Original Article

Efficacy of Recreational Hunters and Marksmen for Host Culling to Combat Chronic Wasting Disease in Reindeer

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ABSTRACT Most populations of large mammals in developed countries are managed by human hunting, but there are surprisingly few empirical studies about the benefits and limitations of using recreational hunters to achieve specific management objectives. In particular, the extensive host culling required to markedly reduce population densities to combat some wildlife diseases may conflict with the management aims of landowners and hunters. This is particularly acute in the case of chronic wasting disease (CWD) in cervids, which has now emerged in reindeer (*Rangifer tarandus*) in Norway. We analyzed the relative efficacy of approximately 1,000 recreational hunters and 30 professional marksmen during the eradication of the entire CWD-infected population of >2,000 reindeer in Norway. The government changed a series of legislation that would normally limit the efficacy of recreational hunters; these changes were linked to the duration of the hunting season, the specificity and size of the quotas, and spatial access rights. Efforts were taken to reduce both the searching time (hunters were given information on herd whereabouts) and handling time (helicopter aid for transport) of the recreational hunters. We compared 1) recreational hunting under ordinary legislation (up to 2016), 2) recreational hunting with less legislation (2017), and 3) culling by marksmen that were allowed to use both snowmobile and helicopter. Despite all of the changes in legislation, harvest by recreational hunters only increased from 241–316 during 2014–2016 to 582 reindeer in 2017 and was below management targets, while marksmen culled 1,399 reindeer, with a daily average and maximum offtake well above that of the hunters. The hunters shot more animals in the early season and during weekends. Offtake by both the hunters and marksmen were equally negatively affected by fog, which reduced visibility. We discuss the relative merits of using hunters and marksmen for wildlife control in general and limits to how legislation can increase offtake. We highlight the need for more research into how the use of marksmen comes with a cost in terms of social conflict. © 2019 The Authors. *Wildlife Society Bulletin* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS cervids, chronic wasting disease, disease ecology, disease management, host culling, hunting legislation, searching and handling times.

During the past century, populations of cervids have increased in density and expanded their geographical distributions both in Europe and North America (McShea and Underwood 1997, Apollonio et al. 2010). Most cervid populations are managed by hunting and constitute important aspects of livelihood,

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culture, and recreation. Management aims and systems vary across cultures and can considerably affect population development (Milner et al. 2006, 2011). Only a few studies report the ability of hunters to regulate ungulate numbers in different cultures in Europe, including moose (*Alces alces*; Solberg et al. 1999, Fryxell et al. 2010) and reindeer (*Rangifer tarandus*; Strand et al. 2012) in Scandinavia, roe deer (*Capreolus capreolus*) in Germany (Hothorn and Müller 2010), and wild boar (*Sus scrofa*) in Spain (Quirós-Fernández et al. 2017). In contrast, there are numerous studies of harvesting white-tailed deer (*Odocoileus virginianus*) in the United States (Harden et al. 2005, Van Deelen et al. 2010, VerCauteren et al. 2011, Williams et al. 2013) and Canada (Fryxell et al. 1991, Giles and Findlay 2004, Lebel et al. 2012, Simard et al. 2013).

There are currently declining numbers of hunters in both Europe and North America (Riley et al. 2003, Heberlein 2007, Winkler and Warnke 2013). This is already regarded as a severe limitation for the ability of hunters to control wild boar populations in Europe (Massei et al. 2015) and white-tailed deer populations in the United States (Brown et al. 2000). It is therefore important to understand the different limitations of hunters to increase 'offtake,' defined here as the number of individuals removed over a given period. Offtake by hunters can, to some extent, be regulated by quotas (Boulanger et al. 2011), license prices (Schorr et al. 2014), property structure and access rights (Brown et al. 2000, Walberg et al. 2018) as well as hunting tactic (Weckerly et al. 2005) and use of technology, bait (Kilpatrick et al. 2010), and dogs (Godwin et al. 2013). Nevertheless, little empirical evidence exists outside of North America about these relationships. Available time also constrains recreational hunters, which is not easily controlled by management (Diekert et al. 2016). There was greater effort and offtake during weekends for red deer (*Cervus elaphus*) among recreational hunters in Norway (Rivrud et al. 2014) and elk (*C. canadensis*) in Idaho, USA (Gratson and Whitham 2000). Caribou (*R. tarandus*) in Canada were shot more often near roads because they enable easy access (Plante et al. 2017). Further, weather affects the effectiveness of hunters (Rivrud et al. 2014). Some conditions, such as extreme wind and cold or heavy rain, may keep hunters at home, or such weather may change the behavior of animals toward seeking shelter (Mysterud and Østbye 1999), making them less prone to getting exposed to hunters (Lone et al. 2014).

In recent decades, cervid management in Europe and North America has mainly involved growing populations with the aim to either allow or limit further growth to balance numbers relative to the carrying capacity (e.g., forage production; Strand et al. 2012), to reduce browsing pressure to allow tree regeneration (Hothorn and Müller 2010), or lower the number of deer–vehicle collisions (Williams et al. 2013). It would be more challenging to use recreational hunting when the management aim is to more drastically lower or even eradicate a population. Such aims come in conflict with the interest of hunters and landowners, and hunters may not have the time required or be willing to pay as much for hunting if it is seen more as a duty to someone else. Dense populations of game pose a disease risk (Gortazar et al. 2006). Host culling is used to combat certain wildlife diseases, including chronic wasting disease (CWD) in cervids (Wasserberg et al. 2009). In Wisconsin, USA, recreational hunters were not lowering deer densities when the CWD epidemic started (Heberlein 2004, Holsman et al. 2010). The use of professional marksmen in Illinois, USA, has been more effective in lowering CWD prevalence (Mateus-Pinilla et al. 2013, Manjerovic et al. 2014). We thus need to know more about 1) what limits the efficacy of recreational hunters, and 2) the alternative of using professional marksmen in efforts to control or eradicate cervid populations under different circumstances.

In 2016, the first cases of CWD in Europe were found in a wild alpine reindeer population in Norway (Benestad et al. 2016, Viljugrein et al. 2019). Host culling is currently the best supporting management tactic to combat CWD (Manjerovic et al. 2014); therefore, the Norwegian government decided to eradicate the whole reindeer population (>2,000 individuals) via a legal regulation (Department of Agriculture and Food 2017). We have previously presented the timeline and gross numbers of harvested reindeer in a commentary paper (Mysterud and Rolandsen 2018). Here, we provide an overview of the legislation changes made by local and governmental management to increase the efficacy of recreational hunters in 2017 compared with 2014–2016. We measured the effect of the change in legislation in terms of the number of reindeer shot and demographic composition of the harvest. We further present a statistical analysis of the relative efficacy of recreational hunters versus marksmen during the eradication process of the entire reindeer population. We hypothesized that recreational hunters were limited by the time available for hunting and that offtake would be greater early in the season and during weekends. We further quantify how much low visibility due to fog limited offtake.

METHODS

Study Areas and Reindeer Management

The Nordfjella wild reindeer management area was situated in the southern mountain ranges of Norway. Reindeer are managed independently in the 2 regions, labeled Zone 1 and Zone 2 (Fig. 1). Data come from Nordfjella Zone 1, which was approximately 2,000 km². The alpine part was demarcated by the county road (FV50) Hol-Aurland in the southwest and state road (RV52) Hemsedalsfjellet in the northeast, while deep valleys with fjords or forest provided barriers in the other regions. The high elevation led to a cold and harsh climate. The coastal western areas had more precipitation and warmer climates than the colder and drier inland regions. The reindeer population of approximately 2,000 animals had been regulated by ordinary recreational hunting until the discovery of CWD.

Reindeer hunting in Norway is regulated through a hunting license (quota) system (Strand et al. 2012). The total number of licenses for a given reindeer management area (such as Nordfjella) is set annually by a reindeer management board and then evenly distributed to the hunting units ("vald"). The local hunting units are either private or on communal land. A landowner has full rights to licenses and hunting on the private land. They typically sell expensive hunts to nonlocals. An open ("bull") license is typically ≥EUR$1,000. Communal areas have a mountain board determining distribution of licenses. They sell licenses to local (resident) hunters at a much cheaper price (EUR $250 for open license). During the 2017 hunt, however, communal areas also opened and sold license to hunters living outside of the municipalities.

Overview of Legislation

We gathered data on legislation mainly by contacting hunters, local reindeer management boards, and state-level managers (Norwegian Environment Agency and Norwegian Food Safety Authority). We also retrieved information and
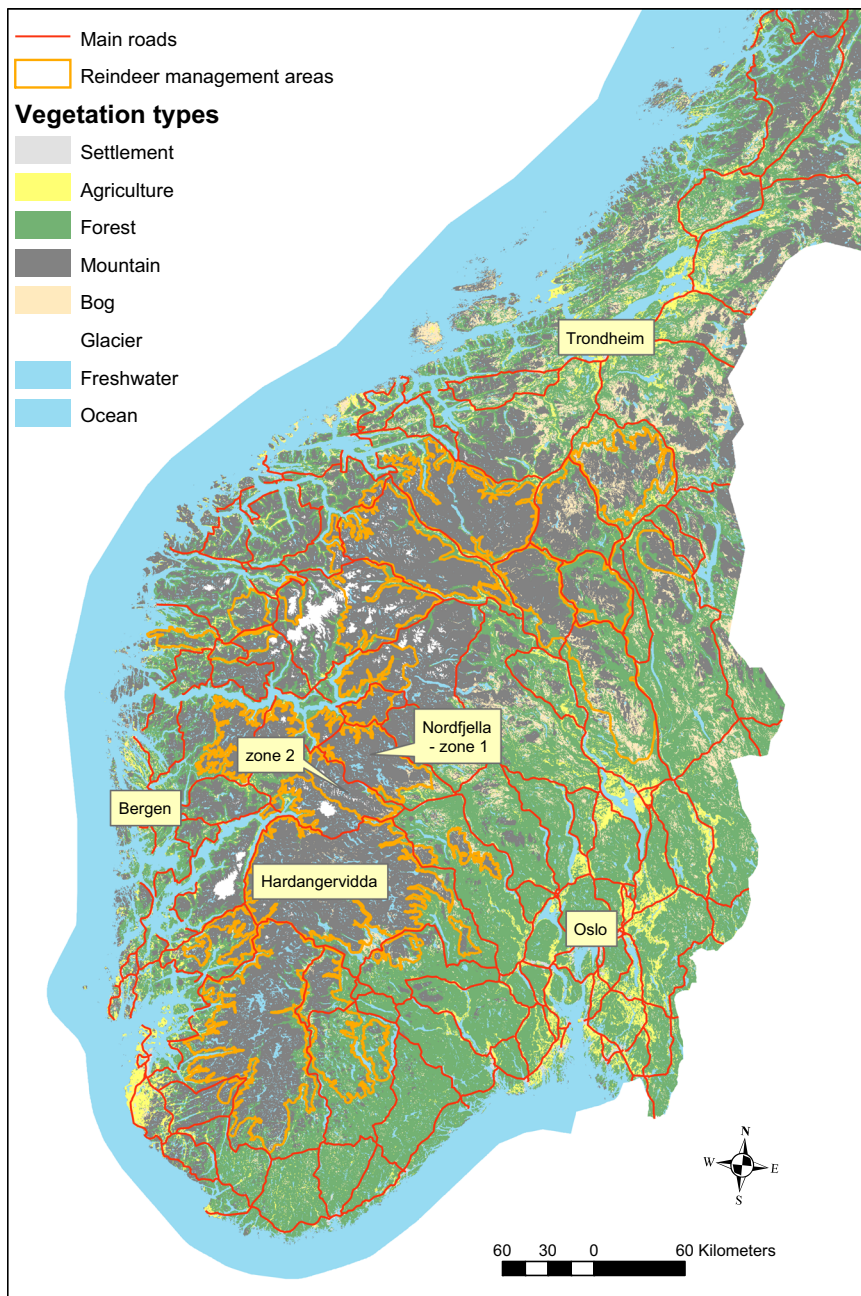
Figure 1. A map of southern Norway with Nordfjella Management Zone 1 and 2, Hardangervidda and major cities demarcated.

experiences as part of our involvement in the organization of the sampling from reindeer in connection with CWD testing, and by participating in hunting in the area for years including the last hunt.

Data from Recreational Hunting and Marksmen Culling

We retrieved hunting and culling statistics to enable a comparison of ordinary hunting, the last hunt in 2017 (with changed legislation), and marksmen culling. We retrieved data on the number, age group, sex, and kill date of harvested reindeer. These were reported by hunters to the local reindeer management board by using the standard reporting system for cervid hunting in Norway—the Cervid Register (www.

hjorteviltregisteret.no)—which is owned by the Norwegian Environment Agency. The Cervid Register contains the total number of harvested reindeer differentiated by sex and age group for all reindeer management areas in Norway. The 582 total reindeer from 2017 included 12 animals taken with licenses from Management Zone 2 that were harvested within Management Zone 1. In addition, for most of the individuals in Nordfjella, hunters also reported the kill date in 2017.

We retrieved the daily data log from the professional marksmen (available freely online; http://www.hjortevilt. no/skrantesyke-statlig-uttak-nordfjella-sone-1/). Thirty professional marksmen were hired through the Norwegian Environment Agency (unit SNO). Half of them were already employees of SNO, while the other half was

specially assigned for this task. The marksmen were organized into 3 teams of 10 each. Each team worked 7 days before a new team took over. The marksmen started culling after the ordinary hunt on 7 November (Fig. 2). They finished herd removal on the 25 February with the last known single individual on the 16 April 2018, well ahead of the management aim of 1 May. We restricted analyses to the period until 25 February when the last herd was removed and the main operation ended (111 total days). After this, only a few solitary animals were found (Mysterud and Rolandsen 2018). We only included animals that were actively culled by the marksmen, although they also removed additional reindeer found dead due to natural causes. Hunters and marksmen together removed 2,024 reindeer (Mysterud and Rolandsen 2018).

Data on Visibility (Fog)

Data on the lowest visibility (in m) were available from a weather station situated in the small town of Geilo at 841 m above sea level (met station no 25640). This location is approximately 10 km away from the southeastern border and approximately 50 km from the northwestern border of Nordfjella, but on the other side of a mountain range (Hallingskarven). Usually, fog is defined as visibility below 1 km, but to obtain a more even distribution of data into the categories 'fog' and 'clear,' we used a 10-km threshold. The visibility metric was averaged based on readings at 0700, 1300 and 1900, and visibility below the chosen threshold indicates periods of fog. To ensure that data on the lowest visibility from the weather station gave a fair indication of the conditions in Nordfjella, we checked these data against a qualitative scoring ('good,' 'fair,' 'demanding,' or 'impossible') available from the marksmen for the period from 7 November 2017 to 25 February 2018. Only 8% of the days marksmen noted as 'good' in Nordfjella had fog at the weather station, while 75% of the days marksmen noted as 'impossible' in Nordfjella had fog at the weather station. Hence, visibility data from the weather stations were a fair proxy for the weather conditions in Nordfjella.

Statistical Analysis

We analyzed the number of harvested reindeer per day in Program R version 3.4.1 (R Development Core Team 2016). Factors were the type of culling (recreation hunters–marksmen), type of day (weekend–workday), and visibility (fog–clear) as well as their interactions. For marksmen, we included the Christmas holiday with no culling as weekend days in the analysis. To see whether offtake changed over time, we counted the number of days from 10 August for recreation hunters (83 days) and from 7 November for the marksmen (111 days). We standardized ($\bar{x} = 0$, SD = 1) the variable 'days after onset of hunting' independently for the 2 periods of ordinary hunting and marksmen culling. We started with generalized linear models and an ordinary Poisson distribution, but zero counts accounted for 51.5% of the data because we included both days without hunting–culling and when not successful. We therefore used the glmmADMB library and found that using zero inflation on the intercept and a negative binomial distribution improved model fit (Skaug et al. 2006). We calculated day length as a descriptive statistic for discussion purposes using the library geosphere for latitude 60.7° (Forsythe et al. 1995), but did not include it in the analysis because it is a direct function of the Julian date. The Akaike Information Criterion (AIC) was used to select the most parsimonious model.

RESULTS

The legislation of the last hunt (2017) was changed relative to ordinary hunting in several ways (Table 1). The hunting season was extended from 32 to 83 days by earlier onset and later termination. Quota size was hugely enlarged from 600–828 in 2014–2016 to 3,500 in 2017. During ordinary hunting, licenses were calves, females including yearlings of both sexes, and open licenses. During the last hunt, 1,750 of the licenses were open and not specific regarding age or sex, and on each of these licenses an additional calf could be shot (i.e., a quota on 3,500 reindeer in total). Spatial restriction of hunting is strict during ordinary hunting. These restrictions
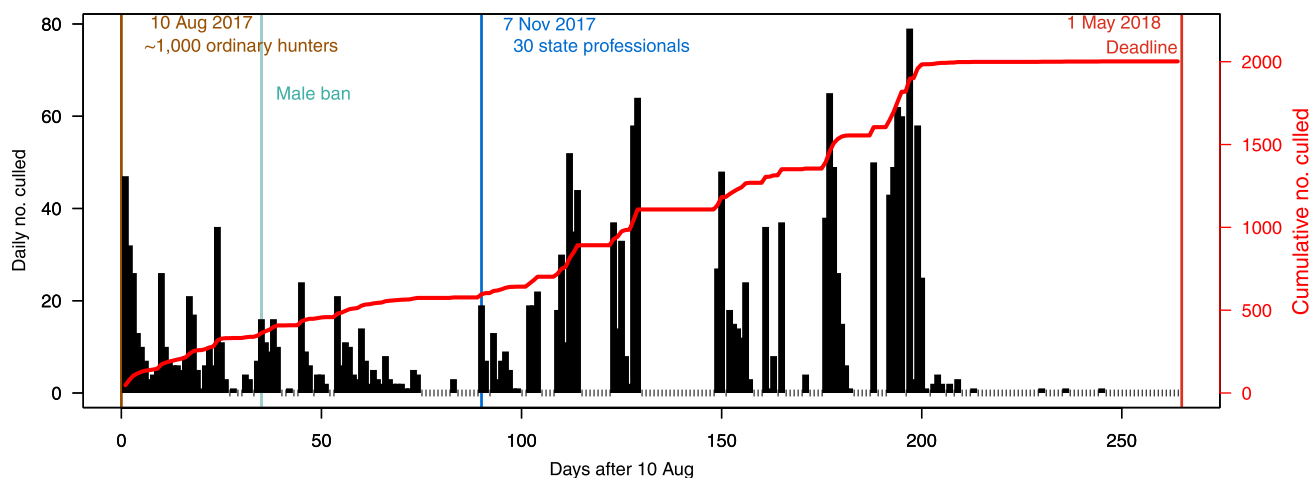
Figure 2. The detailed timeline of the eradication of the population of reindeer infected with chronic wasting disease in Norway from 2017 to 2018.

Table 1. An overview of conditions and management actions implemented to increase the efficiency of recreational hunters and marksmen during the chronic wasting disease (CWD) eradication in Nordfjella, Norway, in the autumn of 2017. We have also included the likely consequences for the economy and assumed conflict levels locally.

Parameter	Ordinary hunting before CWD	Hunt of 2017	Marksmen
Reindeer removed	241–316	582	1,399
Daily average reindeer removed	7.8–10.2	7.0	12.5
No. of days	32	83	111
Conditions			
Snow cover	Bare ground	Bare ground	Snow
Daylight ($\bar{x}$)	13.5 hr	12.6 hr	7 hr
No. of hunters	Hundreds	Approx. 1,000	30
Motivation		Variable	High
Social norms	Use meat	Use meat	Meat discarded
Skill level	Variable, recreational hunters	Likely lower. More hunters in the area for the first time	Extreme skill level
Searching time	Scouting, communicating with team members on the radio, eavesdropping on the radio	State management central daily info to hunters on herd whereabouts	Patrolling with helicopter and snowmobiles
Handling time	Gutting and skinning, carrying out meat on backpacks	Gutting and skinning, carrying out meat on backpacks, some assistance by helicopter for lifting out carcasses	Helicopter lift out of whole carcasses; all meat discarded, only lymph nodes and brain tissue for testing sampled
		Disease containment measures lowering efficiency	Disease containment measures and animal welfare issues lowering efficiency
Legislation			
Quota	Age- and sex-specific	Open licenses with an extra calf for each license	None
Season	20 Aug–20 Sep	10 Aug–31 Oct	1 Nov–31 Apr[a]
Spatial restrictions	Hunting-area-specific	Mainly hunting area specific, some collaboration	None
Local regulations			
Legal hours[b]	0700–1900	0700–1900	All
Rut-related ban on male hunting[c]	After 15 Sep	After 15 Sep	None
Economy			
Hunters	Limiting	Probably limiting	Not limiting
Landowners	Earn money	Earn money	Loss of income
State	Free & earn from state tax on each shot deer	Free, but no state tax	Expensive
Bounties	None	None	None
Conflict level	Low	Low	High

[a] This was the planned period. In reality hunting started on 7 Nov and the last herd was taken out on 25 Feb (i.e., 111 days as reported above).
[b] To reduce stress to the animals.
[c] Meat from rutting reindeer males is often not edible.

were modified in some areas allowing other hunters in, but only after specific agreement and mainly later in the season. However, both the legal hours of hunting (0700–1900) and rut-related ban on male hunting (after 15 Sep) were retained during the last hunt (Table 1). In addition, aid was given during the last hunt in the form of information of herd whereabouts by radio and providing helicopter transport of carcasses.

Recreational hunters removed 582 reindeer in 2017 during the 83 days, of which 339 were removed the first 32 days (duration of an ordinary season). This represented a success rate of 58.2% relative to the management aim of >1,000 reindeer and 8.1% relative to the quota of 3,500 licenses. This number was considerably greater than previous years (2014–2016) with 241–316 reindeer harvested with 32 days of hunting (Table 1; Fig. 3). The demographic composition of the harvest was 30.1% adult males, 37.0% adult females, 10.7% yearlings, and 22.0% calves averaged over 2014–2016, whereas it was 33.7% adult

males, 29.6% adult females, 10.5 yearlings, and 23.0% calves in 2017 (Fig. 3). Hence, slightly more adult males compared with adult females were harvested in 2017 compared with 2014–2016. The number harvested per day in Zone 1 during hunting was 9.9 in 2014, 7.5 in 2015, and 9.0 in 2016 with 32 days hunting season, but declined to 6.8 with 83 days hunting in 2017.

Marksmen culled 1,399 reindeer (Fig. 2). On average, ordinary hunting removed 7.0 reindeer/day, with a maximum of 47 on the most successful day; whereas, the culling of reindeer by marksmen removed, on average, 12.5 reindeer/day and peaked at 79 on the most successful day. There was no culling on 19 days of ordinary hunting (22.9%) and on 58 days of marksmen culling (52.3%). The high proportion of days without culling was due to weather giving low visibility (i.e., the marksmen classified 39 days as 'demanding' and 28 days as 'impossible'). On average, marksmen had 7 hours of daylight from 7 November to 25 February, whereas ordinary hunters had a mean of 12.6 hours of daylight from 10 August to 31 October.
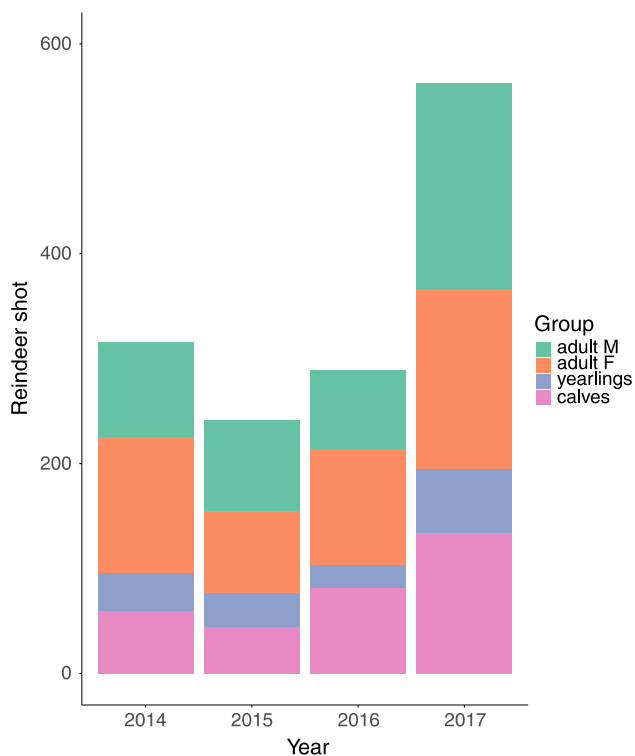
Figure 3. The total number and composition of reindeer shot in the chronic wasting disease (CWD)-infected population in Zone 1 during ordinary hunting 2014–2016 and during the 'CWD-hunt' of 2017 with marked change in legislation in Norway. F = females; M = males.

Analysis with number of reindeer harvested per day as a response showed that marksmen culled more reindeer per day than did recreational hunters (Table 2). More reindeer were culled during the weekends for the recreational hunters but not for the marksmen (Fig. 4A; Table 2). Similarly, the rate of harvest by the recreational hunters declined over the season but not for the marksmen (Fig. 2; Table 2). Fog reduced the number of felled reindeer similarly for recreational hunters and marksmen (Fig. 4B; Table 2)—adding an interaction term for the type of hunting and fog did not improve the model fit (ΔAIC = 1.20). The interactions type of day × fog (ΔAIC = 1.90) or type of hunting × type of day × fog (ΔAIC = 63.30) also led to less parsimonious

Table 2. An analysis of the daily culling of reindeer by recreational hunters and marksmen using a negative binomial model with zero inflation during the eradication process from 10 August 2017 to 25 February 2018 in Norway. st = standardized variable ($\bar{x} = 0$, SD = 1). Baseline for categorical variables were marksmen, weekend and fog.

| Model variables	Estimate	SE	z	P
Intercept	1.855	0.138	13.41	<0.001
Hunter vs. marksmen	1.480	0.185	8.01	<0.001
Workday vs. weekend	0.636	0.222	2.87	0.004
st(date of harvest)	−0.452	0.111	−4.07	<0.001
Clear vs. fog	−0.562	0.181	−3.09	0.002
(Hunter vs. marksmen) × (workday vs. weekend)	−0.648	0.325	−1.99	0.046
(Hunter vs. marksmen) × st(date of harvest)	0.721	0.150	4.82	<0.001

models. A more detailed overview of model selection is given in Supporting Information (Table S1).

DISCUSSION

The ability of ordinary recreational hunters to control ungulate populations is of increasing concern, particularly when facing severe wildlife disease epidemics (Holsman et al. 2010). The most urgent cases are African swine fever spreading among wild boar in Europe (European Food Safety Authority Panel on Animal Health and Welfare et al. 2018), and the outbreak of CWD in cervids that poses a great challenge for wildlife management in Europe (Mysterud and Edmunds 2019), as it does in the United States and Canada. Combating CWD involves taking drastic management actions such as extensive host culling (Uehlinger et al. 2016). Chronic wasting disease was only recently discovered in Europe (Benestad et al. 2016); therefore, hunters in Europe have little knowledge and understanding about CWD and the necessity of taking such drastic actions. Before CWD, the annual harvest of reindeer in the affected area was in the range of 241–316 reindeer during years before the change in the legislation. The management aim was to eradicate the entire population of >2,000 reindeer (Department of Agriculture and Food 2017), with a recreational hunting goal of >1,000 reindeer (The Norwegian Food Safety Authority and The Norwegian Environment Agency 2017). Although recreational hunters (probably up to 1,000) shot more reindeer than normal (582 reindeer), this was nevertheless only sufficient to cause a moderate population decline. The 30 marksmen culled 1,399 reindeer, the vast majority of harvested reindeer, during a period of 111 days. Hence, recreational hunters proved to be less effective compared with the marksmen, even with the changes in the legislation. Part of this result was likely due to the time constraints of the recreational hunters because their harvest peaked during weekends and declined over the season. Unfavorable weather conditions, in the form of low visibility due to fog, was a major factor negatively affecting offtake of both hunters and marksmen.

Hunting by Recreational Hunters and Culling by Professionals

Efficiency of individual hunters is complicated for humans, where economy, social norms, motivation, legislation in terms of quotas, hunting seasons, and property access rights severely limit recreational hunters more than they limit marksmen. The number of hunters and their motivation, social norms, and experience are also important for efficacy. Ordinary hunting of reindeer involves either sit-and-wait or active stalking with the frequent use of handheld binoculars in the open alpine areas. The Nordfjella region is topographically hilly, making it difficult to spot reindeer from a distance. Therefore, searching for and finding reindeer is a main limitation to the efficiency of individual recreational hunters. We showed quantitatively how reduced visibility in the form of fog markedly reduces offtake. Ordinary hunting typically occurs before the onset of snow cover, whereas the professional marksmen could benefit from the contrast of the dark animals on the snow-covered ground and from finding
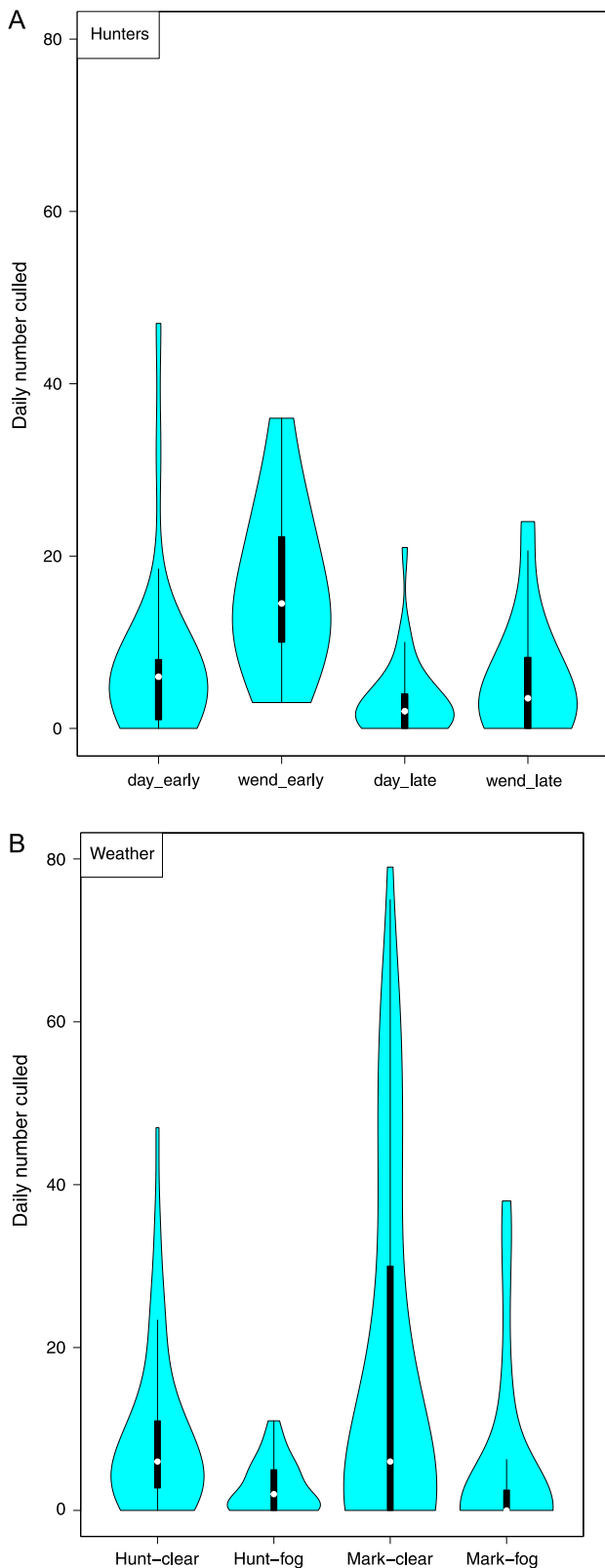
Figure 4. A) For ordinary hunters, offtake was higher during weekends ("wend") than during the workdays ("day") and in the first ("early") compared with second ("late") half of the hunting season. B) For both recreational hunters ("Hunt") and state professional marksmen ("Mark"), weather conditions (fog) during winter were decisive for culling success of reindeer in Norway during 2013–2017. The white spot is the median and the black lines represent the quartiles, while the colored area represents a density kernel of the data distribution.

tracks in the snow. Winter 2017–2018 had early snow cover that enabled the use of snowmobiles. The marksmen used both helicopters (220 hr) and snowmobiles (49,545 km) for patrol, markedly reducing searching time (Mysterud and Rolandsen 2018). Hunters in Norway communicate with the aid of handheld radios during hunting, typically within the hunting team. However, reindeer hunters frequently eavesdrop to the radio channels of competing hunters on neighboring estates to obtain information about herd movements (A. Mysterud, personal observations). For the CWD hunt, the Norwegian Nature Inspectorate (SNO) had a manned office that provided information on the position of the reindeer herds to the hunters via radio, social media or telephone to reduce searching time. In the ongoing efforts aimed at preventing the spread of African swine fever into Germany, hunters are now allowed to use night vision when hunting wild boar in efforts to reduce population densities (J. Müller, University of Würzburg, personal communication). However, how much this action increases efficacy has not been quantified.

Handling time is another essential component. Recreational hunters of cervids in Scandinavia are typically aiming for meat consumption rather than trophies (Andersen et al. 2014). To use the meat is a strong social norm and important for public acceptance of hunting (Ljung et al. 2012). Recreational hunters used the meat from the reindeer, whereas meat from all of the reindeer culled by the marksmen was lifted out by helicopter and discarded to improve efficacy. The reason for the decision to discard the meat was the practical difficulties involved in storing large number of carcasses properly during the period before CWD test results appear. Many hunters also do not have the capacity to handle all of the meat if they shoot many animals. Hunters also need to gut and skin the animals, which will typically take at least an hour, even for trained hunters. In Nordfjella, carrying reindeer meat in backpacks for up to 2–3 hours is normal. Therefore, a single hunter can usually not handle >2 reindeer/day depending on the distance to roads. In the season studied, extra aid was provided by a helicopter for lifting carcasses out of remote areas to reduce the handling time, but typically only if >1–2 animals were shot. This was very popular among hunters and frequently used. In North America, it is well-documented that easy access to roads is a major determinant of harvest offtake (Gratson and Whitham 2000, Plante et al. 2017). Handling time was also increased as a result of several disease-mitigation measures for both hunters and marksmen regarding disposal of offal and taking samples as part of disease testing regimes. Further, animal activists were particularly negative to the marksmen, and even reported them to the police (K.R. Alvseike, Norwegian Food Safety Authority, personal communication). Animal welfare arguments were therefore always on the agenda for the marksmen, assessing stress levels in herds sometimes aborting efforts, and hence this limited offtake. Linked to this, marksmen did not use helicopter for active culling except in final stages with small herds (<20 individuals) so that all could be harvested together. Only 243 total reindeer were felled directly from a helicopter to abide by such animal

welfare restriction, while using helicopter for transport of the carcasses was standard.

Legislation as Limitations to High Offtake

In general, hunters are typically strictly limited by legal harvest quotas, hunting seasons, and property access rights (Mysterud 2011). Several actions were taken to increase the efficiency of the individual hunters compared with under normal conditions. Recreational hunting of reindeer is regulated with sex- and age-specific hunting quotas (Strand et al. 2012). During the CWD hunt (2017), 1,750 open licenses (no restriction with regard to sex and age) were issued, allowing an additional calf on each license without extra payment. Licenses during ordinary hunting are typically open licenses (typically adult males are harvested), females (including yearling males), and calves. This change to open licenses led to a greater proportion of adult males (33.7% vs. 30.1%) and a lower proportion of adult females (29.6% vs. 37.0%) in the harvest of 2017 relative to 2014–2016; but overall, the change in the composition of the harvest was quite moderate. Furthermore, the ordinary hunting season for reindeer is from 20 August to 20 September (32 days), but during the hunting season of 2017, it was extended from 10 August to 31 October (83 days). This extension of season was a key factor—the hunting in 2017 removed 339 reindeer during the first 32 days, which was only slightly greater than overall harvest of 241–316 reindeer in 2014–2016. In the Nordfjella area, hunters were only allowed to hunt between 0700 and 1900, which is normal. This timeframe was chosen so as not to disturb the animals too much, so this timeframe was retained. Also retained was the local ban on shooting males after 15 September on account of rutting activity, because the meat from rutting adult reindeer males usually cannot be used for human consumption.

Another important limitation was that hunters are typically only allowed to search on a given landowner property, while reindeer herds are nomadic and use extensive areas. Marksmen could use all areas without restrictions. In some cases during the CWD hunt, property access rights were relieved also for ordinary hunters, but only after explicit agreement with neighboring hunting areas. Such legal limits to spatial searching are a main hindrance to efficacy because wind direction typically moves the herds toward one region. Therefore, most of the time, recreational hunters likely cannot find reindeer in their areas. In some cases, hunters with reindeer on their properties fill their quotas rapidly, and herds are then left and can stay safe from hunters until the wind direction changes and they are disturbed. Similarly, private property rights severely limit access for deer hunters in the United States (Brown et al. 2000, Walberg et al. 2018), and both elk (Proffitt et al. 2010, 2013, 2016; Ranglack et al. 2017) and white-tailed deer (Rhoads et al. 2013) seek refuges on private land during the hunting season. There were some agreements allowing hunters to use other estates during the 2017 hunt, but this also led to interference. Hunters not experienced in a given area are more likely to disturb the reindeer herds and ruin chances for other hunters. Communal areas mainly allowed resident hunting, but opened for hunters living outside of the municipalities in the 2017 hunt. Similarly, these nonlocals were not familiar with their hunting area; according to local hunters, this caused interference to the extent locals were reluctant to go hunting. Hence, recruiting more recreational hunters does not always result in greater efficacy.

Conflicting Management Aims

There are few case reports regarding the extent to which hunters respond to new management aims and regimes, in particular for such a dramatic goal as population eradication. Deer hunters in Wisconsin showed reluctance to adapt to even minor changes in antler-tine-based harvest restrictions because of their established beliefs and harvesting regimes (Cornicelli and Grund 2011). In Canada, efforts to reduce moose densities down to one-third with the aid of ordinary hunters proved successful (Serrouya et al. 2011, 2015), despite requiring the introduction of antlerless harvest often unpopular in North America. Combating disease using host culling will involve more rapid responses and conflicts of interest with other management objectives or motivational aspects at an entirely new level (Holsman et al. 2010). In Wisconsin, managers raised quotas to increase the offtake by recreational hunters in the initial stages of the CWD epidemic (Heberlein 2004). However, fewer hunters than earlier wanted licenses; consequently, fewer than normal deer were harvested despite the larger quotas. This was partly due to lack of trust in agencies claiming it was safe to eat meat from deer infected with CWD (Heberlein 2004), but also due to an unwillingness to reduce the (host) deer density because it conflicts with social norms (Holsman et al. 2010). The issue of food safety did not seem to worry hunters in Norway because they trusted the testing regime implemented by the Norwegian Food Safety Authority and performed by the Norwegian Veterinary Institute. Hunting for nonlocals was mostly as economically expensive during the CWD hunt as under ordinary hunting. The "earn-a-buck" system in some states in the United States, requiring the shooting an antlerless deer first, has markedly increased the offtake of females (Van Deelen et al. 2010, Boulanger et al. 2011). Bounties could be considered in future efforts; historically this was a common approach with carnivores and pest species (Phja-Mykra et al. 2005), but this was not efficient in combat for wild pigs in Georgia, USA (Ditchkoff et al. 2017).

MANAGEMENT IMPLICATIONS

Use of professional marksmen was successful in reaching the management objectives. However, use of marksmen caused considerable controversy in Illinois (Manjerovic et al. 2014), and the same situation appears to be the case in Norway based on local news coverage and social media (Mysterud and Rolandsen 2018). With marksmen culling, the landowner loses their income from hunting and the recreation value because there was no compensation made to them from the state. Insights from studies on human dimensions have proved essential for understanding the limits of recreational hunters in controlling CWD in the United States (Heberlein 2004; Vaske et al. 2006, 2018; Vaske 2010; Holsman et al. 2010). The perception of using marksmen in general likely depends on whether wildlife is

important for livelihoods. In Australia, marksmen were used to make the culling of western grey kangaroos (*Macropus fuliginosus*) more publicly acceptable in an urban setting (Mawson et al. 2016). Lower wounding rates are likely with marksmen, and the care hunters take when firing a rifle depends on the regulations (Conlin et al. 2009). Therefore, the general public may perceive the use of marksmen more positively than do landowners. However, this is likely also dependent on whether the public accepts the aim of the culling. Governmental badger (*Meles meles*) culling aimed at limiting bovine tuberculosis in the United Kingdom remains highly controversial (Donnelly et al. 2005, Bielby et al. 2014, Donnelly and Woodroffe 2015). Therefore, we call for more research into the motivational, institutional, and economic aspects of recreational hunting and marksmen culling to reach specific management aims, depending on the context.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1. An overview of model selection results using a negative binomial model with zero inflation on the intercept.