

# Use of spatial clusters by red deer (*Cervus elaphus*) to identify transmission hot spots in a Chronic Wasting Disease context

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<http://www.duo.uio.no/>

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## Abstract

In 2016 Chronic Wasting Disease was discovered in Nordfjella, Norway for the first time in a female reindeer (*Rangifer tarandus*). Since then Norwegian nature management have implemented several measures in the affected area in Nordfjella and its surrounding municipalities to stop the spread of the prion disease. The prions' long viability in soil outside of a host body increases the risk of spillover to other cervid species. The risk is especially high for the red deer (*Cervus elaphus*) population of Lærdal being the densest population in the Nordfjella region, and with its overlapping summer ranges with the affected reindeer herd. Norwegian red deer have been studied for a long time and a lot is known about their broad scale habitat selection and seasonal migration patterns. However, little is known about when and why the red deer repeatedly use the same locations on a fine scale, which has become a more relevant topic now as it may facilitate disease transmission. With location data from 14 red deer in Lærdal from 2017 to 2019, and through field work in Lærdal, I have quantified the proportion of spatial clusters containing natural forage, supplemental forage aimed for cervids and supplemental forage not aimed for cervids. I have also been able to quantify the seasonal pattern of number of spatial clusters. I found that non-intentional feeding caused as much as 31% of the clustering in infield habitats, and that most of this was in the form of leftover silage dumped in fields. I found that non-intentional feeding facilitates the contact between cervid species, and that it therefore can facilitate the spillover of Chronic Wasting Disease from reindeer, through red deer, and to roe deer (*Capreolus capreolus*) or other cervid species that do not have overlapping ranges with reindeer. Aggregation in infield habitat and around non-intentional feeding was more frequent during periods with more snow. Lastly, I discovered during the field work that even though there is a requirement of fencing in hay bales to help minimize aggregation of cervids in Lærdal, there were several cases of lack of compliance to this. To reduce the amount of contact within red deer and between cervid species additional measures to limit the amount of silage dumped in fields may need to be installed. In addition, it may be necessary to enforce the requirement of fencing around hay bales to ensure compliance.

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## Introduction

Chronic wasting disease (CWD) is an incurable disease of cervids, always ending in death. Infected individuals may show signs such as weight loss, isolation, hyper salivation, excessive drinking (polydipsia), and excessive urinating (polyuria) among others (Sigurdson & Aguzzi, 2007). CWD is a prion disease caused by the misfolding of host encoded prion proteins (Plummer et al., 2018). Aggregations of abnormally folded prion proteins, called prions, are spread through the infected animal's blood (Mathiason et al., 2006), nervous system, and lymphatic tissues (Sigurdson et al., 2001). The prions transmit between individuals via the saliva, urine, and faeces during an incubation period lasting for two or more years (Haley et al., 2009; Mathiason et al., 2006; Plummer et al., 2017; Tamgüney et al., 2009). It can also spread through the carcass of the deceased animal (Miller et al., 2004). The infectious prions can bind to soil particles and remain in the environment for years without degrading (Miller et al., 2004). Factors that lead to the aggregation of wildlife therefore increase the risk of disease transmission; disease transmission in such places could stem from direct contact between individuals or contracting the disease from the environment (Hines et al., 2007; Wright & Gompper, 2005).

The first reported case of CWD was in 1967 in Colorado, USA (Williams & Young, 1980). At first, scientists believed the disease to be a curiosity restricted to an area of the Rocky Mountains stretching across northern Colorado and southern parts of Wyoming, USA. As of 2020, CWD could be found in 26 states in USA, and three provinces in Canada (USGS, 2020). In USA, the cost of managing CWD racks up to tens of millions of dollars annually (Vaske, 2010). For a while it seemed to only affect mule deer (*Odocoileus hemionus*) (Williams & Young, 1980). It has since then been found in white-tailed deer (*O. virginianus*), elk (*Cervus canadensis*), moose (*Alces alces*), and reindeer (*Rangifer tarandus*) (Becker, 2016; Plummer et al., 2018). A key trait of CWD is the low genetic barrier between cervid species, meaning that an infected individual of one cervid species can infect an individual of another cervid species (Robinson et al., 2012). This means that there is a high risk of spillover among these species in areas where their distribution overlaps (Cullingham et al., 2020).

In March of 2016, the first case of CWD in Europe was discovered in the Nordfjella region of Norway (Benestad et al., 2016). This resulted in one of the most radical decisions in Norwegian nature management history: the complete eradication of a reindeer herd of 2024 animals (Mysterud & Rolandsen, 2018). Following the discovery of CWD in Norway, several mitigation measures were implemented to inhibit further spread. The area of Nordfjella where the herd resided, Nordfjella zone 1 (CWD area), was to be fallowed for at least five years (Mattilsynet & Miljødirektoratet, 2017). However, there was still uncertainty around the infectious status of the surrounding cervid populations, and the level of environmental contamination (Solberg et al., 2019).

Of the 15 municipalities in the Nordfjella region, Lærdal has the densest red deer (*Cervus elaphus*) population, and it also happens to overlap with Nordfjella zone 1. For this reason, spillover to this population is considered an especially high-risk situation (Fig. 1) (VKM et

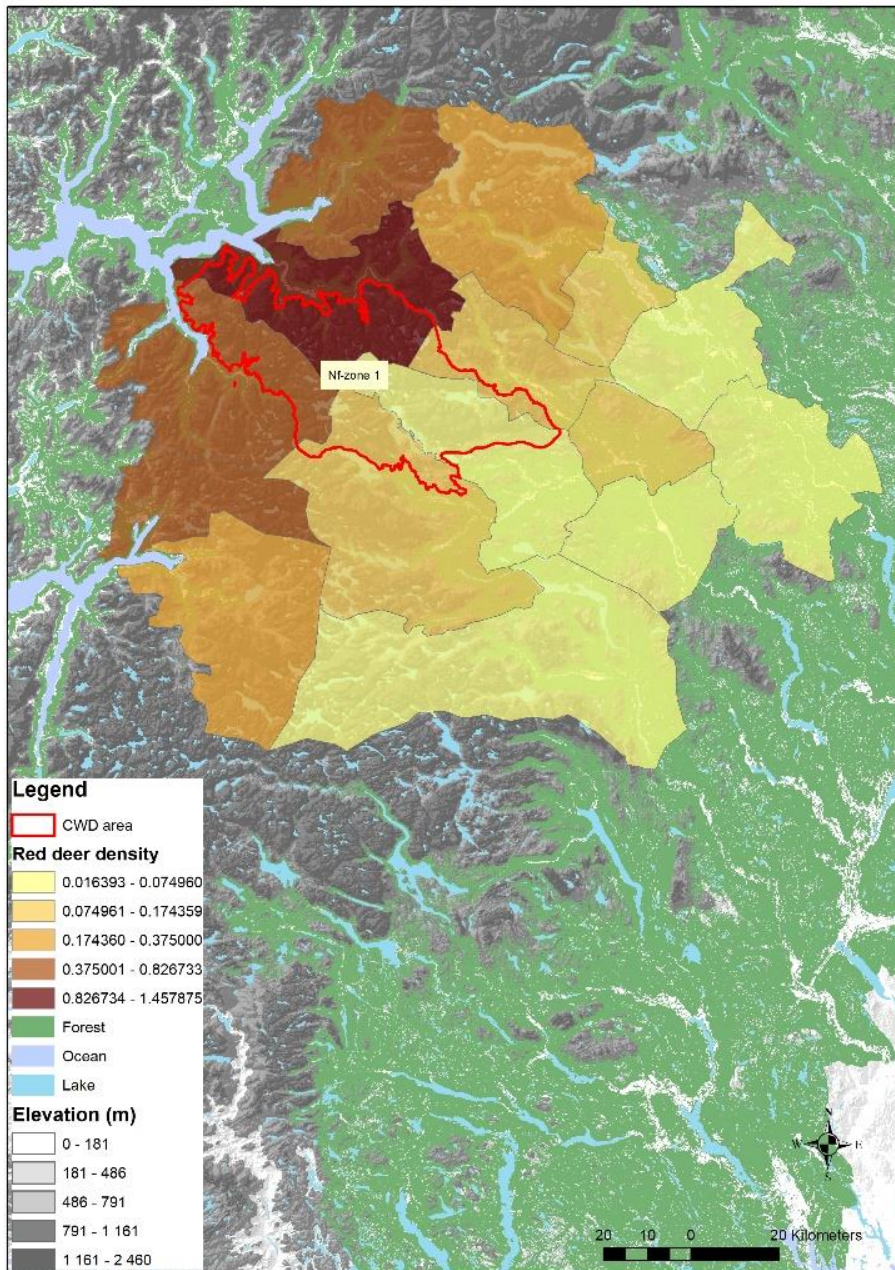


Figure 1. Map of red deer population density in the 15 municipalities surrounding Nordfjella, with Nordfjella Zone 1 (CWD area) marked out in red. Lærdal is the municipality with the highest density, and also overlaps with CWD Zone 1.

al., 2018).

The Ministry of Agriculture and Food issued a regulation concerning “Measures to reduce the spread of Chronic Wasting Disease (CWD)” (“Forskrift om tiltak for å begrense spredning av Chronic Wasting Disease (CWD),” FOR-2016-07-11-913). The regulation was published in 2016 and updated in 2017. The purpose of the regulation was to limit the spread of CWD to cervids and between cervids, where cervids are defined as reindeer, roe deer (*Capreolus capreolus*), red deer, moose and fallow deer (*Dama dama*), see §1 and §2 (“Forskrift om tiltak for å begrense spredning av Chronic Wasting Disease (CWD),” FOR-2016-07-11-913). The regulation included a paragraph (§6) on “Ban on using mineral licks and supplemental

feeding aimed at wild cervids" ("Forskrift om tiltak for å begrense spredning av Chronic Wasting Disease (CWD)," FOR-2016-07-11-913). Why was mineral licks and supplemental feeding banned for wild cervids? Studies have shown how feeding of wildlife can lead to aggregation that is not a part of the animals' normal behavioural patterns (Milner et al., 2014; Thompson et al., 2008). Furthermore, these mineral licks and feeding stations have been shown to be hotspots for disease transmission (Milner et al., 2014; Sorensen et al., 2014). In the case of CWD, this means more contact points for disease transmission between animals of the same species. It also becomes a spot of indirect contact between species, facilitating the spillover of the disease from one species to another. Other factors that lead to the aggregation of cervids are not as well known. Pinpointing these factors, especially if they are human caused, could aid in disease management in the future.

Considering the CWD situation in Nordfjella, and the regulations banning mineral licks and supplemental feeding, new questions arose. Does this ban lead to an increase in non-intentional feeding? For example, do the red deer visit the feeding stations placed for livestock, even though they are designed to keep the red deer out? Do red deer forage on leftover silage from cattle sheds? Are there other factors than supplemental feeding that facilitates the clustering of cervids? For this project, GPS-data from 14 collared red deer from Lærdal was used.

The aim of this thesis is to:

- Quantify the proportion of spatial clusters containing natural forage, supplemental forage aimed for cervids, and supplements not aimed for cervids.
- Quantify the seasonal pattern of number of spatial clusters through the annual cycle of red deer in inland and coastal habitats.

To achieve this, field work was done on snow in Lærdal municipality during the winter of 2019. Spatial clusters from 14 GPS-collared red deer were visited to determine the type of forage and other activities. The GPS-data from 13 red deer in the period 2017 to 2019 was analysed: change in habitat, elevation and proportion of clusters as a response to seasonal variation and fluctuations in weather was investigated. As the red deer migrate to lower elevations for the winter (Bischof et al., 2012), I expected a shift towards more clusters on infield habitats during these months. As more snow leads to less available forage and more energy expenditure during foraging (Parker et al., 1984), I expected to see an increase in clusters with deeper snow. It was also expected that the elevation would be lower and proportion of clusters would be higher during the winter months due to the migratory pattern of red deer, and less natural forage available (Bischof et al., 2012).

## Materials and methods

### Study Area

The field work part of this project was done in Lærdal municipality in Vestland county, Norway (Fig. 2). The estimated population size of red deer in Lærdal was 1099 in winter of 2018 (Solberg et al., 2019). Lærdal is part of the Nordfjella region where CWD was detected in reindeer in 2016 (Becker, 2016). Nordfjella covers 6 municipalities in 2 counties: Hol, Ås and Hemsedal in Viken county, and Aurland, Lærdal and Ulvik in Vestland county. Lærdal is characterized by varied topography dominated by alpine mountain landscape with valleys and fjords. Lærdal has a 51 km long main valley, surrounded by mountains. The bottom of the

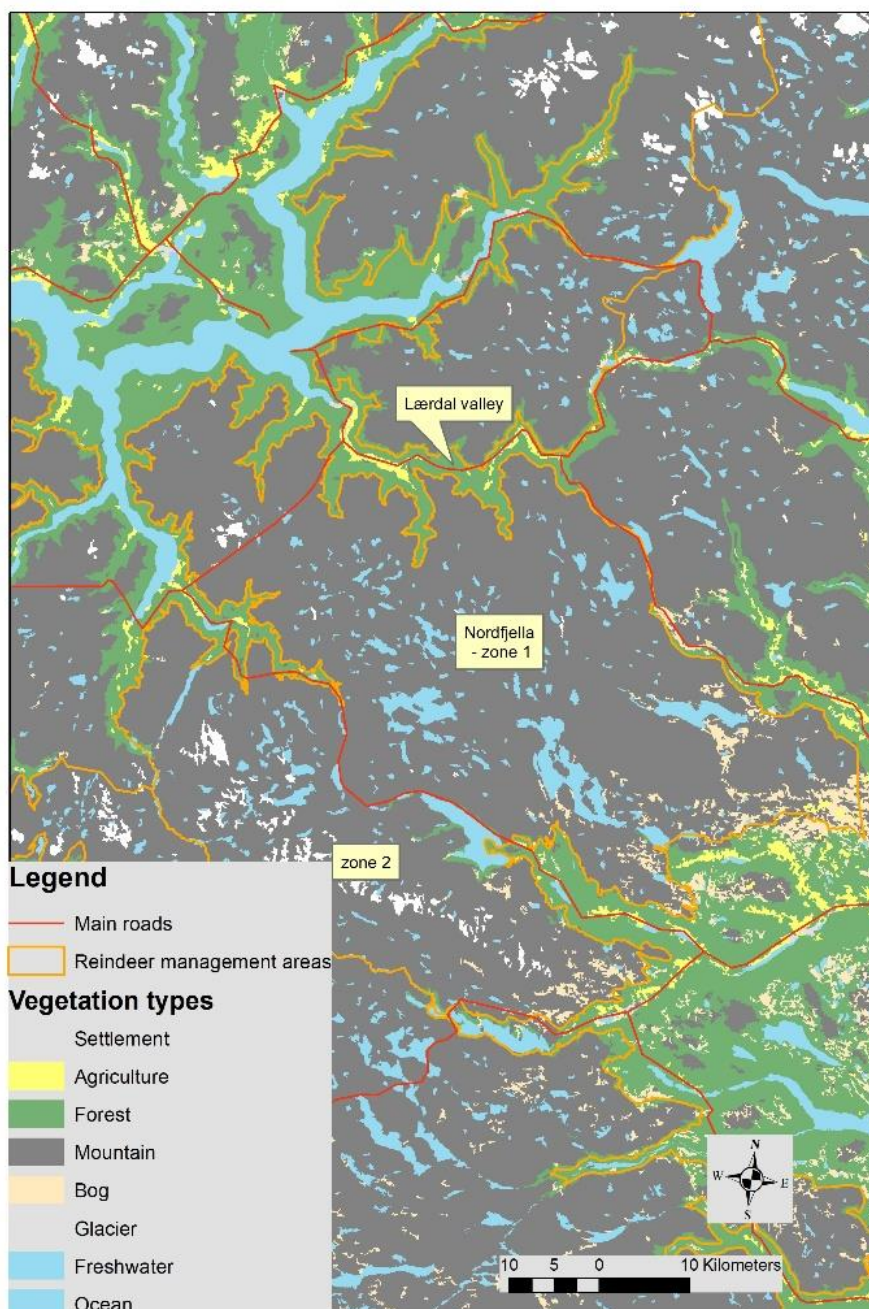


Figure 2. Map of Nordfjella zone 1, zone 2 and Lærdal, with vegetation types.

valley consists of agricultural fields, human settlement, and infrastructure. The slopes leading down to the valley from the mountains are covered in Scots pine (*Pinus Sylvestris*), Norway spruce (*Picea abies*) and deciduous forest, with species such as birch (*Betula* sp.) and Eurasian aspen (*Populus tremula*). The slopes are steep, and in many places there are scree fields. The mean temperature for January and February 2019 in the bottom of the valley was -0.2°C, and the mean precipitation in this period was 1.3 mm/day.

### Study design and field work

The data used was from a subset of 14 out of 30 Global Positioning System-marked animals as part of the University of Oslo and Norwegian Institute of Bioeconomy Research's ongoing project "Red deer in Nordfjella", and had GPS-locations from 2017, 2018, and 2019. During these years, the animals' locations had been registered once every hour. The work was split into two parts: 1) field work based on patterns of movement from winter 2018/2019, where locations from 14 red deer in Lærdal were used, and 2) an analysis of all data, where locations from 13 individuals (with 30 id-years) were used. All animals were from Lærdal to ensure that the seasonal patterns seen in the analysis would not be caused by the red deer residing in different areas when comparing with the field work. For the field work, the number of clusters per individual ranged from 1 to 20, with a mean of 13.2 and a median of 15. For the full GPS-analysis the amount of clusters per individual ranged from 1018 to 5589, with a mean of 3097.1 and a median of 3283.

For the field registrations connected to part one, the data was collected during two periods; from 7<sup>th</sup> to 11<sup>th</sup> of January and from 4<sup>th</sup> to 17<sup>th</sup> of February 2019. Each individual pattern of movement was tracked with the GPS-collar, and before each period of field work, the most recent GPS-positions were used to define spatial clusters. These clusters were defined as a red deer GPS fix with a radius of 20 m where the animal had revisited 5 times or more during a 14 day period, using revisitation analysis (Bracis et al., 2018) (Figure 3). The radius was set to 20 m to account for GPS location error (Godvik et al., 2009). The clusters that were visited in January represented the deer's points of interest in late December and early January, and the clusters visited in February represented points of interest during the time between the two periods of field work.

For field work, there was a trade-off between getting a random sample of clusters and efficient sampling. The main focus was to get as many of the clusters from infield habitats as possible, here defined as sites around human settlement and agricultural areas. This meant clusters closer to roads and hence more readily accessible. Clusters in the cultural landscapes were of higher interest than the ones in distant outfield habitat, here defined as forests, mountains and other habitats not changed drastically by human presence. This was due to potential hotspots for disease transmission in infield habitat being more available, likely to be facilitated by anthropogenic factors and easier to manage. There was nevertheless also gathered data from outfield habitats, to get a more complete picture of the animals' behavioural patterns. From GPS-data, I later estimated how this sampling biased estimates of clustering in infield versus outfield.

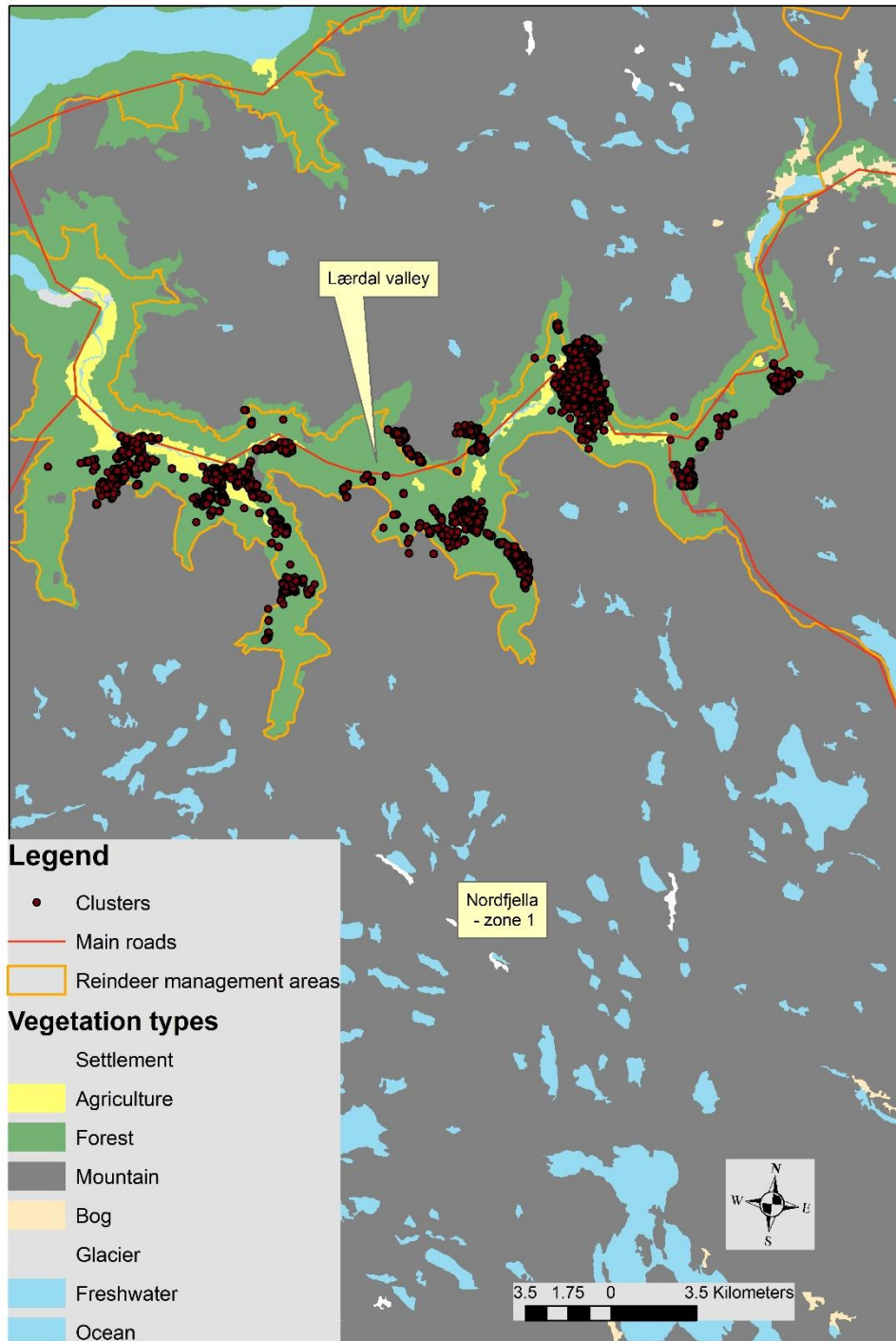


Figure 3. The positions of the spatial clusters of red deer in Lærdal valley, Norway, showing also main vegetation types.

### Site variables and measuring methods

Several site variables were described for each spatial cluster. The same variables were also described for a random paired site to enable assessing local scale selection. These sites were

taken randomly between 50 to 100 m away and in a randomly chosen direction from the spatial cluster. This method of sampling meant that the spatial clusters could be paired with a random site in the same main habitat type. To ensure random sampling, I randomly generated distances between 50 to 100 m and printed out before the field work. The same was done for directions with these being taken randomly between 0 to 400 °.

### *Snow depth and snow age*

Snow depth and snow age (days since last snowfall) was noted at each cluster. Snow depth was measured with a ruler (in cm) in the middle of the cluster, and the age of the snow was assessed and noted. For the first period it snowed on day one, so for the rest of the period snow age was always gathered *in situ*. For the second period it snowed the day before I arrived, which I knew based on local weather reports (yr.no). The rest of the period snow age was again gathered *in situ*. Where it had snowed previous in the day, or for the clusters where it was snowing while the data was gathered, snow age was set to 0.

### *Habitat*

To describe habitat variability, all clusters were categorized as either infield or outfield, each with specific variables. Common habitat descriptors for both infield and outfield was plant coverage (percentage), (percentage), distance to nearest tree (m) and slope (degrees).

For infield clusters, these variables were described:

- Type of infield habitat: the type of infield habitat was described as either field or another form of cultivated land (other).
- Saltlick: the distance to nearest saltlick (m) was measured when applicable. If there was no saltlick in sight this variable was not applicable.
- Hay bales: the distance to any hay bales were measured in the same way as distance to saltlick
- Feeding station: distance to any feeding station for husbandry nearby was measured in the same way as distance to saltlick.

For outfield clusters, these variables were described:

- Type of forest: the type of forest was described as either coniferous, deciduous, mixed or cleared.
- Cutting class: the cutting class of the surrounding forest was described using the 5 categories being standard in forestry (Ray, 1964):
  1. Clear cut
  2. Young trees, typically up to 10/12 m tall, with branches less than 3 m from the ground.
  3. Young production forest
  4. Older production
  5. Ready for felling, growth rate slowed down



For all clusters, these variables were described:

- Plant coverage: Percentage of the different plant groups covering the ground. Plant cover was divided into dead, grass, herbs, heather, ferns and moss. This was only possible to accurately measure where there was little to no snow.
- Canopy cover: This was measured by using a spherical densiometer. The densiometer contained a mirror with 24 squares, and each square was counted as four if it was fully covered, or less if it was only partly covered. This was measured due north, south, east and west, and the total canopy cover was calculated as the mean of these (Mysterud & Østbye, 1999) and then multiplied by 1.04 to get the values in percentage before moving on to analysis.
- Distance to nearest tree: Distance to nearest tree over 2 m was measured. For distances over 10 m, binoculars with distance measure was used. Any distance under 10 m was too short for the binoculars to measure, and I had to measure by counting steps from the middle of the cluster to the tree.
- Slope: Slope was measured using a compass that could measure the inclination of the area in degrees.

### *Signs of animal activity*

To be able to see what factors facilitate the clustering of animals, it was important to note the level of animal activity at the different clusters. This was done by counting the number of faeces, bedding sites and tracks.

- Faeces: Number of red deer dungs within a 5 m radius were counted for each cluster where it was possible. In some clusters where it had snowed recently it was impossible to accurately count number of faeces. In these sites, number of faeces was put as missing data.
- Bedding sites: Bedding sites within a 5 m radius of the clusters were counted. It was easier to see bedding sites if there was snow, and difficult to see where there was no snow. For clusters where it was uncertain whether there were bedding sites, or it was just too difficult to see them, this variable was not applicable.
- Tracks of red deer, sheep, roe deer, moose: Tracks from each species within a 5 m radius was counted. These were also difficult to see without snow. In some clusters they could be counted without snow, because of mud that held the shape of their tracks, but for most clusters without snow this variable was not applicable.

### All GPS-data and broad habitat categories

To quantify the seasonal pattern of number of spatial clusters, as well as the effect of weather, all data from 2017, 2018 and 2019 was included to make the dataset. When analysing the effect of snow depth, data from 2017 was excluded from the dataset, as there was not enough

data from the relevant months for this year. The dataset consisted of clusters, estimated from red deer GPS-data, that each animal had revisited at least five times or more within a 20 m radius from the individual red deer GPS locations, along with the elevation, average monthly snow depth, date and habitat.

To determine the habitat type for each spatial cluster, the broad habitat classes from the AR50 map was used ("AR50," 2017). All clusters in the habitat type 20 (agricultural fields) were categorized as infield, and all clusters from the habitat types 30 (forest), 60 (bog), and 50 (naturally open areas) were categorized as outfield. The few clusters in the habitat type 81 (freshwater) was removed.

Snow depth information was extracted from [senorge.no](http://senorge.no) and was provided by the Norwegian Water Resources and Energy Directorate and the Norwegian Metrological Institute. A daily 1 x 1 km grid of snow water equivalent (here used as measure of snow depth) was used to calculate the monthly average (Saloranta, 2012).

The elevation for each cluster was gathered using a digital elevation model from Geonorge (Kartverket), rasterized with a resolution of 50 m x 50 m.

## **Statistical analyses**

### Local selection of cluster sites

Data gathered from the field work was used for this part of the analysis. To analyse local selection of sites, I used a paired t-test to compare each spatial cluster against the paired random site using R (R Core Team, 2019). For this part of the analysis no additional packages was needed. This was done first for all clusters, then with a subset with just infield clusters, and lastly with a subset of just outfield clusters. Canopy cover, plant coverage (dead, grass, heather, ferns, and moss), distance to nearest tree, slope, number of faeces, bedding sites, red deer tracks, sheep tracks, roe deer tracks and moose tracks were tested for local selection. Before analysis, canopy cover (Pirisinu et al.) was transformed using  $\arcsin(\sqrt{cc/100})$ , to ensure that the data was not limited by, and had unnaturally high values at 0 or 100.

The same paired t-test was run to check for differences in animal activity in infield and outfield spatial clusters.

### Seasonal pattern of clusters

#### Pattern of elevation use

For this part of the analysis the dataset consisting of clusters from 2017 to 2019 was used. A generalized additive model (GAM) of elevation against Julian date was fitted and plotted to check for non-linear patterns of seasonal change in cluster site elevation. For this the `gam()` function in the R library `mgcv` was accessed (Wood & Wood, 2015). Based on this, the data was categorized by season as follows: winter (January-April), spring (May), summer (June-

August), and fall (September-December). The analysis then moved forward with linear mixed effects models to investigate whether the variation in elevation was best explained by year (i.e. 2017, 2018 and 2019), season (winter, spring, summer and fall), year and season, or season x year interaction. To do this the lmer function from the lme4 library was accessed (Bates et al., 2015). Mixed models were used as the clusters in the dataset were non-independent (Zuur et al., 2009): each individual had several clusters. Id was set as random effect to correct for variation between individuals so it would not affect the results. Backwards model selection in the form of Akaike Information Criterion (AIC) was used to find the most parsimonious model (Burnham & Anderson, 2002). The predict() function was used to calculate predictions for cluster elevation pattern using the model found through AIC model selection (Hijmans et al., 2015). Finally, a bootstrap with 100 replicas was run to calculate confidence limits, and the predictions were plotted to visualize the seasonal pattern of elevation. To plot the results the R package gplots and the function plotCI was used, to visualize confidence intervals in the plots (Hijmans et al., 2015).

To look at effect of snow depth on the elevation of clusters, the analysis was limited to the months that surpassed 300 mm snow. In this case that meant making a subset with only clusters from January – April. Data from 2017 was therefore automatically left out as there was no data for these months in 2017. Linear mixed effect models (Tamgüney et al., 2009) with year, snow depth, year and snow depth, and year and snow depth with year x snow depth interactions were made. These were tested using AIC model selection to find the most parsimonious model. The predict() function was used to predict the elevation of clusters at different snow depths based on the model with the best AIC score. Then, a bootstrap (Chernick & LaBudde, 2014) of 100 replicas was run, and the results were plotted to visualize the effect snow depth had on elevation.

#### Habitat selection

To analyse and plot predictions for the seasonal pattern of habitat selection I used the same procedure as was used to run analysis on elevation. Here, the clusters were subsetted into categories of 0 for infield or 1 for outfield habitat before anything else was done. Due to this I used a binomial distribution and ran generalized linear mixed effect models instead of linear mixed effect models (Bates et al., 2015). The same division for seasons as for elevation was used.

For the analysis of snow depth effect on habitat selection the same procedure as for predicting and plotting snow depths effect on elevation on clusters was used. Once again, the clusters were subsetted into infield or outfield, and I therefore had to a binomial distribution and run generalized linear mixed effect models. For this analysis, as well as for snow depths effect on elevation of clusters, a subset of clusters from January to April was made.

#### Number of spatial clusters

To analyse and plot predicted average number of spatial clusters per individual per month in a seasonal pattern I used the same procedure as I did when analysing elevation patterns. The same division for seasons as for elevation was used.

For analysing and plotting predictions of snow depths effect on average number of spatial clusters per animal per month I used the same procedure as was used for analysing snow depths effect on elevation of clusters. Again, a subset of clusters from January to April was used.

## Results

### Local selection of cluster sites

In total, 185 spatial clusters were visited during field work, as well as 185 paired random sites. Of these, 31.9% (59) were located in infield habitat, and the other 68.1% (126) were located in outfield habitat. For the full GPS-data analysis 20% of all clusters were in infield habitat, and for the winter seasons 2017 to 2019 39% were in infield habitat. Non-intentional feeding was found in 11.9% (22) of all spatial clusters visited in field. Of these clusters, 18 were in infield habitat, making up 31% of the infield clusters. Only one of the clusters had a salt lick (0.54%). None of the spatial clusters had hay bales within the cluster site itself. In 3.8% of all clusters, and 11.9% of the infield clusters, hay bales were within sight. The mean values for all variables are presented in Table 1, except for tracks from sheep and moose, as there were none found in the field.

### *Habitat variables*

There was no significant difference in canopy cover between all the spatial clusters and random sites. However, there was a significant difference between clusters and nearby random sites when analysing infield and outfield separately. There was on average lower canopy cover for spatial clusters in infield, and higher coverage for spatial clusters in outfield relative to nearby random sites.

For plant coverage, the variables dead, grass, herbs, heather, ferns, and moss, had no significant difference for all sites, nor infield or outfield.

There was no significant difference in distance to nearest tree when comparing all sites. For infield sites, there had on average been further to the nearest tree in spatial clusters compared to random sites, and for the outfield sites the opposite was true.

For slope, there was no significant difference when comparing all spatial clusters against random sites. On average, there were less steep slopes in spatial clusters in infield compared to random sites, and for outfield clusters the opposite was true (Table 2).

### *Signs of animal activity*

There was a significantly higher number of faeces and bedding sites in spatial clusters compared to nearby random sites, and the same result could be seen when comparing infield and outfield sites separately. For red deer, there were more tracks in the spatial clusters than

in the random sites, both when comparing all sites, and when looking at infield sites separately. However, there was no significant difference for outfield sites in number of red deer tracks. Roe deer tracks were only found in 4.3% of the in total 370 sites visited, and showed no differences for between the sites (Table 2).

*Table 1. Mean value for all variables in spatial clusters and random sites. Split into infield and outfield.*

	<b>Spatial clusters</b>		<b>Random Sites</b>	
	Infield	Outfield	Infield	Outfield
<b>Canopy cover</b> (transformed values)	0.122	1.071	0.825	0.686
<b>Dead (%)</b>	27.780	34.640	23.680	27.600
<b>Grass (%)</b>	70.000	14.460	65.560	22.800
<b>Herbs (%)</b>	0.000	0.000	1.053	0.400
<b>Heather (%)</b>	0.000	5.000	0.000	3.200
<b>Ferns (%)</b>	0.000	0.536	0.790	0.000
<b>Moss (%)</b>	2.222	45.000	13.060	45.600
<b>Distance to tree (m)</b>	31.090	2.301	5.336	10.070
<b>Slope (degrees)</b>	6.525	24.130	19.470	19.750
<b>Faeces</b>	7.768	6.644	2.216	2.417
<b>Bedding sites</b>	0.370	0.574	0.071	0.033
<b>Tracks red deer</b>	7.750	3.559	3.019	2.867
<b>Tracks roe deer</b>	0.250	0.021	0.113	0.111

Table 2. Results from the t-test and p-value for all sites, infield sites and outfield. All t-test results with significant p-values are bolded for emphasis.

Variable	All sites		Sites in infield		Sites in outfield	
	T-test score	p-value	T-test score	p-value	T-test score	p-value
<b>Canopy cover</b> (transformed values)	0.757	0.45	<b>-9.58</b>	<b>&lt;0.001</b>	<b>6.988</b>	<b>&lt;0.001</b>
<b>Dead</b>	0.917	0.365	0.527	0.606	0.737	0.470
<b>Grass</b>	0.061	0.952	0.948	0.357	-1.39	0.181
<b>Herbs</b>	-1.357	0.183	-1	0.332	-1	0.330
<b>Heather</b>	1.363	0.182	No data	No data	1.377	0.185
<b>Ferns</b>	1	0.324	No data	No data	1	0.330
<b>Moss</b>	-1.557	0.129	-1.781	0.095	-0.615	0.546
<b>Distance to tree</b>	1.254	0.212	<b>4.405</b>	<b>&lt;0.001</b>	<b>-4.713</b>	<b>&lt;0.001</b>
<b>Slope</b>	-0.725	0.469	<b>-5.332</b>	<b>&lt;0.001</b>	<b>2.746</b>	<b>0.007</b>
<b>Faeces</b>	<b>8.675</b>	<b>&lt;0.001</b>	<b>5.161</b>	<b>&lt;0.001</b>	<b>6.925</b>	<b>&lt;0.001</b>
<b>Bedding sites</b>	<b>6.346</b>	<b>&lt;0.001</b>	<b>2.939</b>	<b>0.005</b>	<b>5.664</b>	<b>&lt;0.001</b>
<b>Tracks red deer</b>	<b>4.011</b>	<b>&lt;0.001</b>	<b>4.008</b>	<b>&lt;0.001</b>	1.624	0.110
<b>Tracks roe deer</b>	-0.420	0.675	1	0.323	-1.371	0.176

The only sign of animal activity that showed a significant difference when comparing infield and outfield spatial clusters was red deer tracks. The results showed that there were more red deer tracks in the infield clusters ( $T = 3.8478$ ,  $p < 0.001$ ).

## Seasonal pattern of clusters

### Pattern of elevation use

AIC model selection showed that cluster site elevation was best explained by the full model which included season, year and season x year interaction (Table 3). Model estimates are in the appendix (Appendix table 1)

*Table 3. AIC model selection to investigate which variable(s) best explained the variation in elevation: intercept (elevation), year, season, year and season, and year and season interaction with degrees of freedom  $\Delta$ AIC: the models AIC score minus the best models AIC score.*

	<b>Degrees of freedom</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
<b>Season x year</b>	12	512952.1	0
<b>Season and year</b>	8	514002.8	1050.7
<b>Season</b>	6	515088.0	2135.9
<b>Year</b>	5	540403.3	27451.2
<b>Intercept only</b>	3	544024.0	31061.9

The clusters averaged at lower grounds for the winter months (ca. 300-500 m above sea level) compared to spring, summer and fall (Fig. 4). However, the difference in elevation between winter and spring clusters was small. The clusters averaged at the highest elevation in the summer months (ca. 700-900 m above sea level). In the fall, the clusters were at slightly lower elevations (ca. 500-800 m above sea level) again compared to the summer months, and around the same elevation as for spring (ca. 400-600 m above sea level). There was not much difference between the years (Fig. 4).

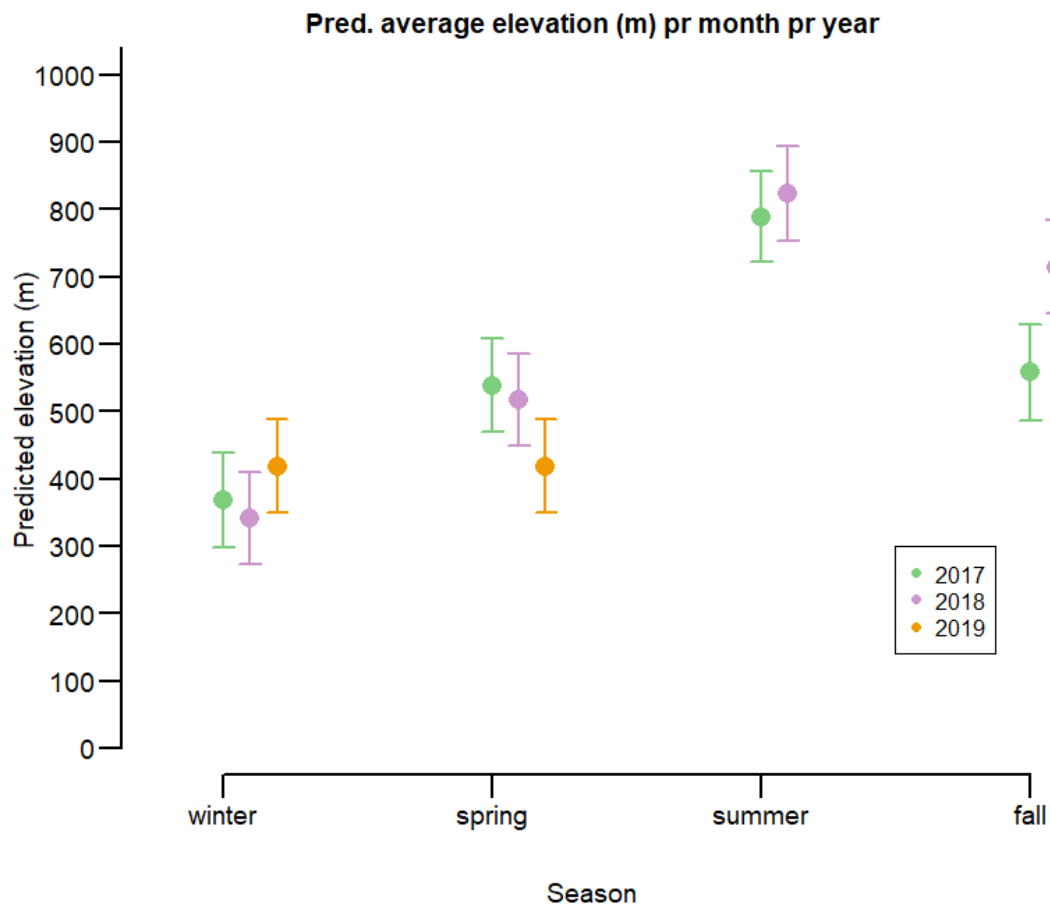


Figure 4. Predicted average elevation (m) of red deer spatial clusters through the seasons for 2017, 2018 and 2019, based on a generalized linear mixed effects model.

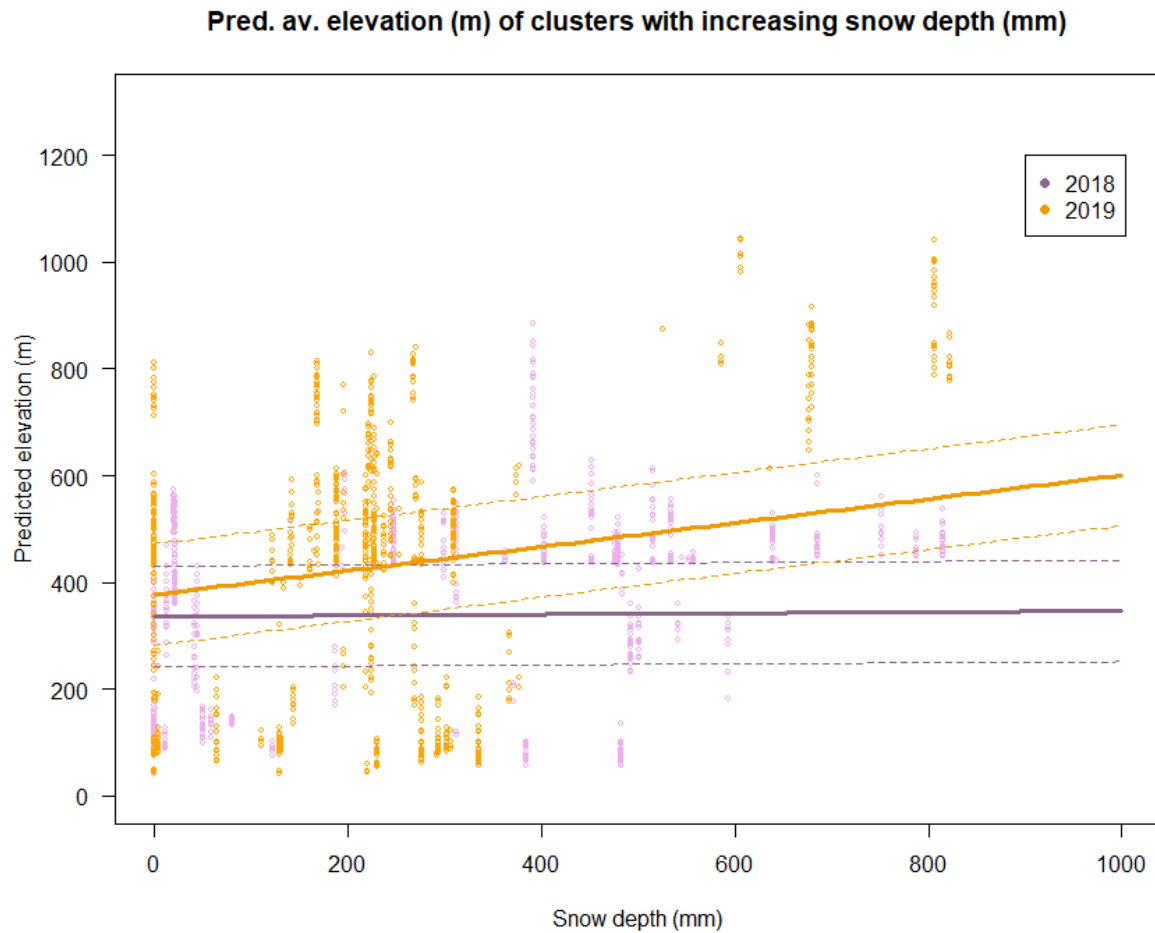
When analysing how elevation depended on snow depth, the model with the lowest AIC score was the full model with snow depth, year and snow depth x year interaction (Table 4). Model estimates are in the appendix (Appendix table 2).



Table 4. AIC model selection to find what variable(s) best explained the variation in elevation of red deer spatial clusters during snowy months (January – April) for years 2018-2019: year, snow depth and year, snow depth, and snow depth x year interaction, with degrees of freedom.  $\Delta$ AIC: the models AIC score minus the best fitting models AIC score.

	<b>Degrees of freedom</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
<b>Snow depth x year</b>	6	193556.9	0
<b>Snow depth and year</b>	5	194297.0	740.1
<b>Snow depth</b>	4	197762.1	4205.2
<b>Year</b>	4	194748.4	1191.5

The average elevation of the clusters increased slightly as the snow depth increased in 2018, but stayed between 300-400 m above sea level (Fig. 5). The same pattern but with a stronger response could be seen for the clusters in 2019, moving from just below 400 m above sea level at 0 mm in snow depth, to just below 600 m above sea level at 1000 mm in snow depth. It can also be read from the plot that the individual clusters were more spread between high and low elevations in 2019. In 2018 the individual clusters were at lower elevations overall (Fig. 5).



*Figure 5: Predicted average elevation (m) of red deer clusters with increasing snow depth (mm) for 2018 and 2019 (lines), based on a generalized linear mixed effects model. Each spatial clusters' elevation plotted against snow depth for 2018 and 2019 (points).*

### Habitat selection

For the analysis of change in habitat selection through seasons, the model with the lowest AIC score was the full model with season, year and season x year interaction (Table 5). Model estimates are in the appendix (Appendix table 3)

*Table 5 AIC model selection to find what variable(s) best explained the variation in habitat selection: intercept (habitat), year, season, year and season, year and season interaction, with degrees of freedom  $\Delta$ AIC: the models AIC score minus the best models AIC score.*

	<b>Degrees of freedom</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
<b>Season x year</b>	12	25929.5	0
<b>Season and year</b>	8	26129.0	199.5
<b>Season</b>	6	27208.0	1278.5
<b>Year</b>	5	29894.0	3968.6
<b>Intercept alone</b>	3	29894.2	3964.7

The predicted probability of clusters being in agricultural fields varied by season and by year, and there was interaction between year and season. There was a higher predicted probability of clusters being infield in the winter months, and the lowest predicted probability of being infield in the summer. However, there was not much difference between spring, summer and fall months, as they all had a high predicted probability of being outfield (Fig. 6). There was also significant variation across years. In 2017, spatial clusters were most likely to be infield in the winter, with predicted probability of being outfield ca. 0.5. Spatial clusters in the spring of 2017 were less likely to be infield, with predicted probability of being outfield just above 0.7. However, for 2019 clusters, there was seemingly no difference between winter and spring in predicted probability of being in agricultural fields, both at a predicted probability of around 0.85 (Figure 6).

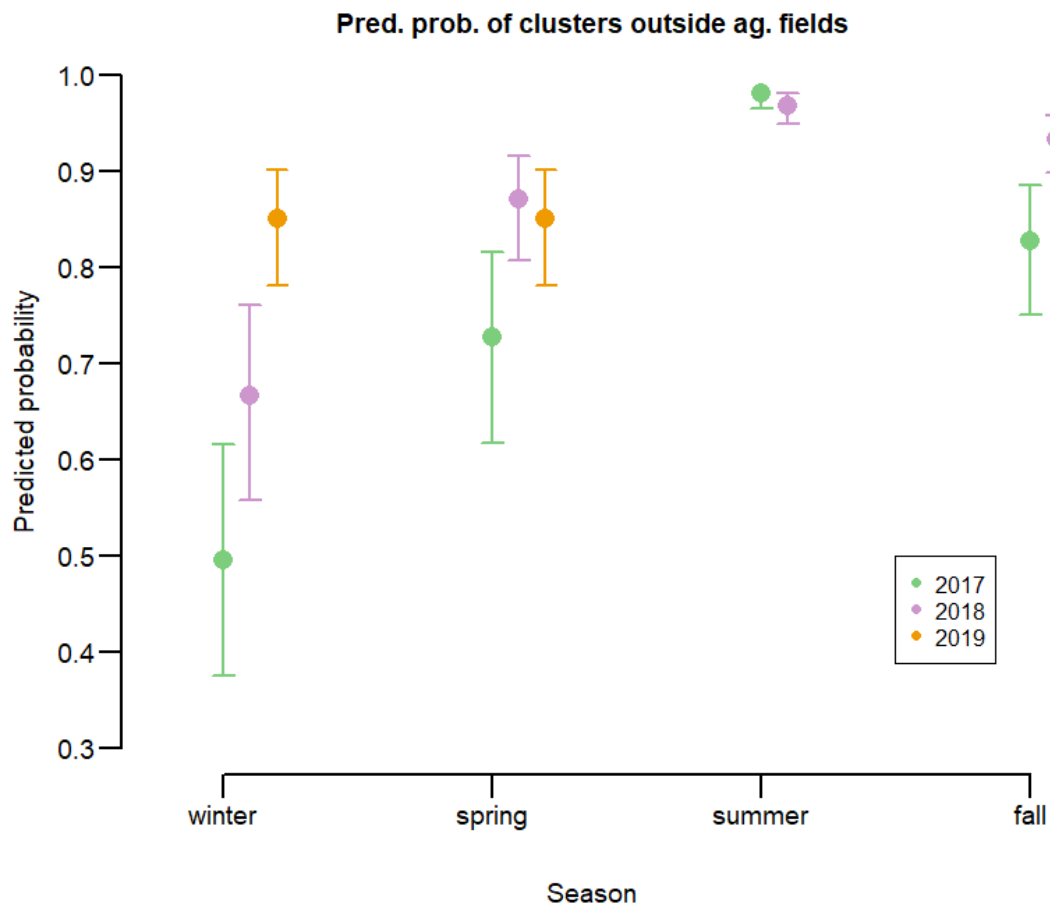


Figure 6: Predicted probability of spatial clusters being outside agricultural fields (infield) through the seasons for 2017, 2018 and 2019, based on a generalized linear mixed effects model.

In analysing the effect of snow depth on habitat selection, the model with the lowest AIC score was the full model with snow depth, year and snow depth x year interaction (Table 7). Model estimates are in the appendix (Appendix table 4)

Table 7 AIC model selection to find what variable(s) best explained the variation in habitat selection during snowy months (January – April): year, snow depth and year, snow depth, and snow depth x year interaction, with degrees of freedom  $\Delta AIC$ : the models AIC score minus the best models AIC score.

	Degrees of freedom	AIC	$\Delta AIC$
<b>Snow depth x year</b>	6	16306.78	0
<b>Snow depth and year</b>	5	16350.41	43.63
<b>Snow depth</b>	4	17050.69	743.91
<b>Year</b>	4	16682.19	375.41

The predicted probability of the clusters being in agricultural fields decreased with an increasing amount of snow. The predicted probability of clusters being in outfield in 2018 was at around 0.55 at 0 mm snow depth, and increased to about 0.8 at 1000 mm snow depth. Spatial clusters from 2019 showed the same increase, but not as strong, ranging from 0.8 at 0 mm snow depth to just below 0.9 at 1000 mm snow depth (Fig. 7).

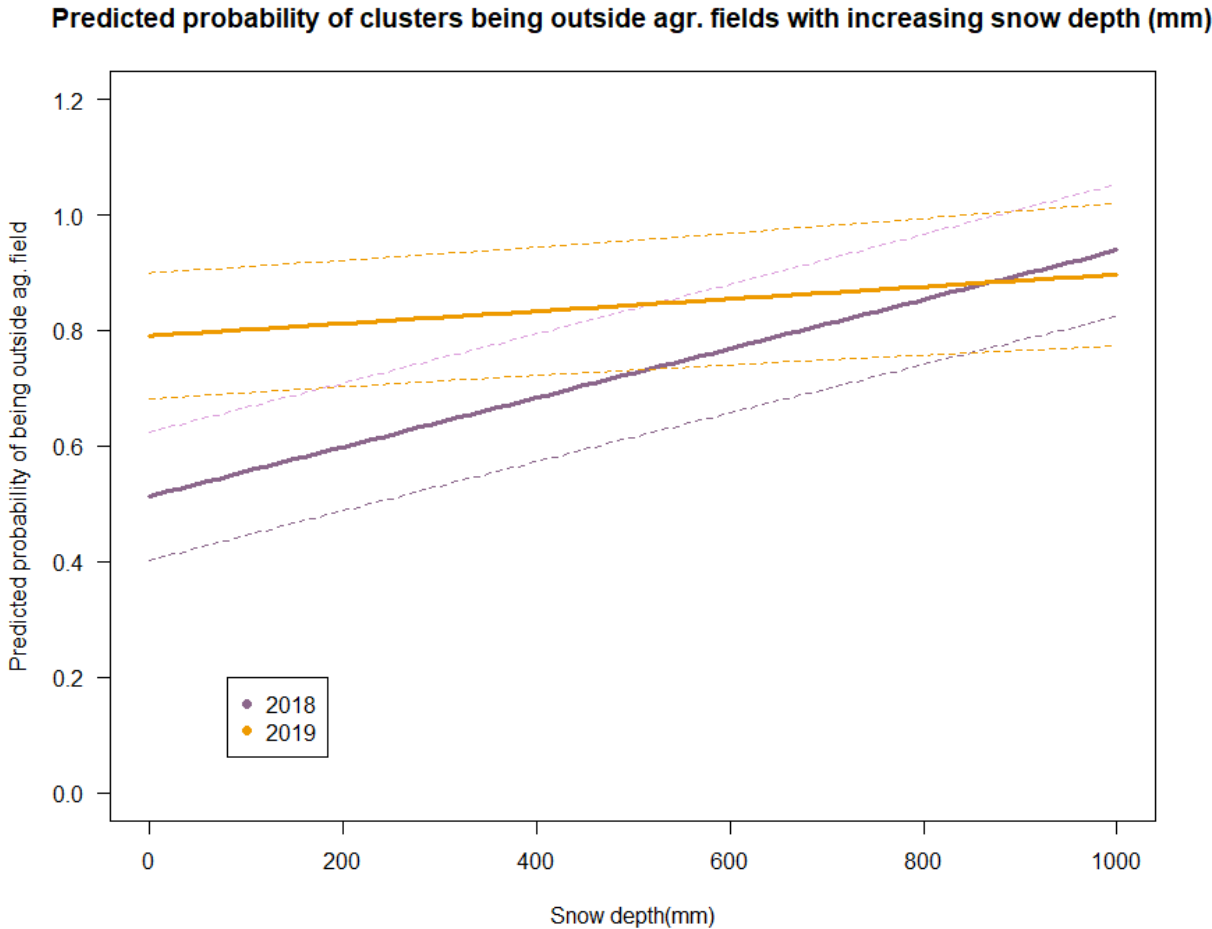


Figure 7: Predicted probability of spatial clusters being outside agricultural fields with increasing snow depth (mm) for 2018 and 2019, based on a generalized linear mixed effects model.

**Number of spatial clusters**

For the variation in number of clusters through the seasons, the model with the lowest AIC score was the full model with season, year and season x year interaction (Table 8). Model estimates are in the appendix (Appendix table 5).

*Table 8 AIC model selection to find what variable(s) best explained the variation in number of clusters: intercept (number of clusters), year, season, season and year or a season x year interaction  $\Delta$ AIC: the models AIC score minus the best models AIC score.*

	<b>Degrees of freedom</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
<b>Season x year</b>	12	478882.6	0
<b>Season and year</b>	8	480396.1	1486.5
<b>Season</b>	6	486022.7	7140.1
<b>Year</b>	5	482778.8	3896.2
<b>Intercept only</b>	3	487611.8	8729.2

The average monthly number of spatial clusters per animal varied by season and year. There were the least amount of clusters in 2017, with below 150 spatial clusters per animal per month in winter, spring and summer, and just below 200 per animal per month in fall. In 2018, there were more clusters in winter and spring, between 250 and 350 clusters per animal per month, than in summer and fall, between 200 and 250 clusters per animal per month. This year also had the highest monthly average of clusters per animal for all seasons. In 2019, the average number of clusters from winter and spring was intermediate to 2017 and 2018, with around 200 clusters per animal per month for each season (Figure 8).

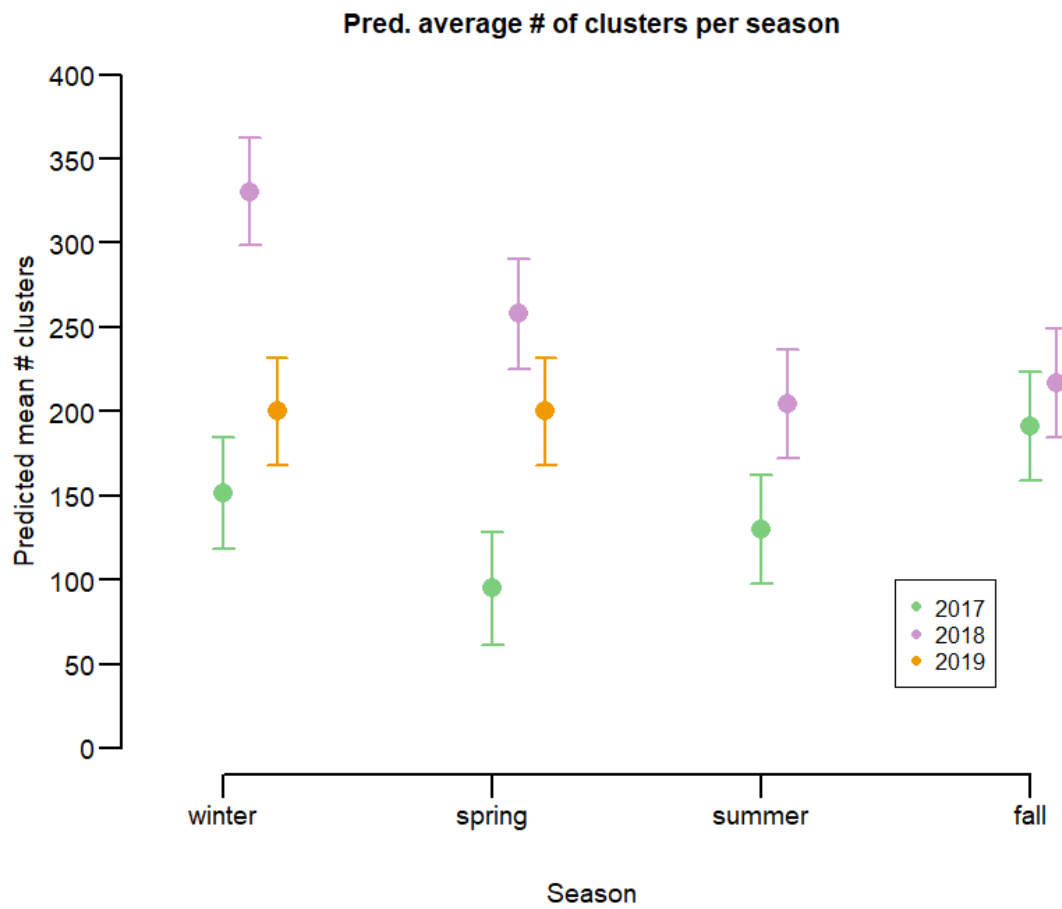


Figure 8: Predicted average number of spatial clusters per animal through the season for 2017, 2018 and 2019, based on a generalized linear mixed effects model.

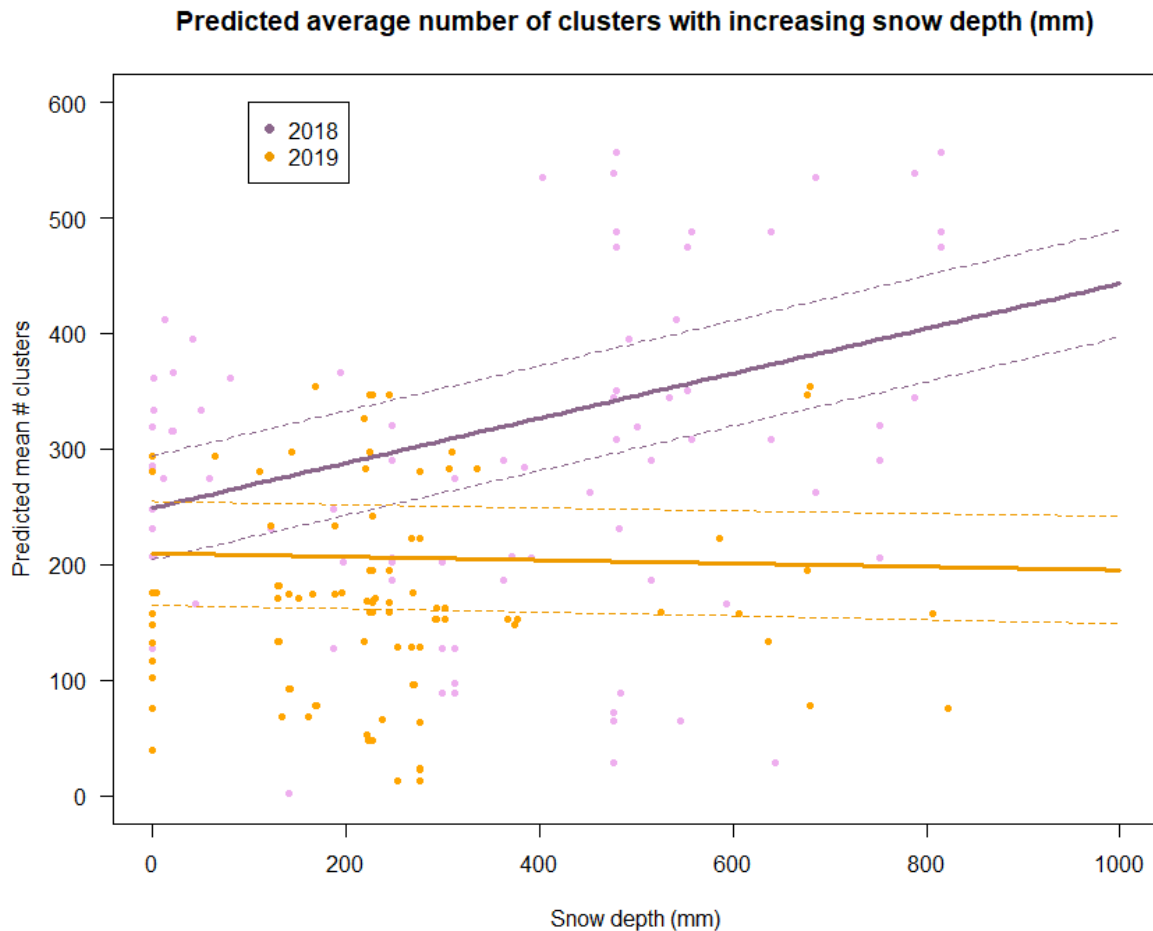
For the analysis of how number of clusters varied with varying snow depth, the model with the lowest AIC score was the full model with snow depth, year and snow depth x year interaction (Table 9). Model estimates are in the appendix (Appendix table 6).

*Table 9 AIC model selection to find what variable(s) best explained the variation in number of clusters in the snowy months (January – April): year, snow depth and year, snow depth, and snow depth x year interaction, with degrees of freedom.  $\Delta$ AIC: the models AIC score minus the best models AIC score.*

	<b>Degrees of freedom</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
<b>Snow depth x year</b>	6	195524.5	0
<b>Snow depth and year</b>	5	196151.7	627.2
<b>Snow depth</b>	4	199104.6	3580.1
<b>Year</b>	4	197412.4	1887.9

The average number of spatial clusters per animal increased with increasing snow depth in 2018. Average number of clusters in 2018 ranged from around 250 at 0 mm snow depth, to around 450 at 1000 mm snow depth. In 2019, there was a very minimal change, but the number of clusters decreased slightly with increasing snow depth. Number of clusters in 2019 ranged from just above 200 at 0 mm snow depth to just below 200 at 1000 mm snow depth. Again, there was a higher average of clusters per animal in 2018 compared to 2019 especially at higher snow depths (Fig. 9).





*Figure 9: Predicted mean number of spatial clusters per animal with increasing snow depth (mm) for 2018 and 2019 (lines), based on a generalized linear mixed effects model. Number of spatial clusters per animal plotted against snow depth for 2018 and 2019 (points).*

## Discussion

The recent outbreak of CWD makes it relevant for Norwegian wildlife management to understand what factors may be causing cervids to cluster, and to find ways to limit these factors. It is already known from previous studies that aggregation of animals facilitates the spread of disease, and that supplemental feeding causes aggregation (Milner et al., 2014; Sorensen et al., 2014; Thompson et al., 2008). Since CWD can transmit both within species and between cervid species, it became increasingly important issue to contain the outbreak. The risk of spillover of CWD from reindeer is especially high for the dense red deer population in Lærdal (VKM et al., 2018). Pinpointing cluster-facilitating factors and implementing measures to limit these, alongside the measures already implemented, could prove vital if a CWD outbreak occurs among red deer. One of the most important factors is anthropogenic sources to aggregation, as they will be easier to manage and keep track of, especially if they are in infield habitats. If these types of aggregation-causes make up a

substantial amount of the overall number of clusters, it would be of interest to eliminate these sources.

Natural forage in this thesis would be everything not categorized as supplemental feeding, as I split food sources into categories of natural forage, supplement not aimed for cervids and supplements aimed for cervids. By this definition, fields would automatically fall under natural forage, even though they are sown and therefore not completely natural. My thesis shows 11.9% of the spatial clusters contained supplements not aimed at cervids. Of the infield spatial clusters, 31% contained supplements not aimed at cervids. None of the spatial clusters contained supplements aimed at cervids. I found evidence that non-intentional feeding facilitated contact between cervid species (roe deer and red deer) in 7% of the infield clusters (2% of all spatial clusters). Number of clusters increased from around 250 to about 450 clusters monthly per animal with increasing snow depth. The highest predicted probability of clustering in infield habitats was during the winter, but there were yearly differences. Clustering in this context means revisitation of an area by the same individual, as mentioned in materials and methods. However, an area of interest for one individual will most likely be of interest to other individuals as well. This causes aggregation and raises the risk of contact between animals.

### Factors causing red deer to cluster during winter

Winter is considered a critical period for cervids due to low abundance and quality of food. Foraging during the winter at northern latitudes also requires more energy due to the energy expenditure of traveling and digging for forage in snow (Fancy & White, 1985). It has been shown that northern herbivores build up their fat layer through the summer and fall months, and that how much food is available during this time is critical to their winter survival. Foraging through the winter is important to not burn through this stored energy too fast (Mautz, 1978). One study showed that black tailed deer (*Odocoileus hemionus sitkensis*) were in negative energy balance through the winter (Gillingham et al., 1997). Cervids spend their time in alternating bouts of ruminating and foraging during the winter (Gillingham et al., 1997). The low quality and quantity of forage at this time leads the animals to search for alternative, human provided food sources (Cotterill et al., 2018). One study showed that Norwegian red deer use infield habitats such as fields more during the spring and fall seasons, and that infield habitats are used more at night, while the daytime is spent in forest habitats (Godvik et al., 2009). While red deer habitat selection is well described on a broad scale, on a fine scale little is known about the specific factors causing the red deer to aggregate. My thesis have been in pursuit of uncovering such factors. Such knowledge could prove useful in management of red deer, and by extension other cervid species, in preventing CWD and other diseases from spreading. The results showed that 31.9% of the spatial clusters visited during the field work were located in infield habitats. For comparison, the analysis of seasonal clustering patterns using red deer GPS-data showed that 15% of the spatial clusters were in infield habitat during the winter the same year.

## Non-intentional feeding

Previous studies have shown that contact with the environment was more frequent at anthropogenic sources compared to natural sources of forage (Mejía-Salazar et al., 2018). In addition, at such sites deer interacted more frequently and over longer periods of time with other deer (Dunkley & Cattet, 2003; Miller et al., 2007; Ozoga, 1972; Thompson et al., 2008; Vicente et al., 2007; Weeks Jr, 1978). Non-intentional feeding encountered in Lærdal consisted of silage dumped in or around the edge of fields in 20 of the 22 clusters (Fig. 10). One of these also had a salt lick among the discarded silage. One cluster had non-intentional feeding in the form of potatoes dumped in large quantities around the edge of a small field (Fig. 11). Another had supplemental feeding intended for cattle. In total, four of the 22 spatial clusters were found in outfield habitats, and the remaining 18 were found in infield habitats, making up 31% of the infield clusters. None of the spatial clusters visited had hay bales



*Figure 10 Silage dumped in field in one of the spatial clusters visited during the field work.*



*Figure 11 Potatoes dumped in field in one of the spatial clusters visited during the field work.*

directly within them, but 7 clusters, all in infield habitats, had hay bales in the near vicinity. This makes up 11.9% of the infield clusters. In any case, 31% of infield clusters is a substantial amount that can be linked back to anthropogenic sources. It helps in management of these sources that most of them stem from the same type of non-intentional feeding in the form of leftover silage. Implementing other ways to dispose of silage may eliminate a lot of the aggregation in infield habitat. This would help in minimizing the amount of contact

between individuals, especially since clusters around non-intentional feeding have a higher level of animal activity around them than other clusters.

### Other fine-scale selection

A study by Lande et al. (2014) found that red deer preferred meadows over other types of agricultural land. When looking at the difference in selection between sexes, they found that females selected intensely fertilized meadows of intermediate age, whilst males did not show preference of age or degree of fertilization (Lande et al., 2014). As previously mentioned, red deer spend more time in pastures with less cover at night when foraging, and more time in the forest during the daytime, when they are less active. Infield pastures offer less cover but more forage of higher quality, whilst outfield forested habitats offer cover for when the animals are resting and ruminating (Godvik et al., 2009).

The results showed that infield clusters had on average less canopy cover, longer to nearest tree, less steep slopes, more faeces, bedding sites and red deer tracks than the paired random sites. In outfield habitat, the clusters had on average more canopy cover, was closer to nearest tree, had steeper slopes, more faeces and bedding sites than the paired random sites. In both infield and outfield clusters, there seems to have been little to no fine scale selection on plant coverage to forage on. More tracks in infield spatial clusters shows that there was more animal activity around these aggregation sites, and therefore there was a higher chance of contact and disease transmission. It cannot be said for certain, however, whether more tracks are connected to several animals gathered at one site, or if the tracks stem from a few or just one individual. I can only assume that more tracks here means more animals. In a management point of view, this tells us that when trying to prevent transmission of CWD among cervids, the focus should be on aggregation sources in infield habitats first.

### Red deer, hay bales and fencing requirement



*Figure 12 One of the spatial clusters visited, with hay bales in the background that had no fencing around them.*

The Norwegian Food Safety Authority required all hay bales in Lærdal to be fenced in from 31<sup>st</sup> of March 2017 as part of the measures implemented to reduce the risk of disease transmission (Sælthun, 2017). From what I observed there was varying compliance. In one area there were hay bales that were not fenced in, surrounded by four spatial clusters (Fig. 12). One spatial cluster was near hay bales that had been properly fenced in. In one last area, with two spatial clusters nearby, there were hay bales with a fence in place that was not properly closed (Fig. 13). In total, 6.7% of the infield clusters were near hay bales with no fence, 3.3% were



*Figure 13 Hay bales near two of the spatial clusters visited, where there is an opening left in the fence.*

near hay bales with an open fence, and 1.6% were near hay bales that had been fenced in. Assumedly the open fence was due to needing access to the hay bales during the day. It cannot be said for certain whether the fence was open during the night. If the fence was left open this could easily be a cause for aggregation.

The area I visited where there was no fence around the hay bales had a lot of signs of animal activity, as well as left over silage dumped in the field not far from the hay bales. The high level of animal activity in the surrounding clusters points to the possibility of other red deer foraging on these hay bales. If the varying level of compliance to the requirements set by the Norwegian Food Safety Authority is a widespread issue, some reinforcement may be necessary.

#### Red deer overlap with other cervid species

Norwegian red deer migrate between higher elevations in the summer and lower elevations in the winter, driven by snow and forage availability and quality (Bischof et al., 2012; Mysterud et al., 2012). Roe deer stay in the cultural landscape year round and do not migrate to higher elevations (Mysterud et al., 2012). For this reason, roe deer will most likely not come in direct contact with reindeer, which have their ranges in the Norwegian mountains (Benestad et al., 2016). However, red deer have overlapping ranges with reindeer during the summer, and overlapping ranges with roe deer during the winter. Because of this, red deer may facilitate the spillover of CWD from reindeer to roe deer even with little direct overlap of the two latter species.

In 4.3% of the spatial clusters, and in 10% of the infield clusters, roe deer tracks were found. In 6.7% of the infield clusters roe deer tracks were found alongside non-intentional feeding. These numbers may be higher in years with less natural forage available. However, this shows that red deer and roe deer would aggregate and forage on the same anthropogenic resources. This hence provide a possible place for spillover among these cervid species. To support this, one study from Scotland found that niche overlap between red deer and roe deer diets increased in winter (Latham et al., 1999). Another study from Poland found that even though the diet of red deer and roe deer have different proportions of each food type, their food niches still had a high amount of overlap (Obidziński et al., 2013). In places where their ranges overlap it is therefore especially important for nature management to limit contact between cervid species when combatting CWD.

## Temporal pattern of aggregation

The red deer migratory patterns are more distinct in areas of the country with varying landscape and topography (Bischof et al., 2012). When migrating they do not gradually follow the green wave of spring to their summer ranges, but rather migrates with few or no stops (Bischof et al., 2012). This is most likely driven by the need to reach summer ranges before calving, to escape predation risk and to not be slowed down by new-born calves (Bischof et al., 2012). In the fall the red deer migrates to lower elevations when snow makes forage in the mountains unavailable. In years with more snow the distinction between summer and winter ranges and timing of migrating is more evident (Bischof et al., 2012). Knowing when, where and why red deer cluster on a broad scale could be useful for knowing where to invest in resources to prevent aggregation.

## Seasonal pattern of clustering

The annual pattern of elevation of clusters followed a clear trend corresponding to the red deers' migratory pattern: lowest in winter, highest in summer, intermediate in spring and fall. Spring clusters were at lower elevations than fall clusters. This corresponds well with annual pattern of habitat selection: highest chance of being in infield habitat in winter, lowest in summer, and intermediate in spring and fall. In a previous study, Godvik et al. (2009) found that red deer changed between forest habitat and pastures during spring and fall, and stuck more to forest habitats during summer and winter. This was thought to be due to forest forage being of similar quality as pastures in the summer, and during the winter the snow made the pastures more difficult to forage on. This trend could have been different had I looked at positions and not clusters. Perhaps the red deer spent more time in infield habitats in spring and fall, but with less snow they did not cluster as much. For the analysis of number of clusters per animal, there was a lot of variation from year to year, and no clear pattern through the seasons. This was true for all seasons, but the yearly differences were especially noticeable in winter and spring. The highest average of clusters per animal was in 2018 for all seasons. Red deer are social animals that stay in groups (Bonenfant et al., 2004). Therefore, in periods with more clustering the risk of disease transmission may be higher, as the chance of groups encountering one another is also higher. Finding no clear correlation between season and clustering intensity points towards other factors affecting clustering intensity more, as I will discuss later under snow effect. I did expect there to be more clusters in general during the winter, but it seems that as long as there is little snow and forage is readily available, this does not happen. Even though the amount of clusters did not go up during the winter as expected, the amount of clusters at lower elevations and in infield habitat did. It is clear that the season with the highest risk of red deer aggregating around anthropogenic sources is the winter. It is therefore vital during this time that mitigation measures put in place are upheld. Any new measures should also be primarily focused around this time of year.

As expected, there was some bias when visiting spatial clusters during the field work. In the data from the field work 31.9% of the clusters were in infield habitats, but from the full GPS-data only 15% of the clusters that winter had been in infield habitats. However, due to this bias a lot of data and information was gathered from infield clusters, like the percentage of

clusters in infield containing non-intentional feeding. This can be used to estimate how many clusters there are on anthropogenic sources each winter for the red deer population of Lærdal. This is assuming that the relative amount of clusters on non-intentional feeding stays the same. By multiplying probability of being infield with average number of cluster per animal, and multiplying this with the amount of non-intentional feeding, I found that the average amount of clusters on non-intentional feeding per animal for the winter of 2019 was 21.7. Knowing that the population of red deer in Lærdal anno 2019 was estimated to be 1099, this means that there were about 10 732 clusters on non-intentional feeding in infield habitats that winter. If I assume that the population size was the same for 2017 and 2018, I can calculate (Table 10):

*Table 10 Estimated amount of clusters on non-intentional feeding in infield per animal, and for the red deer population of Lærdal for the winter of 2017, 2018 and 2019.*

<b>Winter of year</b>	<b>Clusters on non-intentional feeding per animal</b>	<b>Estimated number of clusters on non-intentional feeding</b>
<b>2017</b>	21.7	23 848.3
<b>2018</b>	23.19	25 485.81
<b>2019</b>	9.77	10 731.74

In reality the population size will have yearly variation, but this gives a good image of how many clusters may be caused by human activity during the winter months. The number for 2018 was probably even higher, as the red deer would have difficulty finding natural forage this year and would search for alternative food sources.

#### Snow effect on aggregation

It may be of interest to note that 2018 had an extreme amount of snow fall, compared to normal winter conditions (Skafjeld & Syed, 2018). To compare 2019 had little snow during the period of field work. At the bottom of the valley the ground was completely bare for longer periods of time. Higher up in the valley there was more snow, but also here there were periods with no snow and bare ground. As the red deer home ranges become increasingly smaller with deeper snow (Rivrud et al., 2010), the risk of contact between individuals and therefore the risk of disease transmission increases.

The elevation of clusters increased as snow depth increased in 2019. One could think that elevation of clusters would go down as increasing snow depth pushed the animals further down in the valley. Had I been looking at positions and not clusters, that is probably what I would have seen. However, the snow depth would have been deeper at higher elevations. Therefore, the animals residing higher up in the valley would cluster more when searching for food. At lower elevations where the snow was not as deep, forage was more readily available.

This meant that the animals could move around more when foraging, rather than staying in one place to kick up the snow layer. This would cause less revisiting of sites and hence less clusters. The increase in cluster elevation was a lot less steep for 2018. In addition, the individual clusters in 2018 did not go as high up as for 2019. The large amount of snow this year pushed the animals further down to lower elevations. Even though this shows that with deeper snow there is more clustering at higher elevations, it also shows that with deeper snow the animals stay at lower elevations overall. The trend for probability of being in outfield habitat also went up as snow depth went up. Considering how Lærdal is a valley with steep hillsides, outfield habitats is mostly at higher elevations and have deeper snow and therefore the animals residing here cluster more. The spatial clusters in winter of 2018 generally had a higher chance of being infield than for the winter of 2019, except at the deepest snow depths. This reflects back to the difference in amount of snow for the two years. The red deer did not cluster as much in infield habitat when there was less snow and therefore more forage available in outfield habitats. This shows that red deer aggregate more in infield habitats in years and in areas with more snow. In addition, the number of clusters went up with increasing snow depth in 2018. For 2019 there was almost a flat response in number of spatial clusters with increasing snow depth. This could again reflect back to the little amount of snow that year compared to the year before, and the results would probably have been different if there had been more snow. With more snow, the red deer moved further down and into infield habitat and clustering increased. In winters with more snow, and in places of the country where the snow is deeper during the winter, it is therefore more important to implement measures to limit aggregation.

#### Management of risk of CWD spillover

Norwegian wildlife management was quick to respond when CWD first arose as a threat. After eradication of the affected reindeer herd, the immediate surrounding area of Nordfjella (zone 1) was fallowed (Mattilsynet & Miljødirektoratet, 2017). This would last for at least five years. In practice this means that no reindeer herd will be reintroduced to the area before this time has passed. Fear of spillover to the surrounding red deer population and other cervid species led to some additional measures being put in place to limit the contact between individuals. It was decided that the population size of the red deer in the immediate surrounding area was to be reduced by 50%. This reduction was to be carried out by regular hunting during 2019 and 2020 (Solberg et al., 2019). This was implemented for the 15 municipalities surrounding the Nordfjella region and Zone 1: Årdal, Lærdal, Aurland, Ulvik, Eidfjord, Vang, Vestre Slidre, Nord-Aurdal, Sør-Aurdal, Nes, Gol, Hemsedal, Ål, Hol and Nore og Uvdal. All these municipalities either have areas that overlap with Nordfjella Zone 1, or have cervid populations that for parts of the year range near or in the fallowed area (Solberg et al., 2019). This would aid in limiting the contact between individuals, especially considering the high density of the red deer in Lærdal, one of the affected municipalities.

In addition, the regulation concerning “Measures to reduce the spread of Chronic Wasting Disease (CWD)” (“Forskrift om tiltak for å begrense spredning av Chronic Wasting Disease (CWD),” FOR-2016-07-11-913) issued in 2016 included this regulation: §6 Ban on using



mineral licks and supplemental feeding aimed at wild cervids. As previously mentioned, the Norwegian Food Safety Authority also required all hay bales stored in Lærdal to be fenced in to reduce aggregation around these (Sælthun, 2017).

The drastic measures implemented after the first case of CWD was discovered likely aided in limiting the spread of the disease. However, the prions' long viability outside of a host makes it difficult to determine if these measures alone were enough, or if there will be another outbreak. Knowing more about the causes of aggregation and its anthropogenic sources before such an outbreak could be critical. It is also critical that the measures already implemented are upheld.

As seen from the results there was still aggregation around anthropogenic sources. From what I observed in the field, it seemed like these clusters also had more signs of animal activity around them than other infield clusters. As mentioned, this has also been proved in a previous study by Mejía-Salazar et al. (2018). This higher level of activity around anthropogenic sources facilitates more contact between individuals than clusters around natural forage does. Such hot spots should be reduced as much as possible to avoid disease transmission. Spreading awareness about these non-intentional feeding sources and implementing measures to limit them could be vital in combating disease transmission. Especially considering how they may be the cause of between 10,000 and 25,000 clusters in Lærdal each winter.

I also noted the varying level of compliance to the requirement of fencing around hay bales. Even though none of our clusters from the field work reflected a high level of interest in these, there may be more activity in years with more snow. Foraging on hay bales is more difficult than foraging on bare or nearly bare fields due to the plastic wrapping. However, in years with deep snow when natural forage is of lower quality and energy consuming to acquire, hay bales are a good alternative for cervids. Red deer have been known to forage on hay bales when needed (Haugset, 2005). Hay bales could therefore be a hot spot for disease transmission during winters with deep snow. Especially considering how number of clusters increase and move towards infield habitats with deeper snow. Some enforcement may be necessary to make certain that hay bales are properly fenced in to avoid aggregation around them.

From the results and observations in the field I can see that there is more that can be done to aid in combating the spread of CWD. Finding ways to dispose of silage so the red deer and other cervids cannot forage on it will minimize anthropogenic sources of aggregation even more. Enforcing the requirement of fencing around hay bales will also help limit the contact between individuals. This will be especially important during winters with deep snow and in areas where there is generally more snow as this leads the red deer to cluster more frequently. It is also more important that these measures are enforced during the winter in general, as the red deer cluster more on infield habitats during the winter season. Eliminating these transmission hot spots could further reduce the risk of spillover of CWD to red deer and other cervid species.

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## Appendix

*Table 1 Model estimates for predicted average elevation of clusters per animal per month for each season for red deer in Lærdal. Standard deviation for random effect (id) = 135.6. Sesong.yearcat is a variable with season (sesong) and year (yearcat) concatenated into one variable.*

	<b>Standard error</b>	<b>t-value</b>	<b>p-value</b>
<b>(Intercept)</b>	37.761	14.769	3.78e-09
<b>sesong.yearcatfall.2018</b>	3.953	39.724	< 2e-16
<b>sesong.yearcatspring.2017</b>	8.248	-2.360	0.0183
<b>sesong.yearcatspring.2018</b>	5.090	-8.054	8.27e-16
<b>sesong.yearcatspring.2019</b>	7.560	-4.944	7.69e-07
<b>sesong.yearcatsummer.2017</b>	5.488	42.158	< 2e-16
<b>sesong.yearcatsummer.2018</b>	4.160	63.853	< 2e-16
<b>sesong.yearcatwinter.2017</b>	7.204	-26.365	< 2e-16
<b>sesong.yearcatwinter.2018</b>	3.718	-58.244	< 2e-16
<b>sesong.yearcatwinter.2019</b>	4.193	-33.117	< 2e-16

*Table 2 Model estimates for predicted elevation of clusters with increasing snow depth for red deer in Lærdal.. Standard deviation of random effect (id) = 174.84. Baseline is 2018.*

	<b>Standard error</b>	<b>t-value</b>	<b>p-value</b>
<b>(Intercept)</b>	4.852e+01	6.922	1.59e-05
<b>snow.depth</b>	4.069e-03	2.607	0.00915
<b>yearcat2019</b>	2.283e+00	17.949	< 2e-16
<b>snow.depth:yearcat2019</b>	7.712e-03	27.695	< 2e-16

Table 3 Model estimates for predicted probability of clusters being in outfield habitat for red deer in Lærdal. Standard deviation for random effect (id) = 0.8708. *Sesong.yearcat* is a variable with season (*sesong*) and year (*yearcat*) concatenated into one variable.

	<b>Standard error</b>	<b>z-value</b>	<b>p-value</b>
<b>(Intercept)</b>	0.23926	6.546	5.89e-11
<b>sesong.yearcatfall.2018</b>	0.07062	15.146	< 2e-16
<b>sesong.yearcatspring.2017</b>	0.11657	-5.014	5.34e-07
<b>sesong.yearcatspring.2018</b>	0.09185	3.746	0.00018
<b>sesong.yearcatspring.2019</b>	0.16193	6.662	2.70e-11
<b>sesong.yearcatsummer.2017</b>	0.19636	11.953	< 2e-16
<b>sesong.yearcatsummer.2018</b>	0.09367	19.729	< 2e-16
<b>sesong.yearcatwinter.2017</b>	0.09638	-16.446	< 2e-16
<b>sesong.yearcatwinter.2018</b>	0.05635	-15.501	< 2e-16
<b>sesong.yearcatwinter.2019</b>	0.06934	2.467	0.01361

Table 4 Model estimates for predicted probability of clusters being in outfield habitat with increasing snow depth for red deer in Lærdal. Standard deviation for random effect (id) = 0.1990. Baseline is 2018.

	<b>Standard error</b>	<b>t-value</b>	<b>p-value</b>
<b>(Intercept)</b>	5.576e-02	9.206	6.80e-07
<b>snow.depth</b>	2.109e-05	20.171	< 2e-16
<b>yearcat2019</b>	1.191e-02	23.297	< 2e-16
<b>snow.depth:yearcat2019</b>	3.982e-05	-8.016	1.16e-15

Table 5 Model estimates for predicted average number of clusters per individual per month for red deer in Lærdal. Standard deviation for random effect (id) = 67.89. *Sesong.yearcat* is a variable with season (*sesong*) and year (*yearcat*) concatenated into one variable.

	Standard error	t-value	p-value
<b>(Intercept)</b>	18.955	10.086	2.64e-07
<b>sesong.yearcatfall.2018</b>	2.445	10.456	< 2e-16
<b>sesong.yearcatspring.2017</b>	5.101	-18.886	< 2e-16
<b>sesong.yearcatspring.2018</b>	3.147	21.263	< 2e-16
<b>sesong.yearcatspring.2019</b>	4.675	-20.252	< 2e-16
<b>sesong.yearcatsummer.2017</b>	3.394	-18.041	< 2e-16
<b>sesong.yearcatsummer.2018</b>	2.573	5.121	3.05e-07
<b>sesong.yearcatwinter.2017</b>	4.455	-8.912	< 2e-16
<b>sesong.yearcatwinter.2018</b>	2.299	60.622	< 2e-16
<b>sesong.yearcatwinter.2019</b>	2.593	3.340	0.000838

Table 6 Model estimates for predicted amount of clusters per animal per month with increasing snow depth for red deer in Lærdal. Standard deviation for random effect (id) = 81.17. Baseline is 2018

	Standard error	t-value	p-value
<b>(Intercept)</b>	2.257e+01	11.03	1.15e-07
<b>snow.depth</b>	4.317e-03	44.96	< 2e-16
<b>yearcat2019</b>	2.422e+00	-16.23	< 2e-16
<b>snow.depth:yearcat2019</b>	8.182e-03	-25.48	< 2e-16