ORIGINAL ARTICLE

Effect of legal regulation of supplemental feeding on space use of red deer in an area with chronic wasting disease

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Abstract

Supplemental feeding of cervids during winter is a widespread management practice, but feeding may increase the risk of disease transmission. Therefore, legal regulations to limit supplemental feeding are often implemented when dealing with severe infectious diseases, such as chronic wasting disease (CWD) in cervids. However, it is currently unclear whether these regulations result in decreased spatial clustering and aggregation as intended. Supplemental feeding is expected to restrict the movement of cervids. Therefore, a ban on feeding may also result in wider space use and a risk of geographic spread of disease. The space use of 63 GPS-marked red deer (*Cervus elaphus*) was investigated before ($n = 34$) and after ($n = 29$) the implementation of a legal regulation aimed at limiting the supplemental feeding of cervids during winter in a CWD-affected region of Nordfjella, Norway. Snow depth was the main determinant of the space use for red deer. A moderate reduction in the number of GPS positions in spatial clusters was evident during periods of deep snow once the ban was in place. Sizes of core areas (Kernel 50%), home ranges (Kernel 95%), and dispersion (MCP 100%, number of 1 km^2 pixels visited per deer) declined from January to March and with increasing snow depth. Dispersion (number of 1 km^2 pixels visited per deer) did not depend on snow depth after the ban, and red deer used larger areas when snow depth was high after the ban compared to before. The ban on supplementary feeding had no effect on size of core areas or home ranges. Several potential factors can explain the overall weak effect of the ban on space use, including the use of agricultural fields by red deer, other anthropogenic feeding, and landscape topography. This study highlights that snow depth is the main factor determining space use during winter, and it remains to be determined whether the moderate reduction in spatial clustering during deep snow after the ban was sufficient to lower the risk of disease transmission.

Keywords Chronic wasting disease (CWD) · Home range · Spatial clustering · Implementation uncertainty · GPS · Winter feeding · Wildlife diseases

Introduction

Supplemental feeding of cervids is a widespread practice across the Northern Hemisphere (Putman and Staines 2004), with the main aims being to increase the overwinter survival (Schmidt and Hoi 2002) or to divert cervids from browsing on economically important forests or close to traffic (Kubasiewicz et al. 2016). However, feeding may have adverse effects by increasing the risk of disease transmission (Sorensen et al. 2014; Milner et al. 2014). Feeding lead to aggregation of animals, affecting the amount of direct contact and environmental contamination of pathogens, thus increasing the risk of disease transmission between individuals. Bans on anthropogenic feeding of cervids are imposed to combat contagious diseases of deer (Carstensen et al. 2011; Cosgrove et al. 2018), with the intention of lowering local transmission by limiting deer spatial clustering and aggregation of animals. They may, however, also cause animals to travel further in search of alternative and more widely distributed food sources and, therefore, could increase their range sizes and the spread of disease. Indeed, previous research has shown that supplemental feeding during winter reduced the home range size of both roe deer (*Capreolus*

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capreolus) (Guillet et al. 1996; Ossi et al. 2017) and moose (*Alces alces*) (van Beest et al. 2010). Deer (host) space use is a main predictor of the geographic spread of chronic wasting disease (CWD) (Nobert et al. 2016). Therefore, any management action leading to wider dispersion of deer risks furthering the geographic spread of CWD (Mysterud et al. 2020). Other wildlife disease management actions, such as culling, sometimes cause a trade-off between lowering disease transmission in a given location and controlling the geographic spread of disease (Donnelly et al. 2005; Ham et al. 2019), but whether this is the case for ceasing supplemental feeding of deer has not been assessed.

CWD is a particularly serious and lethal disease affecting cervids (Spraker et al. 1997), causing reduction in deer population in endemic areas of the USA (Edmunds et al. 2016; DeVivo et al. 2017). The causative agents of CWD are prions that are shed by infected deer via the saliva and excretion of urine and faeces (Tamguney et al. 2009; Davenport et al. 2018). CWD can be transmitted between deer through direct contact and through the release of prions into the environment (Zabel and Ortega 2017). Deer aggregation points lead to increased environmental contamination of prions (Plummer et al. 2018) and are regarded as transmission hotspots (Mejia-Salazar et al. 2018). Therefore, when CWD recently emerged among reindeer (*Rangifer tarandus*) in Nordfjella, Norway (Benestad et al. 2016; Mysterud et al. 2019a), legal regulations were implemented to limit supplemental feeding of cervids in order to lower CWD transmission (Landbruks-og matdepartementet 2016; Mysterud et al. 2019b). Given that CWD has the potential to spillover between cervid species (Robinson et al. 2012; Cullingham et al. 2020), red deer (*Cervus elaphus*), which are sympatric

with the CWD-infected reindeer around Nordfjella, are one of the populations at most risk (VKM et al. 2018). Red deer are often fed with hay bales during winter (Mysterud et al. 2019b), and they regularly use agricultural meadows (Godvik et al. 2009); their winter home range size is also affected by prevailing weather and snow depth (Rivrud et al. 2010). Therefore, the quantitative extent to which a legal regulation on supplemental feeding is sufficient to affect spatial clustering, home range size, and dispersion is uncertain.

In this study, we aimed to assess whether the legal ban on supplemental feeding affected the space use and worked to reduce spatial clustering and aggregation of red deer in the CWD-affected region of Nordfjella, Norway (Fig. 1). We also aimed to quantify whether the ban led to potentially adverse side effect of wider space use and dispersion. This was done by estimating spatial clustering and broader space use (core area, home range size, and dispersion) of GPS-marked red deer before (2009–2012, $n = 34$) and after (2017–2019, $n = 29$) the legal ban was introduced. We use the term 'spatial clustering' (or revisitation) to refer to multiple revisits of an individual deer to the same main location, i.e. a cluster of GPS positions, while 'aggregation' refers to multiple deer at the same location.

Material and methods

Study area

The study area surrounds the Nordfjella mountain region in Norway (Fig. 1), where CWD was detected within the reindeer population. This includes the municipalities Aurland, Årdal,

Fig. 1 A map of the GPS positions of red deer relative to the where the CWD outbreak occurred in the Nordfjella reindeer area, Norway
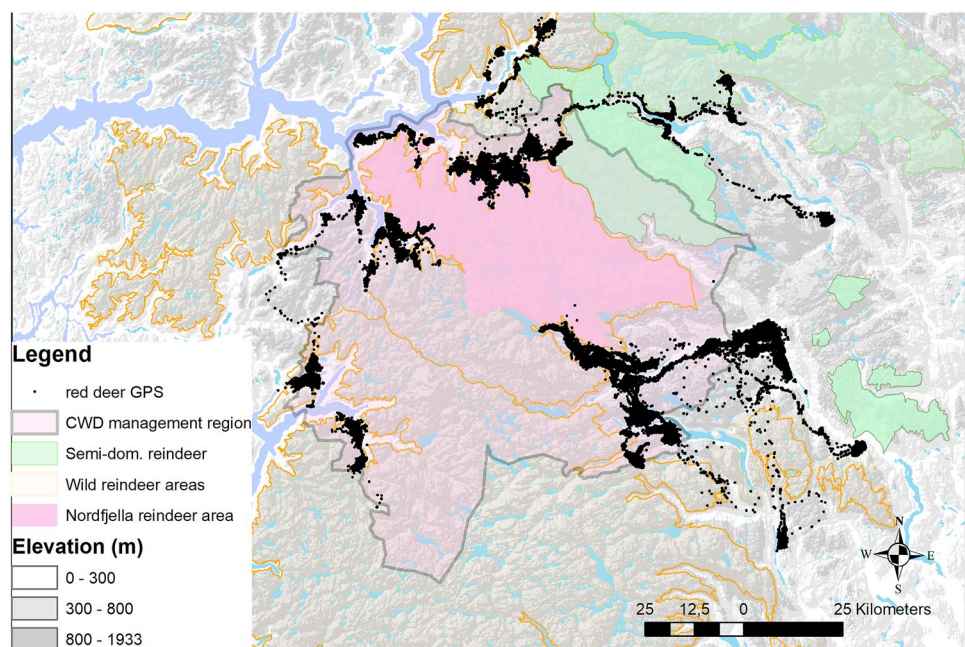
and Lærdal in Vestland county on the western side of the mountain range towards the west coast, and the more inland municipalities of Hemsedal, Ål, Gol, and Hol in Viken County. The climate in the western areas is more coastal with higher precipitation and warmer and shorter winters. The mean snow depth for January–March was 42 cm (maximum: 134 cm), while mean temperature was -4.7 °C (minimum: -14.7 °C; maximum: 2.4 °C). The area is dominated by steep elevation gradients from valleys and up to mountains above 1000 m above sea level, but the western valleys are situated at lower elevations than those inland. The western area is dominated by deep and steep valleys with agriculture and human settlements in the flatter areas. The slopes towards the mountains are covered with deciduous forest consisting mainly of birch (*Betula* sp.) and alder (*Alnus incana*), with scattered stands of planted Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). The eastern part is naturally forested and dominated by Norway spruce on richer soils and Scots pine on poorer soils. Birch is dominating at higher elevations up towards the open alpine habitat. There is very little human disturbance in these areas apart from close to human infrastructure, as the forested areas are not used for recreation during winter mainly due to a difficult and impassable topography.

The red deer population is dense in the western areas and markedly lower in inland areas, where the red deer winter at higher elevations. There is no explicit knowledge of how important the supplemental feeding sites were to red deer. It is clear that they use natural forage to a large extent, but anecdotal evidence suggested high mortality in the first and severe winter when supplemental feeding was banned.

Design and marking of red deer

Our design relied on comparing red deer space use before and after the ban on feeding was implemented. We have no indication that vegetation, land use, or agricultural practice has changed notable over the time period apart from CWD mitigation measures, such as closing supplemental feeding sites and salt licks. The eastern and western side of the mountain range provide wintering areas differing in elevation, and hence, potentially red deer being more relying on supplemental feeding in the eastern region. Deer were marked in both regions to allow testing for this possibility. The red deer were marked between 2009 and 2012 in a project from the eastern region (Mysterud et al. 2012) and as a part of the 'Hordahjort' project in the western region (2009–2011). Red deer were also marked during winters between 2017 and 2019, both east and west of the Nordfjella mountain range, as part of the ongoing project, 'red deer in Nordfjella', that was initiated due to the outbreak of CWD among reindeer. All markings of red deer followed standard procedures (Sente et al. 2014) and were

approved by the Norwegian Food Safety Authority (FOTS ID 19,113) and the Norwegian Environment Agency. The dataset used in the analyses included 53 females (≥ 1 years old) and 10 males (≥ 2 years old, Table 1).

The deer were darted either at supplemental feeding sites or along roads from a car in the same main areas from February to April. All marking of animals prior to feeding ban was carried out at winter feeding sites ($n = 34$ deer, 14 feeding sites). Before ban, feeding was close to ad libitum during periods of marking, from early February to mid-April. Some animals were also marked on short-term feeding sites once the ban was in place ($n = 17$ deer, 8 short-time feeding sites), but only after access was granted by the regulators. Feeding at these sites was kept to a minimum, with fewer locations, short feeding duration just around marking date for each deer, and feeding was terminated after marking ended. To avoid introducing bias in measuring the ban's effect, marking red deer at feeding sites was avoided where possible. This was done on a subsample of 12 red deer in the western region in 2017–2018 (mainly marked along roads); no feeding occurred in 2019.

GPS collars (VECTRONIC Aerospace GmbH, Berlin, Germany, collar weight: ca. 850 g, 0.5–1.0% of animal body weight) with an integrated VHF-transmitter were used, and the collars logged positions every 1 h (females) or 2 h (males); all locations collected within 24 h of marking were excluded. GPS position outliers were removed following standard procedures (Bjørneraas et al. 2010), resulting in a deletion of less than 0.05% of the locations. The animals included were followed usually for 2 years, but at least 1 year and up to 3 years depending on duration of collar battery and survival of a given individual. Further variation in number of positions arise due to start and end dates of successful collar deployment (marking in winter), and since collars not always achieve 100% fix rate.

Estimation of spatial clustering

The overall population of red deer in the study area counts thousands of individuals, and we can only GPS-mark a small proportion of the population. We did contact analysis

Table 1 An overview of the number of GPS-marked male and female red deer before (2009–2012) and after (2017–2019) a legal ban on supplementary feeding of cervids in the regions east and west of Nordfjella, Norway. All red deer were adults (females ≥ 1 year, males ≥ 2 years)

Sex	Region	Before	After	Total
Females	East	20	4	24
	West	11	18	29
Males	East	0	3	3
	West	3	4	7
Total		34	29	63

identifying contacts between pairs of individuals defined as GPS locations being within 40 m (based on cluster diameter used in cluster analysis) and 30 min (based on GPS fix schedule) of each other to investigate whether the marked individuals largely were part of stable groups. There was large variation in contact rates between years, but overall marked animals were typically not part of the same stable social group even when marked in the same main location (Supplementary Table 1). Hence, we do not have sufficient number of animals marked to do social network or similar analysis. Increased revisitation leads to spatial clustering of GPS positions. Based on snow tracking, we documented in previous work a correlation between spatial clustering of GPS positions of a given individual and aggregation of animals (Mysterud et al. 2021). Hence, conditions leading to spatial clustering also lead to aggregation of red deer at these sites. Spatial clustering of GPS positions arising from revisitation is likely a relevant measure of deer contact and risk of disease transmission.

The ban on feeding intends to minimise behaviours likely to increase the risk of disease transmission, i.e. spatial clustering and aggregation of animals. Data were restricted to the winter months January, February, and March to target the potential effects of supplemental feeding. Density-based spatial clustering of applications with noise (DBSCAN) was used to identify the number of spatial clusters used by red deer (Hahsler and Piekenbrock 2021). We estimated clusters for each individual on a monthly scale, retaining only individuals with at least 100 relocations in a month. Each individual GPS location was overlaid a radius of 20 m and identified as clusters when there was a minimum of 10 GPS locations from the given individual (and month) within this radius. For each cluster, we calculated the number of positions within the radius. All analyses were performed using the statistical software R vs. 4.1.2 (R Development Core Team 2021).

Estimation of home range and dispersion

The actual GPS positions (not clusters) were used in the following analysis of home range size and dispersion. The monthly home range size for January, February, and March was estimated separately, and we included only individuals with at least 100 GPS locations available for a given month. The average number of locations per individual per month was 557 (100–744). Home ranges were calculated using the 'adehabitatHR' library in R (Calenge 2006). The 95% kernel density was used as an estimate of the main home range size (Worton 1989), the 50% kernel density was used to estimate core home range size, and the 100% minimum convex polygon (MCP) (Mohr 1947) was used as an estimate of dispersion. While MCP usage is often criticised in home range estimation because it is sensitive to outliers, it is a useful

tool for investigating broad dispersion at landscape scales. To provide another metric of dispersion, the study area was rasterised at 1×1-km resolution, and the number of unique 1-km^2 pixels visited per individual within a given month was recorded. Hence, the response variable (see below) for each individual deer in a given month was the number of unique 1-km^2 pixels visited.

Snow depth and temperature

Information on snow depth and temperature within each home range was extracted as these are major factors determining red deer home range size (Rivrud et al. 2010). Mean snow depth and temperature were extracted from monthly 1×1-km grids covering the study area. Grids were provided by the Norwegian Water Resources and Energy Directorate (snow depth) and the Norwegian Meteorological Institute (temperature). The grids were built from modelling and statistical downscaling from existing weather stations covering Norway (Saloranta 2016; Lussana et al. 2019). Median and mean monthly snow depth and temperature were calculated within the 95% monthly kernel home range for each individual. These covariates were highly correlated ($r = 0.940$ and $r = 0.994$ for snow depth and temperature respectively), and we used the mean snow depth and temperature for analysis. Correlation between mean monthly snow depth and temperature was sufficiently low ($r = -0.307$), allowing for both to be fitted in the models.

Statistical analysis

The main sampling unit was the individual deer. We tested for differences in number of spatial clusters and number of GPS positions per spatial cluster, home range size, or the number of 1-km^2 pixels (all log-transformed) using a mixed model approach, in the 'lme4' library (Bates and Maechler 2009) in R. v. 4.1.2, with feeding or ban, month, and sex as categorical fixed effects, snow depth and temperature being continuous fixed-effects, and region, year, and individual animal as random intercept effects. We examined interactions between environmental variables and the ban to see if deer responses in space use during feeding and when banned differed. Feeding ceased in the winter of 2016/17, so data were categorised as 'feeding' and 'ban' for 2009–2012 and 2017–2019, respectively. The analysis focused on the winter season, and the month was used as a categorical variable. Sex (male/female), month (Jan/Feb/Mar), and feeding ban (feeding/ban) were used as candidate categorical variables and snow depth (cm) and temperature (°C) at the monthly home range scale as candidate continuous variables. The interaction terms between ban and the covariates snow depth and temperature were also included in the model as snow depth and temperature may affect movement differently

depending on supplemental forage availability. For all analyses, we also added the total number of locations per individual each month as a covariate to correct for different sampling intensity and period. The number of locations was added as a basis spline, to account for asymptotic relationships between the sampling intensity and the response.

The inclusion of random terms within a model with only an intercept was tested first. Individual ID, year, and region (east/west), and all combinations of these were candidate random intercepts; the region was included as a potential random term rather than a fixed effect due to some region-wise imbalance in the number of individuals marked before and after the ban (Table 1). Models with different random terms were compared using the Akaike information criterion (AIC) to identify the most parsimonious model. When random term structure was identified, we used backwards model selection by AIC on fixed effects of the full model to identify the most parsimonious model. We considered models with $\Delta AIC > 2$ as different from each other. From the full model, the effect of taking out single variables using the 'drop1()' function was compared, and the variable that increased the AIC the most was removed from the model. The procedure was repeated until the most parsimonious model was identified. All models were checked with standard diagnostic tools to assess patterns in the residuals, looked for influential values, and ensured that the model assumptions were met. We found no strong patterns in the residuals.

Results

Including all three terms (individual ID, year, and region) as random intercepts gave the most parsimonious model for the number of positions per spatial cluster. The terms individual ID and year were included for the number of clusters and home range estimators, while individual ID was the only term included for analysing the number of pixels used (Supplementary Table 2). An overview of the model selection of the fixed effects is provided in Supplementary Table 3.

Pattern of spatial clustering of positions

The mean number of spatial clusters ($\pm$ SD) was 10.1 (4.5) in January, 8.9 (4.3) in February, and 7.3 (4.5) in March with a mean number of locations per cluster of 37.1 (29.5), 39.7 (37.1), and 44.1 (36.6), respectively. The number of spatial clusters was determined by month only. More clusters were formed in February than in January, while the number of clusters formed was similar between January and March (Table 2). The number of GPS positions in each spatial cluster was determined by the month, the legal ban on feeding, snow depth, and the interaction between snow depth and ban (Table 2). The number of GPS positions in each spatial

cluster increased more substantially with snow depth before the feeding ban was implemented (Fig. 2). The number of GPS positions in each spatial cluster was higher in March than in February, but there were no significant differences between the remaining combinations of months. Sex was not retained in the most parsimonious model explaining the number of GPS positions in spatial clusters.

Home range size and dispersion

The mean size of the core area was 0.63 km^2 in January, 0.30 km^2 in February, and 0.32 km^2 in March, while the mean size of the main home range was 3.41 km^2 in January, 1.48 km^2 in February, and 1.55 km^2 in March. The mean dispersion (MCP 100%) was 3.05 km^2 in January, 1.59 km^2 in February, and 2.24 km^2 in March. Similarly, when using 1-km^2 pixels (another measure of dispersion), the mean number of cells visited was 6.8 in January, 4.9 in February, and 4.6 in March.

The categorical variable legal ban was not retained in the models of monthly home range size (kernel 95%), core area size (kernel 50%), or dispersion (MCP 100%), thus implying no marked effect of the legal ban on these movement metrics (Supplementary Table 3). There was a strong decline in home range size over the winter months and with increased snow depth for all home range estimators and for dispersion (Table 2). For core areas, there was an increase in home range size with increasing temperatures. Among the dispersion metrics, only the number of 1-km^2 pixels used by red deer showed a difference between when feeding was legal and when it was banned, but that relationship depended on snow depth (Table 2). The number of unique 1-km^2 pixels used by red deer decreased with increasing snow depths before the ban on feeding occurred, while there was no clear effect of snow depth on dispersion after the ban on feeding (Fig. 3). Sex was not retained in the most parsimonious model for any of the home range estimates or dispersion (Table 2).

Discussion

Ongoing severe wildlife disease epidemics in Europe, such as African swine fever in wild boar (*Sus scrofa*) (EFSA Panel on Animal Health and Welfare (AHAW) et al. 2018) and CWD in cervids (EFSA Panel-on Biological Hazards (BIOHAZ) et al. 2019), elicit radical management responses by governments. Ideally, disease mitigation measures should be evidence-based (Vicente et al. 2019; Mysterud and Rolandsen 2019). However, the efficacy of many measures remains poorly documented, so they are often implemented without knowledge of efficacy or potential adverse side effects. We evaluated effects of a legal regulation of supplemental feeding connected to

Table 2 Parameter estimates from the most parsimonious generalised linear mixed-effects models of number of spatial clusters, number of GPS locations in clusters, home range size, and dispersion (100% MCP or number of unique 1-km^2 pixels used) of red deer during winter before (2009–2012) and after (2017–2019) a legal ban on supplementary feeding in Nordfjella, Norway. Note that the most parsimonious model did not always include the ban on feeding. Individual animal ID, year, and region were fitted as random intercepts in the different models as shown, with standard deviation given in the first row. SE, standard error; CI low and CI high gives the upper and lower boundary of the 95% confidence interval for the estimate. s(monthly GPS locations) gives the estimates for a smoothing spline for monthly sample size, to correct for sampling intensity. Kernel, home range size estimated with the Kernel method; MCP, dispersion or home range size estimated with the minimum convex polygon method. The reference level for 'ban' (ban/legal) is 'ban' and for 'month' is 'January'

Parameters	Estimate	SE	CI low	CI high	ID	Year	Region
No. of clusters							
Intercept	0.560	0.202	0.168	0.959	0.257	0.233	
s(monthly GPS locations, 1)	0.962	0.414	0.145	1.762			
s(monthly GPS locations, 2)	0.891	0.254	0.397	1.395			
s(monthly GPS locations, 3)	1.704	0.180	1.355	2.060			
Month Feb	0.215	0.086	0.046	0.384			
Month Mar	-0.088	0.069	-0.225	0.044			
Positions per cluster							
Intercept	2.596	0.259	2.106	3.073	0.328	0.208	0.115
s(monthly GPS locations, 1)	0.348	0.427	-0.479	1.185			
s(monthly GPS locations, 2)	0.687	0.267	0.162	1.201			
s(monthly GPS locations, 3)	0.514	0.187	0.160	0.886			
Month Feb	-0.080	0.089	-0.252	0.095			
Month Mar	0.112	0.070	-0.025	0.246			
Snow depth	0.008	0.002	0.004	0.012			
Ban	-0.235	0.236	-0.667	0.225			
Ban × snow depth	0.009	0.003	0.002	0.015			
Kernel 95%							
Intercept	5.486	0.373	4.764	6.208	0.670	0.190	
s(monthly GPS locations, 1)	0.827	0.788	-0.712	2.355			
s(monthly GPS locations, 2)	0.123	0.489	-0.814	1.102			
s(monthly GPS locations, 3)	0.190	0.339	-0.476	0.843			
Month Feb	-0.377	0.165	-0.704	-0.061			
Month Mar	-0.495	0.127	-0.744	-0.249			
Snow depth	-0.016	0.003	-0.022	-0.011			
Kernel 50%							
Intercept	4.238	0.432	3.413	5.068	0.706	0.288	
s(monthly GPS locations, 1)	0.864	0.851	-0.804	2.506			
s(monthly GPS locations, 2)	-0.441	0.533	-1.456	0.638			
s(monthly GPS locations, 3)	0.203	0.367	-0.527	0.902			
Month Feb	-0.296	0.182	-0.662	0.051			
Month Mar	-0.654	0.182	-1.003	-0.305			
Temperature	0.053	0.023	0.008	0.098			
Snow depth	-0.017	0.003	-0.024	-0.011			
MCP 100%							
Intercept	4.969	0.352	4.289	5.667	0.610	0.124	
s(monthly GPS locations, 1)	0.532	0.750	-0.995	1.976			
s(monthly GPS locations, 2)	1.280	0.465	0.384	2.191			
s(monthly GPS locations, 3)	0.643	0.322	-0.013	1.262			
Month Feb	-0.533	0.157	-0.848	-0.231			
Month Mar	-0.551	0.121	-0.791	-0.317			
Snow depth	-0.013	0.003	-0.018	-0.007			
Unique pixels (1 km^2)							
Intercept	1.416	0.206	1.018	1.820	0.323		
s(monthly GPS locations, 1)	0.384	0.412	-0.431	1.181			
s(monthly GPS locations, 2)	0.509	0.260	0.007	1.013			
s(monthly GPS locations, 3)	0.413	0.177	0.067	0.753			
Month Feb	-0.218	0.086	-0.384	-0.050			
Month Mar	-0.258	0.067	-0.386	-0.128			
Ban	0.209	0.158	-0.097	0.514			
Snow depth	-0.001	0.002	-0.005	0.002			
Ban × snow depth	-0.007	0.003	-0.013	-0.002			

Fig. 2 Predicted spatial clustering (number of GPS locations per cluster) of red deer as a function of snow depth, before (2009–2012) and after (2017–2019) a legal ban on winter feeding of cervids in Nordfjella, Norway. The predicted values are based on a generalised linear mixed-effects model with individual ID, year, and the spatial region as random intercepts. Ribbons around the predicted lines show the 95% confidence intervals of the predictions. Points show the residuals of the model
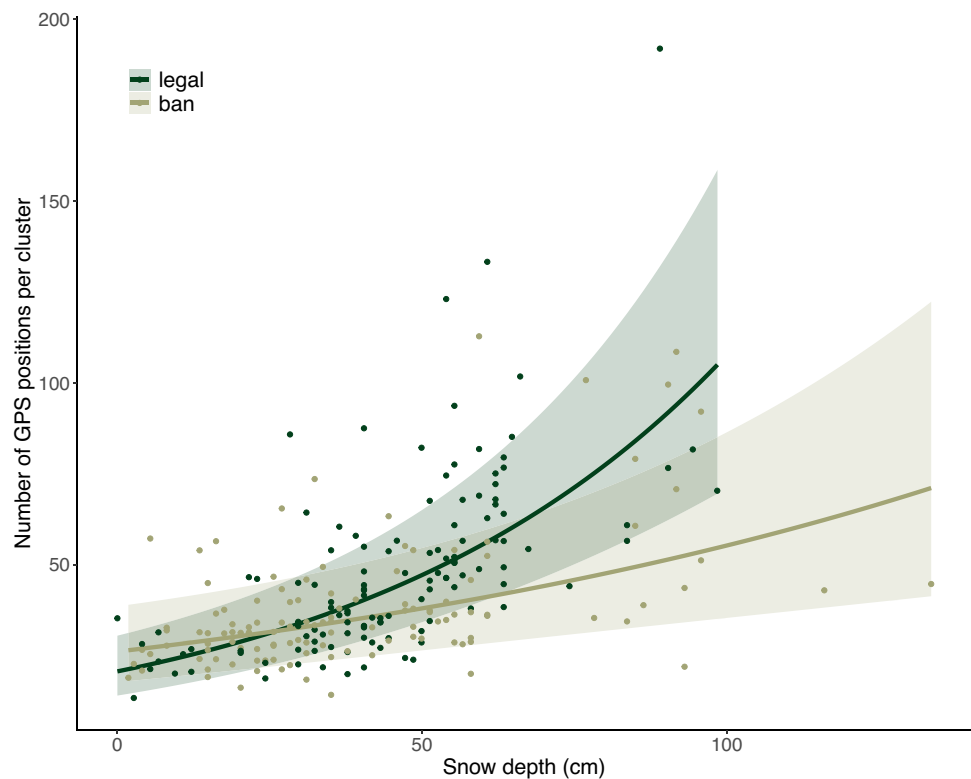

the outbreak of CWD in Nordfjella, Norway, based on data collected from 63 GPS-marked red deer. The regulation led to fewer revisits to spatial clusters during deep snow conditions, which is consistent with the intention of the regulation. It did not, however, reduce the number of spatial clusters as per our definition, i.e. a minimum of 10 GPS positions within a 20-m radius for core positions. Increased dispersion of red deer after the ban on feeding compared to before was only evident at high snow levels when measured as a higher number of unique 1-km^2 pixels visited. Before the ban, red deer showed reduced dispersal with increasing snow levels. The regulation of feeding had no marked impact on home range size or on dispersion measured as 100% minimum convex polygons. Hence, there was weak evidence of potential adverse effects in the form of wider ranging behaviour.

Spatial clustering of positions

Supplemental feeding can lead to increased direct contact between individuals and transfer of pathogens from the environment (Sorensen et al. 2014). Despite these general expectations, moose in Norway using supplementary feeding sites had similar levels of gastrointestinal nematodes compared to non-users (Milner et al. 2013). Whether supplemental feeding affects disease or parasite transmission is likely dependent on how much feeding impacts behaviour and space use relative to other factors. Implementing the movement analysis of hosts into disease ecology is an emerging scientific field

(Dougherty et al. 2018). Aggregation and spatial clustering are likely to be proxies for disease transmission risk. While no direct effect of the feeding ban on spatial clustering was evident here, a lower level of revisits to spatial clusters was recorded after the ban when snow levels were high (Fig. 2). This is consistent with the increased use of supplemental feeding sites by roe deer in Italy during periods of deep snow (Ossi et al. 2020). Hence, some effect of the ban in terms of reduced risk of disease transmission during periods of deep snow was supported. Whether this moderate reduction in clustering is sufficient to markedly affect disease transmission remains to be studied. A limitation of our study is the lack of observations of the direct causes of clustering and that the location of supplemental feeding sites were not mapped before they were closed (and challenging to map). Roe deer remembered the spatial position of supplementary feeding sites (Ranc et al. 2021). It is likely that deer occasionally visited previous feeding sites even after the ban, but such revisitation is likely to decrease over time. The level of supplemental feeding will affect how much behaviour is affected (Arnold et al. 2018). Supplemental feeding in the study area of Norway is much less intensive compared to some areas in central Europe, where feeding even involves fencing of red deer (Putman and Staines 2004). Termination of feeding in some of these areas in continental Europe will likely have a much stronger impact on deer behaviour than what we documented in Norway.

Fig. 3 Predicted dispersion (number of unique 1-km^2 pixels visited) of red as a function of snow depth before (2009–2012) and after (2017–2019) a legal ban on winter feeding of cervids in Nordfjella, Norway. The predicted values are based on a generalised linear mixed-effects model with individual ID as random intercept. Ribbons around the predicted lines show the 95% confidence intervals of the predictions. Points show the residuals of the model
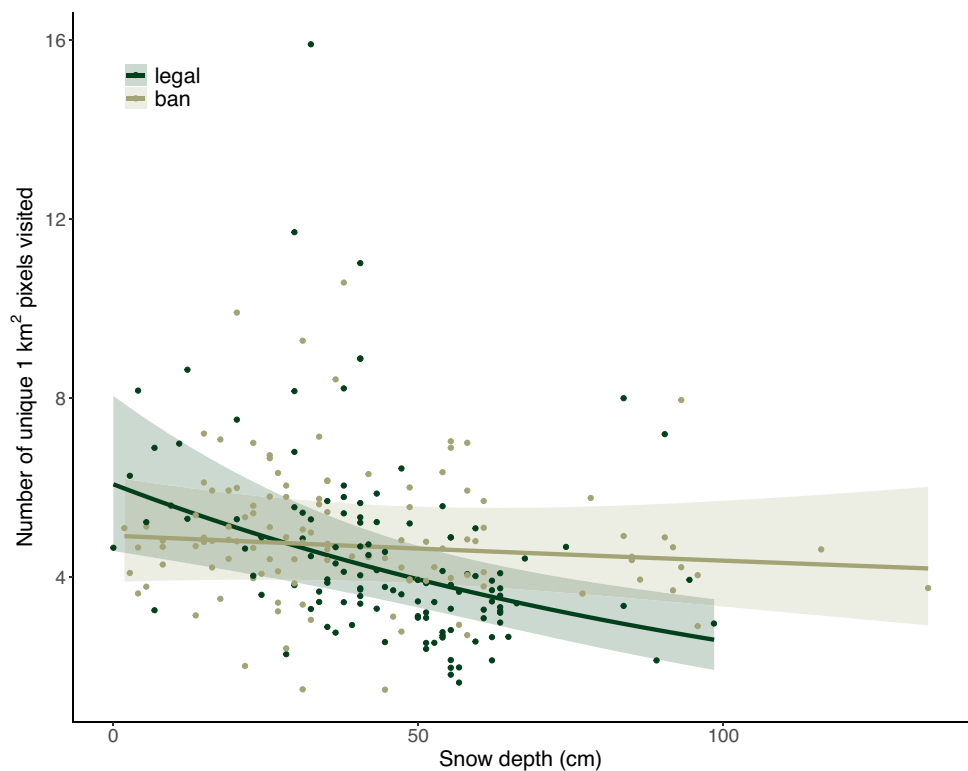
Home range size and dispersion

Management measures to lower the risk of disease transmission may have adverse side effects. Host culling of European badgers (*Meles meles*), intended to limit local transmission of bovine tuberculosis, leads to an increase in the geographic spread of disease as it disrupted the social structure and increased host dispersal (Donnelly et al. 2005; Ham et al. 2019). Supplemental feeding reduced home range size in both roe deer in Sweden and Italy (Guillet et al. 1996; Ossi et al. 2017) and moose in Norway (van Beest et al. 2010). Increased home range size and dispersion of red deer was anticipated following implementation of the feeding ban in this study. The weak effect of the ban on dispersion, limited to periods of higher snow depth, likely stems from the impact of snow on home range size (Rivrud et al. 2010), along with the landscape topography as the deep valleys and snow levels restrict movement. The presence of other anthropogenic sources of forage including agricultural meadows also contributes (Mysterud et al. 2021). Hence, the red deer remained largely in the same area, even after supplemental feeding was stopped. There appeared to be no marked trade-off between limiting local transmission and risking the geographic spread of disease in this region when implementing such a ban. We only assessed the adverse effects in the form of space use. Red deer in the eastern range overwinter at ~600 m above sea level, and they appeared to be heavily reliant on winter supplementary feed when conditions were harsh. Indeed, when one of the winter feeding stations closed during an exceptionally harsh winter, anecdotal evidence suggests that around 50 out of a total of 150 red deer were found dead during the snow-rich winter of 2017/18 (Utti 2018).

Conclusions

Documenting the impacts of disease mitigation measures is important for building a platform that allows an evidence-based response to current and future disease outbreaks in wildlife. As intended with the ban, results indicate fewer revisits to the spatial clusters during periods of deep snow after the ban was implemented. Whether this moderate effect on spatial clustering is sufficient to lower disease transmission remains to be determined. Overall, the effect of the feeding ban on the space use of red deer was weak, and snow depth was the main determinant of space use.

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Declarations

Conflict of interest The authors declare no competing interests.

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