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RESEARCH ARTICLE

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The last moves: The effect of hunting and culling on the risk of disease spread from a population of reindeer

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Abstract

1. Hunting and culling are frequently used to combat infectious wildlife diseases. The aim is to markedly lower population density in order to limit disease transmission or to eradicate the host. Massive host culling can yield a trade-off when combating wildlife disease; it follows that intrusive actions may have unintended behavioural side effects, leading to the geographic spread of disease. The manner in which such excessive hunting and culling of hosts can affect the movement and dispersion of cervids has not been studied.
2. In this study, we quantified the behaviour (daily movements and habitat use) and dispersion of GPS-marked reindeer (n = 24) before and during the eradication of an entire population (>2,000 reindeer) infected with chronic wasting disease (CWD) in Norway. We compared behaviour and dispersion during 10 ordinary hunting seasons (2007–2016), an extended hunting season (2017) and marksmen culling (2017/2018).
3. Seasonality had a major impact on movements. Reindeer movements during the early hunting season (20 August–20 September) did not increase the overall movements compared to that in the pre-hunt season (20 July–19 August), while extended hunting into October (as in 2017) and marksmen culling from November to February markedly increased daytime movements relative to that normally observed in this time of the year. Towards the end of the eradication, the remaining reindeer sought refuge at restricted high-elevation areas with limited forage production. Reindeer used novel areas towards the perimeter of the range, but active herding during culling stopped one herd from leaving the CWD zone.
4. *Synthesis and applications*. With emerging wildlife diseases, host culling is becoming a more frequently used tool for managers in Europe. Our study highlights the potential trade-off between combating disease transmission within a population and the risk of geographic spread. Such insight is important to design mitigation measures, such as perimeter fencing or herding, to avoid the risk of the geographic spread of disease in cases of severe and economically important wildlife diseases.

KEYWORDS
cervids, chronic wasting disease, disease ecology, disease management, host culling, movement ecology, spatial organization, unintended side effects

1 | INTRODUCTION

Combating wildlife diseases may involve extensive host culling (Bolzoni et al., 2014). Culling aims to shorten the infectious period and to lower the population density below the transmission threshold in the case of diseases with density-dependent transmission, such as rabies (Singer & Smith, 2012). In the case of diseases with frequency-dependent transmission, either complete or spatially targeted host eradication are among the management tactics used (Wasserberg, Osnas, Rolley, & Samuel, 2009). These are all invasive actions aiming to lower population densities far below levels usually aimed for during ordinary hunting. Harvesting in general affect wildlife behaviour in much the same way as predation affects prey behaviour (Cromsigt et al., 2013). Excessive culling likely has even stronger impacts than ordinary hunting; unintended side effects of such management actions should be anticipated, due to behavioural changes in the affected populations. A well-known example is the extensive badger *Meles meles* culling that aimed to limit the transmission rates of bovine tuberculosis in the affected populations; at the same time, this led to an increased potential for the geographic spread of the disease owing to the disruption of the social structure of badgers (Donnelly et al., 2005; Ham, Donnelly, Astley, Jackson, & Woodroffe, 2019; Woodroffe et al., 2006). Yet, the trade-off between culling to limit disease transmission and the risk of the geographic spread of the disease remains understudied. The incorporation of movement ecology into disease ecology appears urgent (Dougherty et al., 2018), as unintended behavioural effects require targeted mitigation measures to prevent adverse effects.

Wildlife diseases are of increasing concern world-wide (Jones et al., 2008; Tompkins, Carver, Jones, Krkosek, & Skerratt, 2015). In Europe, the emergence of African swine fever among wild boar *Sus scrofa* (EFSA Panel on Animal Health and Welfare (AHAW) et al., 2018) and chronic wasting disease (CWD) in cervids (EFSA Panel on Biological Hazards (BIOHAZ) et al., 2016) are regarded among the most severe diseases in terms of potential cultural, economic and ecological impact. CWD was first described in captive deer in Colorado, USA, in 1967; it has since spread to wild deer and continues to spread geographically across the USA and Canada (Miller et al., 2000). Surprisingly, CWD was detected in wild reindeer *Rangifer tarandus* in Norway in 2016 (Benestad et al., 2016). Chronic wasting disease was recently included in a list with the most important new issues in biodiversity and conservation research (Sutherland et al., 2018). One of the management tools used to limit CWD is extensive host culling (Uehlinger, Johnston, Bollinger, & Waldner, 2016; Wasserberg et al., 2009). Extended ordinary hunting and culling by marksmen eradicated the entire CWD-infected population in Norway that consisted of more than 2000 reindeer (Mysterud & Rolandsen, 2018; Mysterud, Strand, & Rolandsen, 2019). Despite numerous culling efforts by both ordinary hunters (Conner et al., 2007; Uehlinger et al., 2016) and marksmen (Manjerovic, Green, Mateus-Pinilla, & Novakofski, 2014; Mateus-Pinilla, Weng, Ruiz, Shelton, & Novakofski, 2013), there is no published information on how control efforts may affect the risk of the disease spreading geographically. There are several studies on how ordinary hunting affects the movement and habitat selection of cervids from North America (Little et al., 2016; Proffitt et al., 2010; Ranglack et al., 2017) and Europe (Ericsson & Wallin, 1996; Lone, Loe, Meisingset, Stamnes, & Mysterud, 2015; Picardi et al., 2019; Rivrud et al., 2016); in contrast, studies on how excessive harvesting pressure aimed at wildlife disease control affects the movements, habitat use and dispersion of cervids in the context of the risk of the geographic spread of diseases are scarce.

In this study, we used the host eradication process in Norway to learn about how ordinary hunting during a normal and an extended hunting season as well as marksmen culling affected reindeer movement distances, habitat use and dispersion and, consequently, the potential risk of the spatial spread of the disease by host movements. We compared the behaviour and dispersion of GPS-collared reindeer in years where ordinary hunting took place (2007–2016), during a year with an extended hunting season and pressure (2017) and during marksmen culling (2017–2018) in the CWD-infected reindeer population in Nordfjella zone 1, Norway.

2 | MATERIALS AND METHODS

2.1 | Study areas

The study area was the high alpine region in zone 1 (~2,000 km^2) of the Nordfjella reindeer management area in Norway (Figure 1). The steep topography and fjords in the west and surrounding forests limit connectivity to other alpine areas and movement out of the region is further restricted by roads crossing over the alpine areas. Zone 1 is separated from zone 2 by a county road (Hol-Aurland) in the west, but with a segment where the road goes in a tunnel. Zone 2 has a population of around 650 wild alpine reindeer. Zone 1 is bounded in the east by a state road (Hemsedalsfjellet) towards an adjacent semi-domestic population (Filefjell tamreinlag; ~3,000 reindeer). There was an ongoing fencing along these roads to contain CWD (Mysterud & Rolandsen, 2019). During the winter 2018, the fence along the road over Hemsedalsfjellet had an open section and one third of the fence was snowed down. Along the road Hol-Aurland, only poles had been erected with no actual fence, and also with large

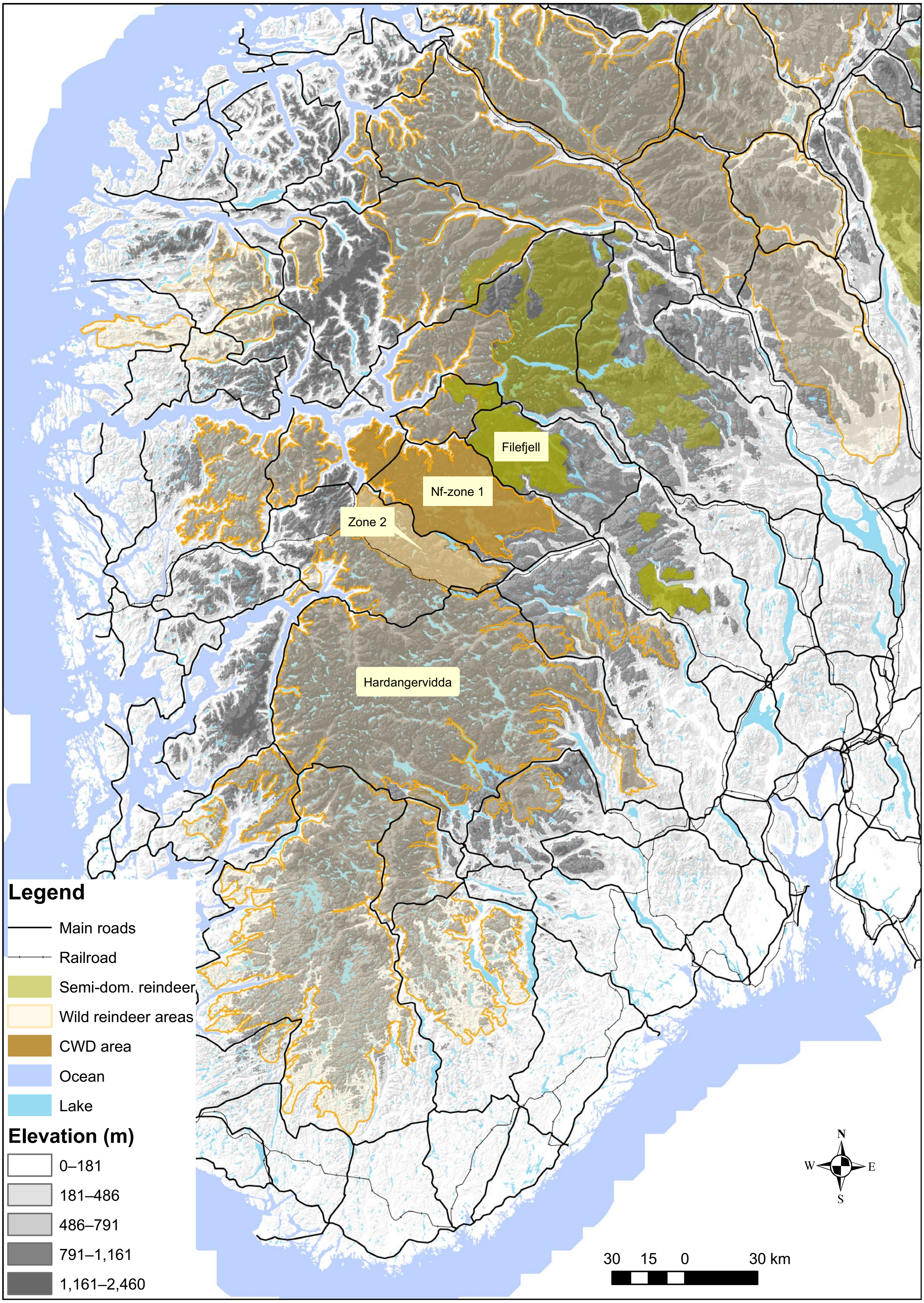

FIGURE 1 An overview of the alpine area of Nordfjella zone 1 relative to adjacent wild (zone 2) and semi-domestic (Filefjell) reindeer populations, Norway

sections being under snow. During the ordinary hunting seasons in 2014, 2015 and 2016, there was shot 316, 241 and 291 reindeer. This increased to 582 reindeer in the extended hunting in 2017, while the marksmen culled 1,399 reindeer (Mysterud, Strand, et al., 2019).

2.2 | Reindeer GPS data

The dataset was collected from 24 female reindeer outfitted with GPS collars (two Vectronics GPS+ and 22 GPS PRO LIGHT) that were followed from 2007 to February 2018 when the last herd was eradicated. Animals were darted from a helicopter during the winter. Marking follow standard procedures and was approved by the Norwegian Environment Agency and the Norwegian Animal Research Authority. The GPS collars were programmed to record a position every 1 or 3 hr; the exact interval depended on the time required to connect to satellites. We used the exact time between positions to calculate movement speed and we only accepted a time window of 3,500–3,700 s for 1-hr positions and 10,700–10,900 s for 3-hr positions. The marksmen had access to positions of the GPS-collared reindeer to locate herds, and collared reindeer were only culled in late stages of population eradication. This may potentially have led to increased movement in herds with marked animals. However, the collared reindeer were distributed well across herds, so we regard their movements to be representative.

We used elevation (m) and remotely sensed peak plant productivity, which is a high-resolution predictor of performance in reindeer (Tveraa, Stien, Bårdsen, & Fauchald, 2013), as measures of habitat quality. Based on the 16-day and 250-m resolution MODIS enhanced vegetation index data, we estimated maximum productivity for each year (full details can be found in Tveraa et al., 2013). For each pixel, we used the average productivity across years (2001–2017) as our measure of habitat quality.

2.3 | Statistical analysis

We performed analyses in R 3.6.3. We used the Akaike information criterion (AIC) when comparing models. Models were checked with standard diagnostic tools to verify that model assumptions were met. We used quantile–quantile plots to check for normality of the residuals, and residual plots to check for nonlinear patterns in the residuals, or patterns in the variances across the fitted values. We also plotted residuals across the different predictor variables and random effects to check for patterns.

Initial plotting using splines indicated a strong impact of season on movement speed and habitat use. We therefore split data into relevant periods for 2007–2016 to compare the effects of hunting: pre-hunt (20 July–19 August), ordinary hunting (20 August–20 September 2007–2016) and post-hunt (October). We contrasted these periods with the first (10 August–20 September) and last (October) part of the extended hunting season of 2017. To facilitate comparison with the first (7 November–23 December 2017) and last (1 January–25 February 2018) period of marksmen culling, we compared these to similar periods in years 2007–2016 during which no hunting or culling took place. We pooled the remaining data into a category 'rest of the year'.

2.3.1 | Movement speed

We used linear mixed effects models in the NLME package with log(speed + 1) as a response variable and individual ID and year as random terms, while serial autocorrelation was controlled for using an autoregressive moving average (ARMA) of order 1 for both the AR and MA part. Our categorical variables of interest were season (categorized above; 10 levels) and time of day (two levels). Time of day was split into day (07:00–19:00; hunting) or night (19:00–07:00; no hunting), as this is the local regulation defining when it is legal to hunt even during the 2017 extended hunting season (Mysterud, Strand, et al., 2019). Time between positions (1 hr/3 hr) was added as a factor variable to account for the GPS fix schedule. We also ran two models on subsets of the data, the extended hunt of 2017 and the marksmen culling, due to more detailed covariates being available. In these two models, we analysed speed with individual ID as a random term and also accounting for serial autocorrelation. Categorical variables were time of day (day/night) and GPS fix schedule (1 hr/3 hr) as in the global model. We also added a variable on visibility (fog/clear), day of week (weekend, weekday), log(number of deer shot in a given day + 1) (Mysterud, Strand, et al., 2019) and daily snow depth for the culling that extended well into the winter season.

2.3.2 | Habitat use

Use of elevation (m) and habitat productivity (remote sensing) were highly negatively correlated ($r_{Pe} = -0.75$, $p < 0.001$). We therefore used elevation as a proxy for both. We analysed the use of elevation (m) with models similar to those used for movement speed.

2.3.3 | Dispersion

We measured dispersion with a standard 100% minimum convex polygon (MCP). Though MCP has limits as a measure of home range size, in our context it was useful as a measure of maximum dispersion. We calculated MCP over a period of 30 days within each period and we included (sqrt) number of positions as a covariate as not all individuals had the same number of fixes over a given period, partly to account for differences in the GPS schedule. We included year and individual ID as random terms. We also identified all pixels at a scale of 1 km^2 used exclusively during the period of extended hunting and culling in 2017/2018 relative to all previous positions.

3 | RESULTS

3.1 | Daily movement speed

The full model with period, time of day, GPS fix schedule and the interaction between period and time of day was superior to simpler models (see Table S1). The movement speed of reindeer followed a seasonal pattern with reduced movements during the winter and increased movements during the summer. Movements during the ordinary hunting period (20 August–20 September) were similar to those of the pre-hunt period (20 July–19 August). Ordinary hunting (20 August–20 September) and the first part of the extended hunting period of 2017 (10 August–20 September) had similar effects on daily movements, while the last part of the extended hunting period of October 2017 led to 60% increased daytime movement speed compared to that during the post-hunt period (Figure 2a, October, see Table S2). Movements decreased during marksmen culling (2017/2018) compared to the ordinary hunting period; but daytime movements during the culling period were two to three times more extensive than what is normal for this time of the year, including both late fall (7 November–23 December) and the winter period (1 January–25 February; Figure 2a).

During the extended hunting period (10 August–31 October 2017), movement speed was higher for days with high hunting pressure and was measured as number of shot deer in a given day, while it was lower during days with fog (see Table S3). We found no difference in movement between weekdays and weekends and no effect of the Julian date over the hunting season, as neither variables entered the best model. During the marksmen culling (7 November 2017–25 February 2018), movement speed was higher for days with high culling pressure measured as number of shot deer in a given day. There was no marked effect of fog or daily snow depth on movement speed, as neither variables entered the best model (ΔAIC > 2). As in the main model, movements were higher during the daytime than during the night for both the extended hunting and culling periods (see Table S3).

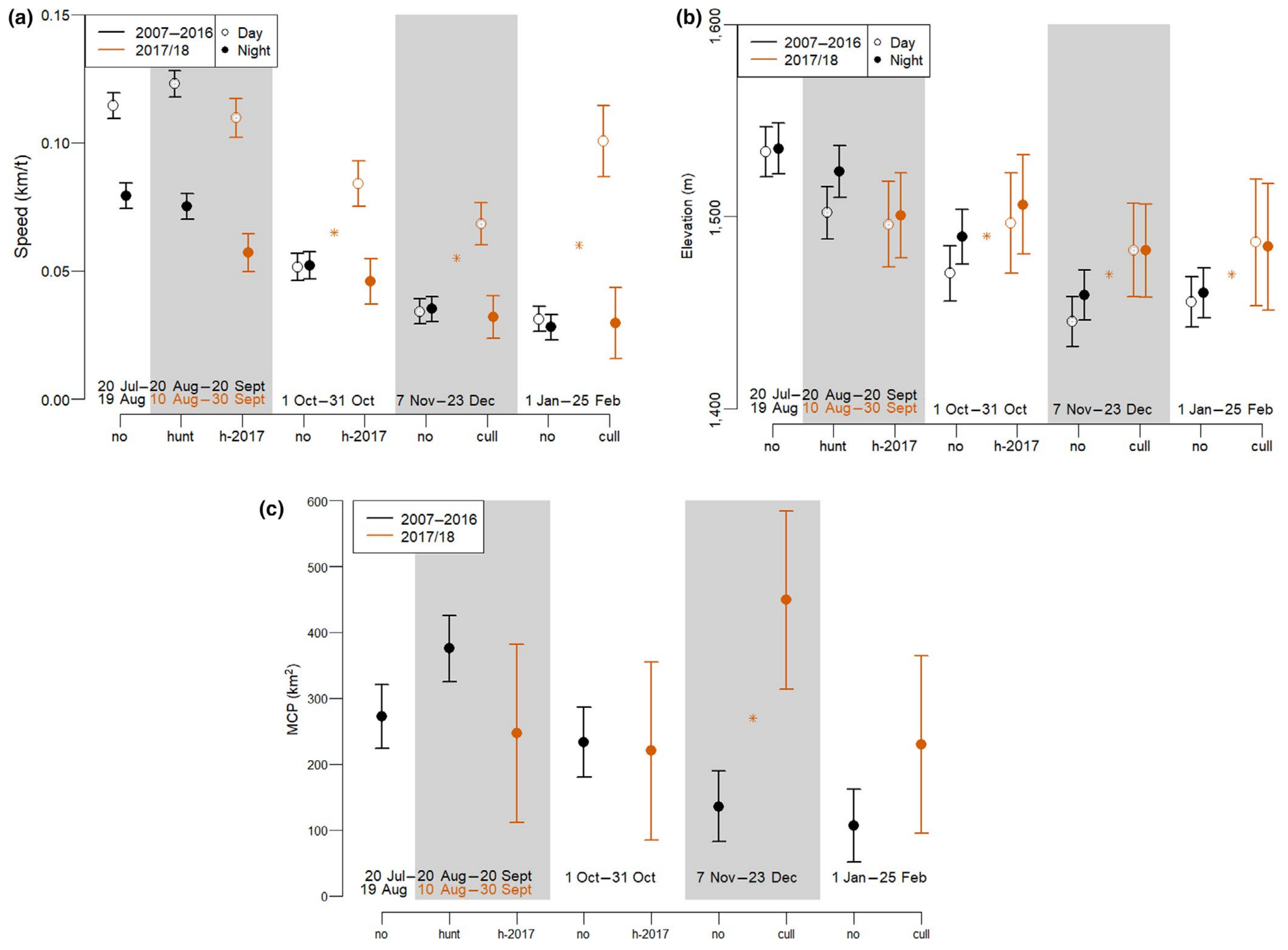

FIGURE 2 The effect of ordinary hunting (2007–2016; 'hunt'), extended hunting (2017; 'h-2017') and marksmen culling (2017/2018; 'cull') on (a) speed of movements (relative to 'no' hunting), (b) habitat use (elevation) and (c) dispersion (minimum convex polygon) of reindeer in the CWD-infected population in Nordfjella zone 1, Norway. Day is defined as hours between 07:00 and 19:00. Values are estimated mean and 95% confidence intervals from models in Tables S2, S4 and S6. Main effect of interest marked '*'

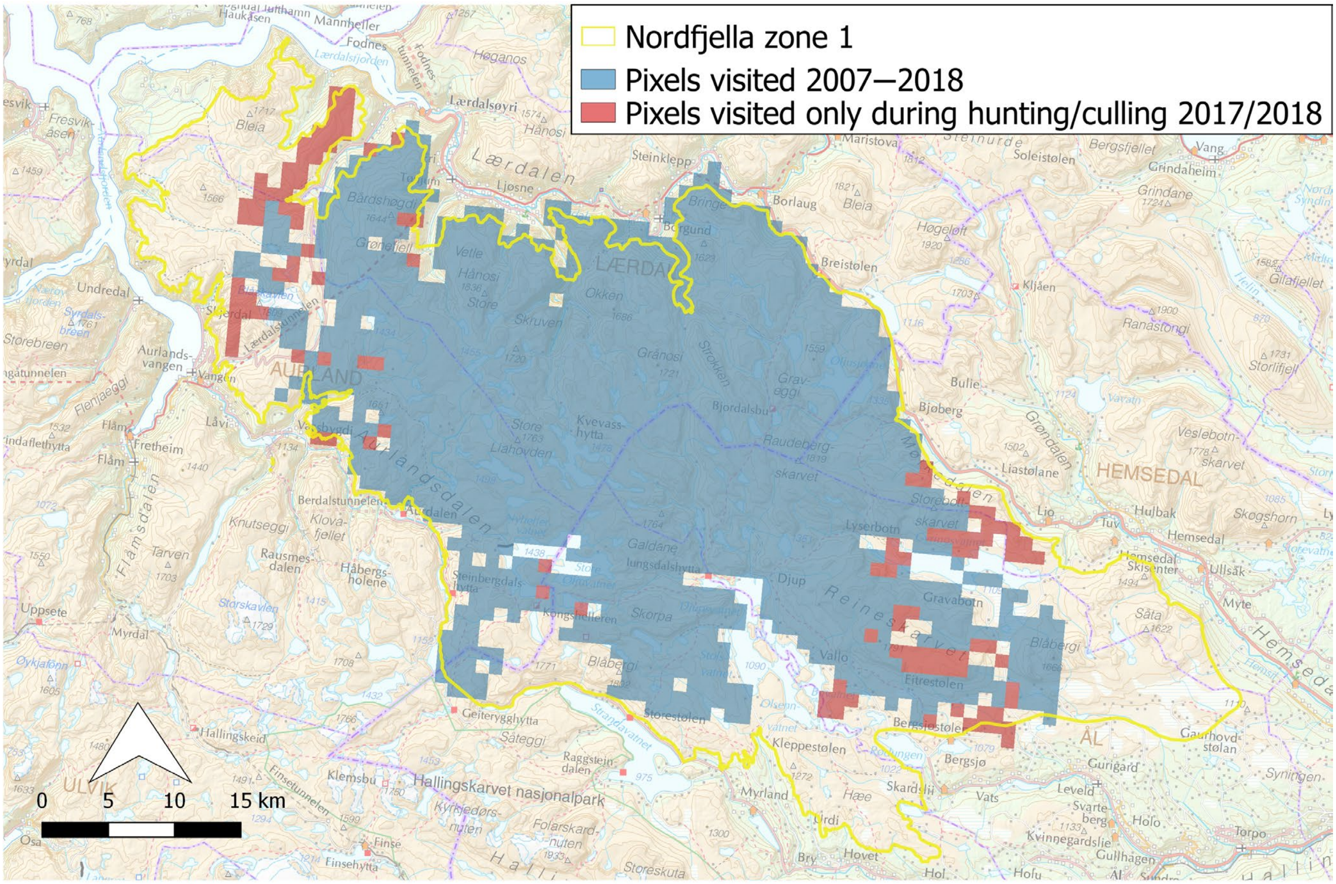

FIGURE 3 The effect of extended hunting and culling during the period 10 August 2017–25 February 2018 on the use of novel 1-km^2 pixels in the Nordfjella mountain, Norway, compared to all previously visited locations

3.2 | Habitat use

Elevation was used as a proxy for habitat quality and was highly negatively correlated with habitat productivity (remote sensing). The model including all variables were also the most parsimonious (see Table S1). Reindeer exhibited a moderate decline in predicted mean elevation from the pre-hunt season (~1,530 m, 20 July–19 August), a period of disturbance by tourists and insects, through the ordinary hunting season towards late fall (~1,500–1,520 m; Figure 2b, 20 August–20 September). Habitat use was similar during the first part of the extended hunting period of 2017 compared to the ordinary hunting seasons (see Table S4). In the last part of the 2017 hunt, reindeer remained at a slightly higher elevation (~1,490 m) compared to what is normal for October (~1,460–1,480 m; Figure 2b, October). During culling, reindeer remained at a higher elevation (1,470–1,480 m) than what is normal for this time of the year (~1,450 m, Figure 2b, 1 January–25 February).

3.3 | Dispersion

The effect of hunting, extended hunting and culling on dispersion, measured as a 30-day home range size (MCP), largely followed the pattern of movement speed. However, there were higher variation within and smaller differences between time periods, and few of which were significantly different (Figure 2c, see Tables S5–S6). Range sizes were quite similar from the pre-hunt to the hunting and during the extended hunting season, while ranges were smaller when no hunting occurred during the winter season (November–February, Figure 2c). The ranges remained quite large during culling, in particular in early stages. Even with no marked effect on home range sizes, reindeer visited another 121 km^2 of novel habitat during the short period (10 August 2017–25 February 2018) with extra hunting/culling, and 11.9% of all 1-km^2 pixels visited in the period were new (n = 1,011). There was a notable extension of new areas towards the perimeter of zone 1 and towards the forested areas in both the south and the north (Figure 3), which represented an 8.5% increase in range relative to all used areas in the previous decade (1,431 km^2).

4 | DISCUSSION

The massive host culling to limit disease transmission is a much used control strategy of wildlife diseases. Well-known examples include badger culling to limit the transmission of bovine tuberculosis (Donnelly et al., 2005), red fox culling to limit the transmission of rabies (Woodroffe, Cleaveland, Bourtenay, Laurenson, & Artois, 2004), hare culling to limit the transmission of louping ill virus (Harrison, Newey, Gilbert, Haydon, & Thirgood, 2010), deer culling to limit the transmission of CWD (Manjerovic et al., 2014) and wild boar culling to limit the transmission of African swine fever (Guinat et al., 2017). Yet, the unintended behavioural side effects of such invasive actions remain understudied. We used data from the historical eradication process of an entire reindeer population infected with CWD in Norway to learn about the complexity of how reindeer responded to a normal and an extended hunting season and increased pressure as well as host culling performed by marksmen using snowmobiles and helicopter in late stages. We study the spread of disease indirectly through host movements, which predicted the spread of CWD among deer in North America (Nobert, Merrill, Pybus, Bollinger, & Hwang, 2016). This insight is crucial to aid the management of mitigation efforts intended to prevent the geographic spread of the disease during culling actions.

4.1 | No movement to new epidemiologic unit

Our study found no evidence that extensive hunting or culling provoked reindeer to move to novel epidemiological units. Movements into novel habitats outside their ordinary home ranges represent the key to the geographic spread of diseases. Reindeer are unique among cervids; they are mainly nomadic without clear home ranges and in Norway they are managed within 24 geographic areas. Topographic barriers like fjords, forest areas, roads and railroads provide barriers to movement thus demarcating populations. In the current context, these populations can be seen as epidemiological entities for reindeer. Historically, considerable movements between Nordfjella zone 1 and zone 2 were recorded (Figure 1), with the last documented herd of ~200 reindeer moving from zone 2 to zone 1 on 25 December 2007, including a GPS-marked female in this study. We found some effect of extended hunting or marksmen culling on dispersion, but no GPS-marked reindeer left Nordfjella zone 1. This could be partly due to the marksmen being cautious and actively surveying and avoiding culling in the periphery areas in the alpine areas. In this respect, we found no evidence that the extended hunting or culling led to the spread of CWD among reindeer.

The use of novel habitat by reindeer recorded towards the perimeter of the range was mainly into lower elevation areas with forest (Figure 3). This does not imply the risk of spread to other alpine reindeer populations, but these novel areas have a high density of red deer *Cervus elaphus* in the west and moose *Alces alces* in the east. Hence, it is possible these movements represent an increased risk of CWD spillover to red deer and moose with increased overlap in space use along the lower elevation, though the time period of overlap was fairly short. Red deer, moose and many other ungulates show higher fidelity to home ranges than reindeer, which may affect how they respond to hunting and culling disturbance. Roe deer *Capreolus capreolus* have strict home range behaviour. Roe deer move less in a protected area than in a hunted area, but remain confined to their usual home range (Picardi et al., 2019). Female red deer have mixed strategies to cope with drive hunting in France. Some individuals show temporary avoidance of the disturbed areas, while others move less to avoid detection (Chassagneux et al., 2019). Female red deer left their home range in 28% of the flights during drive hunts with dogs in Sweden (Jarnemo & Wikenros, 2014), while the onset of hunting triggered migration, therefore longer distance movement, in a more northern red deer population (Rivrud et al., 2016). Wild boar moving out of their home ranges during drive hunts was regarded as a potential risk of spreading classical swine fever (Sodeikat & Pohlmeyer, 2002). It will be more difficult to control any extra movements in forests with more open populations, and details of how to organize the hunting or culling are important for containment of disease.

4.2 | Organization of hunting, containment efforts and risk of disease spread

A mitigation tactic in the open habitat of alpine reindeer was direct herding with a helicopter, which can be aided by surveillance with GPS collars on herd members. In our case, we outfitted females with GPS collars, since females are gathered in the largest herds and represent most of the population. However, sexual segregation is the norm in reindeer and most other sexually dimorphic ungulates. Based on anecdotal evidence, males seem more prone to use wider areas than females; CWD infection was more prevalent among male reindeer in Nordfjella (Mysterud, Madslien, et al., 2019). There was one case of active herding of 22 male reindeer by the marksmen with the aid of a helicopter, around 500 m from the border to the adjacent reindeer population. Hence, our study on female reindeer movements may have underestimated the risk of disease spread. Whether other unmarked individuals escaped from the area is unknown; a key focus of current management strategies is to establish freedom of infection in adjacent reindeer populations.

Marksmen culling of reindeer differs from ordinary hunting in many ways. Ordinary hunting requires a lot of people (several hundreds) being dispersed everywhere, while marksmen typically target one or a few herds per day and only operate in groups of 10 people at a time. However, noise from snow mobiles and helicopters by marksmen can be heard from a long distance and potentially scare herds. Management should target mitigation measures to counter the risk of the spatial spread of disease linked to higher movement rates during excessive culling operations. Active herding is an unlikely alternative for most cervids that are more solitary and live in forested areas. Whether an individual will leave its familiar range depends on a number of factors related to the organization of the hunt, for example type of hunting (stalking, sit-and-wait or drive hunt), use of dogs and the frequency and intensity of hunting. Wild boar had more dispersed resting sites during the season of drive hunting with dogs in France (Maillard & Fournier, 1995); repeated hunts in the same area within a short period were thought to cause an increased risk of extensive movement by wild boar (Scillitani, Monaco, & Toso, 2010). One intrusive containment alternative is perimeter fencing of functionally important movement corridors towards adjacent populations (Mysterud & Rolandsen, 2019), or to implement other measures to increase barrier effects of existing linear structures such as roads.

4.3 | Increased movements during hunting and culling

Although reindeer did not use novel areas outside of the management zone, we found that the reindeer nevertheless altered their spatiotemporal behaviours within their ranges as a result of hunting and culling. There were extensive movements, as indicated by the movement speed (Figure 2a), during the summer season before the onset of hunting, possibly due to disturbance by tourists on foot and harassment by insects. Further, the hunt of 2017 involved more hunters and much larger quotas (Mysterud, Strand, et al., 2019). Nevertheless, the movements during the first period of excessive hunting in 2017, overlapping with the ordinary hunting season, were similar. In contrast, the extension of the hunting season into October 2017 led to more extensive daytime movements than normal for that time of the year. Hence, increased movements were caused by the late extension of the hunting season into October 2017 rather than the increased hunting pressure during the ordinary hunting season. Similarly, the culling that started in November and continued until approximately the end of February led to markedly more movements during daytime than what is normal for this season (Figure 2a). Elk movement rates increase with increasing hunting pressure (Cleveland et al., 2012), and moose increase their step length during hunting in areas of high density in trails used by hunters (Brown et al., 2018). Our study on reindeer documented a more complex interaction between hunting and the seasonal pattern of movement, and it will be important for managers to consider the context in detail when planning hunting and culling efforts to avoid adverse impact.

4.4 | Spatial and temporal refugia and hunter efficacy

There was a marked difference in reindeer movement between day and night during the hunting season. This was partly due to that hunting was only legal during day time (07:00–19:00) due to a locally imposed ban allowing reindeer time to forage (Mysterud, Strand, et al., 2019). The marksmen did not have similar restrictions, but an average of only 7 hr of daylight during winter limited the time they could spend culling; reindeer increased their movement during daytime throughout this period. Temporal and spatial refuges can be defined as periods and areas limiting the contact between predator and prey (Tambling et al., 2015). Dark hours in general provide a short-term temporal refuge against hunting disturbance in most cases. White-tailed deer *Odocoileus virginianus* increase the use of feeders at night, while they avoid areas close to hunting stands during the day (Sullivan et al., 2018). Elk become more nocturnal with the onset of hunting (Visscher, Macleod, Vujnovic, Vujnovic, & Dewitt, 2017). Longer term changes of behaviour as a response to hunting are also apparent. Hunting early in the season is typically more effective in terms of wild boar harvest numbers (Vajas et al., 2020), and red deer males that shift their behaviour at the onset of hunting have higher survival rates (Lone et al., 2015). Changing the hunting opening days affected the timing of movement to private land where mule deer and elk are largely unavailable for harvest (Conner et al., 2001; Vieira, Conner, White, & Freddy, 2003). Hence, managers should consider behavioural changes and that efficacy may not be proportional, for example to duration of hunting season.

Owing to landowner property rights, ordinary hunters do not have legal access everywhere. Anecdotal evidence suggests that reindeer remained in such refugia when local quotas were filled, making them less accessible to other hunters (Mysterud, Strand, et al., 2019). The limited accessibility of ordinary hunters provides spatial refuges and can lower harvest efficacy of reindeer. The use of spatial refuges such as private lands and avoidance of areas with higher hunter access and more hunters is reported both in elk (Proffitt et al., 2010; Proffitt, Gude, Hamlin, & Messer, 2013; Proffitt, Thompson, Henry, Jimenez, & Gude, 2016; Ranglack et al., 2017) and white-tailed deer (Rhoads, Bowman, & Eyler, 2013). Changes in habitat selection and movement rates affect deer vulnerability to harvest (Little et al., 2016). White-tailed deer moved less in areas not open to hunting (Root, Fritzell, & Giessman, 1988). The vulnerability of caribou to hunting depends on landscape (Plante, Dussault, & Côté, 2017). Whether spatial displacement also can affect disease transmission remains to be studied. In our case, the reindeer remained in an area with much higher elevation than normal, characterized by low vegetation coverage, only during the culling period (Figure 2b). The elevational displacement and disturbance of herd social structure and its social interaction may possibly change CWD transmission, but this was likely to be negligible given the slow transmission of CWD relative to the duration of the hunting and culling.

4.5 | Timing and duration of hunting and stress

The ordinary hunting season of reindeer in Nordfjella was 32 days, the extended hunting season of 2017 was 82 days, while marksmen culling was over 111 days. The duration of periods with increased movements is likely to impact animal condition. Evidence on how the timing and duration of the hunting season affect wildlife populations is surprisingly scarce. During marksmen culling, reindeer retreated to smaller areas with lower productivity, but still moved more than usual, and the winter of 2017/2018 had above average snow depth (see Table S7). Thus, reindeer were neither able to compensate the costs of being chased with reduced energy spending nor increased energy intake. Marksmen noted that many animals were emaciated, possibly owing to the disturbance over a long time period when reindeer movements are usually limited to save energy. Reduced animal condition may affect vulnerability to infectious diseases. However, CWD and other prion diseases do not inflict an immunological response in hosts, and hence reduced animal condition is not expected to affect the dynamics of CWD. During this last stage of eradication, variance in movements appeared high; indicating they moved little unless actively chased. Ungulates at northern latitudes rely on stored fat reserves for winter survival and foraging conditions during fall affect winter survival. Late season hunting or culling is likely to have adverse effects on subsequent survival, while in our case, all reindeer were eventually shot. Hence, culling efforts should also take into account how to tackle animal welfare aspects.

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AUTHORS' CONTRIBUTIONS

A.M. had the main idea and wrote the first draft; G.R.R. and B.V.M. helped with data preparation; A.M., I.M.R. and B.V.M. performed the statistical analysis; R.A. and O.S. conducted and organized all GPS marking and provided know-how of reindeer ecology. All the authors contributed to the further writing of the paper and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.1ns1rn8rv (Mysterud et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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