



# The relationship between quotas and harvest in the alpine reindeer population on Hardangervidda, Norway

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## Abstract

Hunting of cervids is commonly regulated by quotas that are specific to sex and age groups. There is substantial cultural variation in how quotas are regulated. In Scandinavia, the entire quotas are often not shot making deer management potentially less predictable. However, the effect of quota size and demographic composition on harvest offtake by recreational hunters has, to a limited extent, been empirically investigated in Scandinavia. Hunters are limited by time and opportunity and may not respond to changes in quota, as anticipated by managers. We analysed the variation in the proportion of quotas filled depending on quota size relative to population size and demographic composition of quotas during the period of 1986–2019 involving a population size varying from approximately 5000 to 15,000 reindeer on Hardangervidda, Norway. We found that the proportion of quota being filled by hunters varied substantially (12–48%) on an annual basis. The quota occasionally exceeded the estimated population size, but the proportion of the quota filled increased the higher the population size was relative to the quota size. The proportion of quota being filled by hunters was markedly lower for calf licences. High annual variation in the proportion of quota being filled by hunters causes considerable implementation uncertainty when managers aim to regulate cervid populations. Nevertheless, there was a strong correlation between quota size and harvest size. Facing new management requirements, a harvest rate of ~47% of the adult male population size was achieved in 2019, compared to an average of 16%. Hence, managers compensated for the low proportion of quota being filled by increasing quotas to reach target harvesting aims, but there remains a limit as to how precisely such a wide-ranging reindeer population can be regulated using recreational hunters.

**Keywords** Harvesting · Hunter effort · Implementation uncertainty · Recreational hunting · Selective hunting

## Introduction

Hunting of ungulates is commonly regulated by setting harvest quotas, usually separated on sex, age, or size categories (Mysterud 2011). There is considerable cultural variation in the way quotas are set (Apollonio et al. 2010). In some countries of Europe, quotas are strictly regulated with detailed management plans and cull targets (Putman 2011). In other cultures, as in many states of the USA and in the Scandinavian countries, the proportion of quotas being filled can be quite variable making deer management potentially less predictable. Filling harvest quotas when population numbers are low is challenging, requiring high effort and motivation (Guttery et al. 2016), and modern recreational hunters are limited by the time they can spend on hunting (Mysterud 2011; Diekert et al. 2016). Despite the widespread use of quotas, little is known regarding their effectiveness in

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regulating harvest and in turn population numbers across different management settings (Strand et al. 2012; Boertje et al. 2020).

The effort of hunters required to fill quotas depends on motivation, and motivation may depend on management objectives (Serenari et al. 2019). Changes in the threshold for number of antler tines for legal harvest relative to established harvesting regimes were not perceived favourably among deer hunters in Wisconsin (Cornicelli and Grund 2011). Incentives such as the “earn-a-buck” system in some states in the USA, requiring the shooting of a female deer first, have markedly increased the offtake of females (Van Deelen et al. 2010; Boulanger et al. 2011). The motivation of hunters is a factor that can influence the achievement of quotas when the aims for harvesting are changing, particularly towards population reduction (Serenari et al. 2019). The deer tag system proved inefficient in increasing harvest offtake when chronic wasting disease (CWD) was discovered in Wisconsin, USA (Heberlein 2004). Part of this was lack of motivation among hunters for heavy harvesting being in conflict with their norms (Holsman et al. 2010).

Quotas for cervids in Scandinavia are specified according to sex and age categories. This is the case for reindeer *Rangifer tarandus* (Strand et al. 2012), moose *Alces alces* (Solberg et al. 1999, 2000) and red deer *Cervus elaphus* (Langvatn and Loison 1999) in Norway. For reindeer in Norway, quotas are most often given as ‘free licenses’, ‘females and yearlings’ and ‘calves’. In sexually dimorphic species, as in most ungulates, males are often more attractive to hunters due to their status as trophies and their large body sizes, yielding more meat. Adult males are therefore usually shot on ‘free licences’. On private estates, the costs of a ‘free license’ for reindeer can be high (300–1000 Euro), while licences are cheaper on communal areas exclusively open to local hunters only. The level of quota filling can be low and variable for cervids in Scandinavia. Yet, we lack documentation as to how changes in quota size and composition affects how hunters are able or willing to fill quotas, and such knowledge is important in order to know to what extent recreational hunters can be used for population regulation.

We analysed the variation in the proportion of quotas filled by recreational hunters historically (1986–2019) in the iconic reindeer population on Hardangervidda, Norway. This is the largest wild alpine reindeer population in Europe, and it covers a period in which the population varied between ~ 5000 and ~ 15,000 reindeer. We predicted that an increasing proportion of the quota would be filled if the quota is low relative to the population size. We further quantified to what extent the proportion of quotas filled depended on demographic composition of such quotas (‘free licenses’, ‘females and yearlings’ vs. ‘calves’), and how an extra calf added to a female or adult license card affected the proportion of quotas filled. Further, we also tested if there was a

significant deviation in the proportion of quotas filled during a ‘hunter boycott’ in 2003 and during ‘disease (CWD) management’ in 2019 with massively increased ‘adult male only’ harvesting. Lastly, we analysed whether or not the size and composition of the (sum or remaining) quota affected further harvest the same season at a large estate.

## Materials and methods

### Study area and harvest data

The Hardangervidda Mountain Plateau covers more than 8000 km<sup>2</sup> and is situated in southern Norway (Fig. 1). In the west, the mountain ends on steep slopes which descend to fjords below, while the topography is more gently rolling in the eastern part. The climate is coastal in the west with significant precipitation, while it has a drier inland climate in the east. The main elevation range is 1100–1200 m above sea level, but with peaks extending to above 1700 m. Most of the Hardangervidda Mountain Plateau has management status as a national park. There are few large carnivores in these areas, and the reindeer populations are regulated by human hunting (Strand et al. 2012). During 1986–1996, the ordinary hunting season was 20th of August–25th of September. During 1997–2018, the ordinary hunting season was 20th of August–30th of September. There were extended hunting seasons in 1999, 2000, 2014, 2016, and 2019 to increase harvest (Table 1). Data from one privately owned area, ‘Juvik’, was included due to detailed account of hunter effort being available. Juvik (59.983° N 8.057° E) is situated southeast at Hardangervidda and covers approximately 31 km<sup>2</sup>.

### Data on harvest, quotas, and reindeer numbers

Data regarding quotas and harvests on Hardangervidda were available from Statistics Norway from 1986–2019. The data were checked against data from the regional reindeer tribunal. There was a very low proportion of quotas filled in 2003. This was owing to a management conflict that caused the regional reindeer tribunal to recommend no hunting that year, despite being overruled by the Norwegian Environment Agency. We refer to this as ‘hunting boycott’ and test whether 2003 was an outlier in the relationship between harvest and quota (see statistical analysis below). In 2004, there was no hunting. In 2019, the Norwegian Food Safety Authority demanded massively increased ‘adult male only’ harvesting on Hardangervidda due to detection of CWD in the adjacent reindeer population in Nordfjella (VKM et al. 2021). We refer to this as ‘disease (CWD) management’ and similarly test whether 2019 was an outlier in the relationship between harvest and quota (see statistical analysis below).



Fig. 1 The position of the mountain plateau Hardangervidda (grey area) and the focal estate Juvik in southern Norway

**Table 1** The raw data used in this paper for Hardangervidda overall. *N*, mean population size; *H*, harvest; *Q*, quota; *adm*, adult male; *c*, calf. *prop.*, = proportion; *tot*, total; *Qtot*, the potential maximum harvest (including calves on adult license cards); *Qcards*, quota given as number of license cards (excluding calves on adult license cards)

Year	Ntot	Nadm	Nc	Qtot	Qcards	Qfree	Qc	Htot	Hc	Hadm	Hunting season
1986	9514	1897	1394	3026	3026	327	748	1337	273	163	20.Aug–25.Sept
1987	10,358	2055	2382	4709	4709	595	1142	1977	361	261	20.Aug–25.Sept
1988	10,616	1936	2448	4659	4659	1048	917	1990	344	457	20.Aug–25.Sept
1989	10,998	2051	2598	4482	4482	582	1110	1501	309	264	20.Aug–25.Sept
1990	11,740	2424	2496	7016	7016	1055	1396	2805	512	496	20.Aug–25.Sept
1991	11,350	2551	2656	7962	7962	1197	1986	2843	574	582	20.Aug–25.Sept
1992	10,301	2485	2027	3494	3494	704	1044	751	172	178	20.Aug–25.Sept
1993	11,655	3022	2369	3992	3992	1013	985	1748	338	534	20.Aug–25.Sept
1994	12,954	3027	3322	5982	5982	918	1782	1612	315	356	20.Aug–25.Sept
1995	14,372	3283	3320	8066	8066	821	2810	2505	568	427	20.Aug–25.Sept
1996	14,973	3861	3421	9014	9014	1368	2699	3622	775	831	20.Aug–25.Sept
1997	13,924	3825	2881	9610	9610	981	2878	3446	736	575	20.Aug–30.Sept
1998	12,878	3855	2699	22996 <sup>3</sup>	11,498	1722	ad <sup>1</sup>	4420	1077	897	20.Aug–30.Sept
1999	9917	3341	1702	23048 <sup>3</sup>	11,524	1755	ad <sup>1</sup>	3550	761	716	20.Aug–10.Oct
2000	8122	2743	1938	22996 <sup>3</sup>	11,498	2301	ad <sup>1</sup>	2683	549	759	20.Aug–10.Oct
2001	6611	2010	1326	10052 <sup>3</sup>	5026	1275	ad <sup>1</sup>	2144	490	553	20.Aug–30.Sept
2002	5423	1769	1089	4285 <sup>3</sup>	2520	755	adF <sup>2</sup>	1417	321	368	20.Aug–30.Sept
2003	4924	1530	1036	958 <sup>6</sup>	958 <sup>6</sup>	356	279	133	23	56	20.Aug–30.Sept
2004	5745	1723	1095	NA <sup>4</sup>	NA <sup>4</sup>	NA	NA	18	4	6	20.Aug–30.Sept
2005	6840	2122	1288	2530	2530	1010	632	864	122	429	20.Aug–30.Sept
2006	7193	2085	1395	3520	3520	1228	884	1038	164	418	20.Aug–30.Sept
2007	7496	2013	1523	1830	1830	637	548	694	149	255	20.Aug–30.Sept
2008	8299	2152	1743	1520	1520	380	455	667	134	165	20.Aug–30.Sept
2009	9092	2406	1681	1523	1523	381 <sup>5</sup>	457	601	140	154	20.Aug–30.Sept
2010	9817	2799	1667	2025	2025	426	398	970	154	248	20.Aug–30.Sept
2011	10,739	3032	2148	5020	5020	731	1507	1388	297	308	20.Aug–30.Sept
2012	11,372	3102	2300	6020	6020	903	1807	1190	192	315	20.Aug–30.Sept
2013	11,890	3263	2001	7025	7025	1755	1760	2087	414	629	20.Aug–30.Sept
2014	11,599	3242	2115	9025	9025	1360	910	2588	508	521	20.Aug–12.Oct
2015	10,128	3007	1393	8020	8020	1205	1205	1682	298	398	20.Aug–30.Sept
2016	9962	3013	1834	14,815	8008 <sup>3</sup>	1203	adF <sup>2</sup>	1846	369	358	20.Aug–9.Oct
2017	8923	2775	1374	9920	6013 <sup>3</sup>	2105	adF <sup>2</sup>	1394	228	551	20.Aug–30.Sept
2018	8414	2677	1103	1522	1522	1056	234	700	81	440	20.Aug–30.Sept
2019	8895	2657	1388	6035	6035	6035 <sup>7</sup>	0	1270	8	1248	10.Aug–22.Sept

<sup>1</sup> An extra calf for every adult license card

<sup>2</sup> An extra calf for every adult female license card

<sup>3</sup> Adjusted relative to Statistics Norway (SSB). SSB did not include the extra calf on adult license cards from 1998 to 2002, but did so in 2016–2017

<sup>4</sup> No ordinary hunting

<sup>5</sup> Corrected relative to Statistics Norway

<sup>6</sup> Many hunters boycotted hunting owing to central management overruling when local management wanted no hunting

<sup>7</sup> Adult male-only licenses

The available quota can be calculated in two ways. (1) *Quota = number of license cards*. Usually, the quota is given to hunters in the form of a physical license card with a permit to shoot one animal. In one analysis, we used the number of license cards as the quota, which is how the quota is perceived by the regional reindeer tribunal. (2)

*Quota = maximum potential harvest*. In some years, it is legal to shoot one calf for every adult license card; hence, hunters can report up to two shot animals on one adult license card. Statistics Norway was not consistent in reporting the total quota for the years with an extra calf following adult license cards. Therefore, we also conducted an analysis

including all calves in the total quota; hence, a female or free license card also allowed for a calf harvest counted as quota for two animals, similar to what Statistics Norway has done for subsequent years (Table 1). The maximum potential harvest was 1.6–2 times the number of license cards. Note that there is no relationship to maximum sustainable harvest.

Due to this way of setting quotas, there are 3 ways to issue a calf permit, either linked to license cards for “adult males/free”, “adult females” or as “own license card”. We refer to this as ‘type of calf permit’.

We used an established population model to estimate population numbers on Hardangervidda down to age classes (adults  $\geq 2.5$  years, yearlings, and calves) of each sex (Nilsen and Strand 2018; Mysterud et al. 2020a). The input to the population estimation model are four annual surveys: (1) Minimum counts performed during the winter using aerial surveys, (2) calving counts performed mid-summer in the form of aerial surveys distinguishing calves from yearlings and adult females, (3) harvest data from fall in the form of the numbers of calves, yearlings and adults of each sex, and (4) demographic structures (sex and age composition) counts from the ground after the hunt and during the rut when sexes are mixed. The model is a hierarchical change-in-ratio model with parameters estimated using Bayesian inference. We calculated population (or quota) growth rate as  $\log(N_y/N_{y-1})$ , where  $N_y$  is estimated mean population size in a given year, and  $N_{y-1}$  the year before. Similarly, harvest rate for adult males in a given year is the percentage of the estimated mean adult male population size corresponding to the number of harvested.

### Data on hunter effort

We used data from the Juvik private estate with detailed data regarding the day of harvest and quota size from 2001–2019. The hunting was internally regulated in detail among the five groups of estate owners. The terrain was divided into three sub-areas. The first part of the season (until 16 September) consisted of four periods of seven days. A defined roll-over system secured equal rights for all groups within a five-year period. The second part was also regulated with respect to days and sub-areas, but was open for members of all groups with the remaining quota.

### Statistical analyses

To screen variables for collinearity before analysis, we estimated correlations among explanatory variables using Pearson correlation coefficient. If one of the variables was a factor (type of calf permit and duration of hunting season), associations were estimated using the adjusted R-square from a simple regression. We used generalised linear regression models to analyse temporal trends in the proportion of

quotas filled. As explained above, there were different standards regarding how to set quotas throughout the relevant period. Therefore, we chose to run models including and excluding calves on adult licenses when conducting analysis of quota filling, that is, quotas in the form of (1) the number of issued licenses (“cards”) and (2) the maximum potential harvest, that is, including calves on adult license cards. We used the number of adults harvested (including yearlings) as a response variable in a negative binomial model with quota of adults as an offset variable using R v. 4.0.3 and library ‘MASS’ (glm.nb). Explanatory variables were (total or adult) quota relative to estimated mean population size, the proportion of free licenses, the proportion of calves in quota (license cards or maximum potential harvest), type of calf permit (linked to license cards for “adult males/free”, “adult females” or “own license card”), duration of hunting season (3 levels, Table 1) and year (as trend) as candidate covariates. Note that all years with an ordinary hunting season had their own license cards for calves. We tested whether year 2003 with ‘hunting boycott’ and 2019 with ‘disease (CWD) management’ represented outliers to the relationship between harvest and quota.

Second, we analysed harvest data from Juvik estate, employing a mixed effects negative binomial model with quota as an offset variable and year as a random effect (using R library ‘glmmTMB’). Candidate covariates were day of week (Saturday, Sunday, or weekday versus Friday), adult quota (sum or remaining), calf quota (sum or remaining) and “day of hunt” (consecutive number of days from onset of hunting).

Model selection was performed with the Akaike information criterion adjusted for small sample sizes (AICc). A lower AICc indicates a more parsimonious model (Burnham and Anderson 2002). As a first step, highly correlated variables were tested in single variable regression models. Then, we compared a range of models with different combinations of predictor variables. We present in tables only a single model, but we considered several models for inference if difference between models ( $\Delta\text{AICc}$ ) was low. In order to indicate the importance of a variable in explaining variation in the data, we presented change in AICc ( $\Delta\text{AICc}$ ) when removing each parameter from the model. The model residuals were assessed for influential points, autocorrelation or remaining patterns (e.g. linearity) with predictor variables.

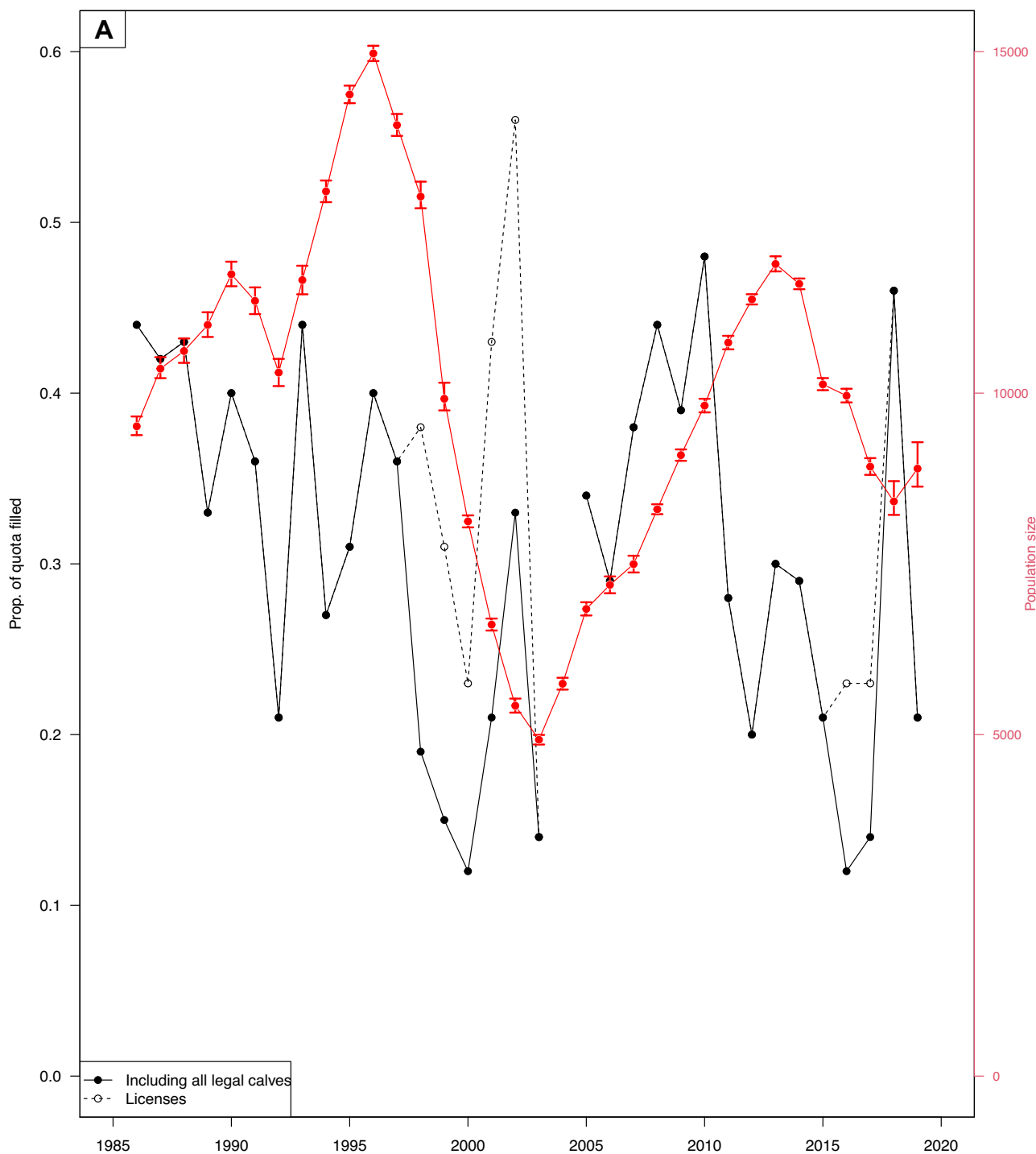
## Results

### Hardangervidda overall

There was a very substantial variation in the proportion of quotas filled by hunters (license cards 14–56%; maximum potential harvest 12–48%) and estimated population size

of reindeer (~5000–15,000) during the observation period of 1986–2019 (Fig. 2A). The mean filling of ‘free’ (adult male) license cards by hunters was 41% (range 15.7–60.7%), while only 28% (range 8–56%) of calf license cards were

filled when given as licenses separate from adults. There was a high correlation ( $r=0.893$ ,  $p<0.001$ ) between (log) total harvest and quota size (number of license cards), and a positive correlation ( $r=0.553$ ,  $p=0.001$ ) between (log)



**Fig. 2** Proportion of harvest quotas filled (black) and population size (red; mean estimates and 95% credible intervals) over time for reindeer on Hardangervidda in Norway during the period of 1986–2019. The filled points are proportion harvested based on the maximum

potential harvest including calves following adult license cards, while open points represent proportion filled relative to number of license cards issued

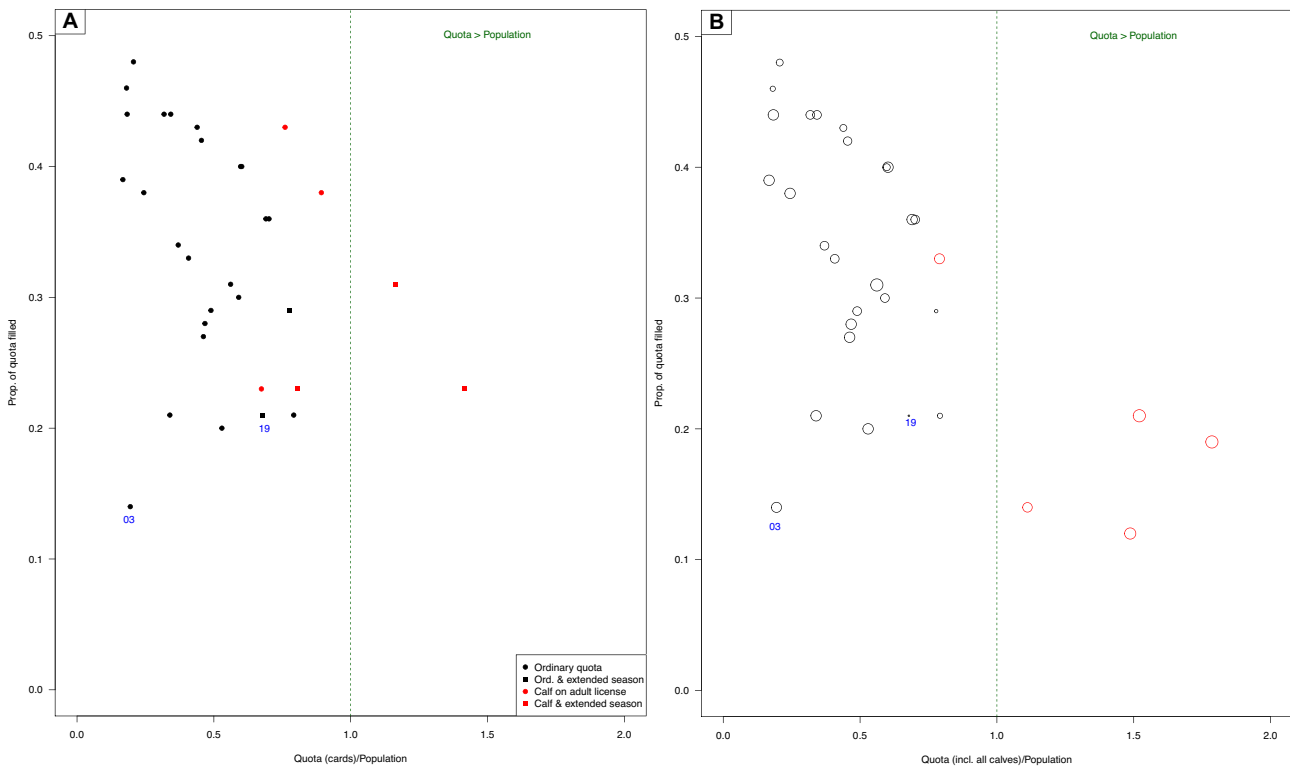


estimated annual population growth and annual growth in quota size given as license cards. The estimated mean harvest rate for males was 16% for the years 1986–2018, which increased to 47% in the “disease (CWD) management” hunt conducted in 2019.

In two years, the total number of license cards issued was higher than the estimated population size (Fig. 3A), while the maximum potential harvest (including calves on adult licences) was larger than the estimated population size in four years (Fig. 3B). The proportion of quotas filled was lower, the higher quota was relative to estimated population size (Fig. 3, Table 2), but the variables ‘total quota relative to population size’, ‘hunting season duration’, ‘the proportion of calf licenses’ and the parameter specifying ‘the type of calf permit’ (linked to free or female license, or own quota) were inter-correlated (Fig. 3). There was a negative correlation between annual changes in the proportion of calf licences and the (log-scale) total or adult quota relative to population size ( $r = -0.491, p = 0.004$ , and  $r = -0.646, p = 0.00006$ ), for total and adult quotas, respectively). Similarly, a significant amount of the variation in adult quotas relative to population size (log-scale) was explained by the type of calf

permit (adjusted  $R^2 = 0.378, p = 0.0003$ ) and by duration of the hunting season (adjusted  $R^2 = 0.309, p = 0.001$ ). There was a weaker association between total quota relative to estimated population size (log scale) and the type of calf permit (adjusted  $R^2 = 0.247, p = 0.005$ ) or the duration of the hunting season (adjusted  $R^2 = 0.249, p = 0.005$ ).

The proportion of adult quotas filled was estimated to be 0.73 times lower (95% confidence interval, ci 0.64–0.82) in those years when the permit to shoot a calf followed adult license cards compared to years with separate calf license card (estimate =  $-0.318, SE = 0.124, \exp(\text{estimate}) = 0.728, p = 0.01$ ). However, a single variable model of adult quota filling using adult quotas relative to population size (AICc = 481.8) performed better than using a function of the type of calf permit ( $\Delta AICc = 9.9$ ) or the proportion of calf quotas ( $\Delta AICc = 6.1$ ), and similar to using the duration of the hunting season ( $\Delta AICc = 1.5$ ). Since there were strong, significant associations between variables, the negative effect of quota relative to mean estimated population size, also explained variation in the proportion of the quota achieved that was contributed by ‘extended hunting season’, ‘type of calf permit’, and ‘proportion of calf quotas’. There were



**Fig. 3** Quota filling as a function of quotas relative to population size for reindeer on Hardangervidda in Norway during the period 1986–2019. Years with an extra legal calf following adult or adult female licenses in red. In 2003, low quota filling was due to hunters boycotting the hunt owing to conflict between central and local management. **A** Quota calculated as number of license cards issued. **B** Quota calcu-

lates as maximum number of potential harvest, i.e. including calves on adult license cards. Sizes of circles are scaled positively to proportion of all calves legal to harvest (potential maximum). The year 2019 (above “19” in blue) was a chronic wasting disease hunt with “adult male only” quota

**Table 2** A negative binomial model (log-link) of the degree of quota filling for recreational reindeer hunting on Hardangervidda, Norway, 1986–2019. (A) Analysis including only adult licence cards, (B) analysis including adult and calf licence cards, and (C) maximum potential harvest also including permits for calves following adult licence cards. Year is scaled to mean zero and variance 1. The  $\Delta\text{AICc}$  is the change in AICc by removing the respective parameter from the model

Parameter	Estimate	SE	<i>T</i>	<i>p</i>	$\Delta\text{AICc}$
<b>A. Adult licence cards</b>					
Intercept	− 1.441	0.058	− 24.80	<0.001	
log(adult quota/population size)	− 0.379	0.052	− 7.25	<0.001	28.6
Year (as trend)	− 0.125	0.031	− 4.07	<0.001	10.3
Year 2003 (as an outlier)	− 1.133	0.207	− 5.48	<0.001	16.5
<b>B. All licence cards</b>					
Intercept	− 1.199	0.063	− 18.90	<0.001	
log(quota/population size)	− 0.427	0.076	− 5.59	<0.001	20.3
Year (as trend)	− 0.160	0.034	− 4.68	<0.001	13.3
Year 2003 (as an outlier)	− 1.169	0.207	− 5.65	<0.001	16.8
Proportion of calf licence cards	− 1.059	0.336	− 3.15	0.002	6.3
<b>C. Maximum legal harvest – all calves</b>					
Intercept	− 1.168	0.116	− 10.11	<0.001	
log(quota/population size)	− 0.464	0.067	− 6.93	<0.001	27.0
Year (as trend)	− 0.169	0.032	− 5.24	<0.001	16.3
Year 2003 (as an outlier)	− 1.171	0.210	− 5.57	<0.001	16.3
Proportion of legal calves	− 1.363	0.293	− 4.65	<0.001	13.2

no residual effects of the type of calf permit or duration of hunting season when accounting for the joint effect of quotas relative to estimated population size (Table 2). There was a decreasing trend in quota filling over the years. In 2003, there was an exceptionally low filling of quotas due to boycotting by hunters. The year with ‘males only’ (2019) with an elevated quota due to ‘disease (CWD) management’ did not deviate significantly from the main pattern. The proportion of free licenses had no effect on the proportion of quotas being filled.

### Hunting effort and harvest at Juvik estate

On the Juvik private estate on Hardangervidda, harvest was highest on Fridays and Saturdays, intermediate on Sundays, and lower during the rest of the week (Table 3). The

**Table 3** A negative binomial model (log-link) for the daily harvest of reindeer on the Juvik estate, Hardangervidda, from 2001 to 2019. There were 674 observations grouped across 16 years (no data for 2003, 2004, and 2013). Day of hunt is consecutive number of days from onset of hunting.  $\Delta\text{AICc}$  is the change in AICc by removing the respective parameter from the model

Parameter	Estimate	SE	<i>Z</i>	<i>p</i>	$\Delta\text{AICc}$
Intercept	− 0.412	0.301	− 1.37	0.170	
Day (Saturday vs Friday)	− 0.86	0.298	− 0.29	0.774	11.0
Day (Sunday vs Friday)	− 0.944	0.357	− 2.65	0.008	
Day (week day vs Friday)	− 0.835	0.255	− 3.27	0.001	
Adult quota	0.048	0.010	4.93	<0.001	16.1
Day of hunt	− 0.085	0.010	− 8.77	<0.001	86.7

expected number of deer shot declined by 0.92 (95% ci 0.90, 0.94) per day over the season. A high adult harvest quota was positively correlated with increased harvest size, while the size of the calf quota had no predictive power for harvest size ( $\Delta\text{AICc} = 16.0$ , if replacing adult harvest quota by calf quota). The proportion of male quota being filled was 82% (range 20–100%) and higher than the average for Hardangervidda, while the proportion of calf quota being filled was 29% (range 0–100%).

### Discussion

Recreational hunters are limited by time and do not always invest extra effort to fill their harvest quotas, at least in Scandinavia. Our study documents enormous annual variation in the proportion of quotas filled for reindeer on Hardangervidda subject to recreational hunting (Fig. 2). The size of the quota relative to population size was the main driver of the proportion of quotas being filled in the most parsimonious model (Fig. 3). However, in years with a high quota relative to population size, an extra calf permit followed adult or female license card, leading to a high proportion of calves in the quota in those years. The filling of the quota for calves was always lower. However, the correlation among these variables makes it difficult to determine whether low filling of quota by hunters was due to the proportion of calves per se, or the type of calf permit (linked to adult or adult female license cards or as own calf license cards). The low and variable proportion of quota being filled by hunters highlights a high level of uncertainty regarding the ability to predict offtake. However, the proportion of quotas filled by hunters



was not markedly lower in 2019 when wildlife managers, due to disease (CWD) management, decided on a quota with ‘adult males only’, achieving a very high harvest rate of 47% of adult males in a single year. Hence, local managers appear to know how to increase quotas sufficiently to at least partly compensate for the low proportion of quotas filled in order to reach management aims.

### Quotas, population size and quota filling

The optimal foraging theory separates predator efficiency into key components of searching and handling time. A clear pattern was the higher proportion of the quota being filled, the lower the quota relative to the estimated population size for reindeer on Hardangervidda. Searching time increases when population density is lower, while a low quota reduces the overall handling time for each individual hunter. A main reason for the low average quota filling on Hardangervidda is that the reindeer often use only a small part of the available range during the hunting season, while quotas are distributed to spatially delimited hunting areas throughout Hardangervidda. A stochastic element in terms of how wind direction affects movement during the hunting season have a major impact on harvest in different hunting areas. Many hunters do not live close to their hunting area and cannot commute daily to the hunting ground (Mysterud et al. 2020b). Recreational hunters are time limited (Mysterud 2011; Diekert et al. 2016). Many recreational hunters in Norway set aside a week at the onset of hunting, but then have only weekends available for further hunting. This was evident on the private estate Juvik with higher offtake linked to weekends, particularly Friday-Saturday. Most estates on Hardangervidda are too remote for daily hunting trips. Hence, hunters may not be willing or able to expend the effort required to complete their quotas. This has benefits in terms of regulation if the population size decreases, as it would in effect reduce the harvest in years of population decline.

Another considerable challenge in population regulation comes from uncertain estimates of population size, stochastic variation in recruitment, and natural mortality. In a period lacking reliable population estimates forming the basis for quotas on Hardangervidda (until 2003), management issued a quota that was larger than the entire population, as estimated with models being available at a much later stage (Fig. 3). Hence, the unusually low proportion of quotas being harvested was mainly due to boycotting of hunting, which made the decline of the population less severe. However, a lower hunting effort has an unfortunate cost if the aim is to reduce population size, as an increase in quota would not lead to a proportional decline in population size if harvest is lower than the recruitment. Uncertainty in estimation of population size will affect estimation

of male harvest rate, the number of years quota was above estimated population size, and quota relative to population size (Fig. 3). The uncertainties in estimation of population size from our model appear small (Fig. 2). However, the estimated uncertainty of population size estimates is restricted under the model assumptions. In reality, the actual uncertainty is much larger than the estimated uncertainty, due to non-measured uncertainty in model structure and assumptions. Nevertheless, the current population estimation model provides a much improved basis for setting quotas in the Norwegian setting.

### Sex and age-specific hunting

There was a very clear pattern, with a low proportion of quotas filled for calf license cards. Calves have a small carcass body mass of approximately 10–20 kg during fall. On the Juvik estate, the remaining quota for calves had no predictive power for further harvesting. Hence, hunters appear not to invest much effort into shooting the remaining calves. On the Juvik estate, they experienced a higher proportion of quotas filled with adult males, partly because this terrain is often used by males. Hence, the local terrain may influence the harvest of this sexually segregated species. Free licenses are expensive and usually mean shooting a large male, often with a carcass mass of 60–80 kg or more for a prime-aged adult. Nevertheless, overall, we did not find a higher proportion of the quota being harvested with more free licenses on Hardangervidda. Also, in 2019 with disease (CWD) management, high quotas for a new license category (adult males only) were within the range of the proportion of quota filled seen before, albeit at the lower range. Local managers making rapid changes in quota size and composition were successful in getting hunters involved in an effort to increase male harvest rates from around 16% for the years 1986–2018 to ~47% as part of ‘disease (CWD) management’ in 2019. Hence, local managers and hunters were able to adjust and increase the harvest of males in connection to the management aiming to detect CWD. As evidenced from the higher quota filling of free license cards, hunters often have a higher motivation for shooting adult males. It is unclear whether a similar large increase in quotas for females or calves would be equally successful.

### Conclusions

Overall, quotas were set much higher than the anticipated harvest to compensate for the low proportion of quota being filled. This way, even a very high harvest rate of ~47% of the estimated mean adult male population was reached in one year (2019) with changes in management aims towards population reduction. However, even a low target for harvest was

not achieved during a hunter boycott (2003), highlighting the important role of hunter motivation. Time available, economics, motivation, legislation in terms of quotas, hunting seasons, distance to roads, and property access rights affect the efficacy of hunters, both in Scandinavia (Mysterud et al. 2019) and North America (Brown et al. 2000; Walberg et al. 2018). The decline in the proportion of quotas filled over time may indicate changes related to aspects such as hunters' available time, effort, and motivation. The ability to regulate wildlife populations depends on both the functional and numerical responses of hunters under such constraints (Mysterud et al. 2020b). If they have a free license, which is usually expensive, reindeer hunters in Norway will mainly aim for adult males. Hunters may not shoot the first reindeer they see, and a number of variables differing among hunters will determine selectivity. Under the existing permit system in Norway, it remains to be determined whether a variety of licenses can lead to an overall higher harvest than even 'free licences' in some circumstances. On the other hand, with a decreasing availability of male reindeer, hunters may shift to shooting other categories of reindeer even on 'free licences'. There remains a limit as to how precisely a wide-ranging reindeer population can be regulated using recreational hunters. Further, the synchronous implementation of changes in quota size, composition, type of licences, and duration of hunting season limit inferences and learning for future actions for the Norwegian setting. With the aim to build an evidence-based wildlife management for Europe, actions should in general be planned also with the intention to maximize learning.

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**Data availability** Data are given in Table 1.

**Code availability** Code are available from the corresponding author upon request.

## Declarations

**Conflict of interest** SEL is directly involved in management of the reindeer population.

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