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ARTICLE

Disease Ecology

Estimating and managing broad risk of chronic wasting disease spillover among cervid species

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Abstract

The management of infectious wildlife diseases often involves tackling pathogens that infect multiple host species. Chronic wasting disease (CWD) is a prion disease that can infect most cervid species. CWD was detected in reindeer (*Rangifer tarandus*) in Norway in 2016. Sympatric populations of red deer (*Cervus elaphus*) and moose (*Alces alces*) are at immediate risk. However, the estimation of spillover risk across species and implementation of multispecies management policies are rarely addressed for wildlife. Here, we estimated the broad risk of CWD spillover from reindeer to red deer and moose by quantifying the probability of co-occurrence based on both (1) population density and (2) habitat niche overlap from GPS data of all three species in Nordfjella, Norway. We describe the practical challenges faced when aiming to reduce the risk of spillover through a marked reduction in the population densities of moose and red deer using recreational hunters. This involves setting the population and harvest aims with uncertain information and how to achieve them. The niche overlap between reindeer and both moose and red deer was low overall but occurred seasonally. Migratory red deer had a moderate niche overlap with the CWD-infected reindeer population during the calving period, whereas moose had a moderate niche overlap during both calving and winter. Incorporating both habitat overlap and the population densities of the respective species into the quantification of co-occurrence allowed for more spatially targeted risk maps. An initial aim of a 50% reduction in abundance for the Nordfjella region was set, but only a moderate population decrease of less than 20% from 2016 to 2021 was achieved. Proactive management in the form of marked population reduction is invasive and unpopular when involving species of high societal value, and targeting efforts to zones with a high risk of spillover to limit adverse impacts and achieve wider societal acceptance is important.

KEYWORDS
disease management, host range, moose, multihost pathogens, niche overlap, Norway, population estimation, red deer, reindeer

INTRODUCTION

Wildlife disease transmission is often complex and involves multiple host species (Downs et al., 2019; Johnson et al., 2015; Rigaud et al., 2010; Woolhouse et al., 2001). Management tactics used to combat wildlife diseases include culling and other intrusive actions (Delahay et al., 2009; Miguel et al., 2020). The effects of culling targeted wildlife species to limit transmission have occasionally not worked as anticipated because of multiple host reservoirs (Gortázar et al., 2015). Targeting the entire competent host community is likely to be the key to the successful mitigation of multihost wildlife diseases (Joseph et al., 2013), but there are few reports on how to approach this complexity in practical management (Portier et al., 2019). Wildlife species differ in their habitat niches, and spatially targeting the culling efforts of multiple hosts would benefit from the quantification of high-risk areas for spillover facing multihost pathogens.

Infectious wildlife diseases are transmitted either directly between individuals or indirectly through the environment with or without the involvement of vectors (Gortazar et al., 2014). The risk of indirectly transmitted diseases can be estimated using spatial or habitat-based niche overlap indices (Dougherty et al., 2018). Niche overlap, and hence the risk of transmission, can be strongly influenced by migration among hosts (Merkle et al., 2018; Rayl et al., 2021). Furthermore, approaches for estimating the risk of disease spillover using indices of habitat overlap recommended from a spatial ecology framework do not explicitly consider population density. Transmission rates of indirectly transmitted diseases and the likelihood of spillover are linked to the population density of the species involved (Portier et al., 2019). Hence, both habitat niche overlap and the population densities of competent hosts are relevant to enabling targeted mitigation efforts, as has been previously shown for transmission risk of brucellosis between elk (*Cervus canadensis*) and livestock (Rayl et al., 2019).

Chronic wasting disease (CWD) is a lethal prion disease detected in the mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), elk, and moose (*Alces alces*) in the United States and Canada (Haley & Hoover, 2015). The recent detection of CWD among reindeer (*Rangifer tarandus*) in Norway, which share a range with red deer (*Cervus elaphus*) and moose, makes the risk of CWD spillover an urgent issue to address (VKM et al., 2018). These species are susceptible to CWD, and CWD cases have been confirmed in both moose (Baeten et al., 2007) and captive red deer in North America (Schwabenlander et al., 2013). CWD can be transmitted either through direct contact or indirectly through the ingestion of soil or plants infested with CWD prions (Zabel & Ortega, 2017). Currently, there are no studies on seasonal niche overlap among cervids in Europe as a basis for understanding the risk of disease spillover. The first CWD-infected reindeer population has been eradicated (Mysterud & Rolandsen, 2018), but prions can remain infectious in the soil for years (Smith et al., 2011; Zabel & Ortega, 2017). Hence, niche overlap continues to pose a risk for CWD spillover. However, the population density and level of the spatiotemporal niche overlap of other cervids with previously CWD-infected reindeer populations remain uncertain.

Here, we aimed both to (1) quantify the risk of spillover (through species niche overlap) relevant for disease mitigation and (2) evaluate success in the management of risk by population reductions. (1) We quantify the pairwise environmental niche overlap for different seasons between reindeer from the CWD-infected population and red deer and moose and provide risk maps where species co-occurrence was also adjusted for population densities. We used a unique dataset, including 25 GPS-marked reindeer, 51 red deer, and 25 moose, derived from the CWD region of Nordfjella, Norway. (2) The central management authorities set the aim of managing the risk of CWD spillover by reducing moose and red deer populations to approximately 50% of their winter densities in 2016 using recreational hunters (Figure 1), and we evaluated whether this was achieved by the end of 2020 (winter density in 2021).

MATERIALS AND METHODS

Study region

The study region consisted of 15 municipalities surrounding the Nordfjella area in Norway with a previously CWD-infected reindeer population (Figure 2). The demarcation of the study area is defined by the Norwegian Food Safety Authority as a CWD containment zone according to legal regulations (Ministry of Agriculture and Food, 2017). The core area is the alpine

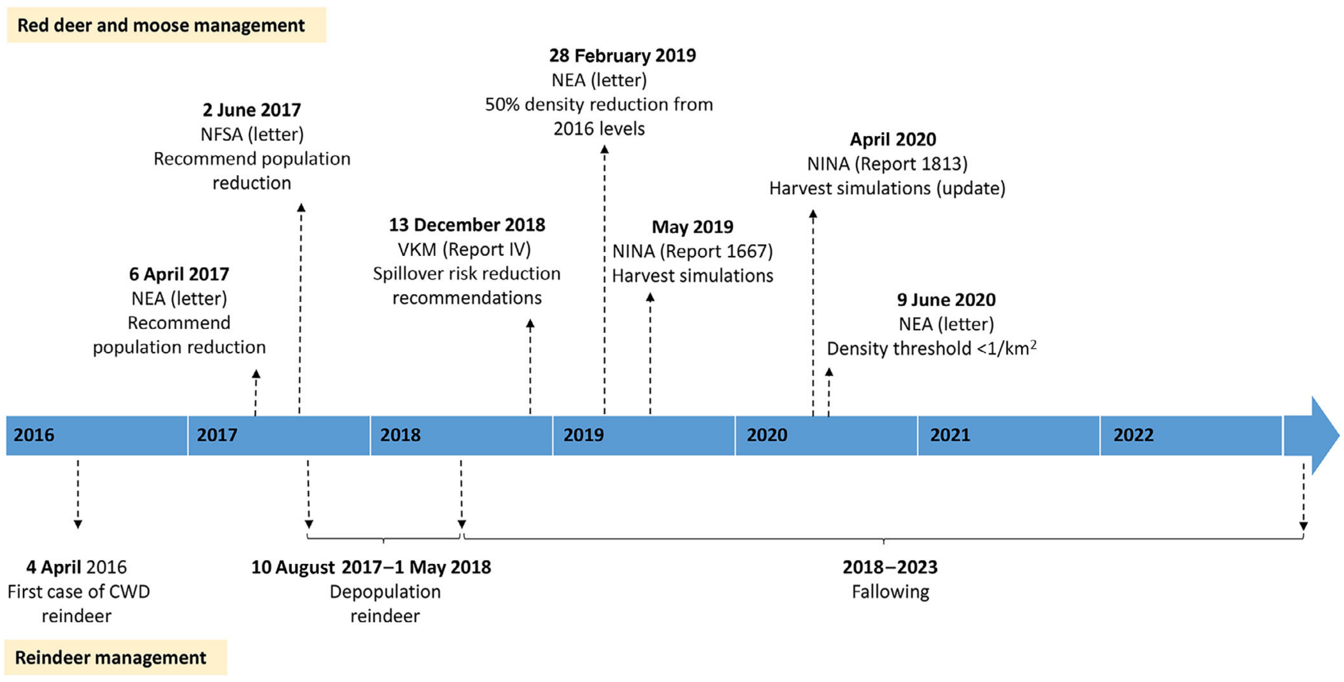

FIGURE 1 An overview of the main steps in the management of risk of chronic wasting disease (CWD) spillover from reindeer to red deer and moose in Nordfjella mountain range, Norway. NEA, Norwegian Environment Agency; NFSA, Norwegian Food Safety Authority; NINA, Norwegian Institute for Nature Research; VKM, Norwegian Scientific Committee for Food and Environment.

wild reindeer management area Nordfjella, which is separated into zones 1 (2000 km^2) and 2 (1000 km^2). CWD was detected only in zone 1. The mountainous area of Nordfjella is surrounded by steep, forested valleys to the west and gentler valleys to the east. The woodland limit is lower in the west than in the east, but approximately 1000 m above sea level and comprises birch (*Betula* spp.) forest. In the west, forests are dominated by deciduous trees at lower elevations with scattered Norway spruce (*Picea abies*) stands, whereas in the east, forests at lower elevations are dominated by spruce and Scots pine (*Pinus sylvestris*).

Red deer had the highest population density in the west, whereas moose had the highest population density in the east (Figure 2). Population sizes of the roe deer (*Capreolus capreolus*) were low and were not considered in this study. There were no large predators with permanent establishments, although there were occasional visits by wolverine (*Gulo gulo*) and lynx (*Lynx lynx*). A total of 60,000 domestic sheep (*Ovis aries*) graze in alpine ranges during the summer season (VKM et al., 2018). To limit the movement of alpine reindeer into Nordfjella zone 1, Norwegian management authorities have erected perimeter fences in the alpine ranges toward the southwest and northeast (Mysterud et al., 2022). However, forest-living cervids are free to enter sympatric ranges through the forests surrounding the alpine areas, and alpine fencing is not likely to affect our primary results, which are based on data collected before installation of the fences.

The ordinary hunting season is 1 September–23 December for red deer and 25 September–23 December for moose, but it was extended in the Nordfjella region for both species to 15 August–23 December and 1 January–31 January for the years 2020–2022 (Ministry of Climate and Environment, 2019).

GPS data

Marking followed standard procedures and was approved by the Norwegian Environment Agency and Norwegian Animal Research Authority. Some animals were marked specifically for this study; however, most data were collected from previous single-species projects.

Reindeer

GPS data from 20 female and 5 male reindeer in Nordfjella were available from 2007 to February 2018 (Mysterud et al., 2020). Individuals were darted from a helicopter during winter and fitted with Vectronic GPS+ or 22 GPS PRO LIGHT. The GPS collars recorded one position every 1 or 3 h. We removed data from the period of active culling of the herd (i.e., data after 10 August 2017).

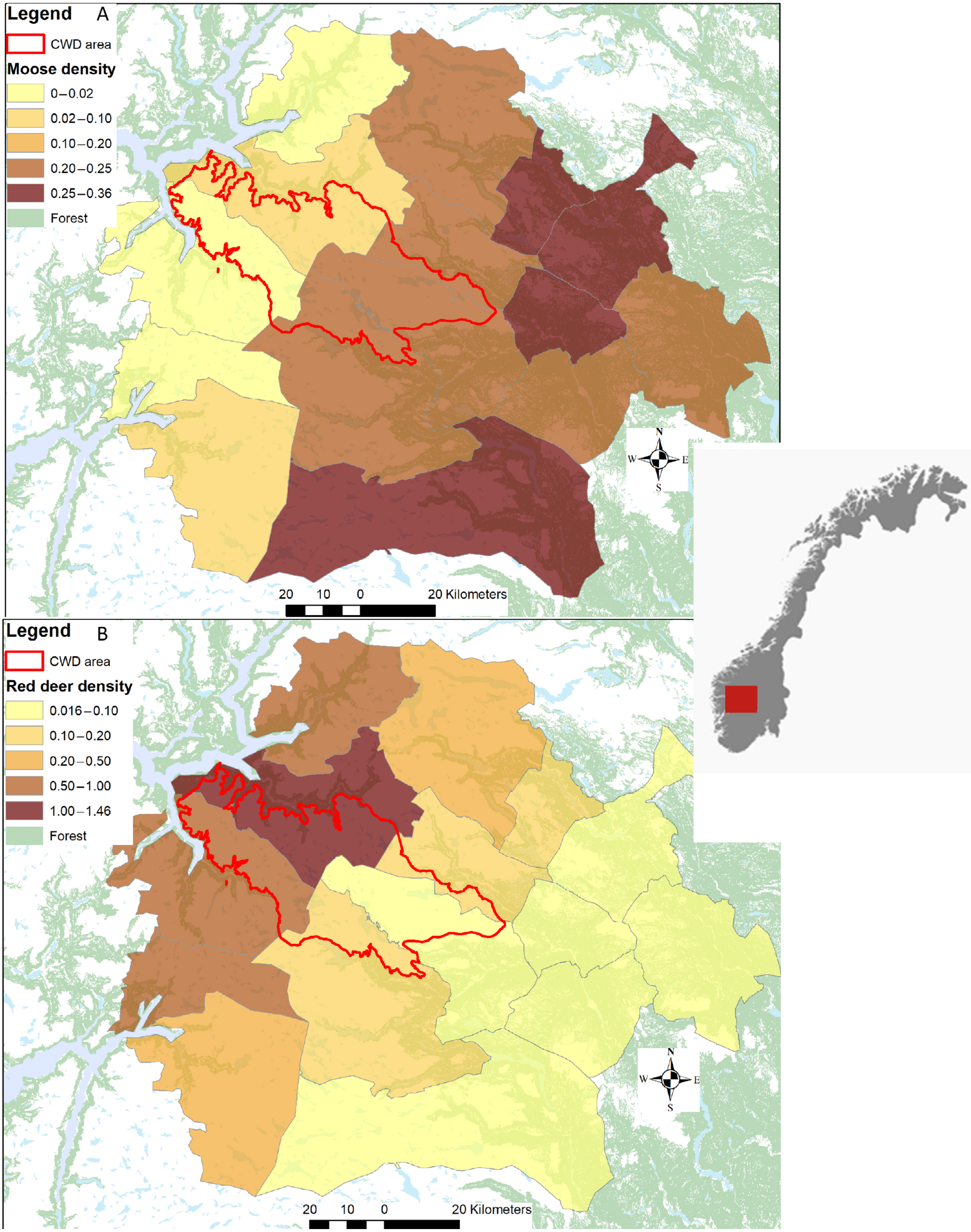

FIGURE 2 The study area surrounding the Nordfjella mountain range consists of 15 municipalities being part of a chronic wasting disease (CWD) containment zone. (A) Moose population density index and (B) red deer population density index (harvest numbers per km^2 of forest and bogs below the tree line).

Red deer

GPS data were available from 42 female (≥1 year old) and 9 male red deer (≥2 years old) marked during 2009–2012 (GPS collars manufactured by Followit) (Mysterud et al., 2012) and 2017–2019 (GPS collars manufactured by Vectronic) (Mysterud et al., 2021). Positions were taken every 1 h for females and every 2 h for males (from 1 September to 30 November). Individuals were darted at short-term winter feeding sites or along roads in the vicinity of the feeding sites from February to mid-April. Red deer are partially migratory, where migrators stay at lower elevations or coastal areas in winter along with resident deer, and at higher elevations or inland in summer. Thus, migration strategies may affect niche overlap between reindeer and red deer. We determined the migration strategy for each individual in each year using net-squared displacement techniques, as described by Bischof et al. (2012) and Rivrud et al. (2016).

Moose

GPS data were derived from 25 female moose (≥1 year old) that were marked during the period 2014–2018 (Solberg et al., 2017). Positions were recorded every 1 or 2 h (GPS Pro light manufactured by Vectronic). Individuals were darted from helicopters or at feeding sites during the winter (February).

We standardized the GPS data by thinning and retaining positions taken at 3-h intervals for all species. The GPS locations were assigned to three different seasons for further analysis. We used our knowledge of reindeer life history and space use as a baseline for setting seasons of functional importance. We separated the seasons into winter (1 February–15 March), calving (1 May–15 June), and summer (1 July–15 August), which are considered key periods for reindeer.

Environmental data

We were interested in the niche overlap related to broad habitat variables known to affect cervid habitat use in this mountainous region. The following variables were retrieved.

1. *Topography*: Elevation (in meters) and slope (in degrees) were retrieved from a digital elevation map at a scale of 50 m × 50 m (raster) provided by Geonorge/Kartverket (http://www.geonorge.no).
2. *Vegetation*: As a measure of vegetation productivity, we retrieved the mean seasonal normalized difference vegetation index (NDVI) at a grid resolution of 250 × 250 m. MODIS NDVI images taken every 16 days were downloaded from the MODIS Land Products data, provided by NASA and accessed using the "MODIStsp" package (Busetto & Ranghetti, 2016) in R (R Development Core Team, 2021).
3. *Snow depth*: We retrieved the mean seasonal snow depth (in centimeters) within each individual's seasonal 95% minimum convex polygon (MCP) home ranges for all species. Snow depth is an important factor in determining the migration and distribution of cervids in the study area. Snow depth was available as a daily grid covering Norway at a grid resolution of 1 × 1 km. The grids were provided by the Norwegian Water Resources and Energy Directorate (http://www.nve.no, https://senorge.no/map) and were downscaled from existing weather stations run by the Norwegian Meteorological Institute (http://www.met.no) (Saloranta, 2014, 2016).
4. *Infrastructure*: We used the distance (in meters) between private and public roads from raster maps with 100 × 100 m resolution. Raster maps were developed from maps of private and public roads in Norway provided by Geonorge/Kartverket (http://www.geonorge.no).

All map processing and variable extraction were performed in R (R Development Core Team, 2021). All variables were extracted at individual GPS location levels on a relevant seasonal scale.

Quantification of seasonal niche overlap

There are two main approaches to measure niche overlap using GPS data: analyzing (1) direct spatial overlap or using (2) habitat overlap (based on environmental covariates). Capturing of moose was not targeting the immediate surroundings of the Nordfjella reindeer range, and hence measures of direct spatial overlap would not represent overlap in niche of moose in the region with reindeer. However, since the habitat for moose around Nordfjella reindeer range is similar to where moose were captured, we can confidently estimate habitat (niche) overlap. Traditional resource selection functions (RSFs) are useful for relating GPS data with habitat variables for single-species analysis. However, since we compare species pairs, we benefit from using an approach with an explicit quantification of habitat niche overlap of two species.

We quantified environmental niche overlap pairwise between reindeer and the other species within each season using ordination techniques (Broennimann et al., 2012) in the "ecospat" package in R (Broennimann et al., 2022). Red deer inhabit both the eastern and western sides of the mountain range and winter at elevations of ~600 m in the east and ~300 m in the west. We assumed that the red deer–reindeer overlap would differ for stationary and migratory red deer; therefore, we analyzed red deer in the east (all migratory) and resident and migratory red deer in the west. All the moose were migratory and located in the east and therefore treated as a single group.

Background data were derived separately for all seasons, species, and categories (migration strategy/regions). To ensure that a sufficiently large area was covered as an available environment, we estimated the seasonal 100% MCPs for each species and category and added a buffer of 2185 m, which is the median individual seasonal home range radius across the dataset. MCP has limits as a measure of home range size, but it was used here only to secure a sufficiently large area for setting the availability of environmental covariates. To account for all possible seasonal environmental conditions, we sampled 10,000 random GPS locations within each seasonal MCP, corresponding to the median number of GPS locations per species and category across seasons. Because NDVI and snow depth require a temporal component when sampling, we randomly assigned each location a season-specific date that fell within the temporal range of the recorded GPS locations before the extraction of environmental covariates.

The seasonal occurrence density of each species in the environmental space was calculated using a kernel smoother (Broennimann et al., 2012). This method uses ordination scores to estimate the occurrence density of observed GPS locations along environmental niche axes, corrected for the density of the background environment (the total available environment) along the same environmental niche axes. The overlap in the environmental space can then be assessed visually and quantified using Schoener's D (Schoener, 1970). Schoener's D quantifies the niche overlap from 0 (no overlap) to 1 (full overlap). We term $D < 0.01$ as very low overlap, $D < 0.1$ as low overlap, $D = 0.1–0.3$ as moderate, and $D > 0.3$ as high. We also investigated univariate seasonal niche dynamics between species along single environmental gradients to assess individual overlap and the contribution of environmental variables to niche overlap.

To assess the direct spatial overlap, we projected the ordination scores of the areas where the species overlapped in space onto background maps. We used the same ordination techniques and estimation of occurrence densities in geographic space to assess the seasonal spatial overlap of the species. This follows the same procedure as when estimating environmental niches but uses GPS coordinates instead of environmental variables as input data. These maps provide the probability of the co-occurrence of species pairs, but only from habitat niche overlap.

We estimated maps of spillover risk by projecting the density of occurrence in environmental space from the niche analyses onto maps for the overlap zones of the different species pairs. By multiplying the maps from species pairs, we estimated the probability of co-occurrence in environmental space, regardless of spatial distribution of individuals. All environmental maps were resampled with a resolution of 50×50 m. The average values were used for the dynamic variables (snow depth and NDVI) when projecting onto maps. To account for spatial variation in the population densities of moose and red deer around the reindeer management area (Figure 2), we adjusted the probability of co-occurrence in environmental space by multiplying the maps with the population density index for 2016 (further details included below). For reindeer, we estimated the relative densities using a density kernel utilization distribution based on the accumulated GPS positions.

Relative spatial and temporal population densities

Population estimates for red deer and moose in the 15 municipalities were made available in stages during the process of managing the risk of CWD spillover. The number of harvested red deer or moose per square kilometers of forest (including bogs below the tree line) at the municipal scale was used as a measure of the spatial variation in density. This simple index is widely used and reflects the broad spatial variation in population density of red deer (Mysterud et al., 2007) and moose (Ueno et al., 2014), but does not provide reliable information on annual variation in population density when management aims and harvest rates are changing.

For temporal development in population density and structure, management relies on indices based on "seen moose" data (Solberg & Sæther, 1999) and "seen red deer" data (Mysterud et al., 2007). All hunters made a daily record of the number of observed animals per sex and age category (calves and adults), as well as the number of hunters and hours hunted, that is, the observation effort. From these data, we calculated the number of moose or red deer observed per hunter-day as an index of population density per municipality per year. From 2018 onward, the instruction for how to count "seen deer" among groups of hunters was slightly modified, including potential double counts among hunters.

For easier visualization and comparison of municipalities differing in absolute size, we ran a linear mixed effect model with either quota, harvest, or seen deer/moose per square kilometers of forest and bog habitat, and with the municipality as a random term in library "lme4" in R version 4.0.3.

Population numbers and harvest requirements

To obtain estimates of absolute density, we used a modified version of the method developed by Hatter and Bergerud (1991). The method depends on contrasting the harvest size in the individual municipality with the population growth rate and structure, based on observed moose and red deer, and is often used to estimate the population sizes of red deer and moose in Norway (Austrheim et al., 2011). We first estimated the winter population size of red deer and moose from 2016 to 2019 and then used the 2019 estimate as a starting point to project (simulate) the harvest required in 2019 and 2020 to reach the management aim.

We first used the following formula to estimate the population size in the winter of 2016:

$$N_{v16} = \frac{H_{16}}{((R_{16} - M_{16})/(1 - R_{16})) - \beta_{16}},$$

where N_{v16} is population size during winter (1 January), H_{16} is the harvest (number of moose or red deer) in 2016, R_{16} is recruitment rate just before harvest in 2016, M_{16} is mean natural mortality across sex and age groups, and β_{16} is the per capita population growth rate. This method requires integration of different data sources to estimate various parameters.

1. *H*: Harvest statistics for moose and red deer are available from all municipalities in Norway and are considered accurate and highly reliable (Statistics Norway, www.ssb.no).
2. *R*: Recruitment rate was calculated as the proportion of calves of all moose or red deer observed during the hunting season after adjusting for the animals harvested.
3. *M*: Estimates of natural mortality were taken from previous studies on marked red deer (Langvatn & Loison, 1999) and moose (Solberg et al., 2017) within or close to the study area. For moose, the estimated mean natural mortality was 6% for the period of 2014–2018 (Solberg et al., 2017), whereas the natural mortality of red deer was estimated to be 7% in an earlier study conducted northeast of our study area during 1977–1995 (Loison & Langvatn, 1998). As there is annual variation in natural mortality rate depending on winter conditions (Loison & Langvatn, 1998), we slightly modified the mortality rate in some years depending on the number of animals killed in traffic or that were found dead for other reasons (https://www.ssb.no/jord-skog-jakt-og-fiskeri/jakt/statistikk/registrert-avgang-av-hjortevilt-utenom-ordinaer-jakt).
4. β: To estimate the population growth rate, we used a combination of deer observations, harvest data, and expert judgment. For all municipalities, we first calculated the number of seen and harvested individuals per hunter-day during the period 2015–2018, and we then estimated the growth rate of these indices for the periods 2015–2016, 2015–2017, and 2015–2018. In this manner, we obtained estimates of both short- and long-term trends in population development. Population growth rates were measured as the geometric per capita growth rate ($\beta = e^r - 1$, where r is the regression coefficient for the log number of seen/shot deer per day against year).

Then, based on the same parameters, we estimated the pre- and postharvest population sizes in 2016, 2017, and 2018, and used the postharvest estimate from 2018 (which is the winter population estimate in 2019) to project the population size and required harvest in 2019 and 2020. For the latter two years, we used the average values from 2016 and 2017 as an estimate of the recruitment rate (*R*) and natural mortality rate (*M*). We used independent data sources to assess the robustness of the population estimates. The number of animals killed in traffic or found dead was available for all municipalities annually (1 April–31 March) from Statistics Norway (www.ssb.no). This is divided into categories of car and train collisions and other sources. This method involves an element of expert judgment (in this case, made by EJS).

RESULTS

Estimation of risk: Seasonal niche overlap

There was an overall limited seasonal niche overlap between reindeer and moose (Figure 3) as well as reindeer and red deer (Figure 4; Appendix S1: Figures S1–S4). The niche overlap (Schoener's *D*, Table 1) for reindeer and red deer was very low during winter (<0.01) but moderate for reindeer and red deer (migratory west) during summer (0.16) and calving (0.17). Moose had moderate niche overlap with reindeer both during winter (0.22) and the calving season (0.19) but was low during summer (0.09). The main difference in elevation included a shift from forest habitats to open mountainous areas. Reindeer used seasonally 94.6%–99.2% of the time in open mountain habitats, while red deer used 0%–18.1% and moose 0.4%–4.7% (Appendix S1: Table S1). The niche of reindeer was at higher elevations, in flatter terrain, in lower productivity vegetation, in areas of lower snow depth, and further from private and public roads, compared with both moose (Figure 3; Appendix S1: Figures S1

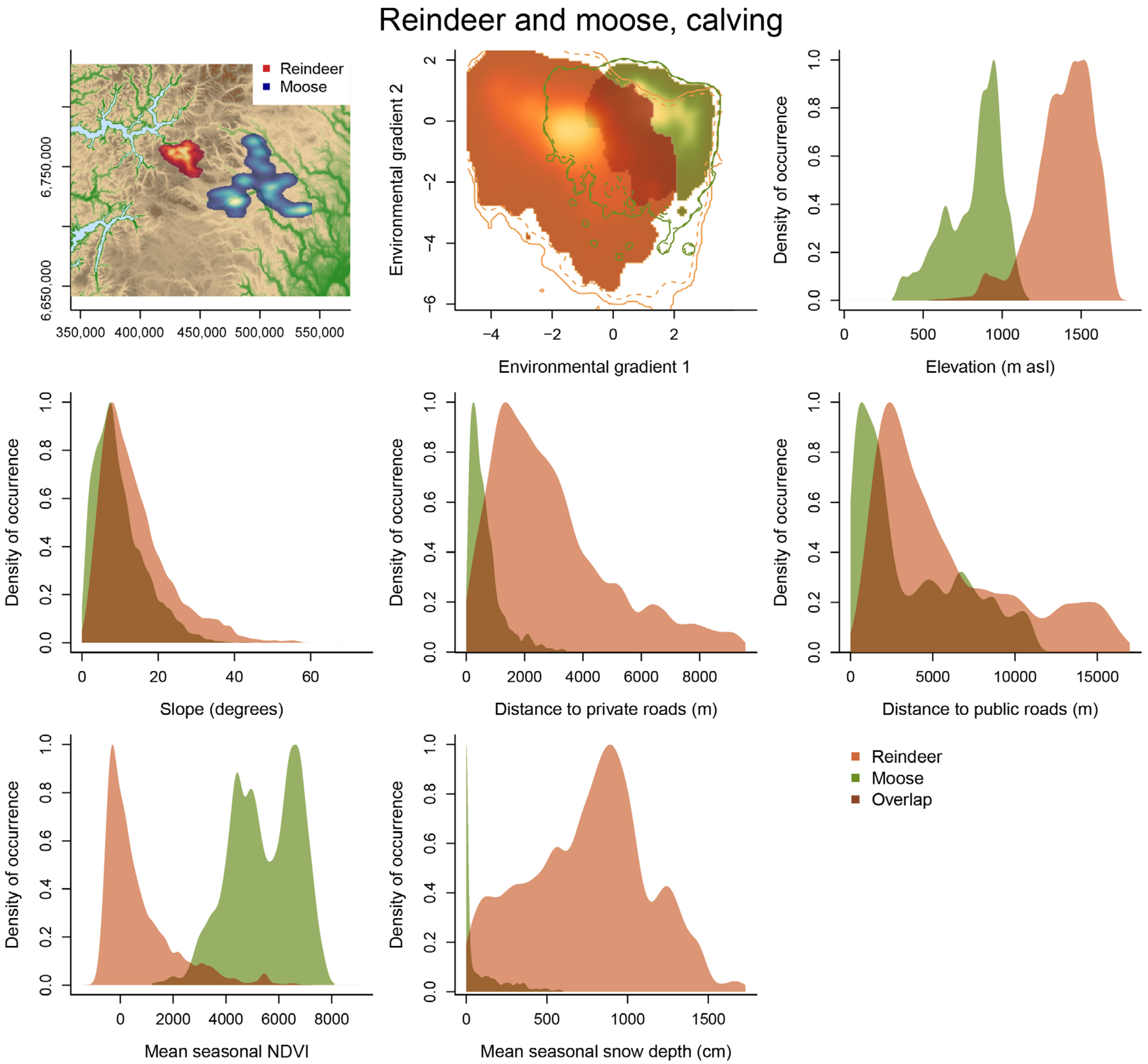

FIGURE 3 The visualized spatial overlap, estimated overall niche overlap (environmental gradient axes 1 and 2), and overlap for the different environmental variables of moose with a chronic wasting disease-infected reindeer population in Nordfjella, Norway, during calving season (1 May–15 June).

and S2) and red deer (Figure 4; Appendix S1: Figures S3 and S4). The direct spatial overlap between reindeer and red deer (Figure 4) was higher than that for reindeer and moose (Figure 3). This was because capturing moose did not target the immediate surroundings of the Nordfjella reindeer range, and thus we do not present estimates of spatial overlap (only habitat overlap).

The risk maps based only on seasonal habitat overlap analysis for reindeer, red deer, and moose identified risk areas near the perimeter of the mountain range (Figure 5A,D; Appendix S1: Figure S5). The maps adjusted for the population densities of moose and red deer and the kernel density of the CWD-infected reindeer population (assumed area of prion deposition) led to a marked narrowing of the main risk areas (Figure 5C,F).

Management of risk: Population density, quota, and harvest

The harvest density of red deer and moose (in 2016) was strongly negatively correlated in space ($r = -0.81$) with high densities of red deer in the west and high densities of moose in the east. The harvest density of moose

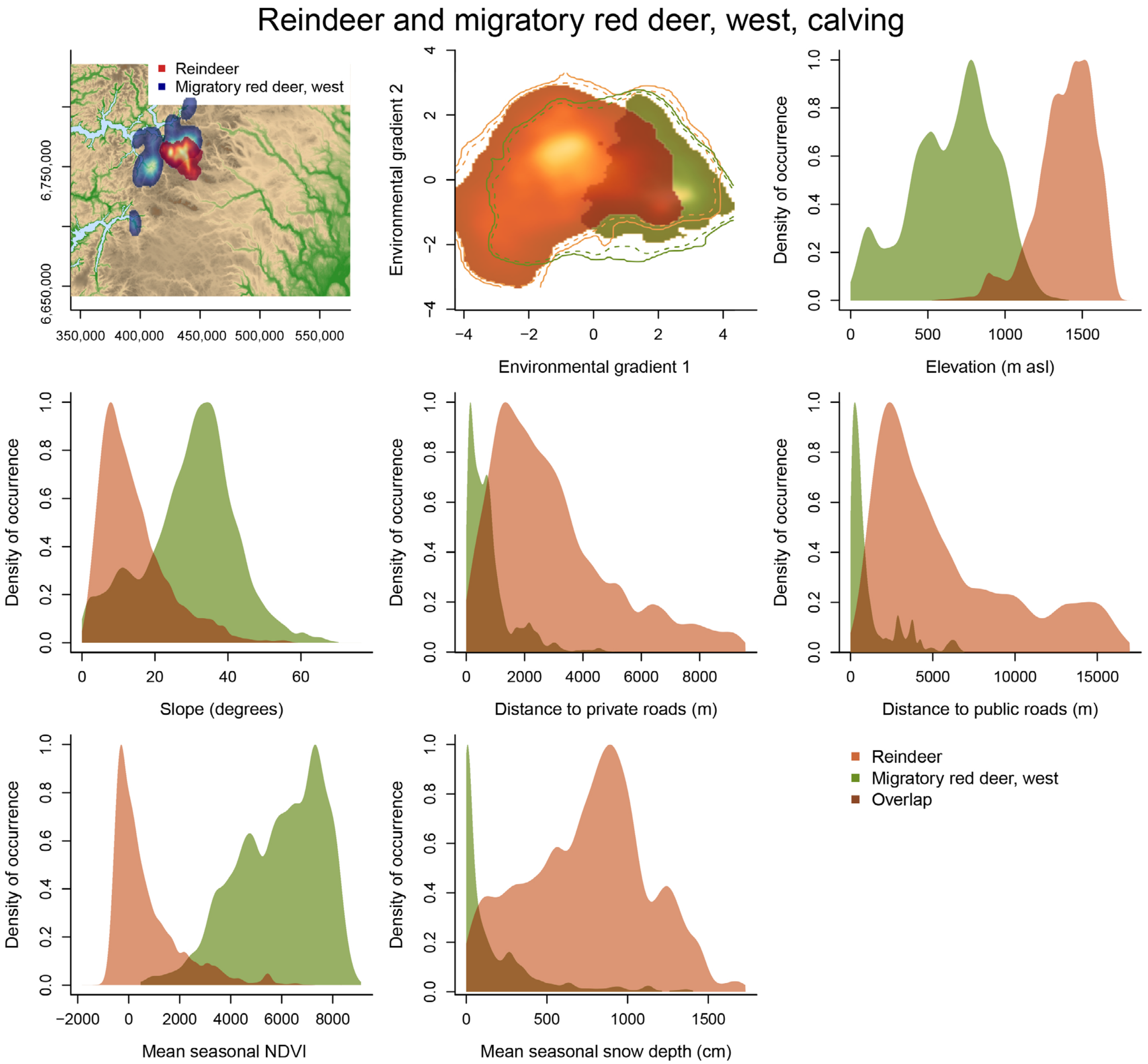

FIGURE 4 The visualized spatial overlap, estimated overall niche overlap, and overlap for the different environmental variables of migratory red deer (in west) with a chronic wasting disease-infected reindeer population in Nordfjella, Norway, during calving season (1 May–15 June).

(in 2016) averaged 0.17/km^2, ranging from 0 to 0.36 for the 15 municipalities around Nordfjella. The harvest density of red deer (in 2016) averaged 0.35/km^2, ranging from 0.02 to 1.46 deer/km^2 (Figure 2).

Moose

In the 10 eastern municipalities in the Nordfjella region, the overall estimated abundance of moose was 5131 before harvest in 2016, with a mean population size of 513 individuals varying between 179 and 901 among municipalities. The overall harvest rate in 2016 was 23.2% of the estimated preharvest population size. To achieve the management aim of halving the population size, the simulations suggested that the harvest would have to be, on average, 215 moose per municipality (harvest rate = 44.7%) in 2019 and 155 moose (harvest rate = 44.7%) in 2020. However, the average harvest per municipality was only 140 moose in 2019 (65.0% of the recommended harvest). While the harvest of 145 in 2020 (93.6% of recommended) was closer to the recommended value for that year, it was unlikely to yield the predicted population decline due to the low harvest in 2019, and

TABLE 1 Niche overlap (Schoener's *D*) between reindeer and the other species and categories for the three seasons: winter (1 February–15 March), calving (1 May–15 June), and summer (1 July–15 August).

Season and species category	Niche overlap (Schoener's *D*)
Winter	
Moose	0.216
Migratory red deer, western region	0.003
Migratory red deer, eastern region	0.030
Stationary red deer, western region	0.005
Calving	
Moose	0.188
Migratory red deer, western region	0.167
Migratory red deer, eastern region	0.107
Stationary red deer, western region	0.086
Summer	
Moose	0.090
Migratory red deer, western region	0.164
Migratory red deer, eastern region	0.047
Stationary red deer, western region	0.109

Note: The covariates used for niche estimation were elevation, slope, distance to public and private roads, mean seasonal normalized difference vegetation index, and mean seasonal snow depth in home range (winter and calving only).

thereby a higher population size than assumed in the simulations. According to the number of moose observed per hunter-day (population density index), this generated a population decrease of less than 20% from 2016 to 2021 (Figure 6A; Appendix S1: Table S3).

Red deer

The overall estimated abundance of red deer in the Nordfjella region before the harvest in 2016 was 6479 individuals, with a mean population size of 432, varying between 79 and 1857 among the 15 municipalities. The overall harvest rate in 2016 was 18.1% relative to the estimated preharvest population size. To achieve the management aim, the simulations suggested that the harvest should be, on average, 141 red deer (harvest rate = 37.4%) in 2019 and 105 (harvest rate = 37.1%) in 2020, but turned out to be, on average, 88 (62.9% of the recommended harvest) in 2019. Although the harvest of 104 in 2020 (98.9% of the recommended harvest) was at the recommended levels, it came after a lower harvest than recommended in 2019 and was therefore relative to a higher population size than assumed in the simulations. The number of seen deer per hunter-day in three main red deer municipalities (Lærdal, Aurland, and Årdal, covering 58.1% of the total population, with the best data, and most overlapping with the CWD-infected reindeer population; Figure 2) declined by only approximately 20% from 2016 to 2021, on average (Figure 6B), that is, well below the management aim of 50% reduction compared with 2016. Notably, the decline in seen deer per hunter-day was low (~28%) even inside Lærdal, despite marked increased harvest early on (from 398 in 2016 to 795 in 2017) and high goal achievement in both 2019 (130% of the recommended harvest) and 2020 (141% of the recommended harvest) in this municipality (Appendix S1: Table S4).

DISCUSSION

Many pathogens can infect multiple host species, which complicates management (Woolhouse et al., 2001). The spillover of CWD from reindeer to red deer or moose, with its wide and continuous geographic distribution, would result in substantial cultural and economic repercussions in Europe. Here we aimed to both quantify the risk of spillover and evaluate the success in management of risk by population reductions. From the GPS data, we documented a moderate seasonal habitat niche overlap between the species (Figures 3 and 4), representing a risk of disease spillover (Figure 5). The first attempt to reduce the risk of CWD spillover among cervid species achieved only a moderately reduced population density of overlapping species (Figure 6). This insight is also relevant for North America with caribou populations being at increasing risk due to the northward expansion of both CWD and white-tailed deer in Canada (Arifin et al., 2020), and more generally for combating other multihost diseases.

Estimation of spillover risk through niche overlap

Most studies on disease spillover have focused on measuring the overlap between wildlife and domestic animals (Barasona et al., 2014; Kaszta et al., 2018; Manlove et al., 2019; Mick et al., 2014; Rayl et al., 2019) and measuring what attracts wildlife to livestock pastures (Pruvot et al., 2014). The risk of CWD spillover among cervids depends on the host *PRNP*-genotype affecting susceptibility and how niche overlap and population density affect exposure (Mysterud, 2023). Reindeer and caribou are northern species with wide distribution ranges, and the use of open alpine versus forest habitats varies largely across

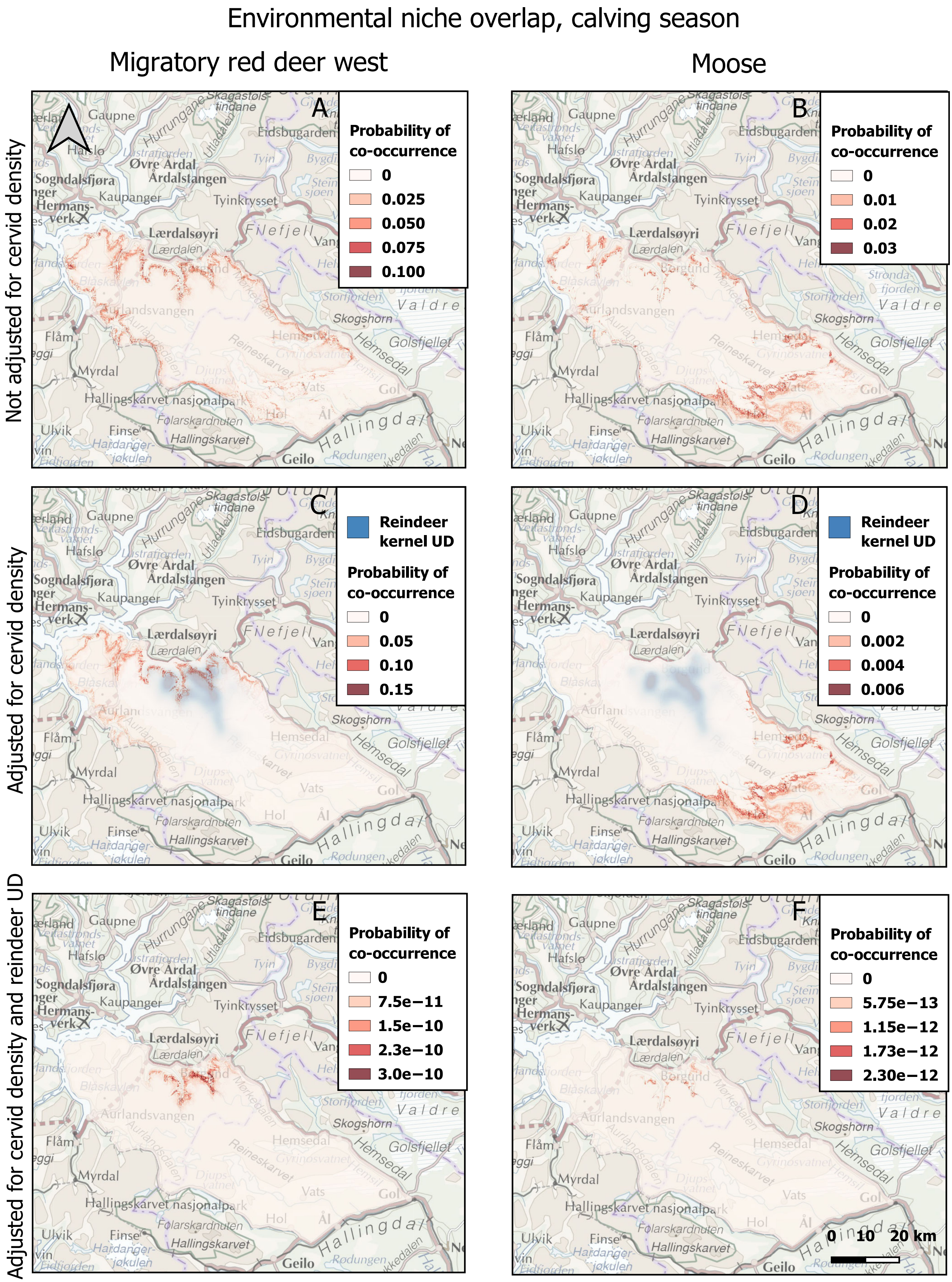

FIGURE 5 Legend on next page.

populations and subspecies. Single-species studies have documented that wild reindeer in Norway mainly use alpine habitat (Panzacchi et al., 2015), while moose (Bjørneraas et al., 2012) and red deer (Godvik et al., 2009) predominantly inhabit forested areas, with occasional seasonal use of higher elevation areas. Our study provides the first quantitative assessment of spatial overlap across species and largely supports this dichotomy in habitat use (Figures 3 and 4; Appendix S1: Table S1). As such, the likelihood of spillover of CWD from reindeer to red deer and moose is low because of habitat separation. However, there was moderate niche overlap during some seasons, and managing this risk is considered important because of the severe consequences of CWD spillover (VKM et al., 2018). A limitation of this analysis was the small number of marked males in all species, which prevented the formal testing of sex effects. Overall, the pattern of elevational use was not significantly different between males and females of the three species (Appendix S1: Table S2); however, this may have slightly underestimated the overlap.

The risk of disease spillover from the GPS data can be estimated using either spatial or habitat niche overlaps (Dougherty et al., 2018). Direct measures of spatial overlap require that a large proportion of both populations are marked, or at least cover the spatial extent of the zone of overlap. Only a small proportion of the population was GPS-marked in our study, which did not cover the entire CWD containment zone (Figure 3), and the measurement of habitat niche overlap appeared to be more appropriate. Methods to integrate movement data into disease ecology are still under development (Manlove et al., 2022; Webber et al., 2023; Wilber et al., 2022). Information solely from space use or habitat niche overlap can be a poor indicator of spillover risk, as they do not directly account for population densities. Developing risk maps integrating both overlap in niche- and population-level data enables improved targeting of risk areas, similar to what was done for the brucellosis spillover from elk to livestock (Merkle et al., 2018; Rayl et al., 2019). In our case, this was important because the mountain range caused a spatial contrast in population densities (Figure 2) and allowed for more targeted risk maps than those based only on habitat overlap (Figure 5). It is possible to create a dynamic temporal risk map similar to that of brucellosis (Merkle et al., 2018; Rayl et al., 2019). However, CWD prions can remain infective in the environment for years (Miller et al., 2004). Hence, accumulated space use over an extended period is likely to reflect the risk of spillover for environmentally persistent pathogens.

Management of risk of spillover by population reductions

Harvest simulations are widely used in the theoretical development of wildlife management principles (Fryxell et al., 2010), but are rarely used operationally in practical management. The planned harvest of red deer and moose in the Nordfjella region was based on simulations, but annual population growth was inherently stochastic and difficult to predict. In Lærdal municipality, the population of red deer was only moderately reduced even with the offtake being above aims derived from simulations. This discrepancy with a higher population size than anticipated after harvest may either reflect underestimation of initial population size and/or higher reproduction, immigration, or lower natural survival. Management authorities set specific targets for CWD management in Norway, even before tools to reliably estimate population size were developed. However, experience suggests that setting vague aims leads to no real effort to markedly reduce numbers. Unfortunately, promising novel population density estimation techniques that rely on unmanned aerial vehicles (drones), camera trapping, or genetic tools for capture and recapture (Forsyth et al., 2022) are costly and logistically challenging to implement on a large scale. Uncertain population estimation remains a general challenge in ungulate population management (Forsyth et al., 2022) and a key challenge for the targeted management of CWD. The results of the modeling approach were presented to local managers in all 15 municipalities in two reports (Solberg et al., 2019; Solberg & Rolandsen, 2020) and several meetings. During meetings with local hunters, there was indeed skepticism about the estimated population numbers because of issues of uncertainty.

Human dimension of hunting and efficacy

The management plan set increasingly specific aims as knowledge of population numbers increased (Figure 1) and provided incentives to increase the harvest.

FIGURE 5 The projected risk maps for chronic wasting disease (CWD) spillover. Maps using only estimated overall niche overlap of (A) migratory red deer (in west) and (B) moose with a CWD-infected reindeer population in Nordfjella, Norway, during calving season (1 May–15 June). Maps adjusted for population densities of (C) red deer and (D) moose with superimposed accumulated use estimated from kernel for reindeer. Maps adjusted for population densities of (E) red deer and (F) moose and using the kernel as density for reindeer. Note that scales are not comparable across maps. UD, utilization distribution.

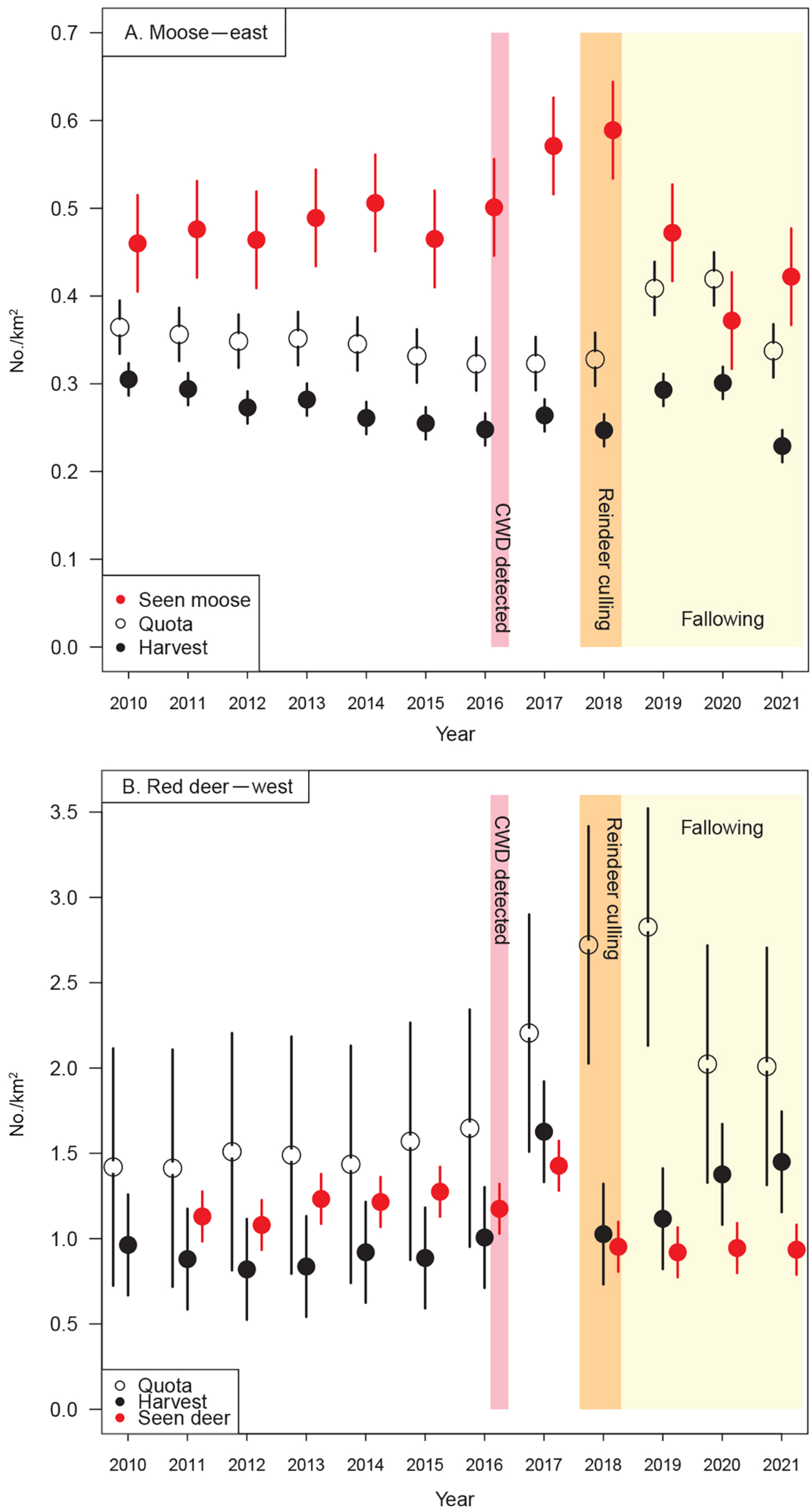

FIGURE 6 Annual variation (mean ± SE) in hunting quotas (permits) and hunted deer per square kilometers forest and bog, and population density indices (number seen per hunter-day) of (A) moose and (B) red deer from 2010 to 2021. Chronic wasting disease (CWD) was detected for the first time in early 2016 and de-population occurred in 2017–2018. In the subsequent fallowing period, the local moose and deer management authorities were asked to reduce the population density to about 50% of the level during 2016. For red deer, results are shown for the three municipalities (Lærdal, Aurland, and Årdal) with the densest populations. For moose, data are from the 10 municipalities on the east of the Nordfjella reindeer area.

Achieving high harvest levels is often challenging (Serrouya et al., 2011). Reducing the population density of popular game species conflicts with the management aims of other stakeholder groups (Heberlein, 2004; Vaske et al., 2006). For the most part, targets for reduction relative to the 2016 population levels were not reached in our case (Figure 6). The population reduction that occurred before CWD detection in red deer and moose is a rare case of proactive management, and it appears challenging to convince all stakeholders that this is more effective than reactive responses. A number of management incentives were used to increase the harvest of red deer and moose: (1) increased quotas; (2) less sex and age specificity in quotas; (3) extended hunting seasons; (4) free transport of carcasses with the help of a helicopter; (5) sale of carcasses (game meat processing facilities); (6) reduced fee to the state for each deer; (7) removal of established population plans and replace with targeted quotas (in a few areas only); (8) meetings and disseminating information to hunters; (9) rent of hunting to others; and (10) focus on other positive aspects of population reduction. Increased quotas and extended seasons are typically implemented in most states in the United States with CWD (Miller & Vaske, 2023), but may not work as anticipated because of hunter responses (Heberlein, 2004). Using recreational hunters comes with challenges in general when aiming for population reduction (Serrouya et al., 2011), as reported for controlling wild boar (Massei et al., 2015) and white-tailed deer (Brown et al., 2000). Hunters are time-limited and may be reluctant to undergo the extra effort required, particularly if they also disagree with the overall aims. Involving marksmen resulted in more effective badger (*Meles meles*) culling to limit bovine tuberculosis in the United Kingdom (Donnelly & Woodroffe, 2015), culling white-tailed deer aimed at limiting CWD in the United States (Manjerovic et al., 2014), and reindeer inhabiting open habitats in Norway (Mysterud et al., 2019). For red deer and moose living in forested habitats, using marksmen over large scales appears unrealistic, both economically and socially in the long term.

Governance refers to how the societal organization of processes leading to decisions affects legitimacy by focusing on social norms and the levels of participation of different stakeholder groups (Armitage et al., 2019), which in turn influences outcomes (in our case, harvest). A stronger focus on governance appears important for future efforts of population reduction linked to the management of CWD and other issues related to population reduction over broader scales in the long term.

AUTHOR CONTRIBUTIONS

Atle Mysterud initiated the study and drafted the first version. Erling L. Meisingset and Atle Mysterud organized data collection on red deer. Geir Rune Rauset and Olav Strand organized data collection on reindeer. Christer M. Rolandsen and Erling J. Solberg organized data collection on moose. Inger Maren Rivrud performed habitat niche modeling and drew maps (Figures 3–5), after discussions with Atle Mysterud, Bram Van Moorter, Manuela Panzacchi, Olav Strand, and Christer M. Rolandsen. Erling J. Solberg gathered population data and estimated population densities of moose and red deer. Atle Mysterud drew Figures 1, 2, and 6, with input from Christer M. Rolandsen in Figure 1. All authors contributed critically to drafts and approved the final manuscript for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and scripts (Rivrud, 2023) are available from Zenodo: https://doi.org/10.5281/zenodo.8204342.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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