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Research article

The role of predation, forestry and productivity in moose harvest at different spatial levels of management units

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Management of ungulate populations to the desired density and/or demographic composition are challenged by contrasting aims of different stakeholders. For example, hunters may want to maximize hunting opportunities whereas commercial forest owners may want to minimize moose densities to mitigate browsing damage. In addition, the return of large predators such as wolves *Canis lupus* affects the possible harvest yield of ungulates and influences the population composition through their selection of specific age classes. The aim of this study was to gain a better understanding of factors related to the variation in moose *Alces alces* harvest. We used moose harvest statistics from the period 2012–2020, wolf annual monitoring data, annual brown bear *Ursus arctos* density, proportion of young forest per management unit, and proportion of agricultural land per management unit (index for productivity and roe deer *Capreolus capreolus* density) to explain variation in moose harvest across different management units at two spatial levels in two bordering countries, Sweden and Norway. The results showed variable responses in total harvest to changes in wolf territory density both at the regional and local management level. The proportion of young forest was correlated with both increased total harvest and proportion of calves. Increased proportion of agricultural land was linked to both increased total harvest and proportion of calves, likely due to that increased roe deer densities re-directed wolf predation from moose to roe deer, and an inverse relationship with brown bear density. Differences between countries may be due to differences in the management regime of moose, both in an historical and present perspective. Improved monitoring for individual hunting areas over time will be important for both the understanding of how different ungulate populations are affected by various factors and for the desired management of wildlife populations shared across borders.

Keywords: carnivore, harvest yield, secondary prey species, ungulate management, young forest

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Introduction

Predation by large carnivores and human hunting are two important factors affecting the dynamics of ungulate populations (Solberg et al. 2002, Bassi et al. 2020, Marrotte et al. 2022). Both large predators and hunters often select for certain categories of prey and can therefore influence the age and sex composition of their prey populations (Ginsberg and Milner-Gulland 1994, Festa-Bianchet 2003, Gervasi et al. 2012, Jonzén et al. 2013). Management of ungulate populations, implemented through regulated harvest, usually includes an objective of the age and sex composition of the living population, which in turn has implications for the selection of age and sex classes to be harvested (Beddington 1974, Law 1974). In addition to harvest, the management of ungulate populations to the desired density and/or composition may be affected by the presence of large carnivores, with their predation in turn affecting the size and composition of the hunter harvest (Mech and Nelson 2000, Nilsen et al. 2005, Vucetich et al. 2005). However, large carnivores predominantly kill non- or low-reproductive individuals (calves, 1-year-olds and old females) (Smith et al. 2004, Swenson et al. 2007, Sand et al. 2008) resulting in a smaller impact on the potential annual growth of the ungulate population compared to hunter harvest, which targets a higher proportion of reproductive females (Ballard et al. 2001, Gervasi et al. 2012).

With the return of large predators, predation can in some ecosystems lead to cascading effects on species at lower trophic levels than that of the main prey (Ripple et al. 2014), such as reduced ungulate browsing on plants (White et al. 2003, Beschta and Ripple 2009). This may be caused by the numerical effect of predation on ungulate density and/or by behavioural changes in ungulate habitat selection to avoid areas of high predation risk (Laundré et al. 2001, Kuijper et al. 2016). However, cascading trophic effects of predators may be context-dependent (Ausilio et al. 2021).

In addition to the effects of harvest and predation, environmental variation also affects ungulate populations. Previous studies have shown that geographical variation in different life history traits (e.g. reproduction) of moose are strongly related to variation in landscape characteristics such as land productivity and food availability (Sand 1996, Solberg et al. 2006, Grøtan et al. 2009, Tallian et al. 2021). For example, population growth rate of moose increased with forage-rich habitat, further emphasizing the importance for the management of ungulates to involve both forest characteristics and harvest (Brown 2011). In addition, availability of both young forest stands providing food and old forest stands providing cover may become more important with climate change (Dussault et al. 2004, Johnson and Rea 2023).

The transition from selective removal of old trees to clear-cutting in Scandinavia in the middle of the 20th century resulted in an increased quantity and quality of forage available to moose (Månsson 2009). Together with the lack of predators and the management regime of sparing reproductive females, this change of forestry practices was the most important factor for the strong increase in moose population size (Milner et al. 2013), with a concurrent increase in hunting opportunities (Lavsund et al. 2003). In Scandinavia, moose hunting has both high economic and recreational value and provides a considerable amount of meat and income to landowners and hunters (Storaas et al. 2001, Boman et al. 2011). While forestry companies and landowners that benefit from forestry have an interest in limiting moose density to reduce moose browsing damage on commercially important tree species (Edenius et al. 2011), a higher moose density will in most non-migratory moose populations lead to increased income from hunting and is a desired state for hunters. However, moose browsing on Scots pine *Pinus sylvestris* during winter often results in losses for landowners through reduced timber quality and lower production of biomass on the damaged stems (Wallgren et al. 2013).

In Europe, human land use through forestry, agriculture, and infrastructure, in combination with climate (e.g. temperature, precipitation), affect the distribution of different ungulate species (Acevedo et al. 2011, Leonardi et al. 2022), which in turn affects the composition of prey species available for large predators (Linnell et al. 2020). In Scandinavia, wolf *Canis lupus* predation rate on the local moose population also depends on the density of alternative prey species, mainly roe deer *Capreolus capreolus* (Sand et al. 2016). In areas where roe deer density exceeds 3 deer km^{-2}, wolves tend to kill more roe deer than moose. High densities of roe deer are generally found in areas with increased productivity and a larger proportion of agricultural land (Mattisson et al. 2013).

The hunting system in Scandinavia is organized in geographical management units where the borders remain relatively stable over time, and moose mortality rate from non-traumatic causes is low (< 4% for both sexes) (Broman et al. 2002). Thus, this management system includes an incentive for hunters to plan for a sustainable harvest in a multi-year perspective (Tuominen et al. 2023). A harvest over several years that is greater than the annual sustainable yield will inevitably lead to a reduction in moose density and thus result in a reduced harvest in the future.

In a previous study (Wikenros et al. 2020), we have shown that wolf territory density affected both moose harvest density and the composition (age and sex) of harvested animals along a latitudinal gradient in Sweden and Norway. It was also shown that the two countries have different harvest strategies regarding, for example, the proportion of calves in the harvest (Wikenros et al. 2020). In parts of the areas re-established by wolves in Scandinavia, the brown bear *Ursus arctos* is sympatric with wolves (Ordiz et al. 2015) and the presence of both predator species has the potential to reduce or even totally preclude a sustainable harvest yield of moose (Jonzén et al. 2013, Tallian et al. 2017, 2022).

The aim of this study was to investigate the role of wolves and other factors, including the known differences of management strategies in the two countries, on moose harvest density and composition, e.g. predation from the two carnivore species present (wolf and brown bear), forest age composition, and the proportion of agricultural land as an index for land productivity, and thereby the presence of alternative prey species (roe deer) to wolves (Bjørneraas et al. 2012, Mattisson et al. 2013), to further improve our understanding of factors important for moose harvest size both at the regional and local scale. We investigated this at different spatial levels of moose management units in Sweden and Norway and expected differences in the two countries as previously shown (Wikenros et al. 2020). We predicted harvest density and the proportion of adults in harvest to be lower in management units of high predator densities as a response to compensate for the numerical effect of predation and to spare animals with high reproductive value. We also predicted an increased harvest and a higher proportion of calves in harvest in management units with a high proportion of young forest due to increased forage availability and its effect on moose reproduction. We predicted a lower impact of wolves on the harvest yield in areas with a higher proportion of agricultural land, as a result of roe deer becoming more abundant and re-directing wolf predation from moose to roe deer (Sand et al. 2016).

Material and methods

Study area

The study was conducted in inner Scandinavia and covers the entire Värmland and Dalarna counties and what was previously Hedmark county (now the eastern part of Innlandet county) in Norway (Fig. 1). The moose population in the study area is one of the densest in Scandinavia (Lavsund et al. 2003, Jensen et al. 2020), with average winter densities within wolf territories of 1.20–3.33 km^{-2} for moose and of 0.05–0.73 for roe deer (Sand et al. 2016). During the 1995–2020 period, the wolf population in Scandinavia increased from 3 to 75 territories with $\geq$ 2 wolves (including territorial scent-marking pairs and family groups) (Wabakken et al. 2001, Svensson et al. 2021). Of the 75 territories recorded during the 2020/2021 monitoring season, 37 were entirely or partly within the study area (Svensson et al. 2021). The brown bear population in Scandinavia has been estimated at about 3000 individuals annually (2012–2018) with the highest number in 2015 (Bischof et al. 2020).

Harvest statistics

The current moose management system in Sweden was introduced in 2012 and consists of regional management units (hereafter RMU, in Swedish 'Älgförvaltningsområden') (Fig. 1). Each RMU manages moose in cooperation with landowners, hunters, interest groups and authorities, and prepares a management plan every third year that must be approved by the county administrative board. An RMU is divided into local management units (hereafter LMU, in Swedish 'Älgjaktområden'). The LMU can, depending on size and land ownership, consist of smaller compartments (hunting areas, hereafter HA) of three different types: management areas (hereafter MA, in Swedish 'Älgskötselområden'), license areas (hereafter LA, in Swedish 'Licensområden'), and unregistered land (in Swedish 'Oregistrerad mark', not included in this study). An MA must have a long-term harvest of at least 10 adult moose per year and a management plan. An LA must be large enough to harvest at least one calf per year. On unregistered land, moose calf harvest may be conducted for a short period. The harvest in MA, LA and unregistered land is reported via the county administrative boards' database 'Älgdata' (www.algdata.se).

In Norway, the equivalent of RMUs are municipalities (Fig. 1) that are responsible for setting quotas and reporting harvested moose to a national register in line with the overall national objectives for ungulate management. The municipalities approve the LMUs (in Norwegian 'Vald'), which are hunting areas or associations of several hunting areas where the holders of hunting rights have applied for a license to hunt moose with quotas based on a 3–5 year management plan. In Norway as well, LMUs are divided into smaller units (HA, in Norwegian 'Jaktfelt'). Hunting statistics are reported at this level and are summarized at LMU and RMU level. However, the spatial extent of the Norwegian HAs was not available in digital form and number of harvested moose not consistently reported for individual HA, therefore, Norwegian HAs were not included in the study.

During the study period in Sweden, the hunting season began on the second Monday in October (except in some areas where hunting was also allowed for three weeks in September) and ended on 31 January in Dalarna and 28–29 February in Värmland. In Norway, the hunting season began on 25 September and ended on 23 December, and there have been a few years of experimental hunting during winter in a few selected RMUs.

The harvest density was calculated for all area covered by forest, bog and agricultural land according to the definition of hunting area given by the county administrative boards in Sweden. In Norway, agricultural land is not included in the official definition. For comparability, we deviated from the Norwegian definition and applied the same rule for estimating hunting area in both countries (Wikenros et al. 2020).

Regional level (RMU) in Sweden and Norway

The average size (± SE) of the Swedish and Norwegian RMU was 1827 ± 205 km^2 (n = 24) and 700 ± 109 km^2 (n = 29), respectively. Harvest for the period 2012–2020 in Sweden was retrieved from 'Älgdata' and analysed based on digital maps for the RMUs used in 2020.

On the Norwegian side, we used digital maps of municipal boundaries from Statens kartverk. Municipalities that include the Glomma River, which is also the border of the Norwegian wolf zone (Energi- og miljøkomiteen 2016), were divided into sub-municipalities east and west of Glomma. Harvest statistics were retrieved from 'Hjorteviltregisteret' (hjorteviltregisteret.no) and 'Viltrapporten' (www.viltrapporten.no) at HA-level, and so aggregated at RMU (municipality) level. Data on harvest quotas follow yet another spatial scale that does not align with Norwegian RMUs,

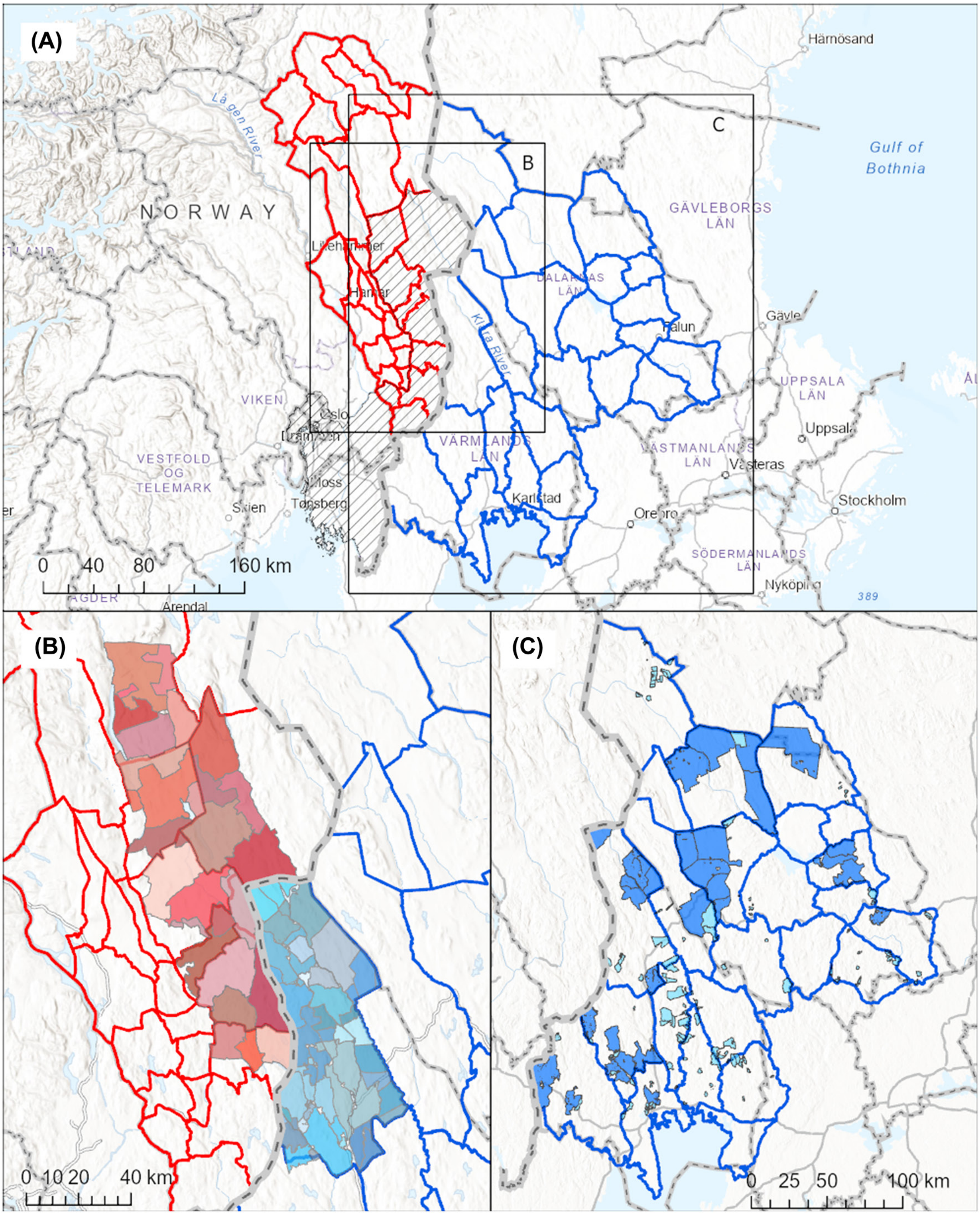

Figure 1. Overview of the management units included in the analyses with (A) regional management units (RMU) in Sweden (blue contours) and in Norway (red contours), (B) local management units (LMU) in Sweden (blue polygons) and Norway (red polygons), and (C) hunting areas (HA) in Sweden divided into management areas (MA, blue polygons) and license areas (LA, turquoise polygons). The hatched area (A) represents the Norwegian wolf management zone.

because some neighbouring municipalities collaborate for moose management and report quotas collectively. Also, municipalities divided by the river Glomma did not report quotas separately for the two areas inside and outside of the wolf zone. Therefore, we did not include harvest quotas in the analyses.

Local level (LMU) across the national border

For a smaller study area for the period 2016–2020 across the national border (Fig. 1) we used annual digital maps for LMU in Sweden and harvest statistics from 'Älgdata'. Maps of Norwegian LMU were partly available digitally, partly on paper maps that we digitized. Harvest statistics at the HA level were obtained from the 'Hjorteviltregistret' and the 'Viltrapporten' and assigned to the different LMU. The Swedish LMU had an average size of 108 ± 18 km^2 (n = 39) and the Norwegian LMU had a size of 209 ± 23 km^2 (n = 26).

Local level (HA) in Sweden

We used data from HAs that had the same area from 2012 to 2020 based on digital maps for 2020 and retrieved from 'Älgdata'. Out of a total of 304 HAs, we excluded the HAs without a harvest quota of at least one adult moose each year during the entire study period (n = 69) and where the hunting area was not the same as in 2020 (maximum difference between years no more than 0.25 km^2, n = 107). This resulted in 28 MAs with an average area of 243 ± 31 km^2 and 100 LAs with an average area of 14 ± 2 km^2.

Wolf index

The wolf population is monitored annually with common monitoring criteria in Sweden and Norway (Åkesson et al. 2022). Wolf territory density per management unit was calculated in R (www.r-project.org). Each territory during the monitoring season (October–March) was represented by a circle with a radius of 18 km from the centre point of the territory. This represents an average-sized territory (1017 km^2) (Mattisson et al. 2013). The resulting raster with a cell size of 1 × 1 km was used to calculate the average wolf index of all cells within a given management unit. As an index of wolf territory density, a parabolic curve was used representing a decreasing probability of wolf territory presence from the centre point (1) to 18 km from the centre point (0) (Ciucci et al. 1997). A wolf territory density of 0 indicates absence of wolf territories, values < 0.5 indicate that only parts of the management unit is covered by wolf territories, 0.5 indicates that the management unit is covered by medium-sized territories, and values > 0.5 indicate that the management unit contains wolf territories that are smaller than medium-sized territories (a higher density of wolf territories) (Wikenros et al. 2020). An index of 0.5 was expected to represent an average wolf territory predation rate of 0.12 moose km^{-2} annually, including about 80% calves (Zimmermann 2014). A short-term effect of wolf predation was defined as the average wolf territory density in the current and the previous monitoring season (hereafter referred to as 2-year wolf index). This 2-year wolf index was later used to explain the variation in the proportion of calves in total harvest, in accordance with the findings of Wikenros et al. 2020. For the long-term effect of wolves on total moose harvest and proportion of females in adult harvest (Wikenros et al. 2020), the average wolf territory density over the last five years (including the current harvest season, hereafter referred to as 5-year wolf index) was used. This time span was motivated by the moose management plans of 3–5 years.

Brown bear density

Brown bear density was estimated as average per km^2 across each management unit, based on a raster with cell size 1 × 1 km of annual estimates on brown bear densities from spatial capture-recapture models (Bischof et al. 2020) based on genetic samples registered in the Scandinavian carnivore registry (www.rovbase.no) for the 2012–2018 period. As data was not available for 2019 and 2020, we used an average of 2012 to 2018.

Forestry

The proportion of young forest per management unit was calculated in R from Global Forest Watch (www.globalforestwatch.org) as the sum of the proportion of clearcuts per year in the current and previous 11 years. The choice to include clear cuts during consecutive 12-year periods was a result of that data from Global Forest Watch was only available for the period 2001–2020 and our study period ranged between 2012 and 2020. The dataset consisted of a raster file with cell size 30 × 30 m, with the z-value indicating the year of tree loss.

Agricultural areas

The proportion of agricultural land per management unit was used as an index of roe deer density (Mattisson et al. 2013) for all years. The proportion of agricultural land was calculated in R as the proportion of arable and pasture land according to the CORINE Land Cover classification (CLC 2018, CLC codes = 12, 16, 18, 20, 21, 26, raster cell size 100 × 100 m) (downloaded from https://land.copernicus.eu/pan-european/corine-land-cover/clc2018).

Statistical analyses

Regional level (RMU) in Sweden and Norway

We used negative binominal regression in the R package 'glmmTMB' (Brooks et al. 2017) to analyse the variation in total number of harvested moose per RMU. We included the hunting area of the RMUs as log-transformed offset. Linear models (LM) were used to analyse the variation in proportion of calves in total harvest and proportion of females in adult harvest. We included the hunting area of the RMUs as a weight in the models, because small units are more susceptible to random changes. In accordance with the results of Wikenros et al. 2020, we included the 5-year rather than the 2-year wolf index as predictor of total number of harvested moose and proportion of females in adult harvest. We did so because moose harvest quotas are decided over a period of 3–5 years, and we therefore expected a long-time effect of wolf territory density. For the proportion of calves in total harvest, we used the 2-year wolf index as predictor. The immediate effect of wolf predation on calves during the summer is why we expected a short-time effect of wolves on the number of calves available to hunters (Wikenros et al. 2020). For all three response variables, we included the wolf index in a three-way interaction with year (factor) and country, as well as the two-way interactions between those variables. The three-way interaction was motivated by the findings of Wikenros et al. 2020 on long-term dynamics of moose harvest. That study found differences between the two countries: the harvest rates were not synchronized in time, Sweden had a higher proportion of calves in harvest, and the relation between wolf index and harvest differed between countries. The predictors proportion of agricultural area and brown bear density were negatively correlated. We included the proportion of agricultural area rather than brown bear density in the models, because the first is a general proxy of landscape productivity and roe deer density. In the full models, we also included the proportion of young forest in interaction with country as predictor variable. The interaction was included due to different land owner structure and forest property size in the two countries. Large areas in Sweden are owned by the forestry industry, while Norway's forests are mostly a patchwork of small private properties. We used backwards stepwise selection and removed non-significant ($p \geq 0.05$) variables from the full model.

Local level (LMU) across the national border

Negative binomial regression was used to model the variation in total harvest in LMUs during the time period 2016–2020. The log-transformed hunting area of the LMUs was used as an offset variable. As predictor variables, we included the three-way interaction of 5-year wolf index × year × country, and proportion of young forest in interaction with country in the full model. We did not include neither the proportion of agricultural area nor brown bear density as predictors because these variables had low values and low variation at the local level of our study area (Fig. 1B). We used backwards stepwise selection and removed non-significant ($p \geq 0.05$) variables from the full model.

Hunting areas (HA) in Sweden

Negative binomial regression was used to model the variation in total harvest in HAs in Sweden during the time period 2012–2020. The log-transformed hunting area of the HAs was used as an offset variable. As predictor variables, we included the two-way interactions between 5-year wolf index and year, 5-year wolf index and hunting area, year and hunting area, proportion of young forest and country, as well as proportion of agricultural area. We used backwards stepwise selection and removed non-significant ($p \geq 0.05$) variables from the full model. All statistical analyses were conducted in R.

Results

Regional level (2012–2020)

Total harvest

In total, 95 976 and 50 475 moose were shot in the Swedish and Norwegian RMUs, respectively, during the 9-year period. The final model included the interactions between country and year, and wolf index and year, proportion of young forest, and proportion of agricultural area (Fig. 2, Table 1, 2). The total harvest was higher in Norway during 2012–2015 and at a similar level as the Swedish harvest during 2016–2020, while the total harvest in Sweden was similar across all years (Fig. 2A). During the first three years 2012–2014, total harvest was independent of wolf territory density in the RMUs

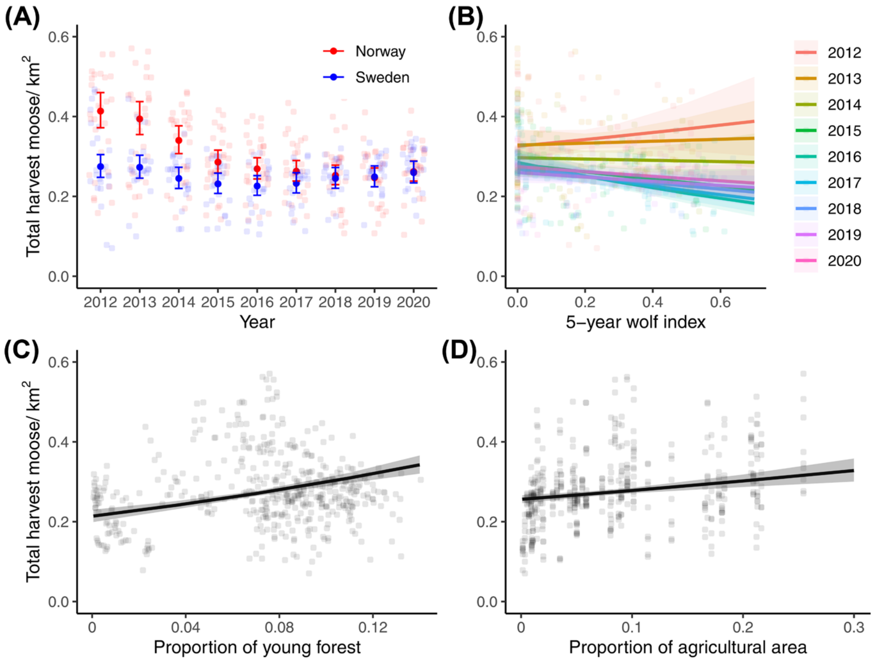

Figure 2. Total harvest of moose per km² in regional management units (RMU) in Sweden (n = 24) and Norway (n = 29), in relation to the interactions between year and country (A) and year and 5-year wolf index (B), proportion of young forest (C), and proportion of agricultural area (D). Figures show predicted means and 95% confidence intervals from negative binominal regression models. Dots represent the observed values and for visual purposes overlapping dots are separated horizontally in A.

Table 1. Overview of the backwards stepwise selection of models for total number of moose harvest, proportion of calves of total harvest and proportion of adult females of harvested adults in regional management units (RMU) in Sweden and Norway, 2012–2020. Explanatory variables are the three-way and two-way interactions between 5-year (for total harvest and proportion of adult females) or 2-year (for proportion of calves) wolf index (W), year (2012–2020 (Y)), country (Sweden, Norway (C)), proportion of agricultural area (A), and proportion of young forest (F) (alone or as an interaction with country). The size of the RMU is included in the models as offset (total harvest) or weight (proportion of calves and proportion of adult females).

Response variable	Intercept	W × Y × C	W × Y	W × C	Y × C	W	Y	C	A	F	F × C
Total harvest	X	X	X	X	X	X	X	X	X	X	X
	X		X	X	X	X	X	X	X	X	X
	X		X	X	X	X	X	X	X	X	
	X		X		X	X	X	X	X	X	
Proportion of calves	X	X	X	X	X	X	X	X	X	X	X
	X		X	X	X	X	X	X	X	X	X
	X			X	X	X	X	X	X	X	X
	X			X		X	X	X	X	X	X
Proportion of adult females	X	X	X	X	X	X	X	X	X	X	X
	X		X	X	X	X	X	X	X	X	X
	X			X	X	X	X	X	X	X	X
	X				X	X	X	X	X	X	X
	X				X	X	X	X	X	X	
	X				X	X	X	X		X	
	X				X	X	X	X			

(Fig. 2B). Thereafter, harvest was lower in RMUs with high, compared to those with low wolf territory density (Fig. 2B). In both countries, moose harvest was positively related to the proportion of young forest, independent of country (Fig. 2C), and to the proportion of agricultural area (Fig. 2D).

Proportion of calves in total harvest

The final model included year, the interactions between 2-year wolf index and country and proportion of young forest and country, as well as proportion of agricultural area (Fig. 3, Table 1, 2). The proportion of calves in the total harvest was higher in the time period 2014–2020 as compared to the first two years (Fig. 3A). In Norway, hunters harvested a higher proportion of calves in RMUs with high compared to low wolf territory density. In Sweden, the proportion of calves in the total harvest was higher than in Norway and only weakly positively related to the wolf territory density (Fig. 3B). The correlation between calf proportion and the proportion of young forest differed between the two countries (Fig. 3C). In Norway, the proportion of calves in harvest increased with increasing proportion of young forest, whereas it decreased in Sweden. The calf proportion was positively related to the proportion of agricultural area (Fig. 3D).

Proportion of adult females in adult harvest

The final model included the interaction between year and country and the 5-year wolf index (Fig. 4, Table 1, 2). Swedish hunters harvested a higher proportion of adult females than Norwegian hunters during the 2016–2020 period (Fig. 4A). The proportion of females in adult harvest was negatively related to wolf territory density, independent of country (Fig. 4B).

Local level across the national border (2016–2020)

Total harvest

For this 5-year period, annual data on total harvest were available for 140 LMUs in Sweden and 94 in Norway including 4449 moose harvested in Sweden and 4522 in Norway. The final model included the interactions between country and year and 5-year wolf index and year, as well as proportion of young forest (Fig. 5, Table 3, 4). Harvest was relatively constant in Norway throughout the time period 2016–2020, but increased during 2018–2020 in Sweden (Fig. 5A). The total harvest was negatively related to increasing wolf territory density during the first three years, but in 2019 and slightly also in 2020, more moose were harvested in LMUs with high as compared to those with low wolf territory density (Fig. 5B). The total harvest was positively related to the proportion of young forest (Fig. 5C).

Local level in Sweden (2012–2020)

Total harvest

In total, 14 589 moose were harvested in MAs and 2340 in LAs. The final model included the interaction between the 5-year wolf index and year, hunting area, and proportion of young forest (Fig. 6, Table 5, 6). In the beginning (2012 and 2013) and the end (2018–2020) of the study period, the total harvest was positively related to wolf territory density (Fig. 6A). In the four years in between (2014–2017), harvest was lower in HAs with high as compared to those with low wolf territory density (Fig. 6A). The total harvest was higher in MAs than in LAs (Fig. 6B) and was positively related to the proportion of young forest (Fig. 6C).

Discussion

We failed to find a uniform support for our predictions as this study showed variable responses in total harvest to changes in wolf territory density both at the regional and local management level. However, as previously shown (Wikenros et al. 2020), the different harvest strategies in Sweden and Norway regarding the proportion of calves in the harvest were

Table 2. Estimates for the selected negative binominal regression model for total moose harvest, and the selected linear models for proportion of calves in total harvest, and proportion of adult females in adult harvest, in regional management units (RMU) in Sweden and Norway, 2012–2020. Explanatory variables are 5-year (for total harvest and proportion of adult females) or 2-year (for proportion of calves) wolf index (W), year (2012–2020), country (Sweden, Norway) and their three-way and two-way interactions, proportion of agricultural area, and proportion of young forest in interaction with country. The size of the RMU is included in the models as offset (for total harvest) or weight (for proportion of calves and proportion of females).

Response variable	Explanatory variable	β	SE	z	p-value
Total harvest	Intercept	−1.253	0.059	−21.097	< 0.001
	Wolf	0.251	0.242	1.039	0.299
	Year 2013	−0.010	0.077	−0.130	0.896
	Year 2014	−0.129	0.077	−1.669	0.095
	Year 2015	−0.238	0.078	−3.040	0.002
	Year 2016	−0.239	0.078	−3.060	0.002
	Year 2017	−0.287	0.078	−3.656	< 0.001
	Year 2018	−0.364	0.079	−4.603	< 0.001
	Year 2019	−0.415	0.079	−5.226	< 0.001
	Year 2020	−0.351	0.079	−4.422	< 0.001
	Country Sweden	−0.409	0.080	−5.120	< 0.001
	Young forest	3.366	0.473	7.112	< 0.001
	Agricultural area	0.827	0.196	4.227	< 0.001
	Wolf × Year 2013	−0.179	0.327	−0.546	0.585
	Wolf × Year 2014	−0.306	0.321	−0.952	0.341
	Wolf × Year 2015	−0.608	0.313	−1.943	0.052
	Wolf × Year 2016	−0.884	0.305	−2.900	0.004
	Wolf × Year 2017	−0.769	0.300	−2.561	0.010
	Wolf × Year 2018	−0.598	0.297	−2.017	0.044
	Wolf × Year 2019	−0.474	0.295	−1.608	0.108
	Wolf × Year 2020	−0.484	0.296	−1.636	0.102
	Year 2013 × Land Sweden	0.042	0.113	0.375	0.708
	Year 2014 × Land Sweden	0.081	0.113	0.716	0.474
	Year 2015 × Land Sweden	0.198	0.112	1.758	0.079
	Year 2016 × Land Sweden	0.235	0.111	2.110	0.035
	Year 2017 × Land Sweden	0.286	0.110	2.592	0.010
	Year 2018 × Land Sweden	0.378	0.109	3.467	0.001
	Year 2019 × Land Sweden	0.419	0.108	3.878	< 0.001
	Year 2020 × Land Sweden	0.399	0.107	3.710	< 0.001
Proportion of calves	Intercept	0.305	0.011	27.373	< 0.001
	Wolf	0.149	0.032	4.692	< 0.001
	Year 2013	−0.008	0.012	−0.652	0.515
	Year 2014	0.009	0.012	0.755	0.451
	Year 2015	0.023	0.012	1.980	0.048
	Year 2016	0.039	0.012	3.389	0.001
	Year 2017	0.038	0.012	3.294	0.001
	Year 2018	0.028	0.012	2.368	0.018
	Year 2019	0.030	0.012	2.533	0.012
	Year 2020	0.023	0.012	1.916	0.056
	Country Sweden	0.118	0.014	8.470	< 0.001
	Young forest	0.305	0.186	1.637	0.102
	Agricultural area	0.182	0.050	3.612	< 0.001
	Wolf × Country Sweden	−0.096	0.037	−2.588	0.010
	Country Sweden × Young forest	−0.480	0.226	−2.126	0.034
Proportion of adult females	Intercept	0.445	0.013	34.358	< 0.001
	Wolf	−0.064	0.014	−4.665	< 0.001
	Year 2013	0.011	0.018	0.616	0.539
	Year 2014	−0.009	0.018	−0.493	0.622
	Year 2015	−0.015	0.018	−0.817	0.414
	Year 2016	−0.042	0.018	−2.295	0.022
	Year 2017	−0.035	0.018	−1.901	0.058
	Year 2018	−0.032	0.018	−1.775	0.077
	Year 2019	−0.031	0.018	−1.690	0.092
	Year 2020	−0.038	0.018	−2.116	0.035
	Country Sweden	0.004	0.016	0.270	0.787
	Year 2013 × Country Sweden	0.014	0.022	0.620	0.536

(Continued)

Table 2. Continued.

Response variable	Explanatory variable	β	SE	z	p-value
	Year 2014 × Country Sweden	0.021	0.022	0.936	0.350
	Year 2015 × Country Sweden	0.023	0.022	1.041	0.299
	Year 2016 × Country Sweden	0.043	0.022	1.972	0.049
	Year 2017 × Country Sweden	0.055	0.022	2.520	0.012
	Year 2018 × Country Sweden	0.056	0.022	2.534	0.012
	Year 2019 × Country Sweden	0.069	0.022	3.118	0.002
	Year 2020 × Country Sweden	0.089	0.022	4.065	< 0.001

confirmed. We found support for our second prediction as the proportion of young forest was correlated with increased total harvest at both management levels. In addition, the proportion of calves in the harvest at the regional level increased with the proportion of young forest in Norway, but showed the opposite trend in Sweden. In line with our third prediction, RMUs with a higher proportion of agricultural land had more moose and a higher proportion of calves harvested, compared to those RMUs with little agricultural land. However, we did not find any relationship between moose harvest and proportion of agricultural land at the local level.

In this study, the correlation between wolf territory density and total harvest differed during the study period. This is in contrast to previous studies from the same system that showed a unified reduction in total harvest and harvest of adult females both immediately after wolf territory establishment (Wikenros et al. 2015) and in a longer time perspective using the same wolf indices as in this study (Wikenros et al. 2020). Another study conducted in the majority of the wolf range showed that changes in the number of moose observations during the first week of the moose harvest season in one or more years often resulted in a corresponding change in the harvest in the following year (Wikenros et al. 2019). However, that study also showed that in the northern part of the current study area in Sweden, the number of moose observations increased during the 2012–2017 period while harvest decreased. This pattern probably resulted in both an increased moose density followed by an increased harvest, as shown in this study, and that this change coincided with an increase in the density of wolf territories. A high browsing damage on pine in this area likely motivated a management decision to increase moose harvest also in areas with high wolf territory density (Zimmermann et al. 2022).

Thus, in our system, hunters initially seem to over-compensate for an anticipated increased mortality in areas exposed to the re-establishment of wolf territories (Wikenros et al. 2015). This may initially lead to increased moose densities and partly explain the variable relationship between total harvest and wolf territory density as shown in this study. This highlights the importance of having long-term data on both

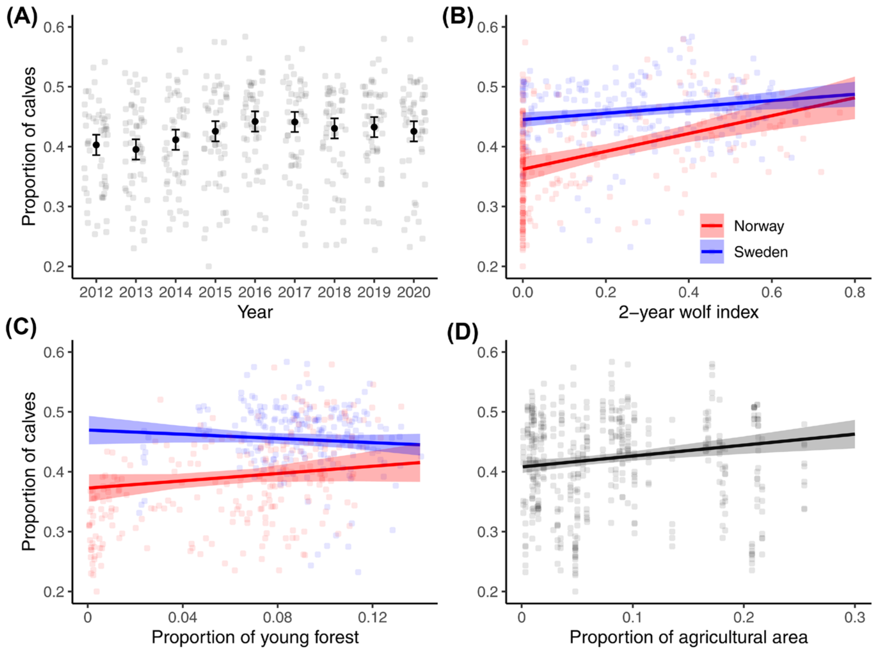

Figure 3. Proportion of calves in total moose harvest in regional management units (RMU) in Sweden (n = 24) and Norway (n = 29), in relation to year (A), the interaction between 2-year wolf index and country (B), the interaction between proportion of young forest and country (C), and proportion of agricultural area (D). Figures show predicted means and 95% confidence intervals from linear models. Dots represent the observed values and for visual purposes overlapping dots are separated horizontally in A.

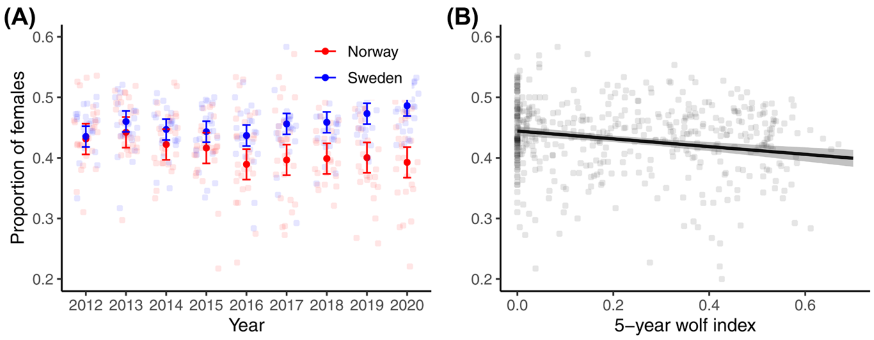

Figure 4. Proportion of adult females in adult moose harvest in regional management units (RMU) in Sweden (n = 24) and Norway (n = 29), In relation to the interaction between year and country (A) and 5-year wolf index (B). The figure shows predicted means and 95% confidence intervals from linear models. Dots represent the observed values and for visual purposes overlapping dots are separated horizontally in A.

ungulate densities and density estimates of carnivores to better balance a sustainable harvest.

This study showed that the total harvest increased with an increased proportion of young forest at both management levels and in both countries. This relationship likely represents an increased availability of high quality forage for moose, which in turn can affect moose density and distribution in the landscape (Maier et al. 2005, van Beest et al. 2010, Bergqvist et al. 2018). Moose density is generally higher in forests that are less than 30 years old compared to bogs and older forests (> 30 years), and this forest age class is also a preferred habitat for moose (Månsson et al. 2007, Månsson 2009, Bjørneraas et al. 2012). An alternative, but not mutually exclusive, explanation for the positive relationship between harvest and the proportion of young forest stands is an allowed higher density of moose by landowners as a higher proportion of young forest would reduce damage levels for a given density of moose (Gicquel et al. 2020). This spatial pattern is also in line with previous findings on the higher importance of forest characteristics, e.g. density of young trees, than the presence of wolves for explaining variation in moose density and moose browsing damage among areas, supporting the hypothesis of a lack of potential for trophic cascades in anthropogenic landscapes (Kuijper et al. 2016, Gicquel et al. 2020, Ausilio et al. 2021).

Geographical variation in different life history characteristics (body growth and reproduction) has previously been documented for moose in Scandinavia, which tend to be linked to climatic conditions and biomass productivity (Sand et al. 1995, Sand 1996, Ferguson 2002, Solberg et al. 2002, Grøtan et al. 2009). In general, the productivity of the moose population tends to decrease towards the north (Sæther and Hagenrud 1985, Sand 1996). It is also likely that geographical variation in the production of moose calves in Scandinavia is affected by current or delayed density-dependent effects, i.e. food competition (Grøtan et al. 2009, Tallian et al. 2021), and/or weather induced changes in forage quality (Holmes et al. 2021) which further complicates quantitative estimates of the effect of predation. The moose productivity gradient also suggests that the impact of wolves and brown bears on the moose population will not be constant but may change with latitude and land productivity with increasing impact towards regions with lower productivity, as has been shown for lynx (*Lynx lynx*) on roe deer (Melis et al. 2009). Although moose is the main prey of wolves in most of their current breeding range in Scandinavia (Sand et al. 2005, 2008), areas with higher densities of roe deer, tend to shift wolf predation from moose towards roe deer (Sand et al. 2016). We therefore predicted a smaller effect of wolf presence on the harvest of moose in management units with a higher proportion of agricultural land, which has shown to be a good index of roe deer density (Mattisson et al. 2013). However, the proportion of agricultural area was spatially inversely related

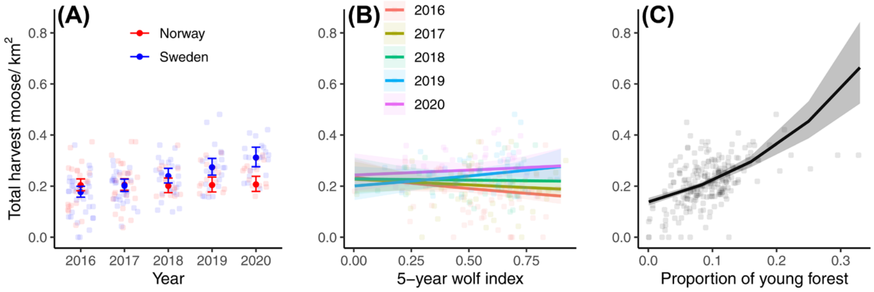

Figure 5. Harvest of moose per km² in local management units (LMU) in Sweden (n = 39) and Norway (n = 26), in relation to the interaction between year and country (A), 5-year wolf index and year (B), and proportion of young forest (C). Figures show predicted means and 95% confidence intervals from negative binominal regression models. Dots represent the observed values and for visual purposes overlapping dots are separated horizontally in A.

Table 3. Overview of the backwards stepwise selection of models for total moose harvest in local management units (LMR) in Sweden and Norway, 2016–2020. Explanatory variables are the three-way interaction and two-way interactions between 5-year wolf index (W), year (20162020 (Y)), and country (Sweden, Norway (C)), and proportion of young forest (F) (alone or as interaction with country). The size of the LMR is included in all models as offset.

Response variable	Intercept	W × Y × C	W × Y	W × C	Y × C	W	Y	C	F	F × C
Total harvest	X	X	X	X	X	X	X	X	X	X
	X		X	X	X	X	X	X	X	X
	X		X		X	X	X	X	X	X
	X		X		X	X	X	X	X	

Table 4. Estimates of the selected negative binominal regression model for total moose harvest in local management units (LMU) in Sweden and Norway, 2016–2020. Explanatory variables are 5-year wolf index, year (2016–2020), country (Sweden, Norway) and proportion of young forest in interaction with country. The size of the LMU is included in all models as offset.

Response variable	Explanatory variable	β	SE	z	p-value
Total harvest	Intercept	−1.815	0.129	−14.052	< 0.001
	Wolf	−0.417	0.252	−1.653	0.098
	Year 2017	−0.109	0.181	−0.599	0.549
	Year 2018	−0.216	0.216	−1.002	0.316
	Year 2019	−0.417	0.224	−1.867	0.062
	Year 2020	−0.294	0.217	−1.357	0.175
	Country Sweden	−0.142	0.084	−1.703	0.088
	Young forest	4.759	0.512	9.290	< 0.001
	Wolf × Year 2017	0.211	0.349	0.603	0.546
	Wolf × Year 2018	0.372	0.377	0.988	0.323
	Wolf × Year 2019	0.774	0.384	2.015	0.044
	Wolf × Year 2020	0.569	0.372	1.527	0.127
	Year 2017 × Country Sweden	0.127	0.117	1.081	0.279
	Year 2018×Country Sweden	0.317	0.126	2.522	0.012
	Year 2019 × Country Sweden	0.436	0.126	3.456	0.001
	Year 2020 × Country Sweden	0.554	0.127	4.356	< 0.001

to brown bear density at the regional management levels in both countries, indicating that the decreased total harvest of moose may also be a response to increased brown bear predation. Wolves and brown bears share the same main prey age category, moose calves, during spring and early summer, and as expected, the same relationship with the proportion of agricultural area was shown for the proportion of calves in the harvest, supporting the effect of predation from both wolves and brown bears that reduce harvest outtake of calves.

In line with a previous study (Wikenros et al. 2020) was the difference between Sweden and Norway in the impact from wolves on the harvest of moose. One plausible explanation may be differences in the management strategies of moose both in a historical and current perspective. For example, the proportion of harvested calves was higher in Sweden than in Norway except in areas with high wolf territory densities, and showed a negative relation with the proportion of young forest in Sweden, whereas the opposite relation was seen in Norway. We speculate that the higher harvest

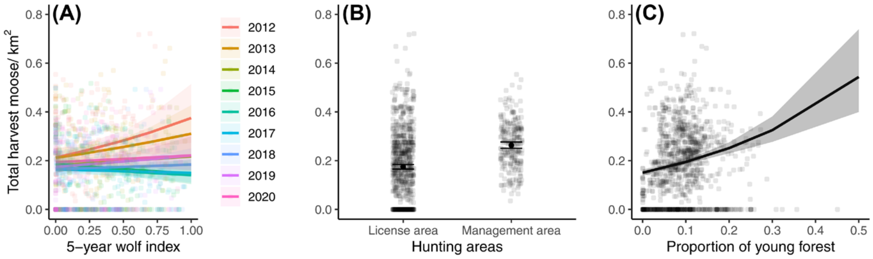

Figure 6. Harvest of moose per km² in moose hunting areas (HA) in Sweden divided into management areas (n = 28) and license areas (n = 100), in relation to the interaction between 5-year wolf index and year (A), hunting areas (B), and proportion of young forest (C). Figures show predicted means and 95% confidence intervals from negative binominal regression models. Dots represent the observed values and for visual purposes overlapping dots are sparated horizontally in B.

Table 5. Overview of the backwards stepwise selection of models for total number of moose harvested in moose hunting areas (HA) divided in management areas (MA) and license areas (LA), 2012–2020. Explanatory variables are the two-way interaction between 5-year wolf index (W), year (2012–2020 (Y)) and type of hunting area (MA or LA), proportion of agricultural area (A), and proportion of young forest (F) in interaction with HA. The size of the HA is included in all models as offset.

Response variable	Intercept	W × Y	W × HA	Y × HA	W	Y	HA	A	F	F × HA
Total harvest	X	X	X	X	X	X	X	X	X	X
	X	X		X	X	X	X	X	X	X
	X	X			X	X	X	X	X	X
	X	X			X	X	X	X	X	
	X	X			X	X	X		X	

Table 6. Estimates of the selected negative binominal regression model for total moose harvest in moose hunting areas (HA) divided in management areas (MA) and license areas (LA) in Sweden, 2012–2020. Explanatory variables are 5-year wolf index, year (2012–2020), type of hunting area (MA or LA), and proportion of young forest (alone or in interaction with HA). The size of the HA is included in all models as offset.

Response variable	Explanatory variable	β	SE	z	p-value
Total harvest	Intercept	−1.875	0.093	−20.262	< 0.001
	Wolf	0.566	0.220	2.578	0.010
	Year 2013	−0.007	0.120	−0.055	0.956
	Year 2014	−0.162	0.123	−1.319	0.187
	Year 2015	−0.130	0.123	−1.055	0.292
	Year 2016	−0.205	0.120	−1.709	0.088
	Year 2017	−0.260	0.119	−2.176	0.030
	Year 2018	−0.253	0.117	−2.171	0.030
	Year 2019	−0.198	0.114	−1.741	0.082
	Year 2020	−0.095	0.112	−0.847	0.397
	Hunting area	0.411	0.038	10.818	< 0.001
	Young forest	2.568	0.384	6.680	< 0.001
	Wolf × Year 2013	−0.182	0.311	−0.584	0.559
	Wolf × Year 2014	−0.383	0.314	−1.220	0.222
	Wolf × Year 2015	−0.807	0.320	−2.525	0.012
	Wolf × Year 2016	−0.775	0.305	−2.539	0.011
	Wolf × Year 2017	−0.656	0.304	−2.155	0.031
	Wolf × Year 2018	−0.459	0.302	−1.523	0.128
	Wolf×Year 2019	−0.328	0.297	−1.103	0.270
	Wolf × Year 2020	−0.432	0.301	−1.433	0.152

of adult moose in Norway may be a deliberate strategy to reduce browsing pressure in areas with more young forest. Also, the proportion of adult females of the total number of adult moose harvested was higher in Sweden than in Norway during the last five years of the study. We acknowledge that this study would have benefitted from information on hunting quotas, but our study design did not allow for that for the Norwegian management units. For future studies, it is desirable to consider deliberate differences in management strategies and include hunting quotas for local moose populations in different administrative units at both regional (RMU) and local (LMU) level as well as the national targets.

Creating conditions for monitoring of individual hunting areas and making comparisons over longer periods of time is important for increasing our understanding of how different ungulate populations are affected by various environmental and management-related factors. This includes creating a system for making data available and linking data of harvest quotas, actual harvest, and estimates of ungulate densities from the same management unit over longer periods of time and in a similar way in neighbouring countries. Such an approach would also facilitate the management of ungulate populations distributed across national borders. Cross-border management of important game species are also challenging due to sometimes contrasting aims from different stakeholders. Knowledge of management strategies and goals in neighbouring countries and bordering management areas that share populations of game species, and a constructive dialogue between stakeholders based on empirical knowledge on population parameters will be one way to improve management of wildlife populations shared across borders.

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Author contributions

Camilla Wikenros: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Håkan Sand**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Writing – review and editing (equal). **Cecilia Di Bernardi**: Data curation (supporting); Formal analysis (supporting); Visualization (equal); Writing – review and editing (equal). **Barbara Zimmermann**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.41ns1rnm9 (Wikenros et al. 2024).

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