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RESEARCH

Retrospective analyses to understand how wolf territory density impacts moose quotas, harvest and observation rate

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Abstract
The ever-growing human population along with the expansion of settlements and land use, and effective hunting methods increasingly influence wildlife populations. Knowledge of management responses to re-establishing large carnivores is important to understand the overall impact of humans on large carnivores and their prey populations. We examined the response of moose (*Alces alces*) harvest, but also population size and composition in relation to wolf (*Canis lupus*) territory density along a latitudinal gradient in two bordering countries in northern Europe. Moose harvest density was negatively related to wolf territory density with model estimates showing that harvest was 35% (Norway) to 39% (Sweden) lower in moose management units (MMUs) with average wolf territory density, compared to MMUs without wolves during the previous five years. The corresponding model estimates for moose observation rate was 21% lower in Sweden and 1% lower in Norway. In both countries, management actions were taken to reduce the total moose mortality (reduced harvest) as well as to maximize productivity in the population (reduced harvest of adult females) in response to increased wolf territory density. Annual changes in quotas were related to fulfilment of last year´s quota and wolf territory density in the previous two years. The annual change in harvest were affected by actual harvest the previous year and by set quotas, showing that harvest followed management plans. Abilities to adjust to new conditions is a key in wildlife management where conflicting societal objectives such as forestry, sustainable ungulate harvest yield, and carnivore conservation should be balanced.

Keywords *Alces alces* · *Canis lupus* · Sustainable harvest yield · Wildlife management

Introduction

Large carnivores and humans have interacted and affected shared prey populations for thousands of years. Along with an increased human population, settlements, land use, and effective hunting methods, humans have successively increased their influence on wildlife populations and habitats. This has led to reductions or even extirpations of many animal populations including carnivores (Ripple et al. 2014). Thus, in many ecosystems, humans have taken over the role as the top predator, as humans kill adult prey with a 14 times higher rate than terrestrial and marine predators (Darimont et al. 2015). During the last decades there has been a change in the view of large carnivores with increased focus on conservation, and large carnivores now return to many areas from where they were once extirpated (Chapron et al. 2014). In these areas, the conditions for game harvest may change as a result of the mutual use of prey populations shared by humans and carnivores (Nilsen et al. 2005; Vucetich et al. 2005; Gervasi et al. 2012). The re-establishment of large carnivores has resulted in an increased need for science-based knowledge of how the mutual use of shared resources may affect ecosystems, prey populations, and wildlife management.

In Europe, human activities, such as land use and harvest of game, now constitute a dominant factor affecting

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ecosystem functions (Kuijper et al. 2016). Game harvest has long cultural traditions and have great economic and recreational value (Storaas et al. 2001). In 2017, > 7.3 million wild ungulates were harvested by ~7 million hunters in Europe (Linnell et al. 2020). During the last 20–30 years, large carnivores have been re-establishing parts of Europe and approximately 30% of the land area now hosts at least one large carnivore species (Chapron et al. 2014) and 90% of the land area hosts up to five species of wild native ungulates (Linnell et al. 2020). Because most of the areas in Europe with large carnivores present are strongly influenced by human activities (Chapron et al. 2014), understanding human responses to re-establishing large carnivores is key to understanding the overall impact of large carnivores and humans on their prey (Wikenros et al. 2015).

Because many large carnivore species select for certain prey types, they have the potential to affect the demographic composition of their prey populations (Ginsberg and Milner-Gulland 1994; Festa-Bianchet 2003; Gervasi et al. 2012). In the perspective of managing local ungulate populations at some desired density or population structure, the effect of predator return is likely to have strong consequences for both the size and the composition of human harvest. A previous study conducted during the first period of wolf (*Canis lupus*) re-establishment in Scandinavia (1995–2008) demonstrated that hunters in Sweden showed an almost instant functional response in their harvest of moose (*Alces alces*) to the establishment of wolves in the area (Wikenros et al. 2015). This behavioural response among hunters reduced the potential for a direct numerical effect of wolf predation on moose density. In addition, the reduction in both total harvest and number of adult females harvested was greater during the first years after wolf establishment compared to areas where wolves had been present for at least 10 years. A more recent study spanning a longer time period (1995–2017) and larger geographical area showed that harvest density was on average 37% (Norway) and 51% (Sweden) lower within averaged-sized wolf territories compared to areas without wolves (Wikenros et al. 2020). However, those two studies did not include detailed information on moose density or hunting quotas both of which likely also influenced harvest density.

In addition to the direct numerical effects of harvest and predation on prey populations, variation in the environment may also impact both the predator and prey populations with implications for the functional relationship between predator, prey, and human harvest. For example, primary productivity changes with climatic conditions which has consequences for the life history of moose (Sæther and Hagenrud 1985; Sand 1996), and annual variation in weather conditions may impact on moose population productivity (Holmes et al. 2021; Tallian et al. 2021).

In Scandinavia, management (e.g., harvest) of moose is regulated by local management plans that include management goals and hunting quotas, which in turn are influenced by moose browsing damage on Scots pine (*Pinus sylvestris*), a commercially valuable tree species, and moose-vehicle collisions. Monitoring is essential in moose management, and several survey methods are used to monitor annual changes in the size and composition of local moose populations, such as pellet group counts (Neff 1968), hunters' moose observations (Ericsson and Wallin 1999; Solberg and Sæther 2018), and harvest data (Lavsund et al. 2003; Rönnegård et al. 2008). Hunters collect large amounts of data that are used to update hunting quotas for future harvest in an adaptive management framework. Management plans and quotas are set in specific moose management units (Sweden) or municipalities (Norway) and the goals should consider the different societal interests such as forestry and hunting (Bjärstig et al. 2014; Johansson et al. 2020) by using data collected by managers (density of wolves, browsing damage on pine) and hunters (moose observation data).

We examined the effect of wolf territory density on moose population size and composition (age and sex), and hunting yield (harvest density), along a latitudinal gradient in two bordering countries in northern Europe (Norway and Sweden) during a six-year period. First, we quantified the impact of wolf territory density on size and composition of the hunting yield (harvest data) and on the moose population (moose observations). We predicted an increased impact of wolf predation on the moose population along with the observed increase in wolf territory density during 2012–2017, i.e., a reduction in harvest density and a change in the age and sex composition of both harvested and observed moose. For moose observation rate, we predicted either a reduction in moose observation rate due to increased mortality due to predation, or an increase due to hunters over-compensate for an anticipated increased mortality as shown during the early phase of re-establishment of wolves in Scandinavia (Wikenros et al. 2015). Secondly, we investigated whether wolf territory density affected annual adjustments of hunting quotas and changes in harvest from year to year, or whether the changes in harvest size merely were a response to changes in harvest quotas or the harvest in the preceding year. Due to the detailed wolf monitoring and volunteer-based hunter census of moose, we predicted that the hunting quotas should be adjusted so to compensate for increased predation in areas with higher density of wolves, i.e., a higher wolf territory density should lead to decreased quotas.

Methods

Study area

The study included data from 63 municipalities in south-eastern Norway and 61 moose management units in six counties in south-central Sweden. In Norway, we split municipalities that partly overlapped with the wolf reproduction zone (the area where wolves are allowed to breed) into inside and outside the zone. We then merged small neighbouring municipalities into lager units to match the size of the Swedish units, resulting in a total of 86 units (Fig. 1). The Swedish and Norwegian units are hereafter referred to as moose management units (MMU).

The objective of the moose management in Sweden is to achieve key political goals by trading off the availability of moose forage, minimizing damage to forestry and agriculture, and reducing vehicle collisions. This management should be based on regular monitoring of moose density and browsing damage. In Sweden, hunters conduct large scale volunteer-based censuses of moose density (pellet counts during spring) that provides one important component to the construction of moose management plans. Whereas there is no similar system in Norway, hunters in both countries register observations of moose during the hunting season which is another key component used in management plans. For some MMUs in Sweden, there are also sanctions if the quotas are not fulfilled, which may be one of the explanations why the percentage of the quotas harvested varies between different MMUs.

Our study system includes a wolf population for which territorial pairs and packs of ≥3 wolves are documented by annual, joint cross-border field monitoring (Åkesson et al. 2022). The wolf population consisted of 65, 68, 68, 70, 74, and 72 territories with ≥2 wolves during the study period 2012–2017 (Wabakken et al. 2018). Moose are the main

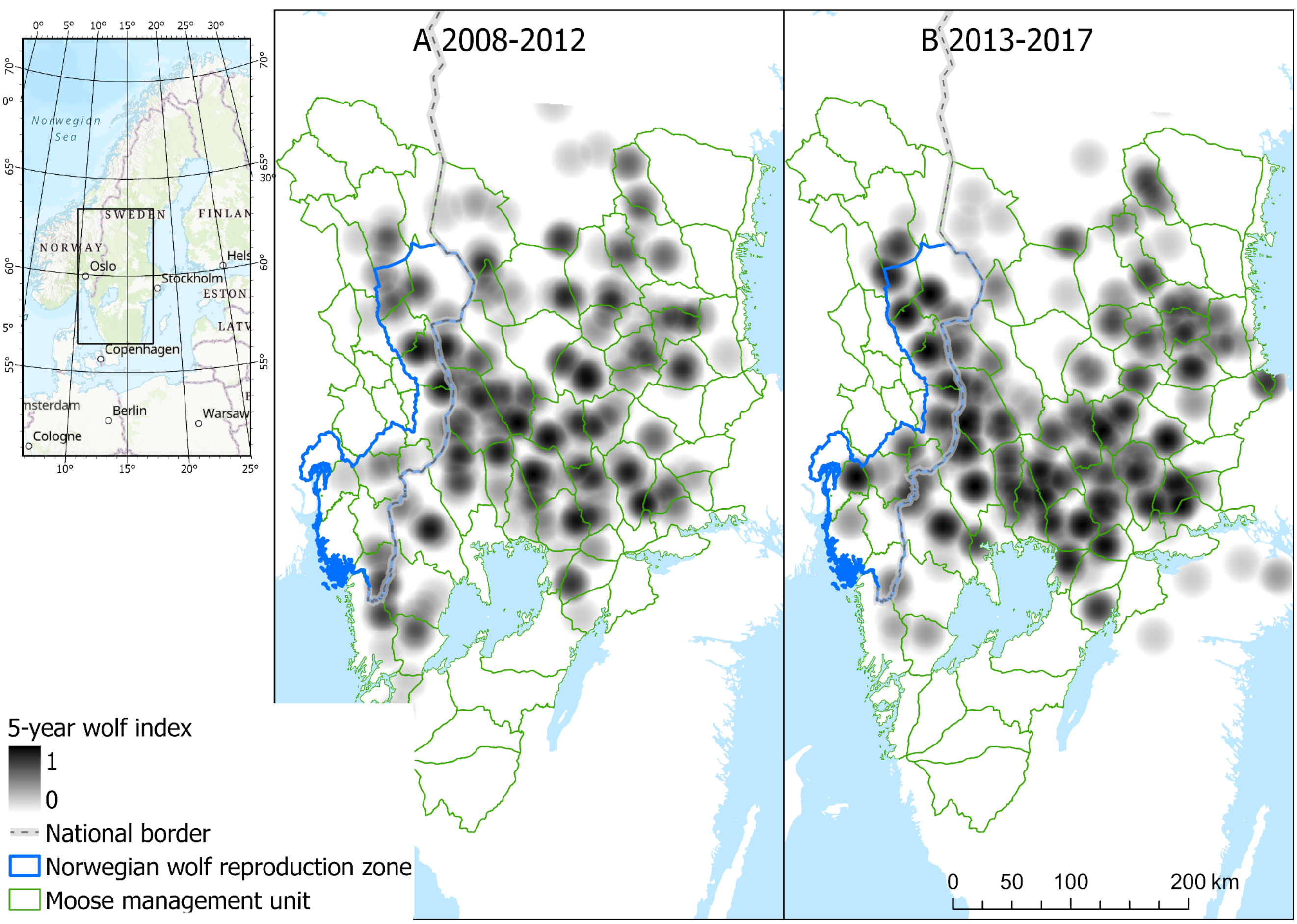

Fig. 1 5-year wolf index in the study area in Norway and Sweden during (**A**) 2008–2012 and (**B**) 2013–2017, calculated as five-year average wolf territory density by using an 18 km buffer from the wolf territory centre each year and a parabolic-shaped decay function of wolf presence from centre (1) to 18 km (0). Today's Norwegian wolf population is limited by the blue border to the west ("the Norwegian wolf reproduction zone"). The green outlines represent the moose management units (MMUs). Maps created with ArcGIS Pro 2.4.2 (Esri Inc), World Topographic Map loaded from https://cdn.arcgis.com/sharing/rest/content/items/7dc6cea0b1764a1f9af2e679f642f0f5/resources/styles/root.json

prey of Scandinavian wolves followed by roe deer (*Capreolus capreolus*) (Sand et al. 2016). Moose occur at an average winter density of 1.3 moose per km^2 within wolf territories (Zimmermann et al. 2015). Brown bears (*Ursus arctos*) occur in the northern parts of the study area (Bischof et al. 2020) and prey on moose during spring (Ordiz et al. 2020). See Wikenros et al. (2020) for a more detailed description of the study area.

Hunting quotas and harvested moose

In Norway, the municipalities are responsible for deciding moose harvest quotas and reporting number of harvested moose to a national registry. The municipalities' objectives must be in line with the national objectives to assure productivity and diversity of ungulate populations and their habitat, ensure sustainable commercial and recreational harvest, and avoid unacceptable levels of damages and inconveniences for societal interests (Ministry of Agriculture and Food 2016). The municipalities approve the hunting areas proposed by the hunting right holders (landowners), with harvest quotas based on a 3-5-year management plan. Several MMUs can cooperate on a common management plan if approved by the municipality. The current moose management system in Sweden was introduced after a parliamentary decision in 2012. Each MMU manages the moose population in cooperation between landowners, hunters, stakeholders, and authorities with the objective of keeping browsing damage on commercially valuable tree species at a level that is acceptable to forest management, and moose harvest at a level that results in a sustainable yield that is acceptable to hunters. Each MMU prepares a three-year management plan that must be approved by the County Administrative Board. The MMUs are responsible for coordinating census of moose density and proposing borders for further division into smaller hunting units. For the MMUs in Norway, no moose density censuses were required.

Since the MMUs varied in size both between and within countries, we compiled harvest density as the number of harvested moose per km^2 hunting area, i.e., all area covered by forest, bog and agricultural land. This definition of the hunting area is used by the County Administrative Boards in Sweden. In Norway, agricultural land does not count as part of the hunting area. To make the harvest data comparable, we applied the Swedish definition also to Norwegian harvest data. For the density of hunting quotas, we had to use the original Norwegian definition (forests and bogs) because the data registry of hunting quotas was based on slightly different geographical units than the MMUs used for the harvest data above. The harvest season in Norway starts on September 25 and lasts until December 23, while in Sweden it lasted from the second Monday in October (except in some areas in the northern part of the study area where hunting was also allowed during three weeks in September) until the last day of January or February during the study period. For each MMU, we extracted the latitude of its centre point in the coordinate system UTM zone 33 N.

Moose observations

Moose hunters in Norway and Sweden report the number of moose of different age and sex categories observed during the hunt, as well as the hunting effort represented by hours (Sweden) or days (Norway) of hunting. Based on previous studies, data from moose observations are accurate (Ericsson and Wallin 1999; Solberg et al. 2000; Ueno et al. 2009) given a sufficient effort and sample size (Sylvén 2000). In Norway, the number of observed animals per hunter per day is reported throughout the hunting season, while in Sweden the number of moose observed is reported per hunter hour, and only during the first seven days of the hunting season. This means that comparisons of absolute numbers of observed moose between the countries are not possible but differences in trends of observed animals over years are comparable.

For Norway, moose observation data were obtained from national cervid registries ("Hjorteviltregisteret" and "Viltrapporten"), where observations and the number of shot moose are reported. For Sweden, we received moose observation data (reported voluntarily by hunting teams) from the Swedish Association for Hunting and Wildlife Management ("Svenska Jägareförbundet viltövervakning"), and used moose observation data from MMUs with a minimum of 5000 hunter hours per week (Ericsson and Wallin 1999). We calculated the number of observed moose per hunter day, the ratio of calves per female, and the proportion of females among adult animals for each MMU and year. We converted reported hunter hours to hunter days, assuming 6 h per day, to approximately scale the Swedish data to the Norwegian data.

Wolf territory density

Wolf territory density per MMU was calculated using data from the annual wolf monitoring in Scandinavia where territorial pairs and packs are identified non-invasively by using DNA from scats, urine or oestrous blood in combination with snow-tracking and camera-traps (Wabakken et al. 2001, 2018; Åkesson et al. 2022), where 0 indicates wolf territory absence, values <0.5 indicate that only parts of the MMU are covered by wolf territories, 0.5 indicates that the MMU is covered by averaged-size territories, and values >0.5 indicate that the MMU contains wolf territories that are smaller than averaged-sized territories (i.e., a higher density of wolf territories). We defined a short-term effect of wolves as an average wolf territory density for the previous and current winter, hereafter referred to as the 2-year wolf index. For long-term effects of wolves, we used the average wolf territory density during the last five years, including the winter after the hunting season, hereafter referred to as the 5-year wolf index. This time span was motivated by the moose management plans of 3–5 years. An index of 0.5 represents an average wolf predation of 0.12 moose per km^2 annually, including approximately 80% calves (Zimmermann 2014). For a detailed description of this methodology see Wikenros et al. (2020).

Statistical analyses

We used Linear Mixed Models (LMM) to estimate the spatial variation in moose harvest density (harvested moose per km^2), number of observed moose per time unit, proportion of harvested calves in total harvest, proportion of harvested females in adult harvest, number of observed calves per adult female, and proportion of females among observed adults. We weighted the observations by the size of the MMU. The random structure (MMU ID alone, year alone, or year combined with MMU ID) was selected by AIC model selection for the full model (including the 5-year wolf index, latitude and country) (Table S1). The two wolf indices (2- and 5-year wolf index) were correlated and we used the one explaining most of the variation in the data (lowest AIC) when testing the full model (Table S1). We then tested all combinations including the selected wolf index, latitude, and country, with country included either individually or in interactions with the other variables, using the dredge function. We used AIC model selection to find the model with the lowest ΔAIC and to calculate Relative Importance Weight (RIW). We used the package "r2glmm" to calculate R^2 for the highest ranked model and for each fixed effect separately.

For the annual change in quotas, we used LMM and the explanatory variables wolf index (2- or 5-year wolf index, see Table S1), the percentage of the hunting quotas filled in the previous year, and latitude. We also analysed the annual change in density of harvested moose by using the following explanatory variables: wolf index (2-year or 5-year, see Table S1), change in quotas, harvest density in the previous year and latitude. In both analyses, country was included either individually or in interaction with the other variables. We conducted all statistical analyses in R (R Core Team 2023).

Results

Impact of wolves on harvest density and number of moose observations

A total of 210,632 moose were harvested during the six-year study period, and annual harvest density averaged 0.31 (95% CI = 0.29–0.33) moose per km^2 in Norway and 0.27 (95% CI = 0.26–0.28) in Sweden. The spatial variation in harvest density was best explained by the 5-year wolf index, latitude, country, and the interaction between latitude and country (Table 1, Table S2). The predicted harvest density was 39% (Sweden) and 35% (Norway) lower in MMUs at an average annual wolf territory density compared to MMUs without wolves (Fig. 2A). Harvest density did not change with latitude in Sweden but decreased from south to north in Norway (Fig. 2B).

A total of 1,129,488 moose observations were reported during the study period. Observation rates averaged 0.42 (95% CI = 0.40–0.43) per hunting day in Norway and 0.43 (95% CI = 0.42–0.45) in Sweden. The spatial variation in moose observation rate was best explained by the 5-year wolf index, latitude, country, and the interactions between wolf index and country as well as latitude and country (Table 1, Table S2). The observation rate was negatively related to the 5-year wolf index in Sweden, with a 21% lower observation rate in MMUs containing average annual wolf territory density than in MMUs without wolves, whereas the corresponding decrease in Norway was 1% (Fig. 2C). The observation rate was negatively related to latitude in Sweden, but positively related in Norway (Fig. 2D).

Impact of wolves on composition of harvested and observed moose

Both proportion of calves in total harvest and proportion of females in adult harvest were on average higher in Sweden than in Norway. Wolf index and country affected the age and sex composition of the harvest, whereas latitude affected only the age composition (Table 1, Table S3). In Norway, the proportion of harvested calves averaged 0.35 (95% CI = 0.34–0.36) and was 34 percentage points higher in MMUs containing average-sized wolf territories during the past two years than in MMUs without wolves (Fig. 3A). The proportion of calves in the harvest in Sweden averaged 0.48 (95% CI = 0.48–0.49) and was 4 percentage points lower in MMUs containing average-sized wolf territories during the past two years than in MMUs without wolves (Fig. 3A). Also the proportion of calves harvested showed opposite latitudinal trends between the two countries where it declined in Sweden and increased in Norway at higher latitudes (Fig. 3B). The proportion of females in the adult harvest was

Table 1 Summary of the best models used to explain the variation in harvest density (moose per km^2), number of observed moose per hunter day, proportion of harvested calves in total harvest, proportion of females in adult harvest, observed ratio of calf per female, and observed females among adult animals in Norway and Sweden, 2012–2017. Wolf index was the average wolf territory density of the management units for the last two ($W_{2\text{-year}}$) or five ($W_{5\text{-year}}$) years. Other variables were latitude (Lat) and country (Cou) with Norway as the reference. Country was included either individually or in interaction with the other variables. The random variable was the management unit ID combined with year or management unit ID (see table S1 for details). Relative Importance Weight (RIW) is a value from 0–1, where 0.9-1 means that the variable has a large weight, 0.6–0.9 is moderate and <0.6 is weak or no measurable weight. R^2 is calculated for the best model and each fixed effect included and lower and upper CL

Response variable		Intercept	W_{5-year}	Lat	Cou	W_{5-year}×Cou	Lat×Cou	Model
Harvest density	β	2.995	-0.253	-0.000388	-2.098		0.000308	
	SE	0.918	0.0285	0.000136	1.0254		0.000153	
	RIW		1.00	0.93	0.89	0.26	0.64	
	R^2		0.26	0.06	0.03		0.03	0.32
	CL		0.20–0.32	0.03–0.11	0.01–0.07		0.01–0.07	0.26–0.39
Response variable		Intercept	W_{5-year}	Lat	Cou	W_{5-year}×Cou	Lat×Cou	Model
Observed moose	β	-1.670	-0.00470	0.000310	5.195	-0.121	-0.000770	
per hunter day	SE	1.122	0.0596	0.000167	1.253	0.070	0.000186	
	RIW		0.99	1.00	1.00	0.59	1:00	
	R^2		0	0.03	0.14	0.01	0.14	0.30
	CL		0-0.01	0.01–0.07	0.09–0.20	0-0.04	0.09–0.20	0.24–0.37
Response variable		Intercept	W_{2-year}	Lat	Cou	W_{2-year}×Cou	Lat×Cou	Model
Calves in total	β	-1.327	0.206	0.000244	3.498	-0.241	-0.000496	
harvest	SE	0.660	0.0378	0.0000979	0.733	0.0428	0.000109	
	RIW		1.00	1.00	1.00	1.00	1.00	
	R^2		0.10	0.04	0.13	0.11	0.12	0.57
	CL		0.06–0.15	0.01–0.08	0.08–0.19	0.06–0.16	0.07–0.18	0.52–0.62
Response variable		Intercept	W_{5-year}	Lat	Cou	W_{5-year}×Cou	Lat×Cou	Model
Females in adult	β	0.445	-0.162		0.0466			
harvest	SE	0.00858	0.0205		0.00970			
	RIW		1.00	0.39	1.00	0.39	0.11	
	R^2		0.21		0.11			0.24
	CL		0.15–0.27		0.06–0.16			0.19–0.31
Response variable		Intercept	W_{2-year}	Lat	Cou	W_{2-year}×Cou	Lat×Cou	Model
Observed ratio of	β	2.286	-0.112	-0.000244				
calf per female	SE	0.359	0.0240	0.0000537				
	RIW		1.00	1.00	0.55	0.16	0.31	
	R^2		0.09	0.13				0.20
	CL		0.05–0.14	0.08–0.19				0.14–0.26
Response variable		Intercept	W_{5-year}	Lat	Cou	W_{5-year}×Cou	Lat×Cou	Model
Observed females	β	2.216	0.00690	-0.000231	-1.393	0.0592	0.000202	
among adult animals	SE	0.325	0.0235	0.0000482	0.363	0.0273	0.0000540	
	RIW		1.00	1.00	1.00	0.80	1.00	
	R^2		0	0.13	0.09	0.02	0.09	0.26
	CL		0-0.01	0.08–0.19	0.05–0.14	0-0.05	0.04–0.14	0.20–0.33

negatively related to the 5-year wolf index in both countries, and generally higher in Sweden (0.46 (95% CI = 0.45–0.46)) compared to Norway (0.42 (95% CI = 0.41–0.43)) (Fig. 3C). In MMUs containing average-sized wolf territories during the past five years, the proportion of females in adult harvest was on average 18 percentage points (Norway) and 16 percentage points (Sweden) lower than in MMUs without wolves. The proportion of females in adult harvest was not related to latitude (Fig. 3D).

The average calf per female ratio in the observation data was 0.63 (95% CI = 0.62–0.64), and did not differ between the two countries. The calf per female ratio was on average 9 percentage points lower in MMUs with averaged-size wolf territories, compared to MMUs without wolves during the past two years (Fig. 3E). The calf per female ratio also decreased with latitude (Fig. 3F; Table 1), irrespective of country. The proportion of females among observed adult animals was higher in Norway (0.66 (95% CI = 0.66–0.67)) than in Sweden (0.65 (95% CI = 0.64–0.65)) (Fig. 3G; Table 1) and was positively related to the 5-year wolf index in Sweden. The proportion of adult females increased by 5 percentage points in Sweden and 0.5 percentage points

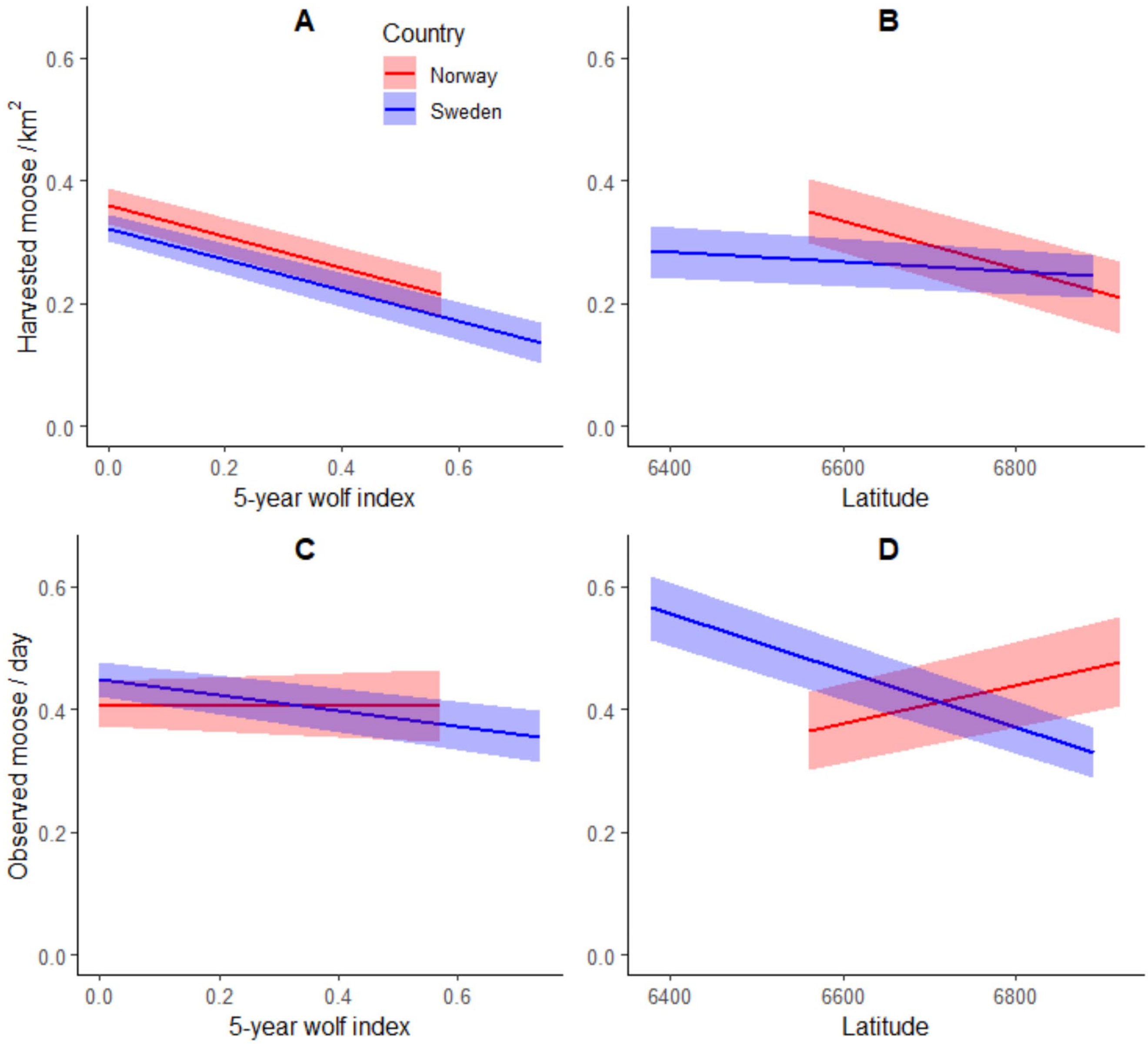

Fig. 2 Predicted density of harvested moose per km^2 (**A**, **B**) and observed moose per day (**C**, **D**) in Norway and Sweden, 2012–2017. The explanatory variables in the best models are the 5-year wolf index (**A**, **C**) and latitude (**B**, **D**). The predictions show average and 95% confidence intervals and are from linear mixed models (LMM) without the random factor (ID of management unit combined with year), and as reference values wolf index 0.25 (**B**, **D**) and latitude 6700 km (**A**, **C**) was used

in Norway with an increase in the 5-year wolf index from MMUs without wolves to MMUs with average-sized wolf territories during the past five years (Fig. 3G). The sex ratio of observed adults was skewed towards more females in the south than in the north in Norway, but independent of latitude in Sweden (Fig. 3H; Table 1).

Factors affecting annual change in quotas and harvest

Hunting quotas averaged 0.47 (95% CI = 0.45–0.49) moose per km^2 in Norway and 0.30 (95% CI = 0.29–0.31) moose per km^2 in Sweden, given the national definition of hunting area, which in Norway excludes and in Sweden includes agricultural land. The annual change in quotas was related to the 2-year wolf index (Fig. 4A) and to the proportion of the quota filled in the previous year (Fig. 4B; Table 2, Table S4). Quotas were reduced by an average of 4 percentage points

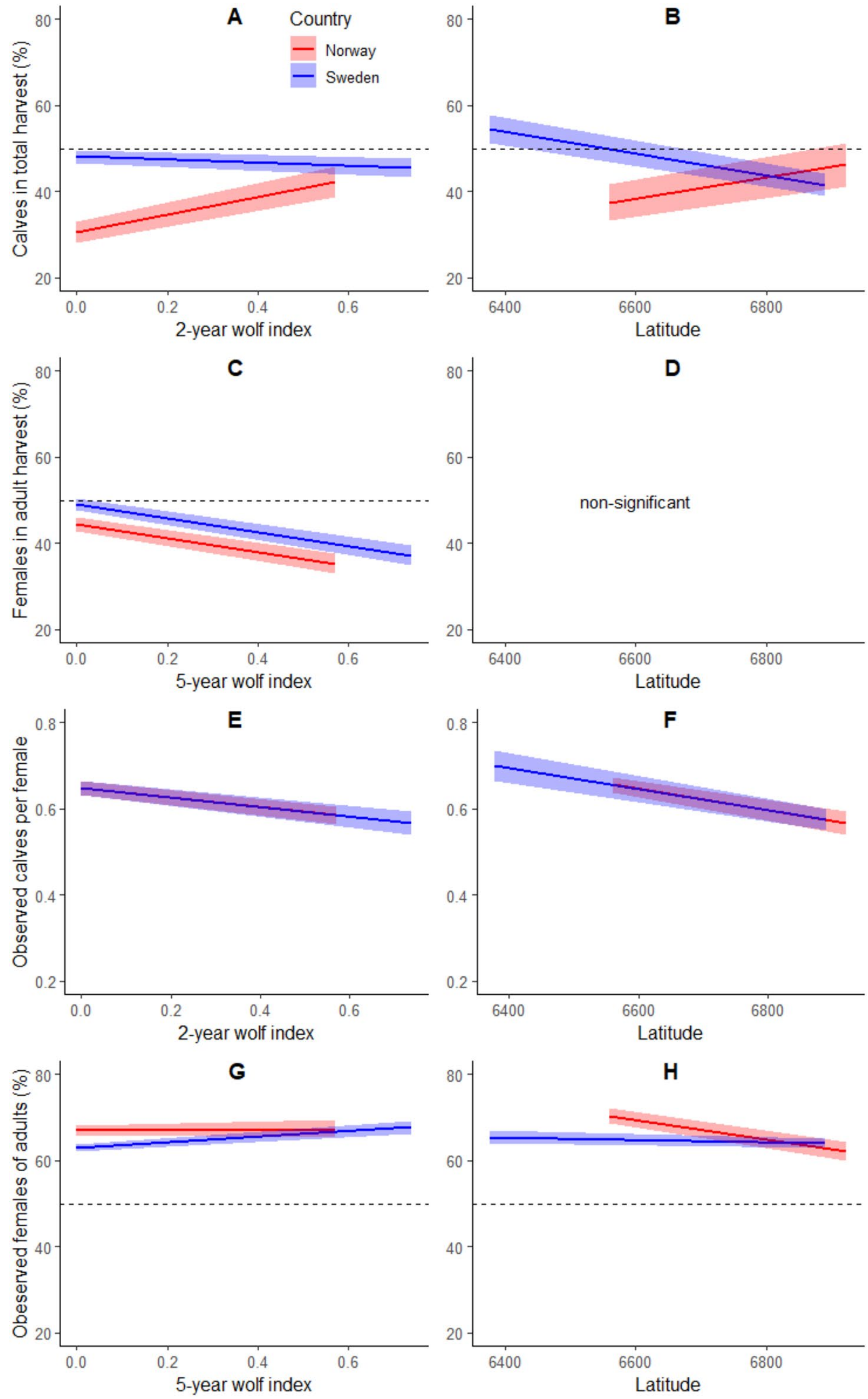

Fig. 3 Predicted proportion of calves in total harvest of moose (**A**, **B**), females in adult harvest (**C**, **D**), observed calves per female (**E**, **F**), and proportion of observed females of adult moose (**G**, **H**), in Norway and Sweden, 2012–2017. The explanatory variables are 2-year (**A**, **E**) and 5-year wolf index (**C**, **G**), and latitude (**B**, **F**, **H**). The predictions show average and 95% confidence intervals and are from linear mixed models (LMM) without the random factor (ID of management unit), and as reference values wolf index 0.25 (**B**, **F**, **H**), and latitude 6700 km (**A**, **C**, **E**, **G**) was used. Dashed line represent an equal proportion of harvested calves and adults (**A**, **B**) and adult females and males (**C**), as well as observed adult females and males (**G**, **H**)

in MMUs with average-sized wolf territories, compared to MMUs without wolves during the past two years (fulfilment of harvest quotas in the previous year set to 0.9, Fig. 4A). MMUs with wolf index 0.25 and a > 90% fulfilment of harvest quotas in the previous year had similar or increased quotas the year after, while MMUs with a lower fulfilment of quotas in the previous year reduced quotas the year after. This effect was stronger in Sweden compared to Norway (Fig. 4B). Latitude did not remain in the best model.

The annual change in harvest was weakly related to the short-term wolf index (Fig. 4C) with an average reduction of 3 percentage points of the harvest in MMUs with

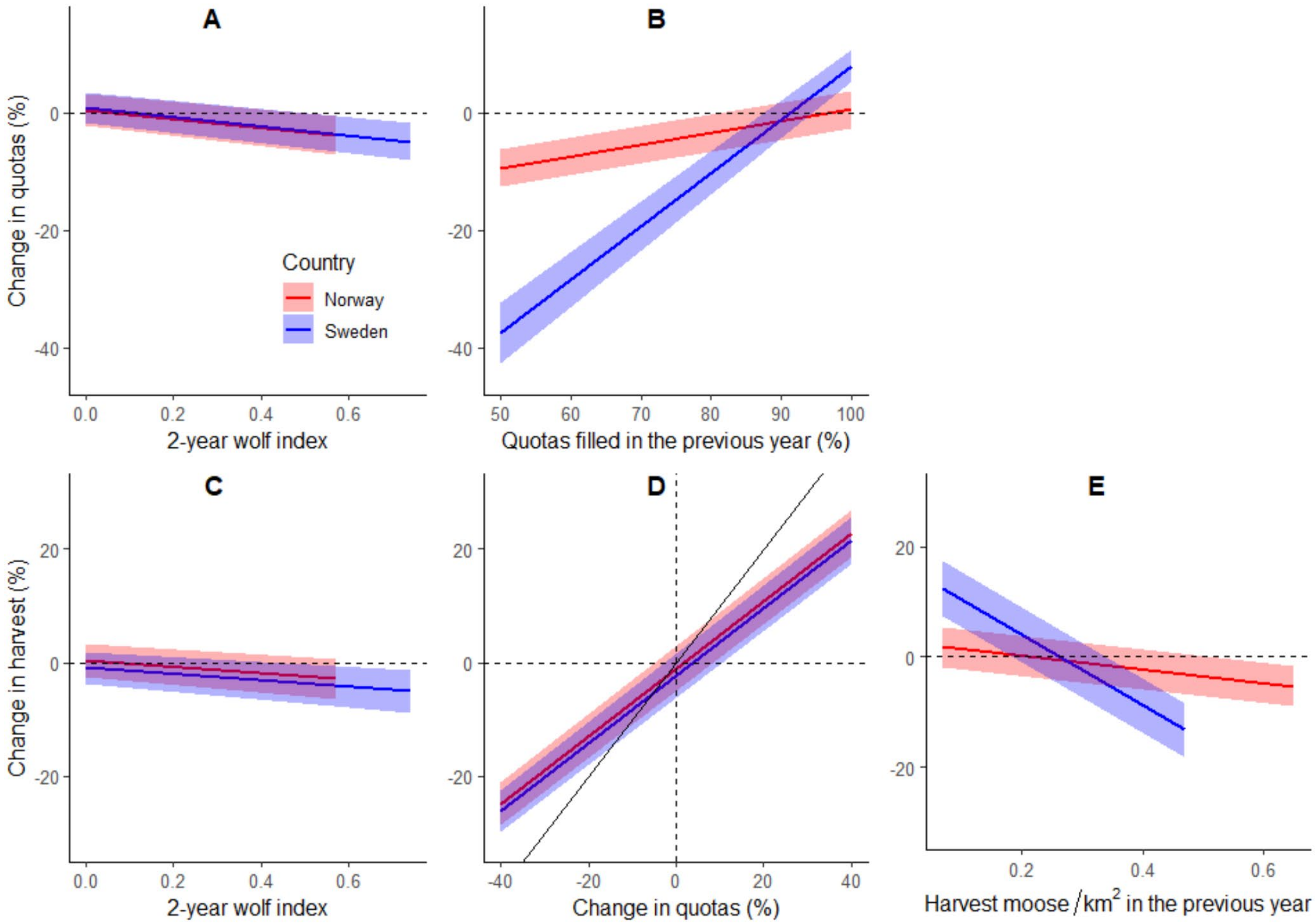

Fig. 4 Predicted annual change in hunting quotas and harvested moose in Norway and Sweden, 2012–2017. The explanatory variables for change in quotas was the 2-year wolf index (**A**), and the percentage harvested moose of the total quotas in the previous year (**B**). For change in harvested moose the 2-year wolf index (**C**), change in quotas (**D**) and harvested moose density in the previous year (**E**) was the explanatory variables. The predictions show mean and 95% confidence intervals and are from linear mixed models (LMM) without the random factor (year), and as reference values the percentage harvested moose of the total quotas 90% (**A**), wolf index 0.25 (**B**, **D**, **E**), change in quotas 0 (**C**), and harvest density in the previous year 0.3 (**C**) was used

Table 2 Summary of the best models used to explain the variation in annual changes in hunting quotas and harvested moose in Norway and Sweden, 2012–2017. The variables were 2-year wolf index calculated as the average wolf territory density of the management units for the last two years ($W_{2\text{-year}}$), the percentage of the hunting quotas filled in the previous year (Harv% t-1), latitude (Lat), country (Cou) with Norway as the reference, change in quotas (ChanQuo), and harvest density in the previous year (Harv t-1). Country was included either individually or in interaction with the other variables. The random variable is year for both models (see table S1 for details). R^2 is a measure of how much of the variation in the response variable is explained by the fixed X-variables (R^2m) and by both the fixed and random variables combined (R^2c). Relative Importance Weight (RIW) is a value from 0–1, where 0.9-1 means that the variable has a large weight, 0.6–0.9 is moderate and <0.6 is weak or no measurable weight

Response variable		Intercept	W_{2-year}	Harv% t-1	Lat	Cou	$Wolf_{2-year}$×Cou	Harv% t-1×Cou	Lat×Cou	Model
Change	β	-0.1738	-0.07766	0.1995		-0.6357		0.7101		
in quotas	SE	0.0359	0.02426	0.0444		0.0663		0.0774		
	RWI		0.99	1.00	0.35	1.00	0.27	1.00	0.12	
	R^2		0.02	0.03		0.14		0.13		0.30
	CL		0-0.04	0.01–0.07		0.09–0.19		0.08–0.18		0.24–0.36
Response variable		Intercept	W_{2-year}	ChanQuo	Harv t-1	Cou	$Wolf_{2-year}$×Cou	ChanQuo×Cou	Harv t-1×Cou	Model
Change	β	0.0400	-0.0559	0.5952	-0.1212	0.1429			-0.5196	
in harvest	SE	0.0215	0.0254	0.0363	0.0427	0.0347			0.1125	
	RWI		0.89	1.00	1.00	1.00	0.45	0.31	1.00	
	R^2		0.01	0.32	0.01	0.03			0.04	0.39
	CL		0-0.03	0.26–0.37	0-0.04	0.01–0.06			0.01–0.07	0.34–0.45

averaged-size wolf territories, compared to MMUs without wolves during the past two years (change in quotas held at 0, harvest density in the previous year held at 0.3 moose / km^2, Fig. 4C). The annual change in quotas was an important explanatory variable for the annual change in harvest (Fig. 4D; Table 2, Table S5). However, the relationship was less than proportional meaning that a 10 percentage point increase in quotas generally resulted in only a 6 percentage point increase in harvest. The change in harvest density in any year was negatively correlated with harvest density in the previous year in Sweden (6 percentage points increase in harvest when harvest density the previous year was reduced by 0.1 moose per km^2), but less so in Norway (1 percentage point) (Fig. 4E). Latitude did not remain in the best model.

Discussion

In MMUs within the range of the Scandinavian wolf population, wolf territory density explained some of the variation in both the dynamics and the management of local moose populations as measured by quotas, harvest and observation rate. The latitude also contributed to explaining the variation in these variables between MMUs and the two countries. In line with our predictions, harvest density of moose was negatively related to wolf territory density, and the composition of harvested and observed moose was also correlated with wolf territory density but with some differences between countries. The decrease in harvest density was in the same range as shown earlier in Norway (37%) but lower than in Sweden (51%, Wikenros et al. 2020). This may be due to high browsing damage on pine resulting in management decisions to increase moose harvest also in areas with high wolf territory density (Zimmermann et al. 2022). Variable relationship between harvest density and wolf territory density has also been shown for parts of the study area included in this study (Wikenros et al. 2024). This highlight the need of also including information about management goals (aiming to decrease or increase the local moose population etc.) and not only quotas as in this study. The decrease in total moose observation rate indicate a decrease in moose population size due to increased mortality according to one of the two diverging predictions.

The relationship between moose harvest regime and wolf territory density was most pronounced for adult females. An increased wolf territory density was associated with a reduction of the proportion of harvested females, and likely as a consequence, an increased proportion of observed females. Because reproduction is closely linked to the age and sex composition of ungulate populations (Gaillard et al. 1998), reduced harvest of adult females may, to some extent, compensate for increased wolf-caused mortality in the moose population. In terms of calf harvest, the management in the two countries appeared to respond differently to wolf territory density. The proportion of calves in the harvest increased in Norway with increasing wolf territory density but remained relatively constant in Sweden and independent of wolf territory density. In general, without wolves the proportion of calves in harvest was higher in Sweden compared to Norway but the difference decreased with increasing wolf territory density during the previous two years (2-year wolf index). Since wolves target moose calves year round (Sand et al. 2005, 2008), these results suggest an effort to maintain (Sweden) or increase (Norway) a high proportion of an age class with relatively low reproductive value in harvest in areas with wolves. Both strategies resulted in a similar decrease in the calf-cow ratio in both countries. The lower proportion of both calves of total harvest and females of adult harvest in Norway compared to Sweden might explain why the calf-cow ratio in the hunter observations was at about the same level in the two countries. Sweden has increased the proportion of calves in harvest since 2005, harvesting approximately 50% calves since 2010 (Wikenros et al. 2020). In contrast, hunters in Norway harvest a larger proportion of yearlings and adults than in Sweden, maybe because there is more focus on hunting effectiveness (larger, but fewer animals are targeted), while hunters in Sweden rather aim for more hunting opportunities. In Norway, maybe due to the goal of keeping sustainable moose populations, calves are harvested close to the same rate as their rate in the population (about 30% calves).

Moose observation data do not allow for comparison of moose population density and composition between different areas (MMUs), since habitat composition (proportion of open areas), hunting method, and effort (time spent hunting) may affect the index (Solberg et al. 2014). In contrast, previous studies have shown changes in observation data on moose between years to be an appropriate index of temporal variation in local moose density, but may underestimate true changes in moose population size (Ericsson and Wallin 1999; Solberg et al. 2014; Ueno et al. 2014). Therefore, it is possible that the real change in moose density due to wolf predation in this study was even greater than found. However, other factors in combination with wolf territory density may also affect the observation rate. For example, wolf territory density could affect the actual mode of hunting, e.g., the use of hunting dogs (since wolves occasionally kill hunting dogs), and thus also the number of animals observed. Changes over time in both the number and composition of moose observations, as well as the associated harvest yield are therefore dependent on a combination of factors such as the management strategy (i.e., the size and composition of the harvest) and the environment.

In Scandinavia, moose harvest quotas represent a deliberate strategy in the MMUs to achieve a desired development of the local moose population. As predicted, data from both countries show that wolf territory density was linked to a reduction in both quotas and harvest. However, in addition to the effect of wolves, the fulfilment of the previous years' harvest quotas also affected the management decisions, i.e., quotas the following year. Areas that fulfilled a low proportion of the quotas generally showed a larger reduction in the quotas the following year, irrespective of wolf territory density. This shows that current quotas are based on both experience from last year's harvest, and information on wolf territory density in recent years. In Sweden, the fulfilment of quotas was a more important factor than wolf territory density for explaining a change in the current quota. Although the size of harvest was affected by actual harvest the previous year, the harvest size was still more influenced by set quotas, and this pattern was the same in both countries. This relationship between quotas and harvest among MMUs shows that the actual harvest closely follows the decided management plans. In Sweden, this relationship improved after the new management system was introduced in 2012, before which the harvest was considerably lower than the quotas (about 0.1 moose lower per km^2) both in areas with and without territorial wolves (Wikenros et al. 2015).

The analyses showed that latitude is of importance for the variation in moose harvest and the number of moose observations. The proportion of calves in harvest increased with latitude in Norway but decreased in Sweden, while the total number of moose observations decreased in both countries with increasing latitude. This may be due to higher brown bear density in the northern parts of the study area in Sweden compared to similar latitudes in Norway (Bischof et al. 2020; Tallian et al. 2021). The presence of both wolves and brown bears can reduce harvest of moose (Jonzén et al. 2013; Sand et al. 2025) and is likely one factor impacting the harvest of calves, particularly in Sweden. This is also supported by another study conducted in parts of the present study area, using a longer time series of harvest data (Wikenros et al. 2024). The decreasing number of moose observations along the south-north gradient may be due to increased calf harvest in Norway and a higher predation pressure from both wolves and brown bears in Sweden in the northern parts of the study area.

An alternative or additional explanation of lower harvest and number of observations in the northern part of the study area relates to the productivity of the Scandinavian moose population. Previous studies have shown geographical variation in various life history characteristics such as weight gain and reproduction in moose (Markgren 1969; Sæther and Hagenrud 1985; Sand 1996; Grøtan et al. 2009). The productivity of the Scandinavian moose population decreases towards the north (Sæther and Hagenrud 1985; Sand 1996). In addition, differences in characteristics of the landscape affect moose productivity (Solberg et al. 2006) and those differences exist in our study area both naturally (Milner et al. 2013) and through supplementary feeding (widely used in Norway before 2017, but not in Sweden). The importance of geographical and temporal variation in nutritional competition within different moose populations, i.e., density dependent resource competition (Grøtan et al. 2009; Tallian et al. 2021), most likely contributes to some of the unexplained variation in the present models.

Our results highlight the importance of access to data in the management of large ungulates (Apollonio et al. 2017; Cretois et al. 2020; Trump et al. 2022). The data in this study (e.g., hunter observations, carnivore density and harvest quota fulfilment) form the basis for decisions to account for increased mortality due to predation. In both countries, data was used and management actions were taken to reduce the total moose mortality (reduced harvest) as well as to maximize productivity in the moose population (reduced harvest of adult females) in response to wolf territory density. Such an ability to adjust to new conditions is key in wildlife management where different conflicting societal objectives such as forestry, sustainable moose harvest yield, and wolf conservation should be balanced.

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Declarations

Competing interests The authors declare no competing interests.

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