



Acknowledgements

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Abstract

Many ungulates perform seasonal migration by moving between high-elevation summer ranges and low-elevation winter ranges. While areas at high elevations often yield high-quality forage during summer, such altitudes may provide harsh winter conditions. Animals may therefore depend on environmental cues, such as temperature, snow depth and plant quality to determine timing of migration. Because management units are often too small to capture the whole migration routes of large ungulates, and because of the spatiotemporal variation in animal abundance caused by migration, there may be an unfair distribution of hunting revenue and cost among different landowners. A way to even the revenue from hunting among landowners can be to adjust the timing of hunting season to better capture animal movements. As an attempt to harvest a higher proportion of red deer in summer areas, the hunting season of Norwegian red deer was advanced from 10th September to 1st September in 2012.

In this master thesis we analysed harvest data from 2000-2013 on red deer before and after the change of the hunting season, together with data on temperature, snow and plant senescence. Our aim was to identify factors that affected the annual variation in the number of harvested red deer per municipality and year, along an altitudinal migration gradient in the core area of red deer distribution in Norway. We were especially interested in finding the effect of the hunting season change.

We found that by moving the start of the red deer hunting season, the proportion of animals harvested at higher elevations increased by ~7 %. The effect found was relatively small, but matched the proportion of individuals migrating between 1st and 10th September. By allowing hunters to begin harvesting earlier, hunters at higher elevations are able to harvest the animals that spend the summer in their areas before they migrate to lower elevations. This means that the hunters are able to benefit from the same animals that potentially cause grazing damage on agricultural areas during summer. The distribution of harvested red deer along the elevation gradient was not affected by variation in autumn weather and plant senescence in a way that reflected migratory behaviour. Our study provides evidence that changing the timing of the hunting season is an efficient management tool to redistribute hunting revenue along an altitudinal migration gradient, and gives insight to the effect of a management decision made to even the cost and benefits of a migratory ungulate.

Sammendrag

Mange store hjortedyr utfører sesongmigrasjon mellom høyereliggende sommerområder og lavereliggende vinterområder. Høyereliggende områder gir dyrene god tilgang på føde på sommeren, men byr på utfordrende forhold på vinteren. Dyrene kan derfor være avhengig av å tilpasse tidspunktet på migrasjonen i forhold til ulike signaler fra naturen, som temperatur, snø og plantekvalitet. Fordi forvaltningsenheter ofte er for små til å fange opp hele migrasjonsruten til store hjortedyr, og på grunn av variasjonen i tilgjengelige dyr på ulike steder til ulik tid avhengig av jakttidspunkt, kan det være en ujevn fordeling av kostnader og jaktutbytte mellom forskjellige landeiere. En måte å jevne ut disse forskjellene, kan være å tilpasse tidspunktet på jaktseasonen for å bedre fange opp dyrenes bevegelser. En slik tilpassing ble gjort på jaktseasonen av norsk hjort, hvor jaktstart ble endret fra 10. september til 1. september i 2012.

I denne masteroppgaven har vi analysert data fra 2000-2013 av hjortejakt før og etter jaktstartendringen, sammen med data på temperatur, snø og plantevisning. Målet vårt var å identifisere faktorer som påvirket den årlige variasjonen i antall høstede hjort per kommune og år, langs en migrasjonsgradient fra høyere- til lavereliggende områder i kjerneområdet til hjort i Norge. Vi var spesielt interesserte i å finne effekten av jaktendringen.

Vi fant at ved å flytte starten av hjortejakten, økte proporsjonen av høstede dyr i høyereliggende områder med $\sim 7\%$. Effekten vi fant var liten, men var proporsjonal med potensialet for omfordeling. Ved å gi jegere i høyereliggende områder mulighet til å begynne jakten tidligere, fikk de adgang til å høste av bestander i sommerområder før de trekker ned til vinterområdene. Dermed får jegere i høyereliggende områder større mulighet til å høste av hjortebestander som påfører innmarka beiteskader. Fordelingen av høstet hjort langs høydegradienten ble ikke påvirket av variasjon i høstvær eller plantevisning på en måte som kan forklares gjennom migrasjon. Studien vår bekrefter at endringen av jaktstart påvirket distribusjonen av høstet hjort langs en høydegradient på en måte som ga en mer jevn fordeling av kostnader og jaktutbytte, og gir innsikt i effekten av en forvaltningsbeslutning.

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Introduction

Seasonal migration is a well-known phenomenon among large ungulates, and enables the animals to secure access to forage even if there are spatiotemporal variations in resource abundance (Fryxell *et al.* 1988). Many ungulates perform seasonal migration by moving between high-elevation summer ranges and low-elevation winter ranges (e.g. moose (*Alces alces*) Andersen 1991; mule deer (*Odocoileus hemionus*) Monteith *et al.* 2011; sika deer (*Cervus nippon*) Igota *et al.* 2004). While areas at high elevations often yield high-quality forage during summer, such altitudes may provide harsh winter conditions (Hobbs 1989). Therefore, animals may depend on environmental cues to determine timing of migration. The green-up in spring is one of the main drivers of spring migration (Hebblewhite *et al.* 2008; Bischof *et al.* 2012), while increasing snow depth and low temperatures initiate the autumn migration (Sabine *et al.* 2002; Ramanzin *et al.* 2007; Fieberg *et al.* 2008).

Most populations of large ungulates are regulated by human hunting (Apollonio *et al.* 2010), but because of their migratory behaviour management can be difficult. It is largely accepted that decision-making in ungulate management should occur at the lowest possible level (Andersen *et al.* 2010). This can enhance local participation and lead to higher efficiency and more use of local knowledge (UNEP 1998). However, management of seasonally migrating animals can be especially challenging because of the extensive area needs of such species (Harris *et al.* 2009; Singh & Milner-Gulland 2011), and because management units are often smaller than the annual space use of even single individuals (e.g. Jarnemo (2008)). This leads to a mismatch between the size of the areas used by the animals, and the size of management units. Because some ungulates can cause damage to forestry and pasture in one area, while bringing incomes as hunting game in other areas, there may be an uneven distribution of cost and benefits among landowners (Skonhøft & Olausson 2005). In addition, different areas may have different harvest success as a consequence of the spatiotemporal variation in animal abundance. This is particularly true if much of the seasonal migration occurs before hunting season. If animals cross several management units during migration, there could be a risk that the areas where animals migrate from will have few animals left when hunting season starts, while others might experience an influx of migrating animals during the hunting season. For migratory ungulates it can therefore be a skew in the proportion of animals harvested in summer and winter areas, thus leading to conflict between stakeholders experiencing an unfair distribution of costs and benefits (Andersen *et al.* 2010).

Adjusting the hunting season to the seasonal movements of a species can be a strategy to increase income at certain points of the migration route. In the U.S., Heusmann and McDonald (2002) studied the change in the proportion of harvested wood ducks (*Aix sponsa*) along their autumn migration routes from northern parts of the country to southern parts, under different hunting season lengths. A management goal had been to increase the hunting opportunity in the southern areas by extending the hunting season. This was done to ensure longer opportunity to harvest migrating ducks as they arrived to the wintering areas. Even though southern areas initiated the extension, hunting seasons were extended along the whole migration route. Longer hunting seasons resulted in an increased harvest in the south, but the lengthening of the hunting season did not lead to an increased harvest in the north. Thus, the management created a greater skew in the proportion of the total harvest between the northern and southern areas. The study illustrates how changing hunting season length and timing can affect the distribution of hunting success along a migration route. A natural management goal could be to spread the revenue of natural resources evenly across stakeholders. However, to our knowledge, no studies have investigated how adjustment of hunting season could impact the geographical spread of hunting success of migrating large ungulates.

Red deer (*Cervus elaphus*) are known as vertical migrators, moving between winter ranges in the lowland and summer ranges at higher elevations (Myserud *et al.* 2011b; Kropil *et al.* 2014). The summer habitat has forage of higher quality, and the red deer start to migrate in the spring to secure prolonged access to newly emerged forage of high nutrition level (Bischof *et al.* 2012; Myserud *et al.* 2012). The red deer usually migrate back to the winter habitats in autumn or early winter (Meisingset 2008). Increasing snow depth and lack of forage can lead to a high energetic cost for red deer staying in the summer areas too long (Schmidt 1993). It is therefore important that they have an optimal timing of the migration. As for other ungulates (Poole & Mowat 2005), avoidance of snow in the high-elevation summer areas is believed to be the ultimate driver of autumn migration in red deer (Luccarini *et al.* 2006), but whether snowfall or frost initiate migration is not known.

In Norway, there has been an almost exponential increase in the number of red deer harvested (Statistics Norway 2015). The population has grown both in distribution and density the last couple of decades (Meisingset 2008). Today, red deer is the ungulate with highest number of

harvested individuals (Statistics Norway 2015), and is thus a species of high economical interest (Olaussen & Mysterud 2012; Skonhoft *et al.* 2013). High red deer density in some areas can, however, represent a significant economic cost to landowners. Red deer frequently cause damage to crops and to productive forest. In the summer areas, the damage is done mainly on pastures, while red deer cause damage to both forest and pasture in winter areas (Meisingset 2008). Several reports have estimated the cost of grazing and browsing damage by red deer (Olaussen & Mysterud 2012; Skonhoft *et al.* 2013), and Thorvaldsen *et al.* (2010) concluded that the overall cost of red deer is very similar to the revenue from hunting. There can, however, be large variation between landowners (Andersen *et al.* 2010).

The traditional timing of hunting season start has been 10th September. In a report from a red deer project studying their habitat use, timing of the autumn migration was found to be around 15th September (Mysterud *et al.* 2011a). The same project examined migration further in the counties Møre og Romsdal and Sør-Trøndelag, and found that 30 % of red deer started migration before the hunting season start on 10th September (Mysterud *et al.* 2011a). Hunters in traditional red deer summer areas at higher elevations could therefore experience the cost of having red deer in the area, while missing the opportunity of harvesting the animals before they migrate (Meisingset 2008). In 2012, the hunting season start was moved from 10th September to 1st September, to meet some of the challenges regarding the migratory behaviour of red deer. One of the goals was to increase harvest success in red deer summer areas (Solberg *et al.* 2014). Whether this change has enabled a more even distribution of cost and benefit, is unknown.

In this master thesis we analysed harvest data from red deer before and after the 10-day extension of hunting season, together with data on temperature, snow and plant senescence. Our aim was to identify factors that affected the annual variation in the number of harvested red deer per municipality and year, along an elevation gradient in the core area of red deer distribution in Norway. We were especially interested in finding the effect of the hunting season change. We hypothesised that the change in hunting season would increase the proportion of harvested red deer at higher elevations. We predicted that more red deer would be available to hunters at high elevations at hunting season start in the period after the change, resulting in an increased harvest compared to before. We also hypothesised that red deer would adjust their timing of autumn migration depending on different cues from the environment, and that this would affect where the deer were shot along the altitudinal

gradient. *First*, we predicted that in years with an early frost (first date with daily mean $<0^{\circ}\text{C}$) red deer would leave summer ranges earlier, resulting in fewer animals harvested at higher elevations compared to years with a late date for first frost. *Second*, in years where the plant senescence started early, we predicted that red deer would begin the autumn migration earlier to prolong their access to high quality forage, reflected in fewer animals harvested at higher elevations. *Third*, as snow makes it difficult to find forage and leads to a high energetic cost for locomotion (Parker *et al.* 1984), we predicted that red deer would move earlier to lower elevations in years with early snowfall, again reflected in a reduced harvest at high elevations compared to low elevations.

Method

Study area

The study area is located along the west coast of Norway (Figure 1). We used data from the counties Nord- Trøndelag (6 municipalities), Sør- Trøndelag (16 municipalities), Møre og Romsdal (24 municipalities), Sogn og Fjordane (24 municipalities), Hordaland (26 municipalities) and Rogaland (8 municipalities).

The topography and climate varies from lower lying coastal areas with milder climate and less snow, to colder inland areas with mountains ranges and more snow (Moen & Lillethun 1998). In the study period (autumn 2000 - 2013), the mean temperature in Sogn og Fjordane for the warmest month (September) was 11.0°C , and 0.8°C for the coldest month (December) (NMI 2015). Mean date for first snowfall was 14th October. In the lowest areas of our study area, the period of snow cover lasts less than 50 days, while the snow cover can last about 150 days at higher elevations (Moen & Lillethun 1998).

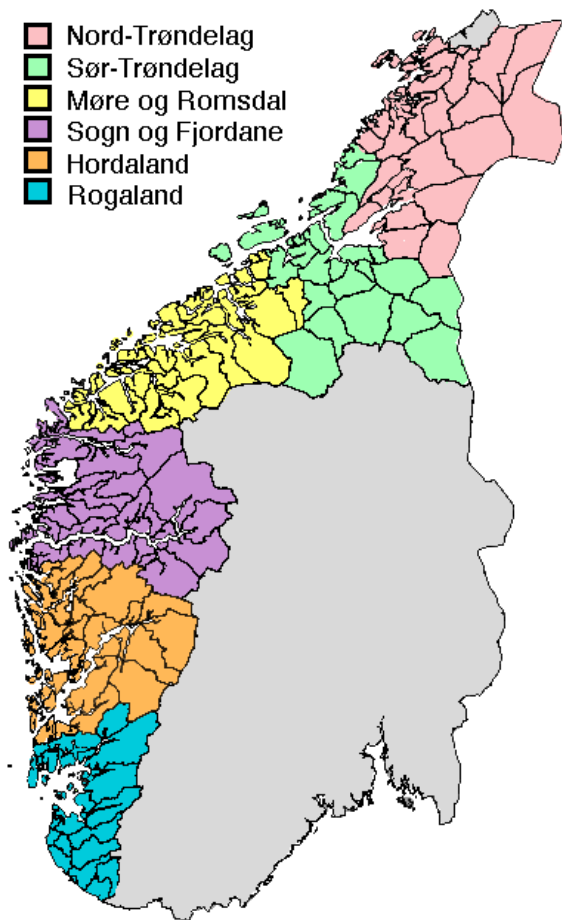


Figure 1: Overview of our study area along the west coast of Norway (coloured areas).

Our study area consists of a mosaic of forested and cultivated areas. The coastal parts of our study area are mostly covered by the boreonemoral zone, dominated by deciduous species such as oak (*Quercus* sp.), ash (*Fraxinus excelsior*), common hazel (*Corylus avellana*), Scots elm (*Ulmus glabra*) and birch (*Betula* sp.) (Moen & Lillethun 1998). The south and middle boreal zone begins further up in the landscape with Scots pine (*Pinus sylvestris*) as the dominating species. At about 800 metres, the alpine zone begins (Moen & Lillethun 1998). Forest plantations, consisting mostly of Sitka spruce (*Picea sitchensis*), occupy a considerable area of our study area (Vadla 2007).

Study species

Our study area is considered the core of red deer distribution in Norway (Meisingset 2008). The population is known to be partially migratory. (Mysterud *et al.* 2011b) found that between 38 % and 77 % (median= 70 %) of the females within our study area performed seasonal migration between summer and winter ranges. The migrants usually move from

high-elevation summer ranges to low-elevation winter ranges in the autumn. Summer areas are roughly between 200 m.a.s.l and 400 m.a.s.l., while winter areas are roughly between 100 m.a.s.l and 200 m.a.s.l. (Mysterud *et al.* 2011b). The length of the migration varies between individuals, but Mysterud *et al.* (2011a) found that the mean distance of seasonal migration in Møre og Romsdal and Sør-Trøndelag was 24.6 km. In the summer the red deer graze on grass, herbs, heather and fresh green shoots, while they prefer rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), willow (*Salix* sp.) and European blueberry (*Vaccinium myrtillus*) in the winter (Meisingset 2008). Red deer forage both in forested areas and in farmland.

Red deer hunting

Compared to other parts of the country, the highest harvest numbers are found in our study area. During the hunting season of 2013-2014 about 93 % (33769 out of 36769 red deer harvested) of the total annual offtake in Norway occurred in this area (Statistics Norway 2015). Within the study area most red deer are shot in Sogn og Fjordane, and Nord-Trøndelag has the fewest harvested red deer (Statistics Norway 2015). Hunting is an important factor controlling the population growth of red deer (Langvatn & Loison 1999), and about nine out of ten red deer born are eventually harvested by hunters (Meisingset 2008).

Hunting occurs both in forest and in farmland areas (Meisingset 2008). Quota are set based on management goals and knowledge about red deer populations in a given area (Meisingset 2008), and are set for calves ($\frac{1}{2}$ year olds), females (1 $\frac{1}{2}$ year olds or older), males (1 $\frac{1}{2}$ year olds or older), and optional animals (Forskrift om forvaltning av hjortevilt 2012). Quotas are distributed among the smallest management units; a geographical area where hunting of red deer is allowed (“vald”) (Forskrift om forvaltning av hjortevilt 2012).

Data

We used R version 3.1.2 (R Core Team 2014) for all statistical analyses.

Data on harvested red deer

Hunters in Norway are obligated to fill out “Seen deer” forms (“Sett hjort” skjema) (Forskrift om forvaltning av hjortevilt 2012). These forms contain information about observed and harvested red deer. Hunters report age (calf, yearling or adult), sex and whether the animal is observed in forest or farmland.

In our analyses we had access to data from “Seen deer” forms from 2000 to 2013. We used data from 1st September to 15th November only. In some municipalities and years the hunting season continued after the 15th November, but to avoid data deficiency we decided to exclude data after this date (Rivrud *et al.* 2014). We removed municipalities and years with zero harvested red deer, because we assumed that this reflected management decisions more than deer density. We also analysed a data set where municipalities that only contributed with harvest data from either the period before the hunting season change or the period after were removed, but this did not qualitatively affect the result, and we decided to keep these municipalities in the data set.

Quota

We had access to harvest quota from 1999-2010 in 11 municipalities only. During this period, the quotas were never filled (median= 79.7 %, 25 percentile= 7.7 %, 75 percentile= 84.9 %). Based on this, we concluded that quotas were rarely limiting the number of harvested deer, and decided to exclude quotas from further analyses.

Weather variables

We used daily data on mean temperature and snow depth extracted from a grid (spatial resolution 1x1 km) covering the study area (<http://www.senorge.no>). Data on mean temperature was available via ftp provided by the Norwegian Meteorological Institute (NMI), Climatology Division (<ftp://ftp.met.no/projects/klimagrid/tam/>), while data on snow depth was provided by the Norwegian Water Resources and Energy Directorate (NVE). The temperature grids were developed using statistical downscaling predicting temperature based on observed temperature records from NMI’s local weather stations. Snow depth was predicted in the same way, based on observed records of precipitation and temperature. From the grid cells covering the individual municipalities, we obtained daily data on temperature and snow depth, and calculated the means within the municipalities.

To investigate threshold values for autumn migration in Norway, we used several measures for temperature and snow (Table 1). For each municipality we extracted the date for the first frost (daily mean below 0°C) and first snowfall within the study period (1st September to 15th November) every year (2000-2013). In several municipalities, the temperatures increased in the days following first frost. To control for this, we calculated the mean temperature over a

seven day period, and extracted the first week with a mean temperature $<0^{\circ}\text{C}$ per municipality and year. We also extracted the dates for first time snow depth exceeded 40 cm, because this is thought to affect ungulate movements (Rudd *et al.* 1983; Sweeney & Sweeney 1984; Sabine *et al.* 2002). If a municipality did not experience any frost or snow during the study period a certain year, frost/snow was set to be at the last day of the year. This was true for 27 observations for first frost, 155 observations for first week with mean temperature $<0^{\circ}\text{C}$, 17 observations for first snowfall and 81 observations for 40 cm snow. We also tried to remove these observations completely in further analyses, but this did not qualitatively affect the results. Because of this, we decided to include the municipalities to avoid systematic loss of municipalities with mild climate in further analyses.

Data on plant senescence

The Normalized Difference Vegetation Index (NDVI) is used in many ecological studies, and makes it possible to assess plant phenology and productivity on a large scale (reviewed in Pettorelli *et al.* (2005)). Chlorophyll in plants absorbs red light (visible light) and leaf cell structures reflects near infrared light (Weier & Herring 2000). NDVI is derived from the ratio between red (RED) and near-infrared (NIR) light reflected from ground surface (Myneni *et al.* 1995):

$$\text{NDVI} = (\text{NIR} - \text{RED})/(\text{NIR} + \text{RED})$$

NDVI values will therefore range from -1 to 1. Green vegetation or dense vegetation will lead to much reflectance of near infrared light and low reflectance of visible red light, and therefore lead to higher NDVI values (Weier & Herring 2000). Areas with little vegetation or bare areas, will have high reflectance of visible red light, and low reflectance of near infrared light, therefore result lower NDVI values. NDVI values near -1 indicate object such as water bodies (Weier & Herring 2000).

NDVI can give measures of rate and start of plant growth and senescence (Pettorelli *et al.* 2005), and has been used in studies to evaluate migration patterns of red deer (Hebblewhite *et al.* 2008; Bischof *et al.* 2012). In our case, we were interested in the change in NDVI during autumn, to assess timing of plant senescence.

A grid with locations spaced 250 metres apart (same resolution as the NDVI raster map) was superimposed on the entire study area, and vegetation type extracted (forest and pasture). The vegetation type was derived from maps provided by the Norwegian Forest and Landscape Institute (Skog og landskap (2007), scale 1:50000). A random subset of 100 locations in forest and 100 locations on pasture was selected per municipality for analysis of NDVI.

NDVI was extracted, processed, scaled between 0 and 1 and smoothed, following the same method as Bischof *et al.* (2012). NDVI time series were constructed based on the images from NASA's MODIS TERRA satellite with spatial resolution 250x250 metres, which were taken 16 days apart. Time series were made for the subsets of the random locations from the year 2000-2013. For these time series, we fitted double-logistic regression models following the green-up and senescence period for each pixel each year (Beck *et al.* 2006; Hird & McDermid 2009). For further details on extraction, processing and curve-fitting of the NDVI-data, see Bischof *et al.* (2012).

Three parameters expressing plant senescence were obtained from the double-logistic regression curves (Figure 2); the start of plant senescence, mid-senescence (the inflection point of the curve) and the rate of senescence (the number of days from mid-senescence and $\frac{1}{4}$ upwards or downwards on the curve) (Beck *et al.* 2006; Bischof *et al.* 2012). The mean of these parameters for each municipality per vegetation type and year was calculated.

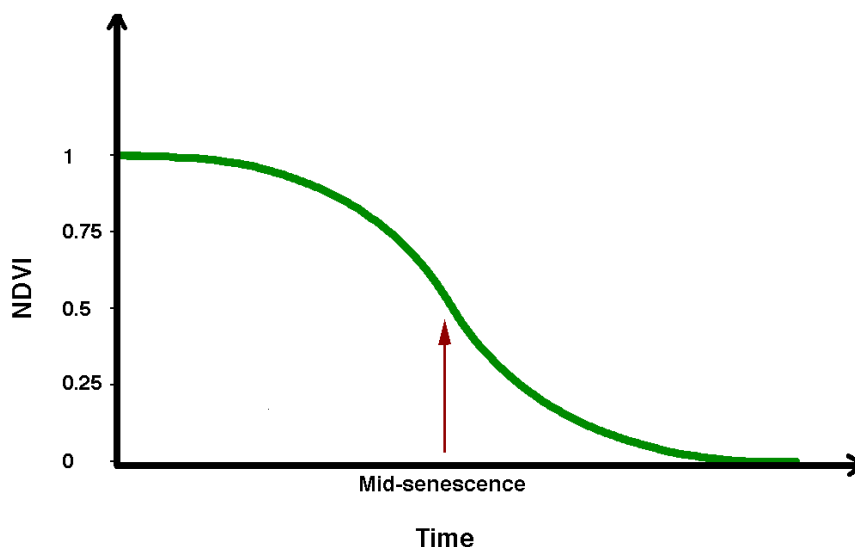


Figure 2: The autumn part of a theoretical normalized difference vegetation index (NDVI) logistic-regression curve over time. NDVI values vary from 0 (barren land) to 1 (dense green vegetation). Mid-senescence is the inflection point where the rate of senescence is the greatest. The figure is based on information from Beck *et al.* (2006) and Bischof *et al.* (2012).

Because of high correlation ($r=0.80$, $p < 0.05$) between the NDVI-variables for forest and pasture, we decided to use data from forest habitat only (Table 1). We used the date for mid-senescence to express timing of plant senescence, because of the high correlation ($r=0.71$, $p < 0.001$) with the date of senescence start.

Table 1: Overview of variables used in the analyses.

Group	Name	Explanation	Type
Response variable	Total harvest	The total number of red deer harvested in the study area.	Continuous
Period	Before	Period before hunting season change, hunting season start 10. September (2000-2011).	Categorical
	After	Period after hunting season change, hunting season start 1. September (2012-2013).	Categorical
Weather variables	First frost	First day with mean temperatures under 0°C.	Continuous
	7-day mean frost	First week with a mean temperature under 0°C.	Continuous
	First snow Snow depth 40 cm	First day with precipitation as snow. First date snow depths was 40 cm.	Continuous Continuous
NDVI variables	Mid-senescence	The date halfway through plant senescence.	Continuous
	Rate of plant senescence	Number of days from mid-senescence and ¼ up or down the curve.	Continuous
Elevation	Elevation	Mean elevation in each municipality. Metres above sea level.	Continuous
	Elevation squared	Square of the variable 'Elevation'.	Continuous

Statistical analysis

We used the Generalized additive models (GAM); fitted with the function 'gam' in the R-package mgcv (Wood 2006), to explore potential non-linearity in the relationship between the number of red deer harvested (response variable) and elevation (explanatory variable) (Crawley 2012). The relationship was clearly bell shaped, and we therefore continued with modelling the effect of elevation as a second order polynomial in a generalized linear model (GLM). GLMs have the added value of enabling interaction effects in the model.

Standardisation of variables by scaling

We standardised elevation using the function 'scale' in R. We also calculated the square of the scaled elevation. Setting the mean to 0 and variance to 1 allowed us to more easily

compare the effect sizes of the variables and for computational ease of incorporating both a first and a second order effect of elevation.

To control for municipality as a spatial component, we also scaled weather and NDVI variables separately for each municipality. This was done because the climate varies from coastal areas to inland areas, so that early and late frost and snow would be dominated by geographical variation. When scaled separately for each municipality, as done in our case, the values instead indicate whether the dates for frost, snowfall and NDVI were early or late for that particular municipality.

GLM and GLMM

The GLM was fitted using the ‘glm.nb’ function in R, with log as a link function (Venables & Ripley 2002) because the response variable was heavily skewed towards a small number of harvested red deer, and was assumed to follow a negative binomial distribution. We started with a model including elevation and elevation squared, period, weather variables and NDVI variables (for details, see Table 1), and their interactions with the elevation variables. To find the most parsimonious model, we performed backwards selection based on maximum likelihood using the ‘anova’ function in R (Crawley 2002). We removed the least significant interactions first. Non-significant main effects were removed if no interactions involving the main effect were left in the model.

There was a large variation between municipalities regarding the number of harvested red deer and the number of years available. To address the importance of municipality, we performed two types of analyses. *First*, we conducted a variance component analysis using the function ‘varcomp’ in the R-package ape (Paradis *et al.* 2004) to estimate the proportion of the total variance explained by municipality. The function is only implemented for normally distributed response variables, and was thus not optimal when analysing our negative binomially distributed data. Although not correct, it does give a good indication of how much of the variation in the data that is due to spatial variation (municipality). *Second*, we extended the GLM to a generalised linear mixed model (GLMM) with a negative binomial distribution, fitted with the R-package glmmADMB (Bolker *et al.* 2013). The GLMM has the same properties as GLM, but also gives the opportunity to add a random term (Bolker *et al.* 2009). In the GLM, parameter estimates could be disproportionately affected by municipalities with a large number of harvested red deer and/or hunting seasons. By adding

municipality as a random intercept in the GLMM, we incorporated the effect of variation between municipalities and reduced this bias (Pinheiro & Bates 2000).

We began with the same start model in the GLMM as in the GLM, and performed model selection following the same method as for the GLM described above. Predicted effects from the best GLM was compared with predicted effects from the best GLMM, to evaluate the effect of allocating the spatial variation captured by municipalities into a random term.

Results

Trends in the raw data

During our study period, the number of harvested red deer has generally increased in all the counties in the study area (Figure 3). Sogn og Fjordane had the largest number of harvested red deer during the entire period, and Nord-Trøndelag had the smallest number.

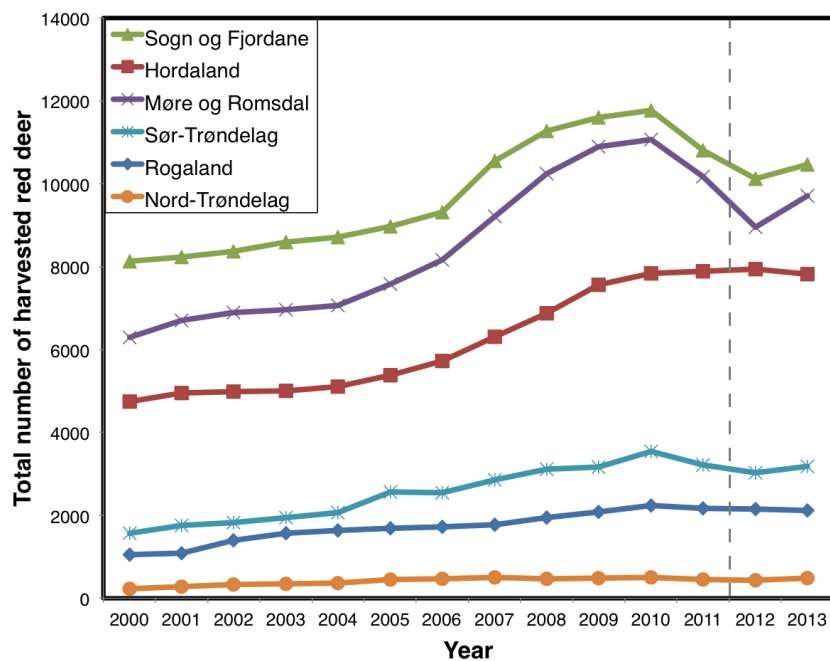


Figure 3: Overview of the total number of harvested red deer per county in the study area from 2000 to 2013. Dotted grey line indicates the shift in hunting season start.

When comparing the total number of harvested red deer in the study area in 2011 (the year before the change in the hunting season) and 2012 (the first hunting season after the change),

there we found a difference in the number of animals harvested in higher elevated areas and lower elevated areas (Table 2).

Table 2: The number of harvested red deer in the year before the hunting season change (2011) and after (2012) in high elevated municipalities and low elevated municipalities.

Year	Elevation	Total harvest
2011 (Before change)	Above 500 m.a.s.l.	6362
	Under 500 m.a.s.l.	6103
2012 (after change)	Above 500 m.a.s.l.	6575
	Under 500 m.a.s.l.	5402

In municipalities with mean elevation above 500 m.a.s.l., the number of harvested animals had increased with 3.3 % in the number of harvested red deer in municipalities with mean elevation below 500 m.a.s.l from 2011 to 2012. The proportion of harvested animals in higher elevated municipalities increased with 7.6 % from 2011 to 2012. Therefore, from 2011 to 2012 our raw data indicated a small redistribution of harvested red deer from lower elevated areas to higher elevated areas.

Factors affecting the distribution of harvested red deer

Generalised linear model

We analysed a final data set consisting of 585 hunting seasons divided between 88 municipalities from year 2000-2013. The interaction between elevation and period, and the main effects of period, elevation and the squared elevation were the factors affecting the total number of harvested red deer per municipality and year in the final GLM (Table 3).

Table 3: Factors affecting the total number of red deer harvested from 2000-2013 in the study area. Estimates are derived from the GLM analysis.

Variable	Estimate	SE	Z value	P value
Intercept	5.62749	0.05775	97.449	< 2e-16
Period (before vs. after)	-0.16876	0.08817	-1.914	0.05561
Elevation	0.24258	0.04821	5.031	4.87e-07
Elevation squared	-0.53129	0.03685	-14.417	< 2e-16
Period x Elevation	0.23243	0.08713	2.667	0.00764

The main effects of elevation and elevation squared were significant (Table 3). More red deer were harvested at intermediate elevation, compared to low and high (Figure 4). The main

effect of period was almost significant, but whether or not more red deer were harvested in the period before the change compared to the period after, depended on elevation (Table 3). The significant positive interaction between period and elevation (Table 3) indicated that there has been a change in the distribution of red deer harvested along the altitudinal gradient. As predicted, the peak of harvested red deer per municipality and year moved towards higher elevations after the change of hunting season start (Figure 4). The number of harvested red deer peaked at ~580 m.a.s.l before the 10-day extension, compared to ~655 m.a.s.l. after the change. At low elevations (~262 m.a.s.l, first quantile) the predicted number of harvested animals before 2012 was 163 (varied between 153-173), compared to 115 (varied between 104-126) after 2012. At the mean elevation (~500 m.a.s.l.) the predicted number of harvested animals was 279 (varied between 263-295) before 2012, and 236 (varied between 216-256) after. At higher elevations (~900 m.a.s.l, third quantile) the predicted number was 172 (varied between 160-184) before hunting season change and 192 (varied between 169-215) after the change. The GLM therefore predicted a small increase in the number of red deer harvested at higher elevations in the period after the change of the hunting season, but a decrease in harvested deer in lower elevated areas.

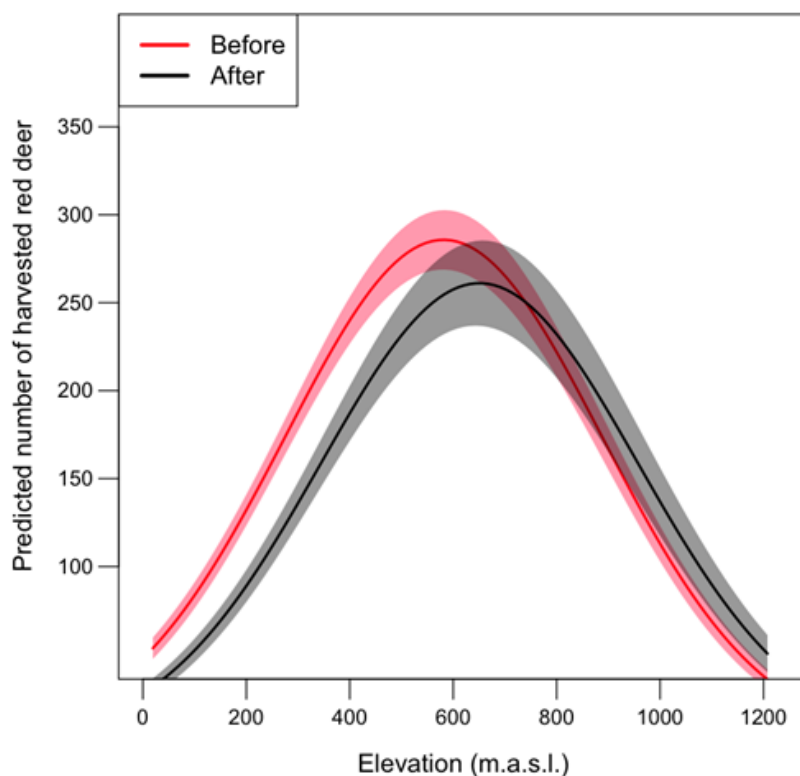


Figure 4: The predicted number of harvested red deer per municipality and year in the study area as a function of elevation. The results are shown with upper and lower limit of standard error. Harvested deer before the hunting season was moved from 10th September to 1st September are shown in red, harvested red deer after the change are shown in black. The predicted values are derived from the generalised linear model.

We did not find support to include any of the weather or plant senescence variables in our final model ($p > 0.13$). Contrary to our predictions, we did not observe a shift in animals harvested at high elevations compared to low elevations that could be explained by snow, temperature or plant senescence in the GLM analysis. The distribution of harvested animals along the elevation gradient did therefore not reflect the migratory patterns we expected to find.

Variation between municipalities - inclusion of a random intercept

The variance component analysis showed that municipality as a random term explained 77.3% of the variation in the data. The analysis indicated that most of the variation in the total harvest numbers was explained by variance between municipalities, and not by variance within each municipality over time. Our data was highly unbalanced, with large variations in the number of years and the total number of harvested red deer in the different municipalities, which could explain the importance of the spatial variation between municipalities found in the variance component analysis. Because of the unbalance in the data and the results from the variance component analysis, we decided to include the results from the GLMM with municipality as a random intercept.

Our results changed when we included municipality as a random term in the GLMM. The variables affecting the total number of red deer harvested were the same as for the GLM, but also included the main effects of plant senescence and first frost, and the interaction between first frost and elevation (Table 4).

Table 4: Factors affecting the total number of harvested red deer in 2000-2013 in the study area. Estimates are derived from GLMM analyses with municipality as a random intercept.

Variable	Estimate	SE	Z value	P value
Intercept	4.6781	0.1782	26.26	< 2e-16
Period (before vs. after)	0.1038	0.0527	1.97	0.04875
Elevation	0.3398	0.1388	2.45	0.01440
Elevation squared	-0.3460	0.1196	-2.89	0.00382
First frost	0.0223	0.0262	0.85	0.39442
Mid- senescence	-0.0790	0.0237	-3.34	0.00085
Period x elevation	0.0961	0.0526	1.83	0.06767
First frost x elevation	-0.0448	0.0253	-1.77	0.07663

Contrary to the GLM, the GLMM predicted that more red deer were harvested in the period after, compared to before. The interpretation of this is that for the average municipality there has been a marginal increase in number of shot deer, and that the results from the GLM were influenced by imbalanced data in space and time across municipalities. The interaction between period and elevation was almost significant, and indicated that there was a trend towards changed distribution of harvested red deer along the elevation gradient. Similar to the GLM results, the peak of harvested red deer moved towards higher elevations after the change of hunting season start (Figure 5). The peak was at ~665 m.a.s.l before the 10-day extension, and at ~705 m.a.s.l. after. At lower elevations (~262 m.a.s.l., first quantile) the predicted number of animals harvested was 67 (varied between 54-83) before the change, and 69 (varied between 52-86) after the change. At ~500 m.a.s.l. the predicted number of harvested red deer was 109 (varied between 91-130) before the change of the hunting season start, and 121 (varied between 101-145) after. At higher elevations (~900 m.a.s.l., third quantile) the model predicted harvest numbers of 95 (varied between 26-226) before the change, and 119 (varied between 33-248) after the change. The GLMM therefore predicted a small increase in the number of red deer harvested at higher elevations and more or less no change in the lower lying areas.

We found no support to include snow or rate of plant senescence in the final model ($p > 0.3222$). First frost and mid-senescence were retained in the final GLMM after model selection, but not in the way we predicted (Table 4). There was a trend indicating that a higher proportion of the harvested red deer was shot in high-elevated municipalities in years with early first frost compared to years with late first frost (Figure I, appendix). This was the opposite of what we predicted. There was also a significant negative effect of timing of autumn on the numbers of red deer harvested (Figure II, appendix). Fewer animals were harvested in years when time of mid-senescence was late, compared to years with early time of mid-senescence.

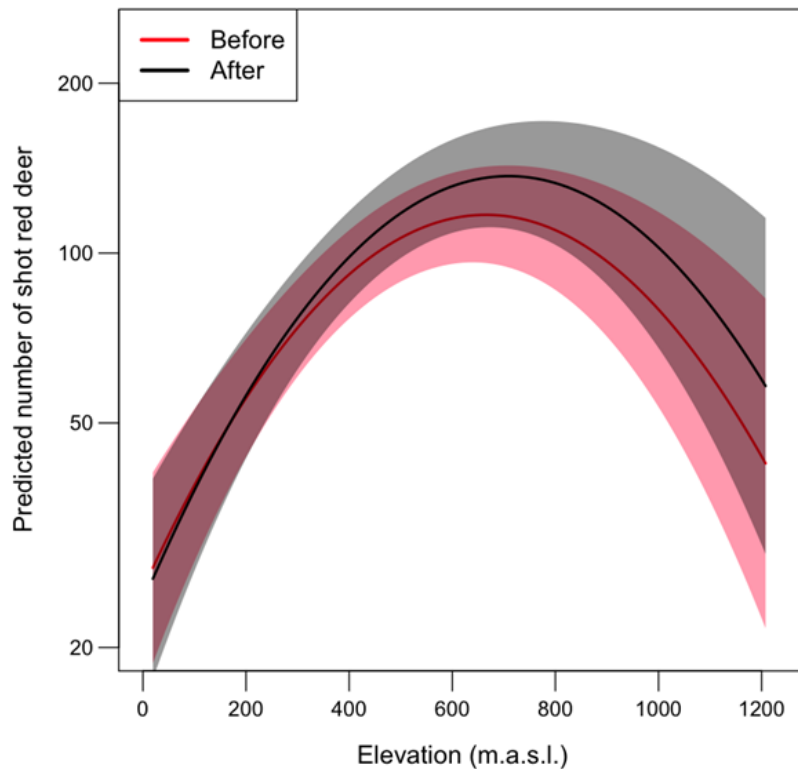


Figure 5: The predicted number of harvested red deer in the study area per municipality and year as a function of elevation. The results are shown with upper and lower limit of standard error. Harvested deer before the hunting season was moved from 10th September to 1st September are shown in red, harvested red deer after the change are shown in black. The y-axis is log transformed based on generalised linear mixed models, with municipality as random intercept.

Discussion

In this study we found that by moving the start of the red deer hunting season from 10th September to 1st September, the proportion of animals harvested at higher elevations increased. The effect found was relatively small, but matched the proportion of individuals migrating between 1st and 10th September. By allowing hunters to begin harvesting earlier, hunters at higher elevations are able to harvest the animals that spend the summer in their areas before they migrate to lower elevations. This means that the hunters are able to benefit from the same animals that potentially cause grazing damage on agricultural areas during summer. Contrary to our predictions, the distribution of harvested red deer along the elevation gradient was not affected by variation in autumn weather and plant senescence in a way that might reflect migration. Our study provides evidence that changing the timing of the hunting season affected the distribution of harvested animals along an altitudinal migration gradient.

Timing and length of hunting season

By moving the start of red deer hunting season from 10th September to 1st September, there was a redistribution of harvested red deer towards higher elevations in accordance to our predictions. The goal of the change in hunting season was to be able to better control the red deer population, and give hunters in typical red deer summer areas an opportunity to harvest animals before autumn migration (Meisingset 2008; Solberg *et al.* 2014).

Our statistical analyses predicted a small change in distribution of harvested red deer along the altitudinal gradient after the 10-day extension of the hunting season. Although the effect was small, this was not surprising. About $\frac{2}{3}$ of the red deer population perform seasonal migration (Mysterud *et al.* 2011b). Mysterud *et al.* (2011a) states that about 20 % of the red deer in the counties Møre og Romsdal and Sør-Trøndelag had already started autumn migration before 1st September. Ten days later (10th September) the proportion of animals that had started the migration had increased to 30 %. The potential increase in the proportion of harvested animals in high-elevated municipalities was therefore ~ 7 %. When comparing harvest numbers in the year 2011 and 2012 (the year before and after the change of hunting season start) we found an increase of 7.6 % in the proportion of harvested animals in high-elevated municipalities. The increase found in our raw data was therefore very similar to the potential increase in proportion of red deer migrants in higher elevated areas. Although the potential increase of available game in higher elevated areas was limited, it seems that the extension of the hunting season has been a successful management strategy, as it looks like the hunters have responded to the extended hunting season by harvesting more red deer before they migrate.

We did not find any evidence that the 10-day extension of the hunting period resulted in more animals shot at lower lying municipalities. The proportion of stationary animals can be quite high. Mysterud *et al.* (2011b) found that between 23 % and 62 % of the female red deer in Sogn og Fjordane and Sør-Trøndelag were stationary. It is therefore not unlikely that these animals may act as a buffer in the winter areas, by allowing hunters in winter areas access to game early in the hunting season before migrants arrive. In addition, an extension of hunting season can lead to an increase in the number of animals harvested (Sunde & Asferg 2014). In our study area, quotas were rarely filled (median = 79.7 %), and it is unlikely to be a limiting factor for hunting in most areas. Under these circumstances, we would expect that there is a potential for an increase in harvest also in lower lying areas. There are, however, other factors

that might explain why we did not detect an increase in harvested red deer in these areas. *First*, the hunting statistics show a small reduction in the number of harvested red deer in recent years (Figure 3), which may indicate a decline in the red deer population, and thus explain the lack of increase. *Second*, variation in hunting effort could affect the patterns in the distribution of harvested red deer we observed. Hunters may adjust their hunter effort in response to animal abundance, by increasing effort at lower population densities (Van Deelen & Etter 2003). It is possible that an increase in hunter effort in periods and areas with low densities of red deer may masque the distribution skew of animals during the autumn migration. It is also possible that old habits have coloured the hunters' effort, and therefore they did not respond immediately to the hunting season change. This is however unlikely, as Solberg *et al.* (2014) found that hunter effort was highest in the first week after hunting season start 1st September. *Third*, because quotas are rarely filled, hunters may have their own aim (often lower than the quota), after which they are satisfied and hunter effort declines. We did not include hunter effort in our analyses, and therefore we could not determine if this has changed in a way that could explain the trend we found. Despite the potential for increased harvest also in low-elevated municipalities, we did not observe any increase in these areas. Therefore, it is likely that the date of hunting season start and length of the hunting season were not limiting factors in low elevation areas.

Effects of weather and plant senescence

We hypothesised that annual variation in autumn weather and plant senescence would affect the timing of autumn migration, and therefore the distribution of harvested red deer along the elevation gradient. Although we used variables known to affect migration in large ungulates (e. g. Albon and Langvatn (1992); Sabine *et al.* (2002); Ramanzin *et al.* (2007); Fieberg *et al.* (2008)), this did surprisingly not give the expected results in our study. In the GLM we did not find that any of these variables affected the number of red deer harvested. Our results from the GLMM suggested a trend that annual variation in autumn temperature affected the total number of red deer harvested along the elevation gradient, but showed the opposite effect of what we predicted. Thus, we found limited support for our hypothesis.

Though both temperature and plant senescence was included in our GLMM analysis, they did not seem to reflect migratory patterns in the altitudinal harvest distribution. The trend we found on temperature indicated that more red deer were harvested at higher elevations in years when the date for first frost was early. The date for first frost correlated with the first

seven day period with temperatures below 0°C, indicating that an early date for first frost was followed by a generally cold autumn. Rivrud *et al.* (2014) found that red deer were more likely to move into farmland during periods with lower temperature, where the possibility of being harvested was higher than in forested habitat. It is possible that this could be a part of the explanation of the trend we observed, if red deer at higher elevations are more inclined to move into farmland in colder periods, compared to red deer at lower elevations. However, we have not been able to find any studies confirming this. A more likely explanation may be that red deer move into open habitat to find forage when forage availability decreases. The annual variation in plant senescence in forest habitat did not affect the number of red deer harvested along the elevation gradient. However, there was an increase in the number of harvested animals in general in years with early autumn. When forage availability decreases, we would assume that red deer move to pasture with greater access to forage (Albon & Langvatn 1992). In such open habitats, it is easier for the hunters to spot the red deer, and the harvest risk is higher (Meisingset 2008; Rivrud *et al.* 2014). Therefore, the effect of temperature and plant senescence probably reflect an increased hunter success because these factors may force the red deer to use habitat where they are more exposed, rather than reflecting migratory patterns.

We were not able to confirm our hypotheses on the effects of the weather and plant senescence variables on the spatiotemporal variation in harvested red deer along the altitudinal gradient. While these factors do not seem to work as triggers for migration, they are crucial for red deer survival (Loison & Langvatn 1998). Because access to high-quality food is important when winter is closing in, it could be fatal for the red deer to be trapped in areas with poor forage availability. Albon and Langvatn (1992) found that plant quality had a more pronounced decline at higher elevations during autumn compared to low-lying areas. Therefore, it could be beneficial for red deer to move to lower elevated areas before plant quality declines. Increased snow depths can also make it more difficult to find forage, in addition to make it tougher to move, and lead to higher energy expenditure (Parker *et al.* 1984). It is therefore probably important for the red deer to leave high-elevated areas before such problems arise. According to Mysterud *et al.* (2011a), over 75 % of GPS-marked red deer in Sør-Trøndelag and Møre og Romsdal had already started the autumn migration before 2nd October. Because the mean date of first snow in our study period was 14th October, and mean date for highest rate of plant senescence was 12th October, most animals had already started their migration before this point in time. Therefore, it is unlikely that the red deer in our study area respond to snow and plant senescence as an autumn migration trigger, but

instead use other cues to time their migration to the winter areas to avoid being trapped in an unfavourable habitat. As both plant senescence and snow limits food availability, it is possible that red deer leave the summer areas before these factors even become relevant, explaining why we did not find an effect of these variables.

The importance of spatial and temporal scale

The spatial and temporal scale used in our study is an important factor determining the results. Because our data consisted of harvested red deer per municipality per year, we did not have the opportunity to examine the number of harvested red deer at smaller spatial and temporal scales. Although we were able to confirm that an earlier hunting season increased the harvest share of high-elevated municipalities, we did not find evidence for our second hypothesis. It is possible that a smaller scale would have been able to capture a more detailed picture of the spatiotemporal variation of harvest data. *First*, a finer spatial scale could have allowed us to investigate harvest patterns caused by migration within the different municipalities. Migration distances vary from a couple of kilometres to over 100 kilometres (Mysterud *et al.* 2011a), and it is not unlikely that animals can have summer and winter areas within the same municipality. Mysterud *et al.* (2011a) found that the average red deer annually used 5 management units (“valds”), but only 1.7 municipalities. Therefore, at the spatial scale we used, movement patterns such as this will not be captured in the analyses. Hunting data are reported at management unit level, but maps of these units are not available digitally, and were thus not accessible to us in this study. Although elevation can be used indicator of summer and winter areas, it does not reflect reality perfectly. Detailed information about migration routes would make it possible to separate summer and winter areas, without having to use elevation as an indication of such areas. GPS-data could have given us information about pairs of summer and winter areas, and therefore increased the precision of our study. *Second*, a finer temporal scale would have allowed us to examine the daily variation of harvested animals. For example, how changes in weather in high-elevated places one day, could have had an impact on harvested animals in lower-laying areas a few days later. It is not obvious that a finer temporal resolution would be beneficial. As hunters may alter their effort depending on for example the weather or the day of the week, a finer temporal scale may lead to a bias towards certain days or periods (Solberg *et al.* 2014). This could therefore confound the results, and not necessarily reflect the seasonal movements of red deer.

Understanding the similarities and differences between the models

Our data set consisted of highly unbalanced data, both in number of harvested red deer in the different areas, and in available years before and after the change of hunting season. GLM is a simpler model than the GLMM, and therefore reflected the distribution of the raw data to a greater extent than GLMM, without taking confounding spatial or temporal patterns into account. In the GLM, municipalities with a large number of harvested red deer, or many years of data, will contribute disproportionately to parameter estimates compared to municipalities with few harvested animals or years. It is possible that municipalities may have responded differently to the hunting season change, and that this might also be a part of the variation between municipalities. Because the variance component analysis indicated that municipality explained a lot of the variation in the data, we wanted to include municipality as a random intercept in the GLMM. By doing this, we controlled for the differences in the number of harvested red deer and years between municipalities, leading to a more even contribution of the municipalities to the parameter estimates (Pinheiro & Bates 2000). Both the GLM and GLMM indicated that the peak of harvested red deer shifted towards higher elevations, but the effect of the change was stronger and more statistically significant in the GLM. The effect of hunting season change was a trend in the GLMM, and indicated that there has been an increase in the harvest at higher elevations, while areas at lower elevations have not been affected. Because the GLMM controls for the spatial variation between municipalities, the estimated effect of the change of hunting season found in the GLMM, should therefore reflect temporal variation to a greater extent than the GLM.

If both high-elevated and low-elevated areas had had a similar harvest response within their groups after the hunting season change, we would expect that more of the variation in harvested red deer would have been explained by the interaction between elevation and period, than what we observed in the GLMM. Because this was not the case in our analyses, it is possible that in addition to large variation in harvest between municipalities, the municipalities may have responded differently to an earlier hunting season start.

We believe that the GLMM shows a more isolated effect of the change in hunting period than the GLM, and thus give a more correct result of the redistribution of harvested red deer along the elevation gradient. Although the effect of the change was small in the model, the fact that the effect was still present and nearly significant even after we controlled for the large

variations in the data, indicates that our findings reflect an actual change in harvest distribution.

Implications for management

Adjusting hunting season could lead to changed distribution of hunting revenue of migrating species. Heusmann and McDonald (2002) found that an extension at the beginning of wood duck hunting season increased harvest in summer areas, most likely because of an increased opportunity to harvest the ducks before autumn migration. Through economic modelling, Skonhøft and Olaussen (2005) found that by allowing an extended hunting season on partially migratory moose in Scandinavia, there was a redistribution of harvest in a way that evened the costs (browsing damage) and benefits (hunting revenue) among landowners. Similar to these studies, we found a redistribution of harvested red deer in Norway after a 10-day extension at the beginning of hunting season. An earlier hunting season start seems to have led to an increased harvest of red deer at higher elevated summer areas, and could be an important management decision to ensure a more even distribution of the hunting revenue of the species between summer and winter areas. Whether summer or winter areas are favoured by a change in hunting season, depends on the timing on the extension. If the goal is to increase harvest revenue in summer areas, it could therefore be beneficial to extend the hunting season early in the season, as was the case in our study. If the goal is to increase harvest revenue in winter areas, the extension should be at the end of the hunting season (Heusmann & McDonald 2002; Skonhøft & Olaussen 2005). We believe that adjustments of the hunting season could be a useful tool for management of migrating species, by allowing hunting season to follow animal movements.

While manipulating hunting season length and timing can be an important tool to obtain management goals, i.e. regulate animal abundance (Christensen & Hounisen 2014) and increase hunting revenue (Heusmann & McDonald 2002; Sunde & Asferg 2014), it can also have unwanted effects on the hunted population. Conner *et al.* (2001) found that the timing of seasonal migration in elk was affected by the timing of hunting season start. An earlier hunting season start led to more elk migrating from summer to winter areas earlier than in periods with late hunting season start. It is possible that the small increased harvest we observed in high-elevated municipalities after the change will disappear with time, if red deer react to an earlier hunting season by migrating earlier. In addition, because the red deer calves can still be quite young in September, it is important to evaluate the consequences of

beginning the hunting season earlier. While the mean date for calving is 17th June, it can vary from early spring to mid autumn in more extreme cases (Loe *et al.* 2005; Meisingset 2008). The calves are weaned in September/October, but they usually follow the hind their entire first year (Meisingset 2008). However, it can be difficult for a hunter to determine whether a hind has a calf or not, and to discover the calf if they are apart. It is possible that an earlier hunting season could increase the chance of shooting a hind without finding the calf first, and therefore risk leaving a calf without its mother. While this may be the case for calves born unusually late, we do not believe the 10-day extension will have any pronounced effect on the probability of discovering most calves. However, considering the relatively small effect of the hunting season change, it is important to acknowledge the implications this change has on the red deer population. If the earlier start will change the migratory behaviour of the animal, or increase the chance of shooting the hind from its calf, these consequences should be weighed against the increase in hunting revenue.

Adjusting the size of management units to better match animal space use could be another way to even cost and benefits of a species. A challenge in many European countries is that management areas are too small compared to the actual space use of ungulates (Apollonio *et al.* 2010). However, making management units larger can be difficult. Landowners may have different goals regarding the ungulate population on their land, and a high level of cooperation would be needed to accomplish successful management (Skonhøft 2005; Apollonio *et al.* 2010). A detailed understanding of the migratory behaviour of ungulates is essential to effectively manage the game species in a fair and sustainable way. Adjusting the management units to capture more of the migration gradient could also be an important step in ensuring a more accurate hunting success in relation to hunting goals and quotas (Jarnemo 2008; Meisingset 2008; Mysterud *et al.* 2011a).

Further research is needed to evaluate the effects of the change in red deer hunting season start, especially because the small effect observed could change with time. In addition, because harvest data did not seem to capture triggers of autumn migration in this study, it could be interesting to see if triggers could be found by using a smaller spatial scale. To be able to examine the results of management decisions is crucial, because this gives the opportunity to adjust management actions to ensure that goals are obtained. Our study gives insight to the effect of a management decision made to even the cost and benefits of a

migratory ungulate. This is an evaluation of how an implemented management action has worked, which is an important part of adaptive management (Allen *et al.* 2011).

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Appendix

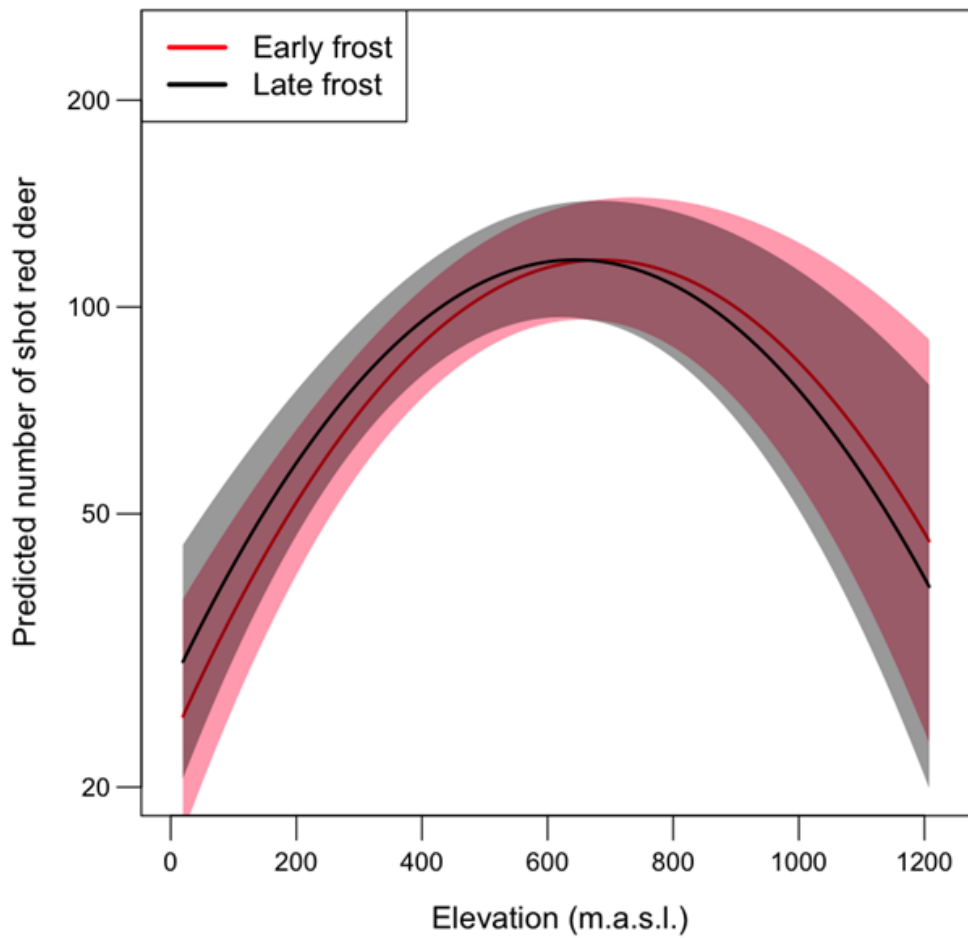


Figure I: The predicted number of harvested red deer in the study area per municipality and year as a function of elevation. The results are shown with upper and lower limit of standard error. Harvested deer in years with early frost are shown in red, years with late frost are shown in black. The y-axis is log transformed based on generalised linear mixed models, with municipality as random effect.

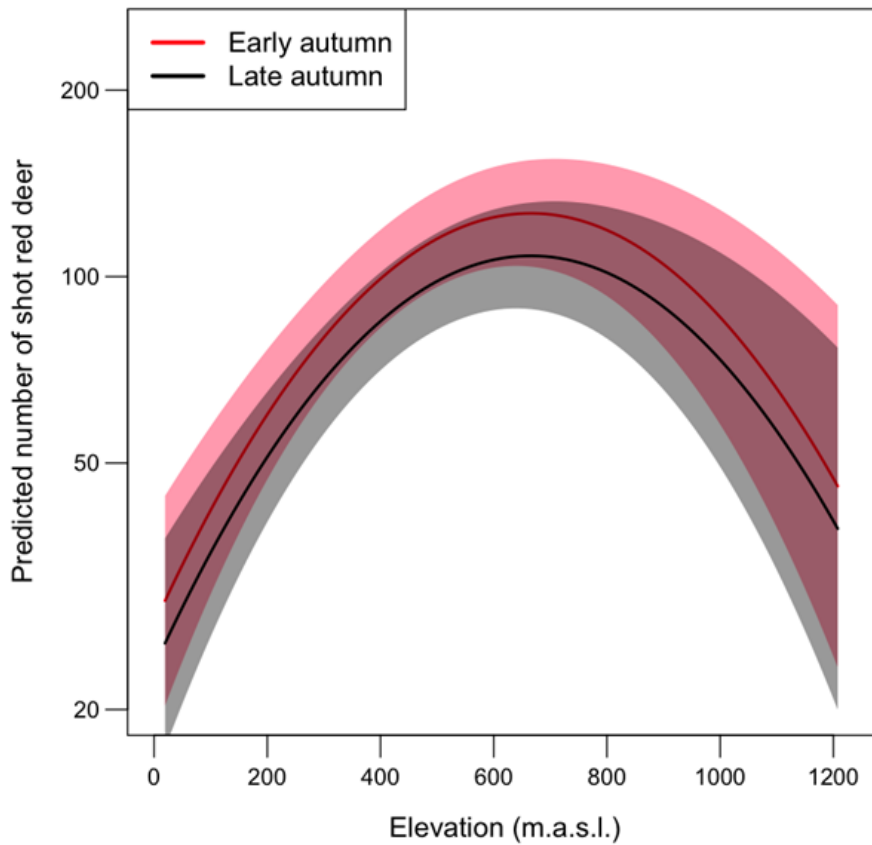


Figure II: The predicted number of harvested red deer in the study area per municipality and year as a function of elevation. The results are shown with upper and lower limit of standard error. Harvested deer in years with early autumn are shown in red, harvested red deer in years with late autumn are shown in black. The y-axis is log transformed based on generalised linear mixed models, with municipality as random effect.



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