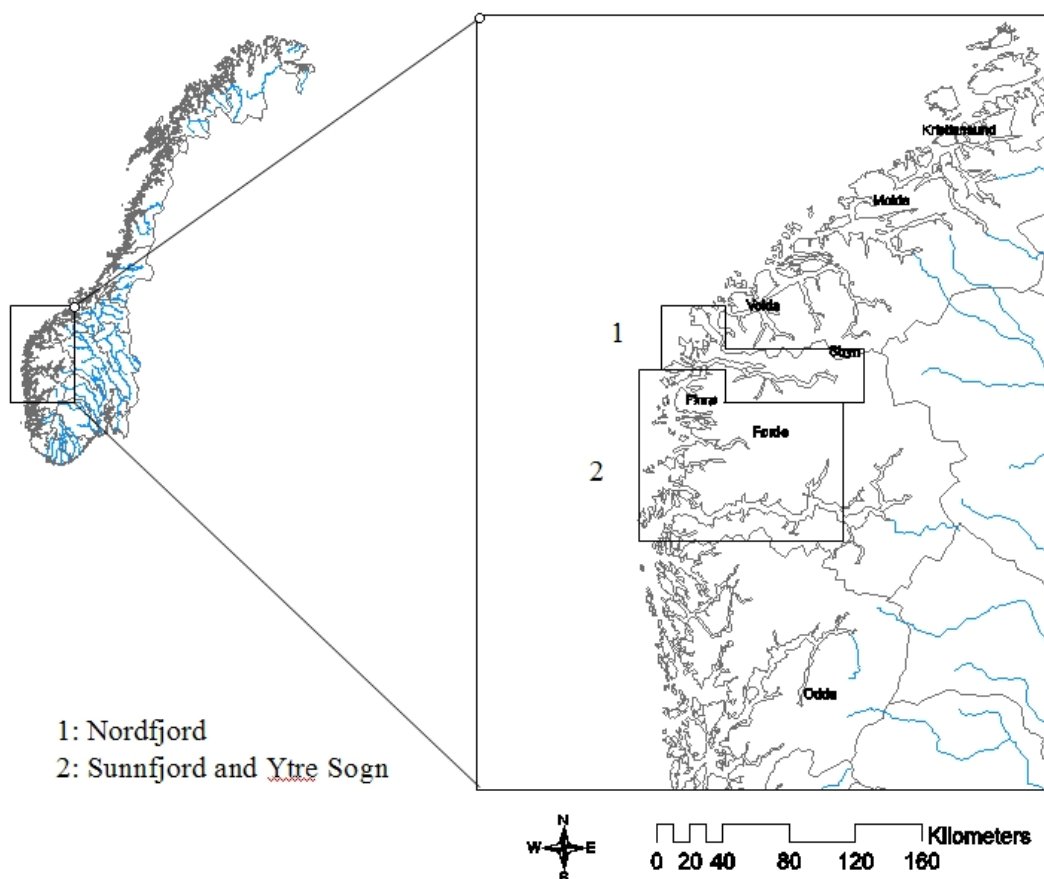


Fig. 1. Map depicting the study area in the western parts of southern Norway. Boxes show the defined areas inhabited by the study animals (Nordfjord and Sunnfjord/ Ytre Sogn).

2.2.2. GPS-collared animals, Sunnfjord

In Sunnfjord (municipalities of Ytre Sogn will also be referred to as Sunnfjord for convenience), 25 female deer were fitted with Televilt GPS collars in January to March 2005. Another 20 female deer were marked in March 2006. Of these, collars of 23 of the 2005 animals and 8 of the 2006 animals (a total of 31 deer) were retrieved by the start of my analysis. Each of them collected data for ca 9-10 months (Jan-Mar to Nov-Dec). They obtained positions at 1 hour intervals throughout the period. In addition they recorded locations at 6 minute intervals for 24 hours every 14 days. The collars were fitted with a drop-off mechanism which facilitated retrieval without killing or immobilizing the animal. After the retrieval of the collars, the saved information was downloaded using the program TPM (Tellus Project Manager, Televilt, Sweden). Locations taken before marking date and on the first day of marking were deleted. Locations where the animal had moved at speeds of more than 10 km per hour (typically less than 0.1% of locations) were inspected, and most of these locations were large GPS errors that could be removed based on impossible speed (in the order of several hundred kilometres per hour). Locations with realistic speed levels were removed if they were present either in water or on the opposite side of a fiord, and then only if the next location was in close proximity to the preceding location.

2.3. Statistical analyses

The year was divided into winter (1st of December- 31st of March), spring (1st of April- 31st of May), summer (1st of June -15th of August) and autumn (16th of August - 30th of November). Information on the VHF-collared animals (Nordfjord) was only available in the months of tracking, and analyses for these animals therefore comprises only five months, summarising the differences between the summer and winter months.

2.3.1. Maps

Digital maps were supplied by the Norwegian Forest and Landscape Institute (NIJOS). I used digital resource maps at 1:5000 with 50 m resolution. As the first step, different classes were combined into 8 groups consisting of 1) agricultural fields (90% grass, Yngve Rekdal, NIJOS, pers.comm.), 2) pastures, 3-5) forest of decreasing productivity classes, 6) marshes, 7) mountains/ bare rock (areas with shallow or uncultivated soil cover and rock outcrops) and 8) ocean, lakes and areas not described. In the following analyses, the habitat map was further simplified into groups of similar characteristics. Class 1 and 2 were combined to form the

agricultural areas, 3, 4 and 5 were combined in forest areas, 6 and 7 were left as separate groups and 8 were left out of the analyses, as deer were not expected to spend a lot of time in the water and no useful information would come from the areas not described. Pastures covered 6%, forests 81%, mountains 12% and marshes 1% of the utilized area in Nordfjord, whereas in Sunnfjord pastures covered 34%, forests 37.5%, mountains 24.5% and marshes 4% (proportions of the combined home ranges of all individuals in the respective area). Because marshes covered such a small part of the areas utilized, this category was not included in the analyses.

2.3.2. Migration

Several descriptive parameters regarding migration were calculated.

Distance. To find patterns of migration, the seasonal home ranges (see below) were plotted in ArcView GIS 3.3 to look for overlap of the summer and winter areas (see Appendix 1 and 2 for illustrations). Migration distance is the distance between mean summer and winter positions for individuals with non-overlapping summer and winter home ranges. We checked for differences in migration distance between Nordfjord and Sunnfjord using a linear model (LM) with distance as response variable and region as predictor variable. A GLM test was run to check the difference in the number of migrating (as opposed to stationary) animals in the two areas Nordfjord and Sunnfjord.

Timing. The time of year of the migration can only be found for the GPS-collared animals (Sunnfjord), as the VHF-collared animals (Nordfjord) only were tracked before and after the migration had taken place. Migration dates were found by plotting the Julian date against the cumulative distance of each location from the marking point (see Appendix 8). From the plots, the exact day of migration start and end could be found. In some cases, the animal travelled the distance between the summer and winter range several times during the summer (see Appendix 8), but there was still clearly defined home ranges, validating the decision to call the animal migratory.

Altitude. Seasonality in use of altitude was addressed by plotting mean altitude by month for the pooled data set (all individuals) with associated 95% confidence limits for the three regions “inland Sunnfjord”, “coastal Sunnfjord” and “Nordfjord”.

2.3.3. Home range

The home ranges were calculated by plotting a 95% minimum convex polygon (MCP, White and Garrott, 1990) and a 95% kernel area (Worton, 1989) for all animals, giving the areas with 95% probability of finding the animal during a given period.

Factors affecting home range size. The digital vegetation map was rasterised, in order to calculate the proportion of each habitat type within the home range of each animal. The mean altitude for each individual was calculated from the altitude of fixes in the GPS-collar and altitude estimated by LOAS from the tracking data. The effect of season, vegetation type, altitude and region on home range size was tested with LM models. Because the sum of proportion of pastures, forest and mountains is very close to one (mean=0.97), all three vegetation types could not be included as predictors in the same model (because one of the factors would be redundant). I therefore chose to analyse the effect of pasture, forest and mountain separately. I used the function stepAIC (in R library MASS) to select the best model, in all cases starting with the most complex model possible (including all predictor variables and combinations of interactions). In addition, the relationships between home range size and proportion of pastures, mountains and forests were plotted for the summer and winter seasons.

2.3.4. Habitat selection

To find the choice of habitat both within season and between areas, a multivariate analysis of variance (MANOVA) was run. The selection of habitat was ranked through an Aebischer compositional analysis of habitat use (COMPANA analysis).

The best model was found through selection based on the AIC criterion (Burnham and Anderson, 1998). Thereafter I present parameter estimates with associated standard errors and p-values from the best models.

I used the statistical programme R (R Development Core Team, 2006) version 2.4.0 with libraries adehabitat for the HR estimations and habitat selection analysis and gplots for the plotting.

3. Results

3.1. Migration

Distance. Partly confirming the first prediction (H1), a total of 52.8% (n= 53) were migratory. The median distance between summer and winter ranges was 6.8 km (range: 2.0- 34.5) and tended to be larger in Sunnfjord (14.1 km; range: 4.7-34.5 km) than in Nordfjord (8.4 km; range: 1.97-25.3 km; estimate=5.67, SE=3.06, t=1.86, p=0.075). There was a higher proportion of migratory deer in Nordfjord (63.6%) than in Sunnfjord (45.2%; estimate= 0.249, SE= 0.0964, t=2.59, p=0.011).

Timing. In Sunnfjord (GPS data), the median date for spring migration was 4th May (range: 17th April - 8th June) and for autumn migration 11th September (range: 19th June - 19th November). Median number of days spent on the migration was 1 in spring (range: 1-19 days) and 3 days in autumn (range: 1-15 days).

Altitude. Confirming the prediction (H1), red deer used higher altitudes in summer than in winter (Fig. 2). This was much more pronounced in the inland municipalities of Sunnfjord than in coastal municipalities in Sunnfjord and in Nordfjord (Fig. 2). In inland Sunnfjord, the animals migrate into higher areas in late spring and stay there during the summer and autumn months (May-October), before returning to the lower areas again in November/December. For the Nordfjord animals, there was not much difference in the use of the altitudinal gradient during summer and winter, but a larger spread was found in the summer than in the winter (Fig. 2).

3.2. Home range size

As predicted (H3), red deer used larger areas in summer (kernel: median=293.84 ha; MCP: median=155.64 ha) than in winter (kernel: 237.92 ha; MCP: 108.81 ha, Table 1). There was no difference between regions according to the kernel estimates and a marginal effect (included in the best model, but not significant) according to MCP estimates (least squares estimate= 0.5702, SE= 0.3938, t= 1.448, p= 0.15399). The distribution of home range sizes was highly skewed, with many animals having small home ranges and a few having very large ones (Fig. 3). Overall, home ranges were larger in Nordfjord than in Sunnfjord and the seasonal differences in home range size tended to be most pronounced in Sunnfjord (the interaction Season x Region in Table 1). Home range size increased with altitude in winter, but not in summer (Table 1; Fig. 4).

Contrary to the predictions (H4), home range size tended to increase with proportion of pastures in Nordfjord. In Sunnfjord there was no relationship between pastures and home range size (the best model presented in Table 1; Fig. 5 and 6). Forests had the predicted effect (H5), by increasing home range size, but in Nordfjord only (Table 1; Fig. 5 and 6). According to the best model, the negative relationship between proportions of woodland and home range size in Nordfjord was less pronounced in winter than in summer. Animals clearly include more mountainous areas in their summer range than in their winter range (points skewed to low proportion in winter; Fig. 5 and 6). Partly confirming the predictions (H6), proportion of mountain increased home ranges in the summer but not in winter in Sunnfjord, whereas in Nordfjord there was a positive relationship between proportion of mountains and home range size in both seasons (Table 1; Fig. 5 and 6).

There were outliers in the datasets, evident in the plots (filled red circles, Fig. 5 and 6). These were removed from the datasets and analyses rerun to check for effects (red lines of predicted values and standard errors, Fig. 5 and 6). Exclusion of outliers only altered the reported patterns to a minor extent (see Appendix 3).

3.3. Habitat selection patterns.

There was a difference in selection of habitat in summer and winter ($t= 0.346$, $p= <0.001$) and also differences in habitat selection between the two regions Sunnfjord and Nordfjord ($t= 0.279$, $p= <0.001$), but the seasonal patterns did not differ between the two study areas ($t= 0.018$, $p= 0.4155$). Forests were the most selected habitat type, closely followed by pastures during the winter season (Table 2). Only in Sunnfjord during winter are pastures ranked before forest, but the selection was not significantly stronger. During summer, the mountainous habitats become more important, but the forested areas are still the most selected habitat.

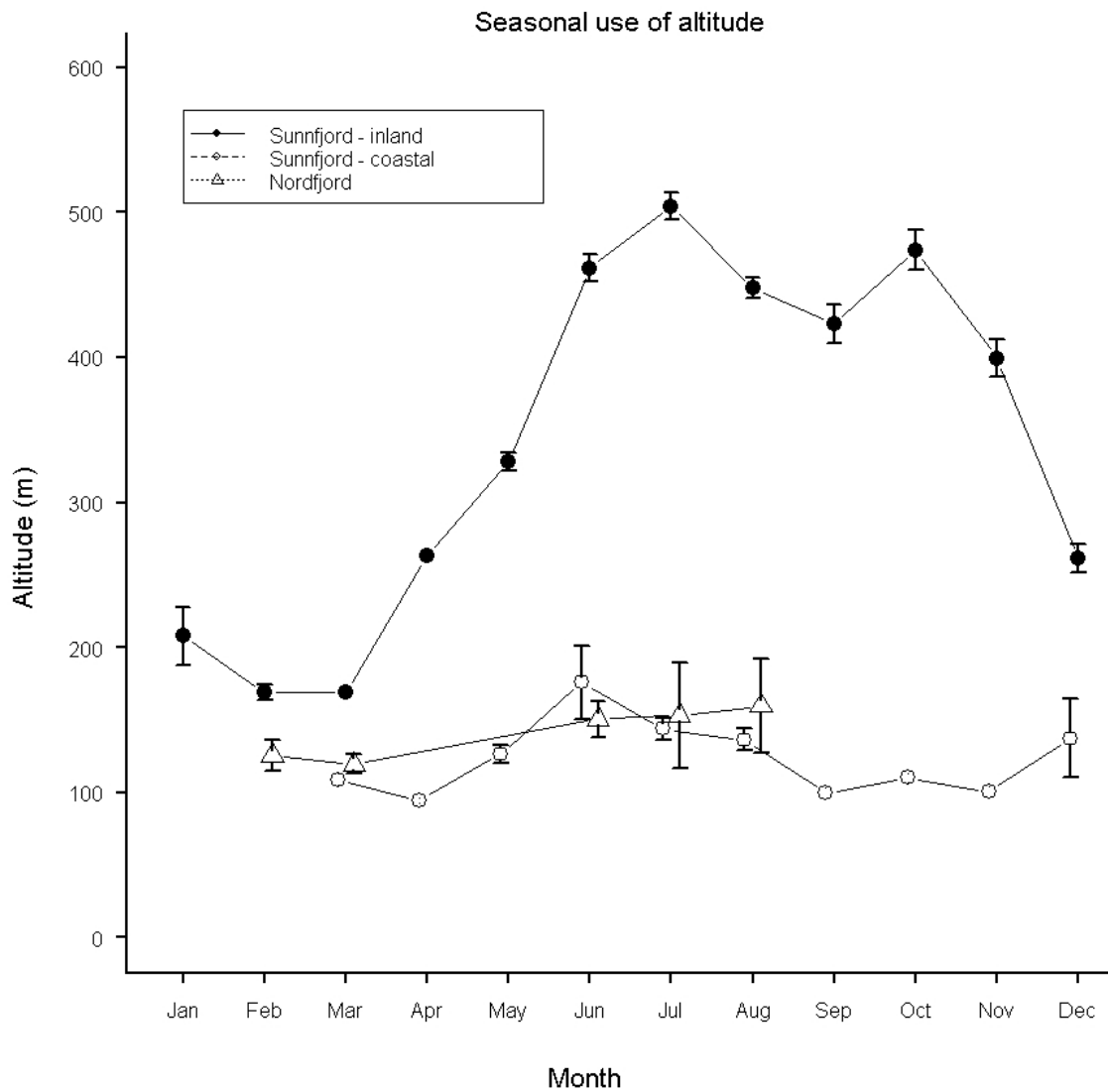


Fig. 2. The seasonal use of altitude by red deer in inland Sunnfjord (municipalities of Balestrand, Gaular and parts of Jølster), coastal Sunnfjord (municipalities of Fjaler and Askvoll) and Nordfjord (Gloppen, Stryn).

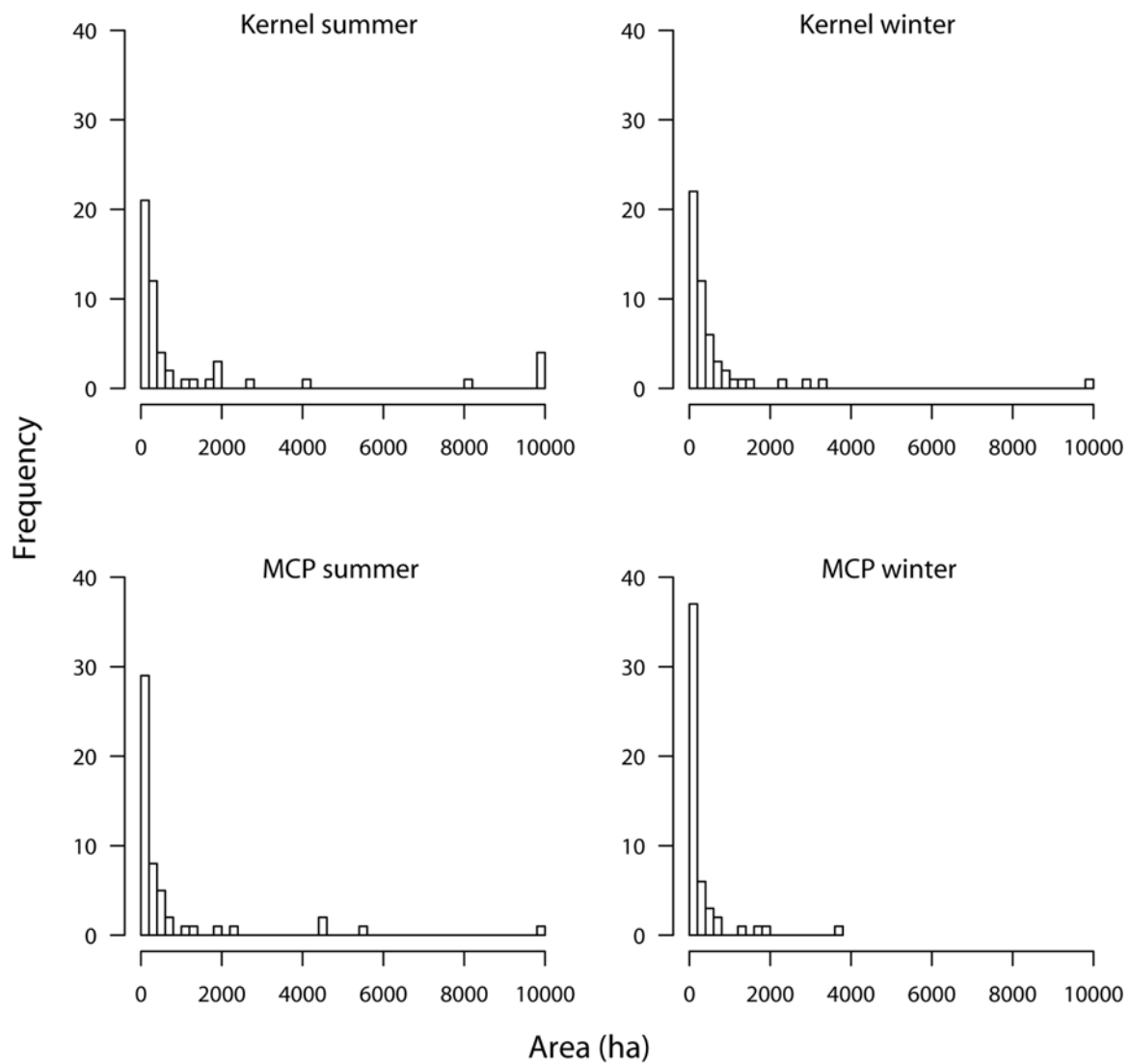


Fig. 3. Distribution of sizes of summer and winter home ranges of red deer in Sogn og Fjordane, Norway. The histogram is truncated at 10000 ha (see Appendix 1 for exact home ranges for all individuals).

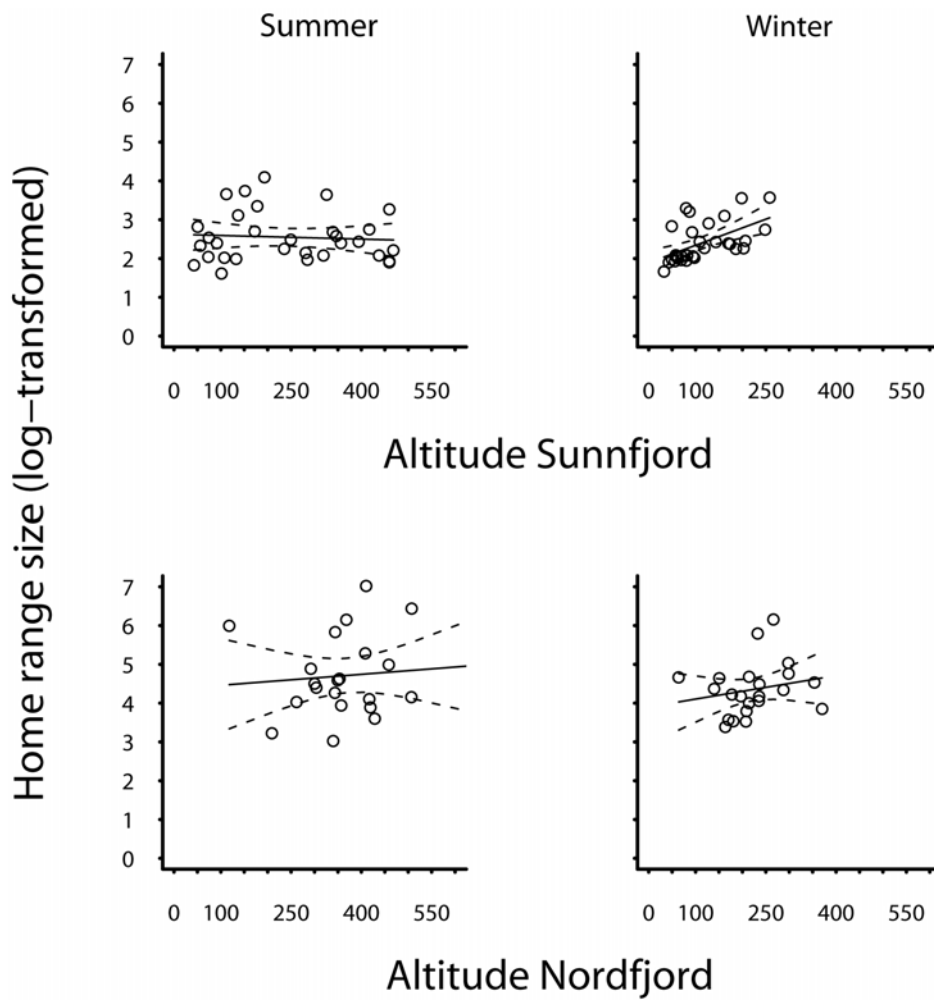


Fig. 4. The size of home range (log) for the red deer in Sunnfjord and Nordfjord depending on altitude, split into summer and winter seasons.

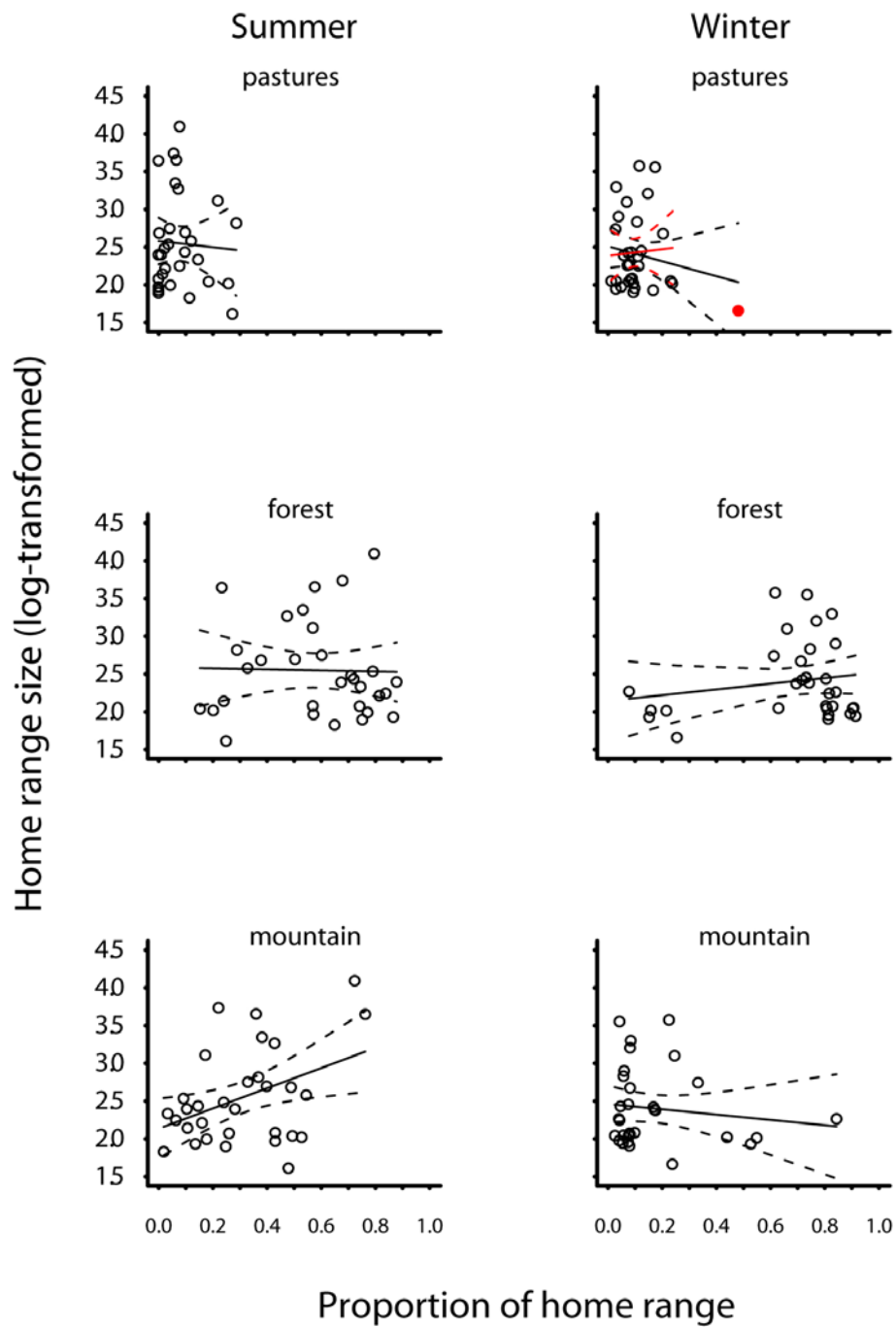


Fig. 5. The size of the home range (log) of the red deer in Sunnfjord, Norway, depending on the proportions of pastures, forest and mountainous areas within their home ranges. The filled red circle in the winter pasture plot signifies outlying point, with new estimate and standard error lines (in red) for parameter estimate excluding the outlier (see text).

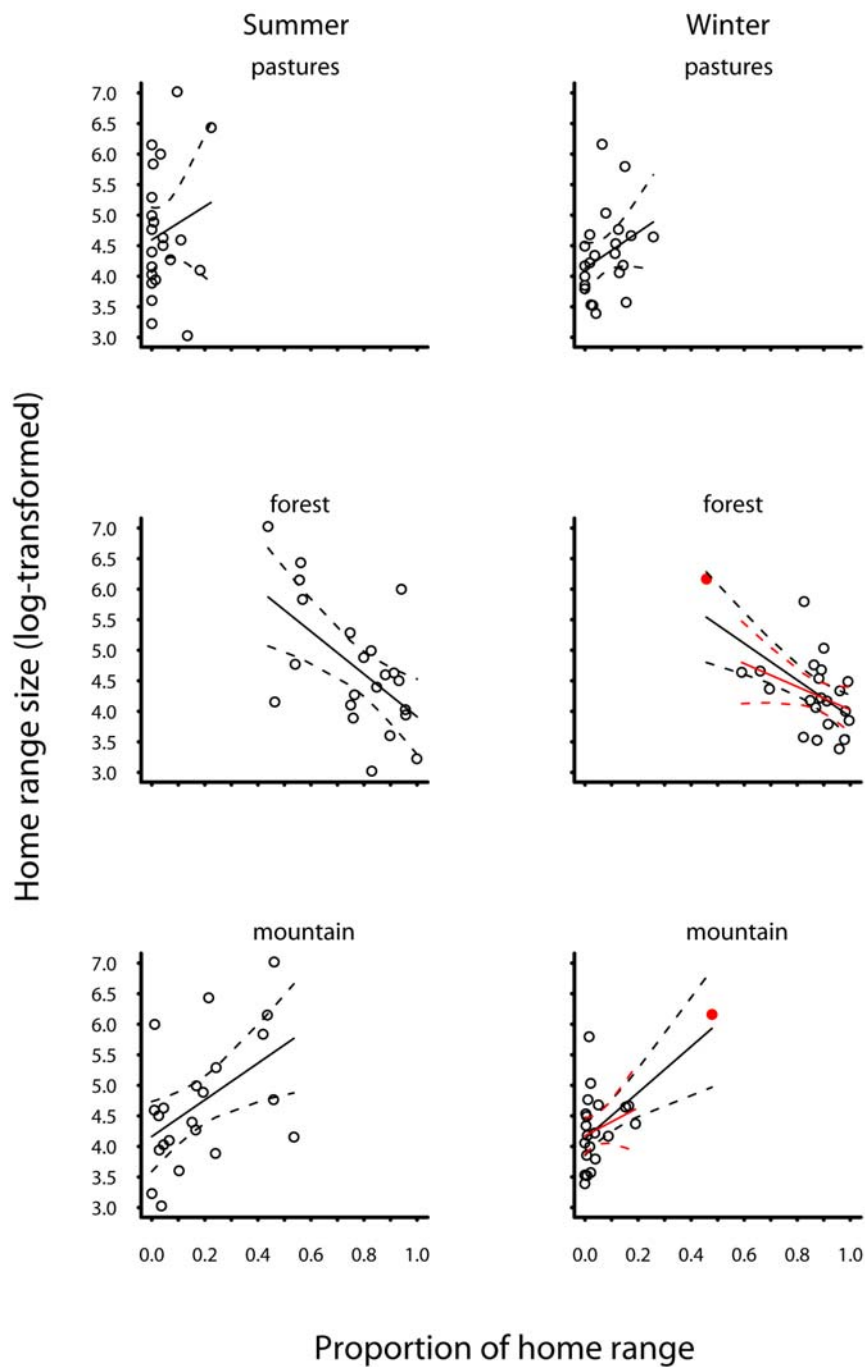


Fig. 6. Size of the home range (log) of the red deer in Nordfjord, Norway, depending on the proportions of pastures, forest and mountainous areas within their home range. The filled red circles in the winter forest and mountain plots signifies outlying points, with new estimate and standard error lines (in red) for parameter estimate excluding the outlier (see text).

Table 1. The best models for home range size (MCP method) in red deer. The reference level for Region is Nordfjord and the reference for Season is summer. Three separate models are run for the effect of proportion of pastures, forest and mountains.

Model	Least squares estimate	SE	t	p
Pastures				
Intercept	4.59	0.318	14.42	<0.001
Proportion pastures	3.47	1.576	2.20	0.030
Season (winter- summer)	-1.32	0.492	-2.67	0.009
Region (Sunnfjord- Nordfjord)	-1.92	0.248	-7.73	<0.001
Mean altitude	-0.0001	<0.001	-0.088	0.930
Proportion pastures x Region (Sunnfjord- Nordfjord)	-3.86	1.62	-2.38	0.019
Season (winter- summer) x Region (Sunnfjord- Nordfjord)	0.79	0.34	2.31	0.023
Season (winter- summer) x Mean altitude	0.0037	0.0017	2.23	0.028
Forest				
Intercept	10.42	0.985	10.58	<0.001
Proportion forest	-5.26	0.760	-6.92	<0.001
Season (winter- summer)	-3.75	0.891	-4.21	<0.001
Region (Sunnfjord- Nordfjord)	-7.56	0.983	-7.70	<0.001
Mean altitude	-0.0045	0.0014	-3.16	0.0021
Proportion forest x Season (winter- summer)	1.34	0.603	2.22	0.029
Proportion forest x Region (Sunnfjord- Nordfjord)	4.64	0.775	5.98	<0.001
Season (winter- summer) x Region (Sunnfjord- Nordfjord)	2.59	0.841	3.08	0.0027
Season (winter- summer) x Mean altitude	0.0091	0.0025	3.68	<0.001
Region (Sunnfjord- Nordfjord) x Mean altitude	0.0042	0.0016	2.63	0.0101
Season (winter- summer) x Region (Sunnfjord- Nordfjord) x Mean altitude	-0.0050	0.0031	-1.60	0.113
Mountains				
Intercept	4.55	0.567	8.03	<0.001
Proportion mountain	7.34	2.20	3.33	0.0012
Season (winter- summer)	-1.36	0.49	-2.77	0.0067
Region (Sunnfjord- Nordfjord)	-2.02	0.61	-3.31	0.0013
Mean altitude	-0.0015	0.0017	-0.90	0.373
Proportion mountain x Season (winter- summer)	-1.20	0.869	-1.38	0.170
Proportion mountain x Region (Sunnfjord- Nordfjord)	-7.08	2.14	-3.31	0.0013
Season (winter- summer) x Region (Sunnfjord- Nordfjord)	0.876	0.39	2.26	0.026
Proportion mountain x Mean altitude	-0.0080	0.0056	-1.43	0.157
Season (winter- summer) x Mean altitude	0.0055	0.0016	3.51	<0.001
Region (Sunnfjord- Nordfjord) x Mean altitude	-0.0004	0.0020	-0.186	0.853
Proportion mountain x Region (Sunnfjord- Nordfjord) x Mean altitude	0.0130	0.0064	2.03	0.045

Table 2. Result of Aebischer analyses ranking habitat use by red deer in Sunnfjord and Nordfjord. > signifies a difference between the habitat types, while no significant difference in use is marked by \geq .

Region - seasons	Habitat rankings
Sunnfjord - winter	pasture \geq forest > marsh > mountain
Sunnfjord - summer	forest > pasture \geq mountain \geq marsh
Nordfjord - winter	forest > pasture > marsh > mountain
Nordfjord - summer	forest > mountain \geq pasture \geq marsh

4. Discussion

I found evidence for differences in seasonal migration and home range strategies among female red deer, as half the individuals migrated between separate winter and summer ranges and the other half remained stationary the year round. Contrary to my prediction (H4), pastures increased home ranges. Forests were the selected habitat year round and decreased home ranges in the way pastures were expected to do. There were clear regional differences in the use of the altitudinal gradient and the animals utilizing mountain habitats had larger home ranges than those with more forested habitats. This suggests that even though animals are prone to move higher in summer in order to feed on highly nutritious forage (Albon and Langvatn, 1992), the more rocky habitats associated with higher altitudes may create a more patchy pattern of high quality food leading the animals to cross greater distances. Surprisingly, the duration of the spring migration was very short, which is not expected (H2) if migration is driven by the altitudinal variations in plant phenology.

4.1. Variation in movement strategies and landscape characteristics

Migration did not seem to be related to habitat quality, as populations with animals sharing winter home range areas had both migrating and stationary animals. The presence of both migratory and stationary individuals in the same population, termed partial migration (Ball et al., 2001), has often been reported. This indicates that migration is not a pure necessity for finding high quality foraging habitats, as plenty of animals stay in vicinity of the winter home range all year round. Had all animals stayed during summer, however, competition for forage would likely be increased. Red deer calves follow their mother through her migratory patterns the first year, and although the hinds may change routes to some extent, they seem to be quite faithful to the general annual pattern of their mother (Nelson, 1994, white-tailed deer). Stags will usually develop their own migratory patterns, but it seems that when a deer has developed a certain migratory pattern, it tends to keep to this for the rest of its life (Nelson and Mech, 1984, white-tailed deer). It seems migration patterns are heavily dependent on inheritance, and are therefore unlikely to change rapidly with variations in density or resources.

The main patterns of movement in the migrating half of the animals closely confirmed the prediction (H1) made on the basis of great amounts of literature on large northern herbivores (see Introduction). The animals kept to one home range during winter and

migrated during spring to a summer range, returning to the winter range during the autumn months (the median month being September). The animals moved to higher elevations during the summer months, a pattern clearly dependent on regional topography, as it was more pronounced in the inland municipalities of Sunnfjord. For the Nordfjord animals and the coastal living animals in Sunnfjord there were no difference in the use of altitude between seasons, but the Nordfjord animals did have a larger spread in the summer compared to the winter months. The larger spread in summer show that some animals stay in the lowlands while others move higher up the mountains as a response to the increasing amounts of available foraging areas following the snow melt in spring, which agrees with earlier studies (Albon and Langvatn, 1992; Bertram and Rempel, 1977; Georgii, 1980; Luccarini et al., 2006). The regional differences correspond to the differences in access to areas of higher altitude, as there are more accessible high areas in the inland.

4.2. Timing and speed of migration

Little information regarding speed of migration is reported in the literature, but with GPS technology it is possible to have this estimated much more precisely. Animals generally spent fewer days on the spring migration (1 day) than the autumn migration (3 days). Such a pattern deviates from what has been reported for red deer marked in Snillfjord, Sør-Trøndelag, which may use up to 3 weeks on migration from the winter to the summer range (Albon and Langvatn, 1992). Langvatn and Albon (1986) points out that patchy vegetation as a result of slow snow melt in some areas may lead to heterogeneity in plant quality, enabling deer to maximize their intake of digestible energy over a longer period in the higher areas than in the lowlands. Clearly, only 1 day of migration in spring cannot be the result of deer following the pace of plant growth on their migration route. The shorter distance between high and low elevation in Sogn og Fjordane may be part of the reason. If there is not much difference in the phenological development occurring over a few hundred metres difference in the altitudinal gradient, the animals may be encouraged to move more quickly during the spring migration in order to get to the most nutritious vegetation quickly. A similar pattern of very short duration of migration has been reported in roe deer (Mysterud, 1999).

The driving force of the initiation of the autumn migration is generally considered to be seasonal cues (Nelson, 1995; Sabine et al., 2002, white-tailed deer) like snowfall, falling temperature and senescence of vegetation. Snow is well known to drive deer down from summer ranges at a higher altitude (Georgii, 1980; Luccarini et al., 2006; Sabine et al., 2002).

In my study, however, some animals started the return migration in June, while others waited until November (see Appendix 5b). Animals which decide to stay until November may be utilizing areas where the vegetation is still of good quality. The combination of a large individual variation in time of departure from the summer area (Appendix 5b) and the longer time spent on the move indicate that severe climatic events (such as snowfall) may be less important in triggering autumn migration in Norwegian red deer than other temperate ungulates (Georgii, 1980; Luccarini et al., 2006; Sabine et al., 2002). Animals leaving the summer range early may be following a consistent alternative migration strategy, but data from several years would be needed to study this.

A pattern not often reported in the literature was that in many cases (35.7% of the migrating animals, Appendix 5b) animals were found to either return to the winter range several times during summer, return to the summer range after an initial autumn migration or even pass through the winter range on its way to another area (Appendix 9). Such trips may be important in discovering new areas of potentially better quality food. Red deer (Bertram and Rempel, 1977) and white-tailed deer (Nelson, 1995) have been reported to return to the summer range after the initial autumn migration in years with mild weather. A changing climate may therefore affect annual migration patterns to some extent. It is believed that a range of stimuli influences deer migration (Nicholson et al., 1997; Sabine et al., 2002). Factors like photoperiod and sudden cold spells may induce some animals to travel to the winter range, while milder temperatures and lack of snow might encourage them to return to the summer range for an additional period. Georgii (1980) points out that relatively open mountain forests can provide both food and shelter within short distances even at a more intermediate altitude, which may be a valuable habitat the deer are ultimately reluctant to leave. Some individuals may therefore delay the return to the winter range for as long as possible, until snow actually starts limiting mobility or food quality is too poor to be attractive. Delaying their migration can be a risky strategy, as the animals may get trapped by sudden snowfalls which increase mobility resistance and decrease forage accessibility (Sabine et al., 2002). In milder seasons with delayed onset of winter, it can be a valuable strategy though, as the growth season may be extended even at higher altitudes.

It is also likely that red deer compete with domestic animals, especially sheep, on the summer ranges, although so far there is no evidence of large scale competition (Myysterud et al., 2002). Increased intra- or interspecific competition in the winter range may induce animals to return to the summer ranges, while fear of getting trapped by snowfalls drive them back to the winter ranges during cold spells.

4.3. Home range size and large scale habitat selection

Seasonal home range sizes are assumed to reflect habitat quality, but energetic demands and distribution of patches are also likely to be decisive. In agreement with earlier studies, the summer home ranges were larger than the winter home ranges (Georgii, 1980; Georgii and Schröder, 1983; Luccarini et al., 2006). That summer ranges are larger is likely due to a higher demand for energy due to lactation and no snow restricting movement. When moving into more rocky areas, patches of high quality might be more widely dispersed inducing movement over a larger area. As snow is likely to inhibit mobility during the winter, it naturally follows that the winter home ranges are likely to be smaller, both because some areas may be inaccessible and since animals will try to reduce energy expenditure by moving less in deep snow. However, this is not always the case. Anderson (2005) found that elk (the same species as our red deer) home ranges in relatively open areas increased in winter and attributed this to the predator pressure inflicted by wolves (*Canis lupus*), population densities and reduced quantity and quality of forage. This suggests that differences in study sites are important. In addition to different topography, elk in North America are, due to the large wolf population, exposed to a completely different predator pressure than Norwegian red deer. This is likely to affect space use patterns.

A few animals had very large home ranges, creating a highly skewed distribution, and there was a greater spread in the summer than in the winter range sizes. That some animals had such large ranges is likely due to differences in habitat quality, as it is necessary to roam over larger areas where there are scattered foraging patches or generally lower forage quality. It may also be that females without calves move over greater areas, but home range size related to presence of calves could not be checked, as I had no information on whether females had a calf or not.

Summer home range sizes did not increase with altitude, which was unexpected, as altitude is generally associated with more rocky areas where preferred forage is likely to be more dispersed. There was an effect of proportion of mountainous areas, however. This discrepancy might partly be caused by a non-linear relationship between altitude and mountainous habitat, with little mountainous areas up to a certain altitude and then a sudden increase up to the highest areas. Home ranges increased with altitude in winter, though, which may be linked to snow depth. When moving higher up the altitudinal gradient where snow is usually deeper, animals are more likely to have to move further in order to find enough patches of food of sufficient quality, or areas where food is accessible at all. In agreement

with the findings of Schmidt (1993), access to high quality habitats is clearly more important than altitude in itself. My findings are therefore consistent with the view that mountainous habitats are inferior deer habitats, as good quality foraging patches are more widely dispersed.

Contrary to my prediction (H4), home range size increased with proportion of pastures in Nordfjord. This was unexpected, as food supply is regarded as being a main determinant of home range size. I assumed that pastures would signify large patches of high quality food, thereby decreasing home range size, as the animals would have more accessible food within a small area. The regional differences suggest that the dispersion of forest and pasture habitat patches likely plays a role (Lovari and San Jose, 1997). Even if the periods of effective foraging are spent within a smaller area, the animals still need to travel between the shelter and feeding areas. While pastures provide abundant food, forest habitats supply the animals with both food and cover. Indeed, true to the predicted scenario (H6), high proportions of forest habitat decreased home range size, suggesting that forests provide access to an adequate mix of food and cover. I did not have access to vegetation maps with specified forest types, but forests of mixed vegetation may give high quality food as well as shelter, thus representing a very important habitat combining sheltering and foraging opportunities. Schmidt (1993) found that animals utilizing foraging stations spent more time travelling than those that did not rely on supplementary feeding. This implies that animals that make use of food related to pastures and general agricultural areas may need to travel further between sheltered resting places and feeding areas, than animals that utilize the naturally available resources. The pastures may also be small and far between in some areas, thereby forcing the animals to travel further to get from one good patch to the other.

5. Concluding remarks

Though the main patterns of migration were similar to many earlier studies, the rapid spring migration seen in this study differs greatly from the studies reporting slow spring migration of deer due to a gradual green-up in the altitudinal gradient (Albon and Langvatn, 1992).

Differences in climate and topography are likely reasons, where the steeper gradients of Sogn og Fjordane cause the deer to rely on other cues than simply the first green-up. This highlights that regional differences in topography, habitat availability or climate may not only affect proportion of migrants and specific details about the seasonal movement patterns of northern ungulates, but possibly also the causes of migration. Elevated summer ranges have nutritious forage but lower biomass. In high-density areas, a rapid migration from winter to summer ranges may contain a competitive aspect in terms of accessing the best vegetation.

A return to the summer range in autumn is likely a matter of competition in the winter range. Winter ranges constitute a more concentrated area which animals are forced into by necessity. By making use of the summer ranges for as long as possible, the time spent in areas of higher animal density can be minimized.

6. References

- Albon SD, Langvatn R, 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* 65:502-513.
- Anderson DP, Forester JD, Turner MG, Frair JL, Merrill EH, Fortin D, Mao JS, Boyce MS, 2005. Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecology* 20:257-271.
- Baker RR, 1978. Seasonal return migration by terrestrial mammals. In: *The Evolutionary Ecology of animal movement*, 1 ed. London: Hodder and Stoughton; 526-555.
- Ball JP, Nordengren C, Wallin K, 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildlife Biology* 7:39-47.
- Bertram RC, Rempel RD, 1977. Migration of the North Kings deer herd. *California Fish and Game* 63:157-179.
- Burnham KP, Anderson DR, 1998. *Model selection and inference: a practical information-theoretic approach*. New York: Springer.
- Burt WH, 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346.
- Börger L, Franconi N, Ferretti F, Meschi F, de Michele G, Gantz A, Manica A, Lovari SaC, T., 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *The American Naturalist* 168:471-485.
- Cederlund G, 1994. Home-range size in relation to age and sex in moose. *Journal of Mammalogy* 75:1005.
- Cederlund GN, 1988. Home range and habitat use of adult female moose. *The Journal of Wildlife Management* 52:336.
- Drickamer LC, Vessey SH, Meikle D, 1996. *Animal Behavior- mechanisms, ecology, evolution*, 4 ed. Dubuque: Wm. C. Brown.
- Edge WD, 1985. Effects of logging activities on home-range fidelity of elk. *The Journal of Wildlife Management* 49:741.
- Georgii B, 1980. Home range patterns of female red deer (*Cervus elaphus L.*) in the Alps. *Oecologia* 47:278-285.
- Georgii B, Schröder W, 1983. Home range and activity patterns of male red deer (*Cervus elaphus L.*) in the Alps. *Oecologia* 58:238-248.
- Institute of Meteorology,
http://met.no/observasjoner/sogn_og_fjordane/normaler_for_kommune_1445.html?kommuner, station no 58070, 58320. Precipitation and temperature information.
- Langvatn R, Albon SD, 1986. Geographic clines in body weight of Norwegian red deer: a novel explanation of Bergmann's rule? *Holarctic Ecology* 9:285-293.
- Langvatn R, Hanley TA, 1993. Feeding-patch choice by red deer in relation to foraging efficiency. *Oecologia* 95:164.
- Langvatn R, Mysterud A, Stenseth NC, and Yoccoz NG, 2004. Timing and synchrony of ovulation in red deer constrained by short northern summers. *The American Naturalist* 163:763-772.
- Lovari S, San Jose C, 1997. Wood dispersion affects home range size of female roe deer. *Behavioural Processes* 40:239-241.
- Luccarini S, Mauri L, Ciuti S, Lamberti P, Apollonio M, 2006. Red deer (*Cervus elaphus*) spatial use in the Italian Alps: home range patterns, seasonal migrations, and effects of snow and winter feeding. *Ethology, Ecology and Evolution* 18:127-145.
- Mysterud A, 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. *Journal of Zoology* 247:479-486.

- Mysterud A, Langvatn R, Yoccoz NG, Stenseth NC, 2001a. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *Journal of Animal Ecology* 70:915-923.
- Mysterud A, Langvatn R, Yoccoz NG, Stenseth NC, 2002. Large-scale habitat variability, delayed density effects and red deer populations in Norway. *Journal of Animal Ecology* 71:569–580.
- Mysterud A, Pérez-Barbería FJ, Gordon IJ, 2001b. The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. *Oecologia* 127:30.
- Mysterud A, Yoccoz NG, Stenseth NC, Langvatn R, 2000. Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *Journal of Animal Ecology* 69:959–974.
- Nelson ME, 1994. Migration bearing and distance memory by translocated white-tailed deer, *Odocoileus virginianus*. *The Canadian Field-Naturalist* 108:74-76.
- Nelson ME, 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. *Canadian Journal of Zoology* 73:1069-1076.
- Nelson ME, Mech LD, 1984. Home-range formation and dispersal of deer in northeastern Minnesota. *Journal of Mammalogy* 65:567-575.
- Nicholson MC, Bowyer RT, Kie JG, 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. *Journal of Mammalogy* 78:483-504.
- O'Neill RV, Milne BT, Turner MG, Gardner RH, 1988. Resource utilization scales and landscape pattern. *Landscape Ecology* 2:63-69.
- Pettorelli N, Gaillard J-M, Laere G, Duncan P, Kjellander P, Liberg O, Delorme D, Maillard D, 2002. Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. *Proceedings of the Royal Society B* 269:747-753.
- R Development Core Team, 2006. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; Statistical programme.
- Sabine DL, Morrison SF, Whitlaw HA, Ballard WB, Forbes GJ, Bowman J, 2002. Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. *The Journal of Wildlife Management* 66:718-728
- Schmidt KL, 1993. Winter ecology of non-migratory Alpine red deer. *Oecologia* 95:226-233.
- Sinclair ARE, 1983. The function of distance movement in vertebrates. In: *The Ecology of Animal Movement* (Swingland IR, Greenwood PJ, eds). New York: Oxford University Press; 240-258.
- Sweaner PYL, 1988. Migratory behavior of related moose. *Ecography* 11:190-193.
- Szemethy L, Mátrai K, Katona K, Orosz S, 2003. Seasonal home range shift of red deer hinds, *Cervus elaphus*: are there feeding reasons? *Folia Zool* 52:249-258.
- Tierson WC, Mattfeld GF, Sage RWJ, Behrend DF, 1985. Seasonal movements and home ranges of white-tailed deer in the Adirondacks. *Journal of Wildlife Management* 49:760-769.
- Tufto J, Andersen R, Linnell J, 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *The Journal of Animal Ecology* 65:715-724.
- White GC, Garrott RA, 1990. *Analysis of wildlife radio-tracking data*. London: Academic Press.
- Worton BJ, 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168.

Appendices

Appendix 1. Kernel and MCP home ranges of all individuals

Kernel and MCP home ranges of all individuals, winter and summer and information on whether the animal is migratory or not.

Region	Municipality	ID	Kernel summer	Kernel winter	MCP winter	MCP summer	Migratory
Nordfjord	Gloppen	2	72.68	146.83	57.95	20.60	Yes
Nordfjord	Gloppen	16	189.80	153.84	47.04	51.51	No
Nordfjord	Gloppen	40	181.08	137.65	34.24	71.54	Yes
Nordfjord	Gloppen	56	192.67	318.05	35.69	63.65	Yes
Nordfjord	Gloppen	62	1897.87	124.21	33.90	342.22	No
Nordfjord	Gloppen	97	320.61	530.13	153.46	117.64	Yes
Nordfjord	Gloppen	107	161.02	660.24	116.96	60.32	Yes
Nordfjord	Gloppen	126	1823.58	702.41	76.66	98.97	No
Nordfjord	Gloppen	142	1088.59	2917.51	474.25	102.40	No
Nordfjord	Gloppen	151	194.37	178.33	54.64	48.76	Yes
Nordfjord	Gloppen	161	159.80	198.09	68.02	56.06	Yes
Nordfjord	Gloppen	192	1670.08	435.31	105.78	403.04	No
Nordfjord	Gloppen	208	19301.58	241.16	93.18	1122.36	Yes
Nordfjord	Gloppen	221	1280.29	178.77	44.37	468.93	Yes
Nordfjord	Gloppen	359	550.81	404.53	107.59	198.14	Yes
Nordfjord	Gloppen	462	680.54	1008.26	329.02	147.38	Yes
Nordfjord	Gloppen	027breim	111.05	208.90	65.34	36.69	Yes
Nordfjord	Gloppen	27foleide	71.11	129.09	29.59	25.14	No
Nordfjord	Stryn	25	284.98	412.22	103.82	90.17	Yes
Nordfjord	Stryn	231	31274.08	278.27	78.99	622.14	No
Nordfjord	Stryn	371	320.59	549.84	89.15	132.31	Yes
Nordfjord	Stryn	5olden	318.85	240.03	64.60	81.12	No
Sunnfjord	Askvoll	034_06	156.22	253.36	85.10	109.73	No
Sunnfjord	Askvoll	175_06	46.83	1542.12	185.54	41.08	No
Sunnfjord	Askvoll	350_06	444.79	125.40	103.39	658.38	No
Sunnfjord	Askvoll	395_06	80.93	66.09	45.78	104.23	No
Sunnfjord	Askvoll	434_06	484.95	126.35	105.02	483.82	Yes
Sunnfjord	Balestrand	009_05	302.70	103.32	90.46	303.08	Yes
Sunnfjord	Balestrand	034_05	228.32	126.28	113.12	248.93	Yes
Sunnfjord	Balestrand	045_05	388.58	623.92	473.53	496.20	No
Sunnfjord	Balestrand	088_05	92.01	98.84	111.27	78.81	No
Sunnfjord	Balestrand	119_05	108.97	134.48	121.08	93.05	No
Sunnfjord	Balestrand	175_05	143.12	82.13	94.34	120.90	No
Sunnfjord	Balestrand	215_05	116.48	101.92	80.33	118.75	No
Sunnfjord	Balestrand	224_05	8175.78	3396.59	1608.26	4509.30	No
Sunnfjord	Balestrand	259_05	80.33	88.78	87.98	85.39	No
Sunnfjord	Balestrand	269_05	105.53	105.25	118.74	98.67	Yes
Sunnfjord	Fjaler	339_05	10614.00	2321.71	1984.87	5486.06	Yes
Sunnfjord	Fjaler	385_05	369.52	851.30	797.88	343.82	No
Sunnfjord	Fjaler	422_05	77.81	355.64	270.71	67.43	No
Sunnfjord	Fjaler	434_05	253.45	152.57	110.03	249.47	Yes

Sunnfjord	Fjaler	445_05	262.08	820.69	680.96	215.12	No
Sunnfjord	Gaular	205_06	784.07	198.24	111.95	1294.88	Yes
Sunnfjord	Gaular	250_06	4071.91	357.79	284.65	4427.56	Yes
Sunnfjord	Gaular	455_06	18786.93	215.65	176.97	12474.42	No
Sunnfjord	Jølster	074_05	152.18	229.01	243.98	379.82	Yes
Sunnfjord	Jølster	205_05	2782.03	1269.82	1255.36	2226.15	No
Sunnfjord	Jølster	250_05	214.51	235.81	239.02	176.85	No
Sunnfjord	Jølster	280_05	1903.79	435.25	551.09	1853.46	Yes
Sunnfjord	Jølster	350_05	151.88	364.87	264.85	163.90	Yes
Sunnfjord	Jølster	360_05	575.43	190.75	182.94	560.61	Yes
Sunnfjord	Jølster	395_05	305.24	24219.06	3756.66	271.93	Yes
Sunnfjord	Jølster	455_05	113.0	121.0	146.0	139.0	Yes

Appendix 2. Numbers of tried and successful GPS fixes

Numbers of tried and successful GPS fixes for each of the GPS-collared animals. Frequency 124088 started working poorly in September, success rate until then was 89%.

Number	Year	Frequency	Tried	Success	% success
1	2005	142088	12053	9249	77
2	2005	142215	15672	12720	81
3	2005	142434	13995	12062	86
4	2005	142074	14676	12975	88
5	2005	142455	13824	12397	90
6	2005	142395	15057	13606	90
7	2005	142250	15769	14480	92
8	2005	142445	13987	12886	92
9	2005	142259	15219	14080	93
10	2005	142422	13994	13354	95
11	2005	142360	14040	13466	96
12	2005	142350	13249	12810	97
13	2005	142175	10700	9310	87
14	2005	142205	16462	14707	89
15	2005	142269	15765	14149	90
16	2005	142034	16583	15371	93
17	2005	142119	14590	11598	79
18	2005	142009	16583	15170	91
19	2005	142339	14042	12637	90
20	2005	142045	16636	14796	89
21	2005	142280	15426	14799	96
22	2005	142385	14699	13908	95
23	2005	142224	16571	14353	87
24	2006	142034	11868	11689	98
25	2006	142175	11868	10127	85
26	2006	142205	12419	10598	85
27	2006	142250	12780	11872	93
28	2006	142350	12971	11949	92
29	2006	142395	12399	11456	92
30	2006	142434	12971	12185	94
31	2006	142455	12782	12106	95
Average:			14182	12802	90

Appendix 3. The best models for factors affecting home range size, excluding outliers

The best models for factors affecting home range size (MCP method) in red deer, excluding the outliers in the datasets. The reference level for Region is Nordfjord and the reference for Season is summer. Compared to Table 1 in the results, there was a slight increase in regional differences with proportion of pastures and a decrease in regional differences with proportion of mountains. “L.s.est” signifies least squares estimate.

Models	L.s.est	SE	t	p
Pastures				
Intercept	5.03	0.384	13.0890	<0.001
Proportion pastures	-11.93	5.244	-2.2750	0.025
Season (winter- summer)	-0.837	0.309	-2.7080	0.008
Region (Sunnfjord- Nordfjord)	-2.293	0.260	-8.8030	<0.001
Mean altitude	-0.001	<0.001	-1.0940	0.277
Proportion pastures x Season (winter- summer)	9.065	4.0670	2.2290	0.028
Proportion pastures x Region (Sunnfjord- Nordfjord)	7.544	4.2580	1.7720	0.080
Season (winter- summer) x Region (Sunnfjord- Nordfjord)	0.522	0.4047	1.2890	0.20
Proportion pastures x Mean altitude	0.034	0.0110	3.0590	0.003
Proportion pastures x Season (winter- summer) x Region (Sunnfjord- Nordfjord)	-7.18	4.6200	-1.5540	0.124
Forest				
Intercept	10.73	2.4112	4.4480	<0.001
Proportion forest	-5.92	2.7622	-2.1450	0.035
Season (winter- summer)	-4.22	2.0284	-2.0810	0.040
Region (Sunnfjord- Nordfjord)	-9.06	2.4731	-3.6640	<0.001
Mean altitude	-0.0055	0.0053	-1.0400	0.301
Proportion forest x Season (winter- summer)	2.68	2.2939	1.1690	0.246
Proportion forest x Region (Sunnfjord- Nordfjord)	7.61	2.8932	2.6310	0.010
Season (winter- summer) x Region (Sunnfjord- Nordfjord)	3.74	2.0996	1.7830	0.078
Proportion forest x Mean altitude	0.0022	0.0064	0.3350	0.739
Season (winter- summer) x Mean altitude	0.0063	0.0016	3.8990	<0.001
Region (Sunnfjord- Nordfjord) x Mean altitude	0.010	0.0058	1.7440	0.085
Proportion forest x Season (winter- summer) x Region (Sunnfjord- Nordfjord)	-3.44	2.4198	-1.4200	0.159
Proportion forest x Region (Sunnfjord- Nordfjord) x Mean altitude	-0.010	0.0073	-1.4290	0.157
Mountain				
Intercept	4.56	0.5859	7.7780	<0.001
Proportion mountain	6.83	2.4195	2.8230	0.0058
Season (winter- summer)	-1.44	0.4925	-2.9140	0.0045
Region (Sunnfjord- Nordfjord)	-1.74	0.6227	-2.7970	0.0063
Mean altitude	-0.0015	0.0017	-0.8510	0.397
Proportion mountain x Region (Sunnfjord- Nordfjord)	-7.61	2.5363	-3.0000	0.0035
Season (winter- summer) x Region (Sunnfjord- Nordfjord)	0.672	0.3776	1.7790	0.079
Proportion mountain x Mean altitude	-0.007	0.0059	-1.1960	0.235
Season (winter- summer) x Mean altitude	0.0056	0.0016	3.4530	<0.001
Region (Sunnfjord- Nordfjord) x Mean altitude	-0.0012	0.0020	-0.5790	0.564
Proportion mountain x Region (Sunnfjord- Nordfjord)x Mean altitude	0.015	0.0069	2.1500	0.034

Appendix 4. Output from the Aebischer analyses.

The lines signify selection of habitats, where forest is selected before the other habitats the year round, only challenged by pastures in the winter in Sunnfjord. Marshes and mountainous areas are the least selected.

Sunnfjord winter				
Habitat type	Pasture	Forest	Marsh	Mountain
Pasture	-----			
Forest	-----			
Marsh			-----	
Mountain				-----
Sunnfjord summer				
Habitat type	Forest	Pasture	Mountain	Marsh
Forest	-----			
Pasture		-----		
Mountain		-----		
Marsh		-----		
Nordfjord winter				
Habitat type	Forest	Pasture	Marsh	Mountain
Forest	-----			
Pasture		-----		
Marsh			-----	
Mountain				-----
Nordfjord summer				
Habitat type	Forest	Mountain	Pasture	Marsh
Forest	-----			
Mountain		-----		
Pasture		-----		
Marsh		-----		

Appendix 5a. Migration information on the Nordfjord (VHF-collared animals)

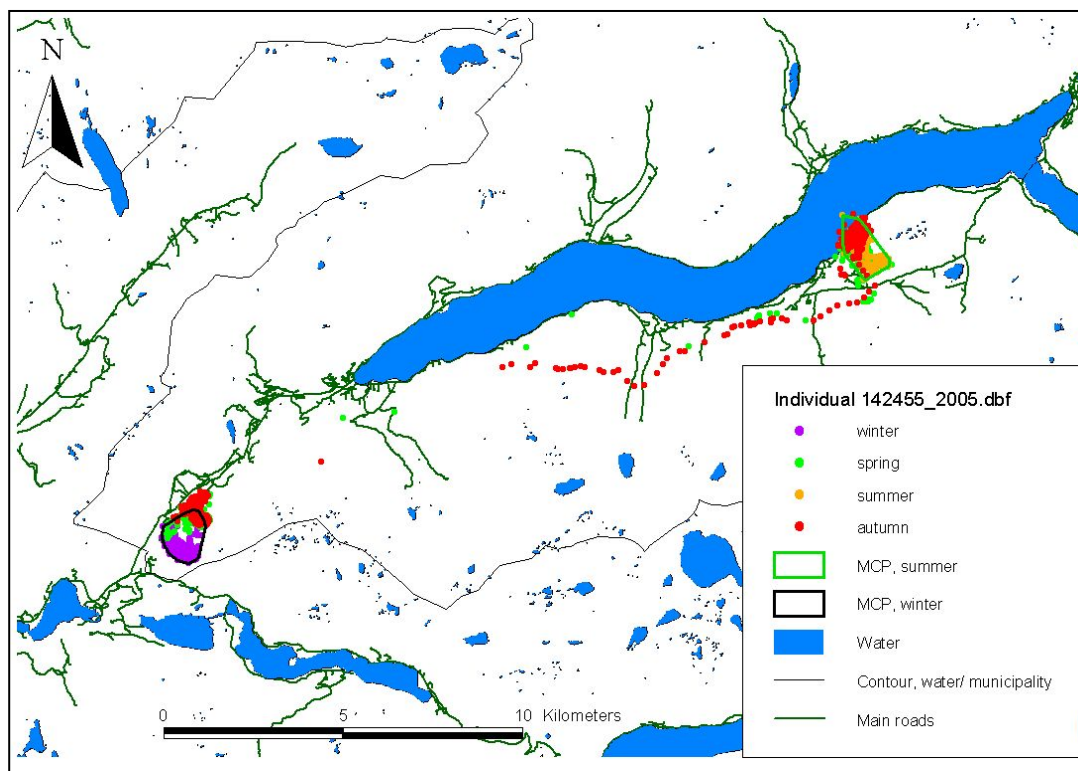
Migration distance between winter and summer home ranges in Nordfjord (VHF-collared animals).

Id	km
107	2.15
151	2.82
161	1.97
2	18.27
208	6.65
221	4.56
25	12.07
27breim	5.75
359	3.95
371	25.25
40	5.95
462	16.08
56	5.73
97	5.71

Appendix 5b. Migration information for the Sunnfjord (GPS-collared) animals

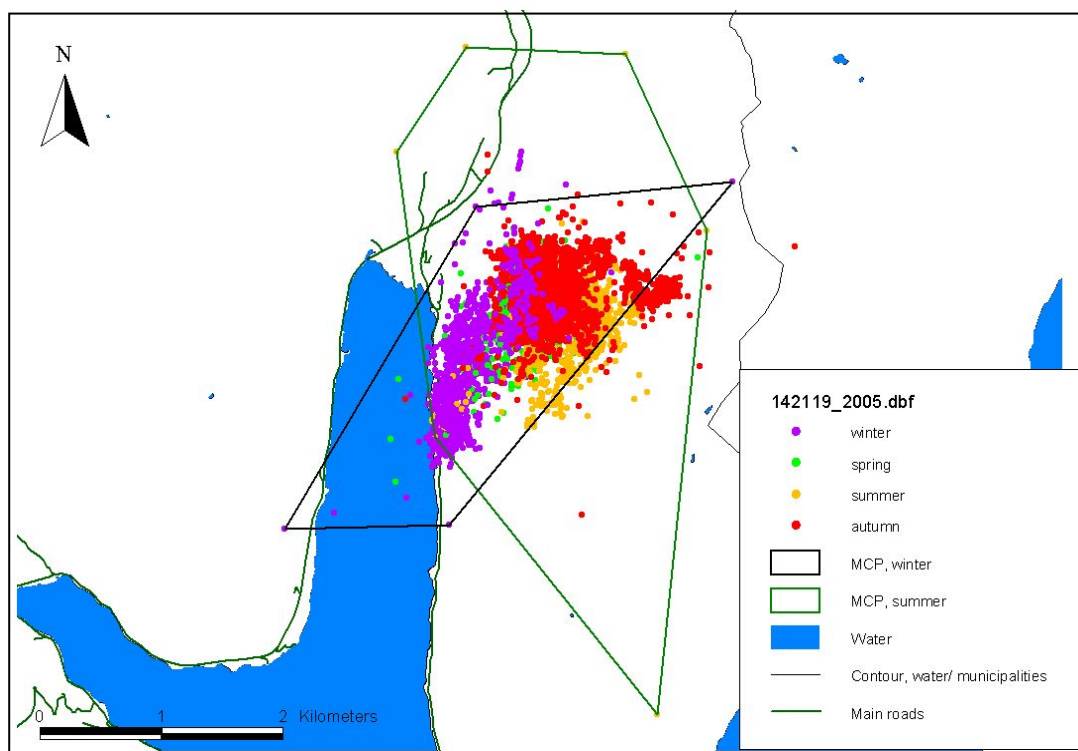
The abbreviation “Migr.” stands for migration, “med” denotes median days. Columns “Days” contains days spent on migration. Return column shows animals that either did trips back to the winter range (Yw), or returned to summer range after initial autumn migration (Ys).

Id	Distance between HR (km)	Migr. start, spring	Migr. end, spring	Days	Migr. month	Migr. start, autumn	Migr. end, autumn	Days	Migr. month	Speed in spring km/hr	Speed in autumn km/hr	Return
009_05	5.23	10.05.2005	11.05.2005	1	May	12.09.2005	14.09.2005	1	Sept	0.315	0.505	N
034_05	4.65	02.05.2005	03.05.2005	1	May	10.09.2005	15.09.2005	5	Sept	0.187	0.255	N
074_05	12.03	24.04.2005	25.04.2005	1	April	18.09.2005	22.09.2005	4	Sept	0.454	0.280	N
205_06	5.32	08.06.2006	08.06.2006	1	June	28.08.2006	30.08.2006	1	Aug	0.414	0.491	N
250_06	34.52	24.05.2006	12.06.2006	19	April	10.09.2006	17.09.2006	6	Sept	0.216	0.630	N
269_05	5.64	01.05.2005	02.05.2005	1	May	15.09.2005	01.10.2005	15	Sept	0.219	0.269	Yw
280_05	15.24	17.04.2005	18.04.2005	1	April	06.11.2005	16.11.2005	9	Nov	0.458	0.347	Yw
339_05	12.92	30.05.2005	30.05.2005	1	May	19.06.2005	22.06.2005	3	June	0.455	0.311	Ys
350_05	12.28	21.04.2005	22.04.2005	2	April	13.11.2005	14.11.2005	2	Oct	0.329	0.614	Ys
360_05	13.77	11.05.2005	13.05.2005	2	May	09.09.2005	10.09.2005	3	Sept	0.402	0.556	N
395_05	18.94	17.05.2005	19.05.2005	2	May	02.09.2005	03.09.2005	1	Sept	0.262	0.626	Ys
434_05	6.94	19.04.2005	19.04.2005	1	April	19.11.2005	20.11.2005	1	Nov	0.314	0.209	N
434_06	28.72	07.05.2006	11.05.2006	3	May	07.09.2006	11.09.2006	4	Sept	0.629	0.542	N
455_05	20.07	17.04.2005	19.04.2005	1	April	07.11.2005	08.11.2005	1	Nov	0.496	0.680	N
				med: 1					med: 3			
												35.7% Y



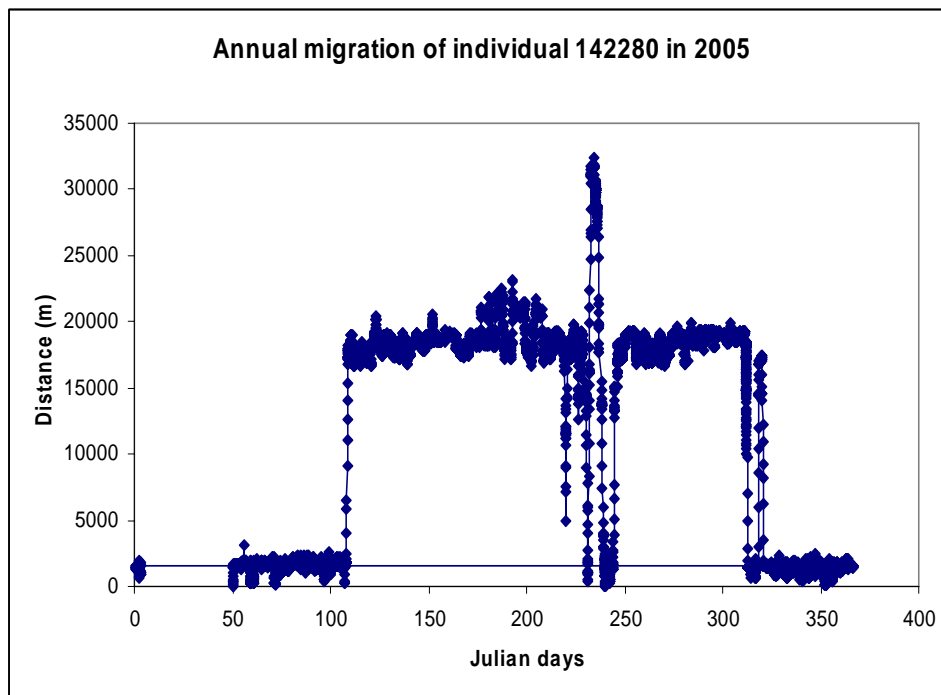
Appendix 6. Annual pattern of a migratory individual

Annual pattern of a migratory individual (142455 in 2005) with clearly separated summer and winter home ranges, and spring and autumn migrations.



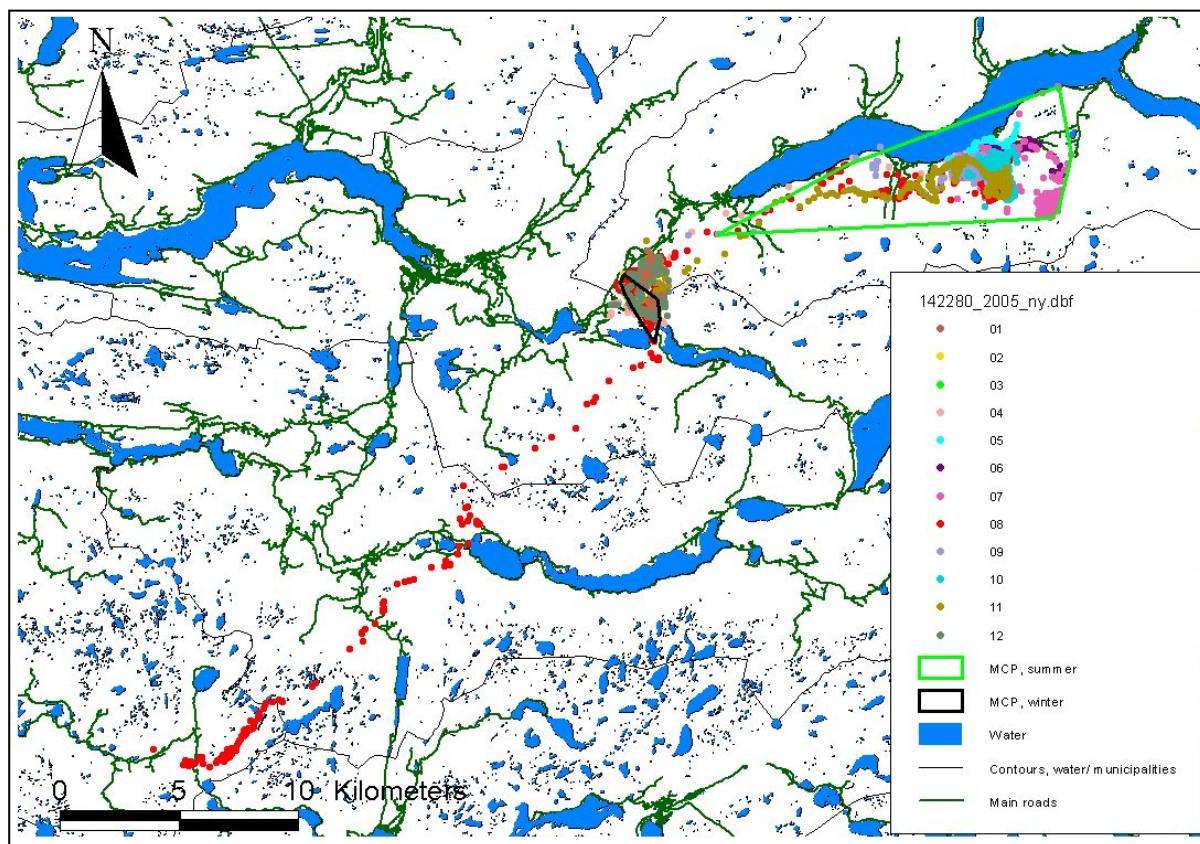
Appendix 7. The annual pattern of a non-migratory individual

The annual pattern of a non-migratory individual (142119) in 2005. The home ranges in winter and summer clearly overlap.



Appendix 8. Julian days vs. cumulative distance from marking point

The animal wandered between the summer and winter range several times.



Appendix 9. Map showing “test trip” outside the normal migration route

Annual migration of individual 142280 in 2005. The summer home range is within the light green area, the winter home range within the black area. The red dots show a long “test trip” undertaken in August.