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Examensarbete i ämnet biologi
Department of Wildlife, Fish, and Environmental studies
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Abstract

Factors predicting moose body condition in Sweden were investigated by means of dressed weight from shot animals and combining a range of potential explanatory variables from public national databases. There were significant differences between regions, sexes and age-classes with considerable variation between years and moose populations. Population sex ratio (male:female) and ungulate species richness (number of sympatric ungulate species present) were highly relevant in the models for the northern region, while densities of other ungulates (red deer, fallow deer, roe deer, wild boar) and human disturbance were significantly correlated with moose body mass in southern Sweden. Calf weights seemed to be mainly associated with abiotic factors like latitude and altitude and also with land use proportions such as available area of transitional habitat (wood-shrub, including young forests and clear-felled areas). Adult moose weights, in turn, were significantly correlated with interspecific variables and population sex ratio. Variation between moose populations was high. As a general trend, relationships in northern Sweden were mostly explained by fewer variables with higher consistence between age-classes. My results indicate that predictability is decreased by climate change creating complexity in food availability, and that managers should try to improve moose sex ratio and continue developing multispecies management approaches in order to maintain a Swedish moose population of high quality.

Key words: moose condition, body mass, multispecies, ungulate, database.

Introduction

It is a general trend in (northern) Europe that ungulate species are growing in numbers and extending their distribution (Apollonio et al., 2010). Along with that, damages to forest trees and agricultural crops by those species are increasing and correspondingly the species' conflict potential (Apollonio et al., 2010). In Sweden, there is a movement from often "moose-centred" single species management towards ecosystem management considering the entire ungulate community (and beyond), a necessary development in order to follow the Malawi principles (Jaren et al., 2003). Despite these tendencies, multi-species interactions in Nordic conditions have so far rarely been discussed in the scientific literature.

This work is an attempt to understand the interactions between northern ungulate species at a landscape level. Applying publicly available data from national databases, I investigate how other ungulate species and additional factors such as climate and available habitat relate to moose *Alces alces* body condition across Sweden, using body mass as an indicator.

Body mass is a key life history parameter in ungulates. It affects population dynamics and fitness of individuals by influencing reproduction, survival and competitive abilities (Mysterud et al., 2001a; Mysterud et al., 2001b): In female moose, body size is strongly correlated with fecundity and onset of reproduction (Saether and Heim, 1993; Sand, 1996; Garel et al., 2009). Reproductive success is higher for heavier males (Malmsten et al., 2015) and (juvenile) overwinter survival increases with body mass (Bonenfant et al., 2009).

Apart from moose, the Swedish ungulate species system consists of roe deer *Capreolus capreolus* occurring in most parts of the country, red deer *Cervus elaphus* and fallow deer *Dama dama* with more scattered populations mainly in the South, and wild boar *Sus scrofa,* which re-colonized Sweden in the 1980's and has after an initial exponential growth phase established stable populations in most of southern Sweden (Lemel, 1999; Tham, 2004). Although their growth rate has stabilized, wild boars continue to increase their range northwards (Apollonio et al., 2010). In addition to those species, mouflon *Ovis orientalis* is present in small local populations (Apollonio et al., 2010) and therefore not considered in this work. As in several other European countries, populations of large predators (mainly wolf *Canis lupus*, lynx *Lynx lynx* and brown bear *Ursus arctos*) are increasing in Sweden (Apollonio et al., 2010). However, including the effect of those species on moose condition would go beyond the scope of this work wherefore I refer to the already existing publications on the subject (see e.g. Olsson et al. (1997); Swenson et al. (2007); Gervasi et al. (2012); Sand et al. (2012); Wikenros et al. (2015)).

Moose management in Sweden on an ecosystem level is organised in moose management areas (MMAs) (Lindqvist et al., 2014). In my study, these MMAs serve as sample units. I investigate the importance of the following factors and their interplay on moose weight:

(1) Intraspecific, i.e. density-dependent factors, including sex (male/female) and age-class (calf/adult), sex ratio of adult moose (male:female) and moose density (with bag size, number of traffic accidents and moose observations per man-hour as density indicators).
Male moose are expected to be heavier than females in both age-classes (Cederlund et al., 1991; Sand et al., 1995; Solberg et al., 2007). I hypothesize that low sex ratios are connected to lower body masses especially in adult males, as males tend to breed

earlier in life under such conditions, retarding body growth in favour of the energetically expensive rut (Solberg and Sæther, 1994). Moose body mass has been shown to be negatively related to population density (Solberg and Sæther, 1994), however density dependence often only sets in at high densities (Garel et al., 2006), conditions rarely achieved in Sweden where moose populations are held well below carrying capacity by active management. Moose observations per man-hour (Ericsson and Kindberg, 2011) may reflect population density better than bag density and traffic accidents, due to moose hunt being licensed and bags thus not necessarily reflecting population composition, and other factors than density possibly influencing the number of moose vehicle collisions (Seiler, 2004; Ueno et al., 2014).

(2) **Abiotic** factors, such as region (North and South of Sweden, divided by the geographical border *Limes Norrlandicus* (Borgegård, 2002)), latitude and elevation, and climatic variables including annual precipitation, mean temperature, snow depth, length of vegetation period and seasonality. Relationships are expected to differ between North and South due to contrasting environmental conditions (e.g. higher productivity, habitat variability and species densities in the South, harsher climate in the North). According to Bergmann's rule (Bergmann, 1848) and various supplementing explanations (Sand et al., 1995; Garel et al., 2006), moose are larger and thus heavier in higher latitudes. Elevation may affect body weight positively due to higher diversity in vegetation at higher altitudes, or negatively due to harsher weather conditions (Hjeljord and Histol, 1999; Ericsson et al., 2002). With moose being a heat-sensitive northern ungulate (Owen-Smith, 2010), temperature is expected to be negatively related to body mass (Solberg and Sæther, 1994; Allen and Singh, 2016). The effect of precipitation on moose weight is debated, if present at all (Sand et al., 1995; Hjeljord and Histol, 1999; Owen-Smith, 2010). Snow depth may either be advantageous with moose being able to reach higher branches and therefore increase their food spectrum, or disadvantageous by increasing energetic costs and actually limiting food availability (Cederlund et al., 1991; Sand, 1996). A longer vegetation period equals higher plant productivity and thus food availability, and is therefore expected to affect body weight positively (Ericsson et al., 2002). Seasonality, i.e. variation between seasons, can also have contrasting effects – higher seasonality may be connected to lower weights due to higher weather harshness, or select for higher body mass to tolerate longer periods with less food availability (Sand et al., 1995; Garel et al., 2006).

(3) **Interspecific** factors, i.e. richness (number) and densities of other ungulate species (roe deer, red deer, fallow deer and wild boar). As an increasing amount of species in a limited area may cause competition for resources, species richness and increasing densities of other ungulate species are expected to decrease moose weights (Stewart et al., 2005). This effect is expected to be stronger in the South due to higher species densities in general, and stronger for ungulates with niches similar to those of moose (i.e. selective feeders like roe deer; Allen and Singh (2016); Hofmann (1989)). Alternatively, ungulates with broader niches (i.e. intermediate feeders) may be more competitive than moose and therefore affect moose body weights negatively (Latham, 1999). Wild boar seem rather disconnected from cervid dynamics and are thus not expected to affect moose body mass (Ferretti et al., 2011; Focardi et al., 2015). Compared to other cervids, moose may be stronger affected by competition due to their large size (Gordon and Illius, 1989); however, other studies have found them to be less affected (Jedrzejewska et al., 1997; Nichols et al., 2015).

(4) **Habitat** conditions, including land cover (artificial, agricultural, different forest types, wetland), diversity and forest age. High proportions of poor habitats (artificial, wetland) in the MMA are expected to influence moose weights negatively, while favourable habitats (e.g. young forest) should have a positive effect (Bjorneraas et al., 2011). I hypothesize that spatial heterogeneity, measured by Simpson's diversity index (Simpson, 1949), affects body mass positively by increasing the range of potential foraging areas (Owen-Smith, 2010; Herfindal et al., 2014). As young forests offer preferred browse to moose, body mass should be negatively correlated with forest age (Bjorneraas et al., 2011).

(5) **Human disturbance,** indicated by human population, road and railway density. Few studies exist on the effects of human disturbances on moose, but I expect high densities of any of these factors to lead to lower body condition (i.e. mass) due to increased disturbance (Neumann et al., 2010; Sahlén, 2016). Alternatively, roads and railways may be advantageous by offering sodium and preferred forage growing along the edges (Laurian et al., 2008; Rea et al., 2010).

The **relative importance** of these different factors in predicting moose body mass **(6)** is the main topic of this thesis. I expect clear differences between the northern and southern region due to contrasting preconditions: In the more sparsely populated North, climate and habitat factors could be paramount, while interspecific factors and human disturbance should be much more important in the southern region. Concerning sex and age-classes, intra- and interspecific factors are expected to affect adult moose stronger than calves, which may primarily be affected by climatic conditions (Solberg and Sæther, 1994; Tiilikainen et al., 2012). Differences between sexes should mainly be apparent for adults, with males being more influenced by intraspecific factors such as sex ratio than females (Solberg and Sæther, 1994). Females could possibly be more affected by habitat factors, as they may actively select their habitat, while males may select areas based on access to reproductive females besides food.

Material & Methods

Study area and time period

The study was conducted at a national scale, covering the whole of Sweden (excluding the island Gotland where moose are absent). Stretching from 55°N to 70°N latitude, Sweden covers several climatic zones and environmental conditions differ strongly along a latitudinal gradient. Productivity, habitat fragmentation, human presence and ungulate richness and densities increase towards the South, with the landscape being more uniform and the climate harsher in the North.

All collected data were adjusted to the scale of moose management areas (MMA), the ecosystem level of Swedish moose management since 2012 (Lindqvist et al., 2014). At present (spring 2017), the country is divided into 149 MMAs with sizes ranging from 20,000 ha in the South to over 3,000,000 ha in the North (Figure 1). MMAs are adapted to moose ecology, following natural borders such as river catchments or railways if possible (SEPA, 2011) and being larger in the North where migration between summer- and winter ranges occurs (Allen et al., 2016). They are supposed to include largely distinct populations of moose, which is why I here use the term "MMA" synonymously with "moose population". As opposed to moose management, management of other hunted species occurs mainly at the scale of smaller hunting parishes (*jaktkretsar*) administered by the Swedish Association for Hunting and Wildlife Management (SAHWM, *Svenska Jägareförbundet*). Bag statistics recorded by hunters at hunting parish level have thus to be transferred to MMA level.

The study period extended from the hunting year 2012/2013 (1 July 2012 to 30 June 2013), i.e. the first year after the implementation of MMAs, until the end of the hunting year 2015/16 (30 June 2016), the last period where data were available in time for the analyses.

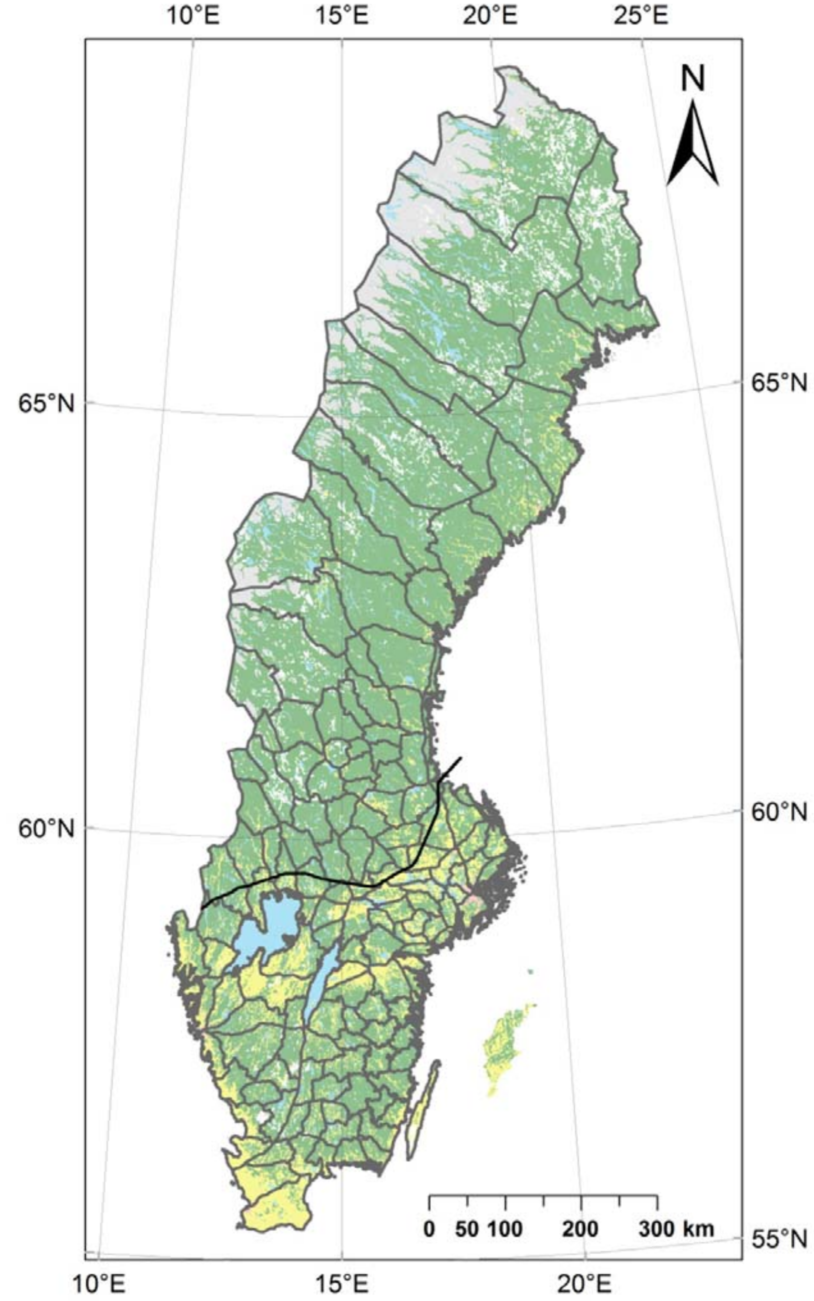


Figure 1. Map showing the study area with moose management areas (MMA, effective 2015/16) as sample units. The area was divided into a northern and southern region based on the *Limes Norrlandicus*, a climatic boundary (black line). Colours indicate approximate habitat types with forests in green, open habitats in yellow, freshwater in blue, urban areas in pink and mountains in grey.

Data

Data on moose body mass were obtained from animals harvested during the regular moose hunting season, in the South starting on the second Monday in October (after the rut) and in the North in the first week of September, with a two-week-break during the rut. It is mandatory for Swedish hunters to report sex and age (calf/adult) of shot moose. For about 38 % of all harvested moose during the study period (N = 138,362 individuals), hunters voluntarily reported dressed weight (kg). Dressed weight corresponds to body mass without head, skin, lower part of the legs, viscera and blood, and comprises around 50 % of body mass (Wallin et al., 1996). In the following, "body mass" is used synonymously with "dressed weight". All reported weights were checked and unrealistic data excluded prior to analysis in consultation with the experts from the SAHWM. To improve statistical power, only MMAs with at least 10 reported samples per age-class (i.e. male adult, female adult, male calf, female calf) and hunting year were included in the analyses. Based on these, means were calculated per MMA for each year and age-class and used as the response variable in all analyses. In preliminary analyses I included coefficient of variation (CV) of moose weights as a second response variable to measure variation in moose body mass. I decided however to exclude it for further analyses as no clear trends were apparent.

Geographical information on administrative units (counties, municipalities and districts/parishes) was derived from the open database by the Swedish National Land Survey (*Lantmäteriet*). I obtained the current MMA borders from the County Administration Board (CAB) in Jönköping and created layers for the previous years by tracing back changes in borders using protocols from meetings of the MMA administration groups. In collaboration with the SAHWM, I compiled and revised the borders for all hunting parishes in the country in order to map ungulate distribution.

All 35 potential explanatory variables for moose body mass were derived from public national databases (Table 1) and quality-checked before analysis. Preparation of all data is described in detail in the Appendix (S1).

Table 1. Description and source of the potential explanatory variables for moose body mass included in the analysis. Hunting year is included as a fixed variable in all analyses and therefore not shown. If nothing else is noted, variables are per hunting year (1 July – 30 June).

Variable	Description	Source
Sex	Male or female	"Moose data" from county administration boards (CAB), www.algdata.se
Age	Calf or adult	"Moose data" from CAB, www.algdata.se
Sex ratio	Ratio male:female moose	"MooseObs" data from CAB, www.algdata.se
Moose density – bag	Number of moose shot per 1000 ha	"Moose data" from CAB, www.algdata.se
Moose density – traffic	Number of moose vehicle accidents per km of road	Swedish Police/National Wildlife Accident Council (NVR), www.viltolycka.se
Moose density – observation	Number of moose observed per man-hour	"MooseObs" data from CAB, www.algdata.se
Region	North or South, divided by	Created in a GIS program based

	Limes Norrlandicus	on SMHI
Latitude	Y-coordinate of MMA centroid	Extracted using a GIS program
Elevation	Height above sea level (m)	Swedish National Land Survey, www.lantmateriet.se
Precipitation	Precipitation sum (mm) [a]	Swedish Meteorological and Hydrological Institute (SMHI), www.smhi.se
Temperature	Mean temperature (°C) [a]	SMHI, www.smhi.se
Snow depth	Mean snow depth (m) [b]	SMHI, www.smhi.se
Vegetation period	Accumulated day degrees >5°C [c]	SMHI, www.smhi.se
Seasonality	Coefficient of variation (CV) of Fraction of Photosynthetically Active Radiation (fPAR) [d]	Dynamic habitat indices (DHI) (Allen, 2016), http://silvis.forest.wisc.edu/dhi
Species richness	Number of other ungulate species present (1–4)	NVR, www.viltolycka.se
Species density – bag	Bag density per 1000 ha for each of the other ungulate species (absent, low, medium, high)	Swedish Association for Hunting and Wildlife Management (SAHWM), www.viltdata.se
Species density – traffic	Number of traffic accidents per km of road with each of the other ungulate species (absent, low, medium, high)	NVR, www.viltolycka.se
Land use proportions	Proportion of each of the 7 land use classes (%) [e]	Corine Land Cover (CLC) habitat data 2012, European Environment Agency (EEA), http://land.copernicus.eu/pan-european/corine-land-cover/clc-2012
Habitat diversity	Simpson's λ index (Simpson, 1949)	CLC habitat data, www.lantmateriet.se
Forest age	Forest age in years [f]	Swedish University of Agricultural Sciences (SLU), Forest Map 2010, www.slu.se/skogskarta
Road density	Length (km) of roads per km^2	Swedish National Land Survey, www.lantmateriet.se
Railway density	Length (km) of railways per km^2	Swedish National Land Survey, www.lantmateriet.se
Human population density	Population size per ha [g]	Statistics Sweden (SCB), www.scb.se

[a] Values per calendar year: E.g. for hunting year 2012/13, values are from calendar year 2012.

[b] Values for September to May of previous year: E.g. for hunting year 2012/13, values are from September 2011 to May 2012.

[c] Mean values for reference period 1961-1990.

[d] Average over the time period 2003-2014.

[e] Land use classes: Artificial, Agricultural/Open, Broad-leaved forest, Coniferous forest, Mixed forest, Transitional habitat, Wetland. Data from 2012.

[f] Data from 2010.

[g] Annual data from 31 December: E.g. for hunting year 2012/14, data from 31 December 2012.

Statistical analyses

Geographical analyses were performed in ArcGIS (ArcMap) 10.3.1 (ESRI, 2017). I conducted all analyses using the coordinate system SWEREF99 (Swedish Reference Frame 1999), the official reference system used by the Swedish National Land Survey since 2007 (Lantmäteriet, 2012). Explanatory variables were collected at different spatial scales (e.g. human population size for municipalities and weather data for single weather stations). In order to obtain values at the scale of MMAs, I created raster files for each variable in question and used the ArcGIS tool *Zonal Statistics as Table* to extract and compile mean raster values at the level of MMAs (see Carricondo-Sanchez et al. (2016) for a similar approach). These were exported to Microsoft Excel and could directly be used as variables in the analyses.

I conducted all non-spatial statistical analyses using R (R-Core-Team, 2016) combined with the user interface RStudio (RStudio, 2016). I applied linear mixed models fit by maximum likelihood (ML) using the R packages lme4 (Bates et al., 2016) and nlme (Pinheiro et al., 2017). Other packages used for different parts of the analyses are specified in the Appendix (S2). To investigate differences in body mass between age-classes and regions prior to modelling, non-parametric Kruskal-Wallis tests were performed due to variance partly violating assumptions of equality. If differences between age-classes and regions existed, modelling was divided into different groups. Mean body mass was the response variable, hunting year (4 modalities, 1213, 1314, 1415, 1516) was included as a fixed effect in all models (as it contained less than 5 levels which would qualify it as a random factor; McGill (2015)) and MMA identity (MMA_ID) as a random effect as I was interested in the general variance that MMAs contributed besides my fixed explanatory factors. All included continuous explanatory variables were rescaled due to their differences in magnitude.

Initial graphical data exploration led to some explanatory variables being transformed in order to fulfil the criteria of a Gaussian distribution. For calves, two extreme outliers were removed for each of the two sexes in the northern region (mean body mass > 120 kg (males) and > 140 kg (females), respectively). Due to many zero values in the density data of the other ungulates, I categorized these variables based on their data ranges (absent, low, medium, high). Specific transformations per variable and definitions of the density categories can be found in the Appendix (S2).

My modelling approach began with defining a baseline model for each group against which to compare the more complex models, including only hunting year as a fixed effect and MMA_ID as a random factor. In order to examine the effects of each single variable on body mass and subsequently limit down the number of potential predictors, I then conducted univariate tests with each potential variable in the baseline model (Zuur et al., 2010). As different climate approximators are especially prone to correlation, I also conducted principal component (PCA) and linear discriminant analyses (LDA) for all climate variables to exclude redundant variables. Using correlation matrices and variance inflation factors (VIFs), I then checked and corrected for collinearity between all continuous explanatory variables. VIFs quantify how much the variance of a coefficient is increased due to multicollinearity. For each model group, I applied a stepwise removal of variables until all VIFs were lower than 2.5 (Zuur et al., 2010; Allison, 2012). I then created a global model with the remaining explanatory variables for each model group.

The following model selection was performed using information-theoretic framework with the Akaike Information Criterion corrected for small sample size (AIC_c) as recommended by Anderson et al. (2001). The model with the lowest AIC_c value represents the most parsimonious one. T-values (Pinheiro and Bates, 2000) and the coefficient of determination r^2 were weighted in as additional factors during model selection. I distinguished between marginal r^2 (variance explained by fixed factors) and conditional r^2 (variance explained by both fixed and random factors) (Bartoń, 2015). First I examined if including meaningful interactions improved the models. I then analysed each explanatory variable's significance (p-value), contribution (assessed by hierarchical partitioning, see Allen (2016)) and relative importance (defined as the sum of the Akaike weights of all models containing this variable (Bartoń, 2015)) and consequently excluded non-relevant variables.

Having obtained the final combination of variables for each model group, I tried to improve the models' quality. I checked each model for heteroscedasticity by plotting Q-Q plots and model residuals vs. fitted values, and, if relevant, tested if including variance functions improved the model (Pinheiro and Bates, 2000). I conducted a similar procedure for testing the models for spatial autocorrelation (SAC). I investigated presence of SAC in the model's standardised residuals using bubble plots, spatial correlograms (Moran's I plots), sample variograms and Moran's I coefficient (per year). If SAC existed, I tried to account for it by applying different correlation structures to the model (Pinheiro and Bates, 2000).

Finally, I performed hierarchical partitioning with each final model in order to report the percentage of explained variation for each variable. I then conducted 10-fold cross validation to determine each model's predictive accuracy as described in Allen (2016), but excluding the random factor hunting year due to incompatibility of random factors with the method (Colby and Bair, 2013).

Limitations to the datasets

This study attempts to collate and combine several publicly available datasets from different sources and with varying quality for the first time. Consequently, limitations in some datasets can be expected.

As moose hunt is based on quotas, the *"Moose data"* dataset may not reflect population composition, which should however not affect reliability of body weight data per sex and age-class. Data may be limited due to the coarse resolution of age-classes which does not allow to account for the asymptotical increase of moose body mass during lifetime (see e.g. Solberg et al. (2008)),

The *"MooseObs"* data may have limitations due to differences in detectability between areas and a possible detection bias between sexes. The method is however scientifically approved and the most widely used density index available. Differences in detectability between areas are a minor issue in this study as I do not compare MMAs between each other, but rather use them as sample units with their variance captured in the random factor of the model.

The *traffic accident* dataset may be compromised by coordinates not always being taken exactly at the accident spot. Although reporting is mandatory, not all collisions (e.g. with smaller ungulates) might be reported and smaller species could thus be underrepresented.

The *bag density* data from the SAHWM may have issues due to the reporting being voluntary for other ungulates than moose and red deer. In connection with that, it is unknown if the reporting proportions within each hunting parish are representative for the whole area. The SAHWM is encouraging reporting and trying to reach good coverage of each parish, therefore the obtained values are expected to be acceptable.

Results

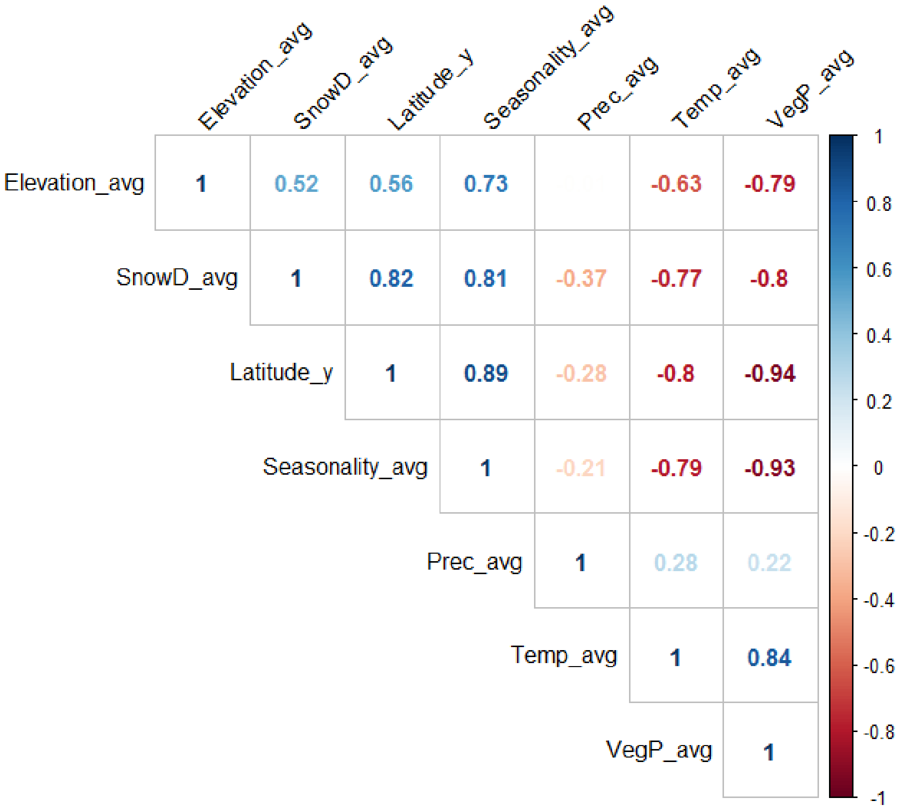
Moose body mass

Moose body mass differed clearly between the different sexes and age-classes as expected (Kruskal-Wallis test, $H = 1747.7$, df = 3, $p < 2.2\times10^{-16}$). Each age-class had significantly higher body mass in the northern region (Kruskal-Wallis test, df = 1, $p < 2.2\times10^{-16}$; MA $H = 133.48$; FA $H = 241.46$; MC $H = 317.6$; FC $H = 292.35$). Hence, I conducted separate analyses for each age-class and region. Mean body mass per group is shown in Table 2.

Table 2. Mean body mass [kg] including standard error (± SE), range and sample size (*N*) for each age-class per region. Regional means and ranges are calculated from means per MMA with at least 10 samples per year. *N* thus equals number of MMAs × number of years (max. 4 years) with samples for the corresponding group.

Age-class	Region	Abbreviation	*N*	Mean body mass ± SE [kg]	Range [kg]
Male adult	North	MA_N	206	190.69 ± 1.01	132.96 – 237.60
Male adult	South	MA_S	281	173.48 ± 0.79	127.27 – 217.69
Female adult	North	FA_N	197	164.89 ± 0.77	130.56 – 197.13
Female adult	South	FA_S	284	147.21 ± 0.48	119.81 – 168.80
Male calf	North	MC_N	207	71.36 ± 0.33	56.15 – 85.56
Male calf	South	MC_S	309	59.89 ± 0.26	45.84 – 71.31
Female calf	North	FC_N	206	66.73 ± 0.29	52.50 – 78.71
Female calf	South	FC_S	296	56.87 ± 0.26	39.47 – 69.07

PCA and LDA with the climate variables (latitude, elevation, precipitation, temperature, snow depth, vegetation period, seasonality) prior to modelling revealed that the variable "vegetation period" was highly correlated with most other climate variables (Figure 2). "Vegetation period" was therefore excluded from further analyses.



	Elevation_avg	SnowD_avg	Latitude_y	Seasonality_avg	Prec_avg	Temp_avg	VegP_avg
Elevation_avg	1	0.52	0.56	0.73	-0.01	-0.63	-0.79
SnowD_avg		1	0.82	0.81	-0.37	-0.77	-0.8
Latitude_y			1	0.89	-0.28	-0.8	-0.94
Seasonality_avg				1	-0.21	-0.79	-0.93
Prec_avg					1	0.28	0.22
Temp_avg						1	0.84
VegP_avg							1

Figure 2. Correlation matrix for the Principal Component Analysis (PCA). Vegetation period (VegP_avg) is highly correlated with most other climate variables.

Selected models

Moose body mass was explained by different factors depending on sex, age-class and region (Table 3). Model parameters for each selected model per model group can be found in the Appendix (S3). Variance structures to correct for heteroscedasticity were implemented for MA_N (Power of covariate function structure with Artificial-% as the variance covariate) and FC_N (Power of covariate function structure with fitted values as the variance covariate). As including a variance structure in the model formula led to extremely low r^2 values for unknown reasons, I decided to report the r^2 values for the corresponding models without variance structures. Spatial autocorrelation was detected for calves in the North (MC_N and FC_N), but no fitting correction structure was found, therefore I assume that it is accounted for by the different regions North and South.

Table 3. Highest-ranking ($\Delta AIC_c < 4$) linear mixed models for prediction of moose body mass per model group (region and age-class, for abbreviations see Table 2). “Hunting year” and "MMA_ID" were included as fixed variables in each model and are therefore not shown. For further explanations on each variable, see Methods section. R^2m is the marginal r^2, i.e. the variance explained by the fixed factors, and R^2c is the conditional r^2, i.e. the

variance explained by both fixed and random factors. Overall MSE is the overall mean square error from the cross validation, calculated from a linear model without random effect with the same variable composition as in the mixed model.

Model group	Selected top model	R^2m	R^2c	Overall MSE
MA_N	Sex ratio + Latitude – Species richness – arcsin(sqrt(Artificial-%)) + varPower(Artificial-%)	0.762	0.929	167
MA_S	– Red deer bag density + Road density – log(Human population density)	0.311	0.611	124
FA_N	Sex ratio – Species richness	0.297	0.630	87.7
FA_S	– Fallow deer traffic density – Red deer bag density – Roe deer traffic density – Wild boar bag density	0.273	0.563	48.6
MC_N	– arcsin(sqrt(Artificial-%)) – arcsin(sqrt(Agricultural/Open-%)) – arcsin(sqrt(Wetland-%))	0.325	0.783	16.1
MC_S	Latitude + sqrt(Elevation) – Precipitation – Fallow deer traffic density – Wild boar bag density + arcsin(sqrt(Transitional-%)) + log(Human population density)	0.518	0.789	10.2
FC_N	sqrt(Elevation) – arcsin(sqrt(Agricultural/Open-%)) – arcsin(sqrt(Wetland-%)) – sqrt(Elevation) × arcsin(sqrt(Wetland-%))	0.255	0.673	14.6
FC_S	Latitude + sqrt(Elevation) – Red deer bag density + arcsin(sqrt(Transitional-%))	0.447	0.758	11.7

Effects of the single predictors

Looking more closely at the single variables, intraspecific factors (apart from sex and age-class) were less decisive for moose body mass than expected. None of the three different moose density indexes showed relationships with body mass. Sex ratio of adult moose was correlated with body mass of adult moose in the northern region, with a clear positive relationship between sex ratio and mass (MA: $r^2 = 18$ %, FA: $r^2 = 12$ % from univariate tests; Figure 3). In line with that, post-hoc Kruskal-Wallis tests also showed that sex ratios were significantly more skewed in the North compared to the South (Kruskal-Wallis test, $H = 28.59$, df = 1, $p = 9.0\times10^{-8}$; North: mean ± SE = 0.54 ± 0.01; South: mean ± SE = 0.58 ± 0.01).

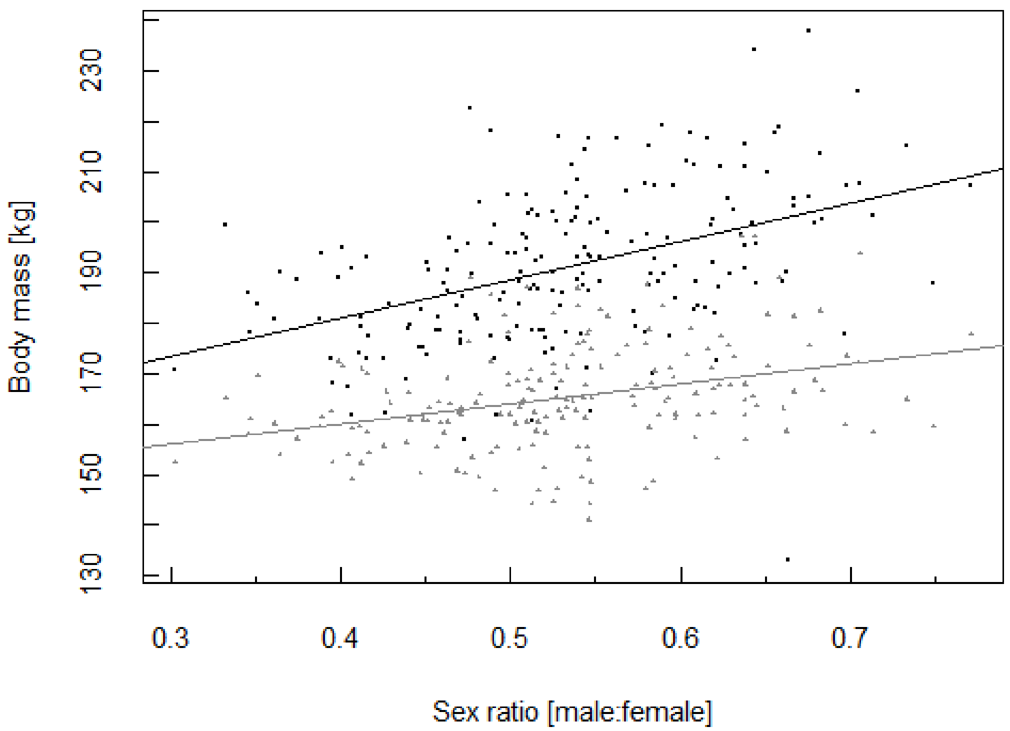


Figure 3. Positive relationship between body mass and sex ratio for adult male (black) and female (grey) moose in the northern region. R^2 (MA_N) = 19.5 %, r^2 (FA_N) = 10.6 %.

The only climate-related relevant variable was, unexpectedly, precipitation. While the net effect of precipitation was weakly negative in the model for male calves in the South, precipitation showed a positive relationship with body mass up to an annual amount of ca. 800 mm (r^2 = 10 %, Figure 4). More important than climate were "stationary" abiotic variables, i.e. latitude and elevation. In adult males in the North, body mass increased linearly up to a latitude of around 62° N where the effect evened out (r^2 = 22 %, Figure 5). Calf body mass in the South increased up to around 57° 30' N latitude, decreased then until 58° 30' N and increased again at higher latitudes (MC: r^2 = 14 %, FC: r^2 = 14 %; Figure 6). Elevation had a net positive effect on calf body mass in the models. In the North, female calf weight increased up to a height of around 250 m a.s.l. and decreased at higher altitudes (r^2 = 6 %; Figure 7). Surprisingly, the effect of altitude on calves was more distinct in the South. For both sexes, weights initially decreased with altitude up to around 50 m a.s.l. and increased continuously afterwards, with the highest altitudes in the South ranging around 250 m (MC: r^2 = 19 %, FC: r^2 = 18 %; Figure 7).

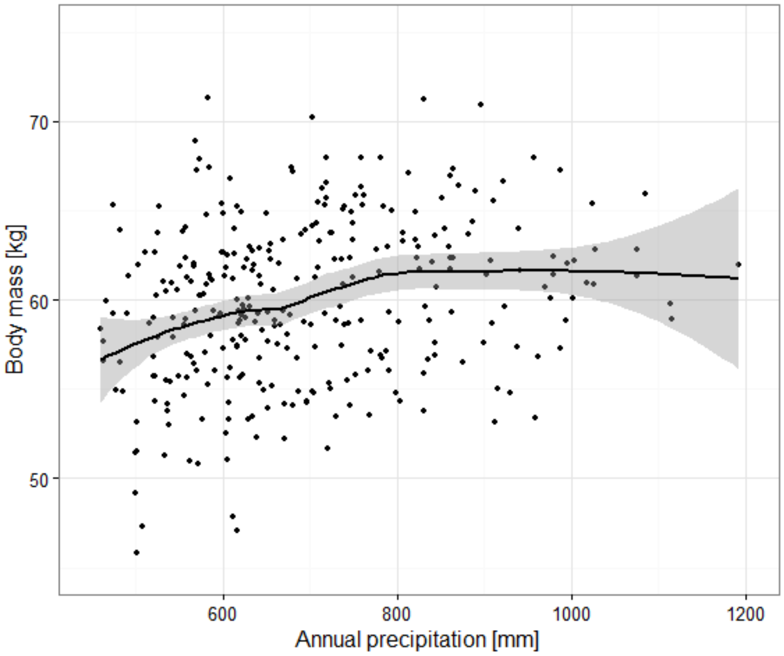


Figure 4. Relationship between body mass and precipitation for male calves in the southern region. The curve is fitted using a LOESS function. The shaded area shows the standard error. Body mass increases with precipitation up to an annual threshold of ca. 800 mm where the effect evens out.

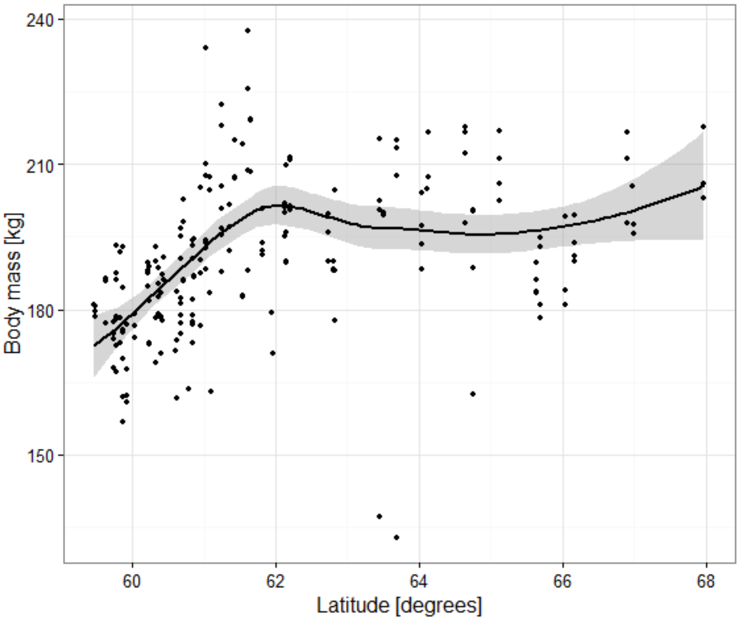


Figure 5. Relationship between body mass and latitude for adult male moose in the northern region. The curve is fitted using a LOESS function. The shaded area shows the standard error.

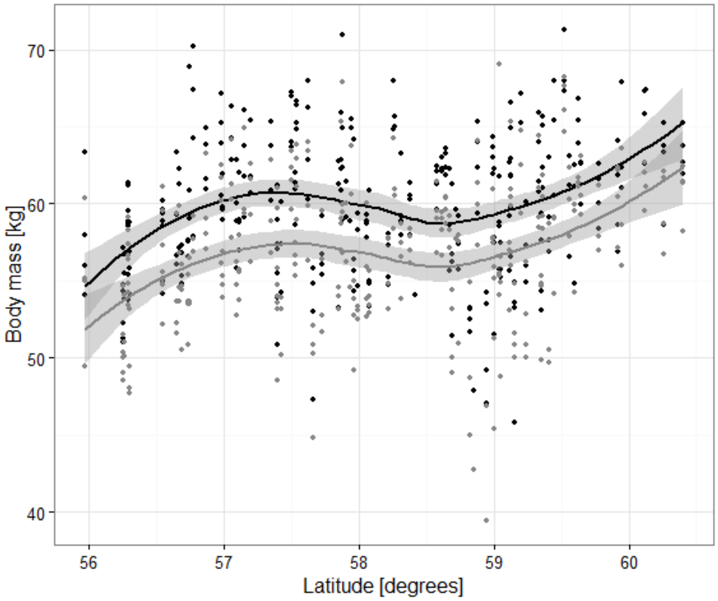


Figure 6. Relationship between body mass and latitude for moose calves in the southern region (black = male, grey = female calves). The curves are fitted using a LOESS function. The shaded areas show the standard errors.

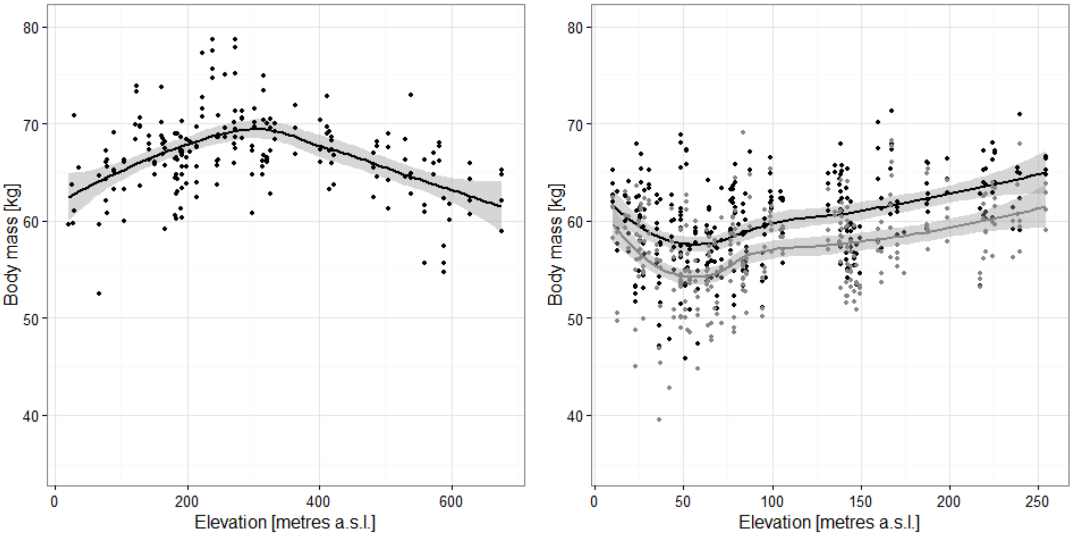


Figure 7. Relationship between body mass and elevation for female calves in the northern region (left) and calves in the southern region (right; black = male, grey = female calves). The curves are fitted using a LOESS function. The shaded areas show the standard errors. Observe the different scales on the x-axes.

Species richness was a significant negative factor only in the North and for adult moose (MA: r^2 = 20 %, FA: r^2 = 22 %). Body mass decreased with an increasing amount of other species. Noteworthy was the much lower observed body mass with three compared to two other species present, while there were only small differences between one or two and three or four species present (Figure 8). Due to little occurrence and therefore small sample size in the North, species densities were only included in the southern models. Both density indexes (traffic accidents and bag statistics) were positively correlated for all ungulates apart from roe deer (r^2: fallow deer 0.79, red deer 0.68, wild boar 0.71), and therefore the index strongly correlated with moose weight was chosen for each species specifically (resulting in bag statistics for red deer and wild boar, and traffic accidents for fallow and roe deer, Figure 9). Increasing fallow deer and wild boar densities were associated with lower adult female (fallow deer: r^2 = 14 %, wild boar: r^2 = 10 %) and male calf mass in the models (fallow deer: r^2 = 16 %, wild boar: r^2 = 14 %) (Figure 10). Increasing red deer density was related in a comparable way to adult moose and female calf mass (MA: r^2 = 17 %, FA: r^2 = 11 %, FC: r^2 = 14 %) and roe deer density had a weaker correlation with adult female mass (r^2 = 5 %, Figure 11).

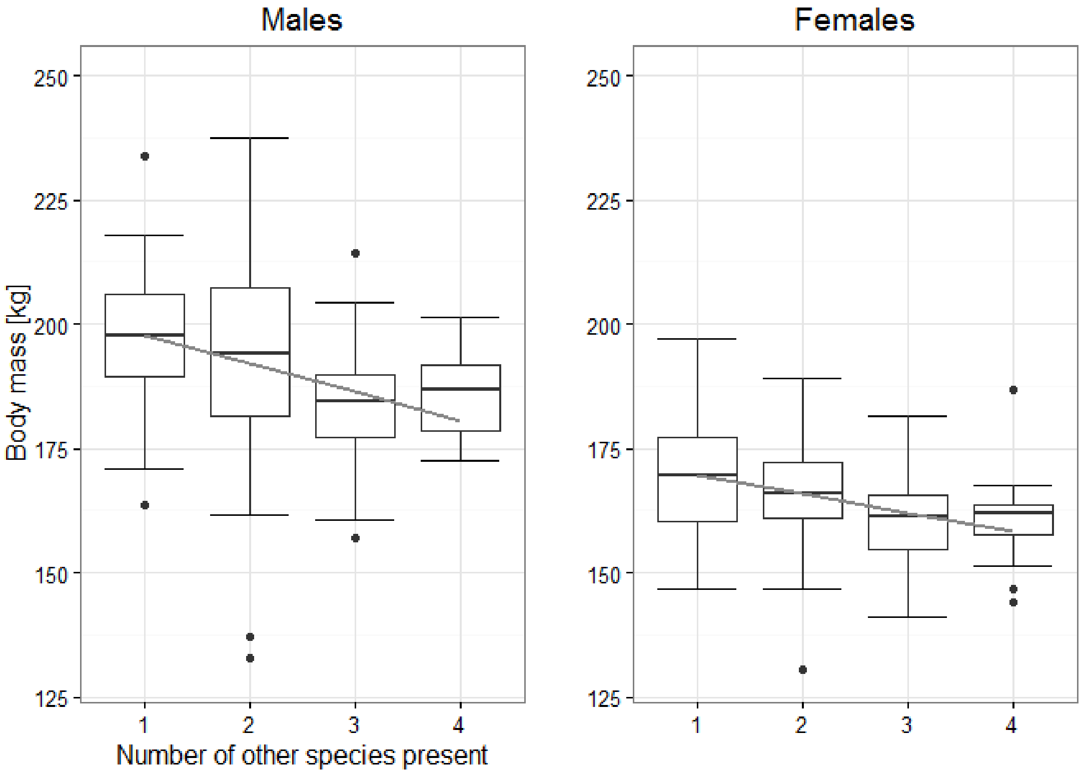


Figure 8. Relationship between body mass and species richness, i.e. amount of species other than moose present, for adult moose in the northern region, including trend lines in grey.

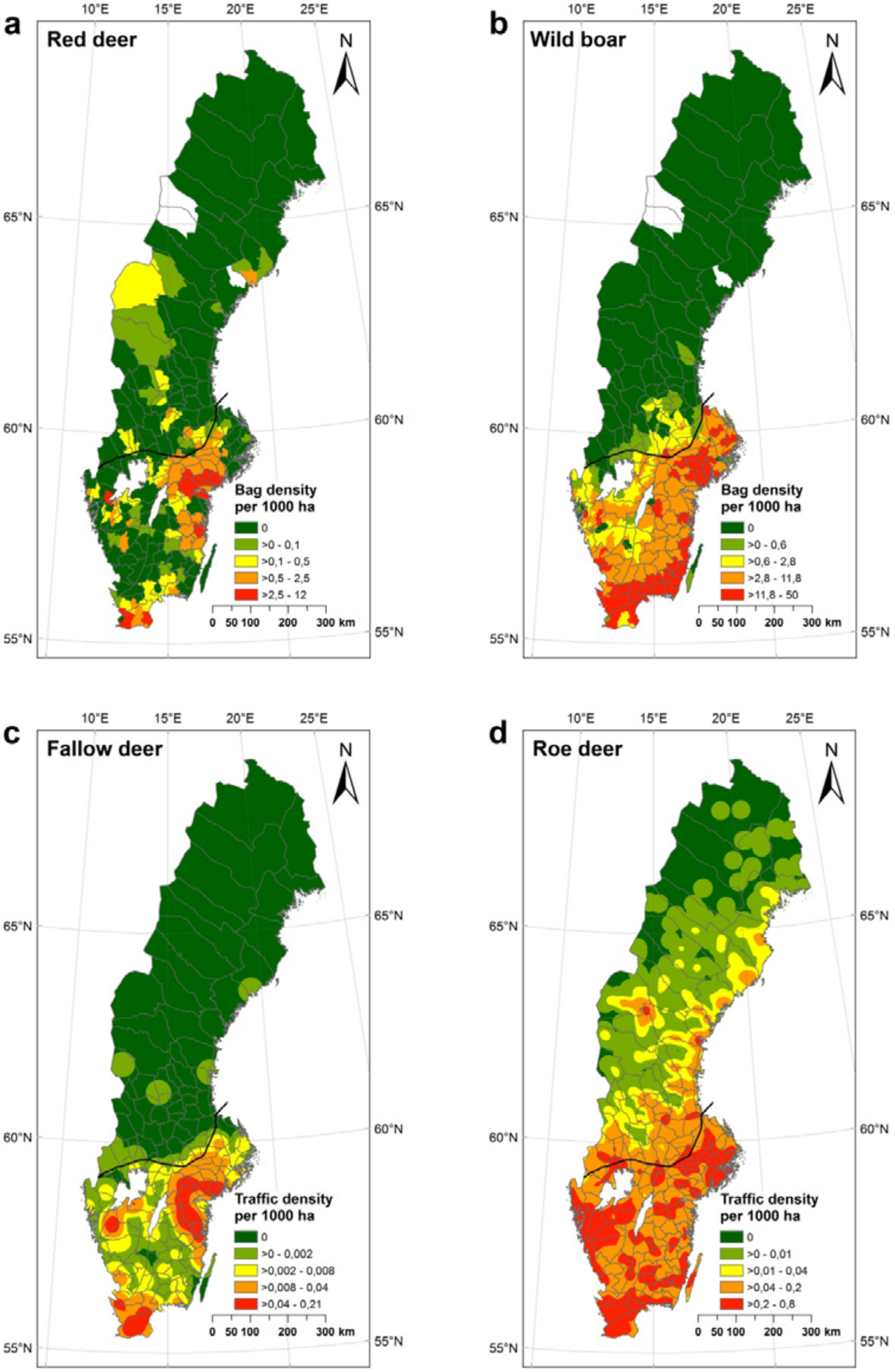


Figure 9. Density indices (effective 2015/16) for the four other ungulate species red deer (a), wild boar (b), fallow deer (c) and roe deer (d). Bag statistics were used for red deer and wild boar, traffic accidents for fallow and roe deer.

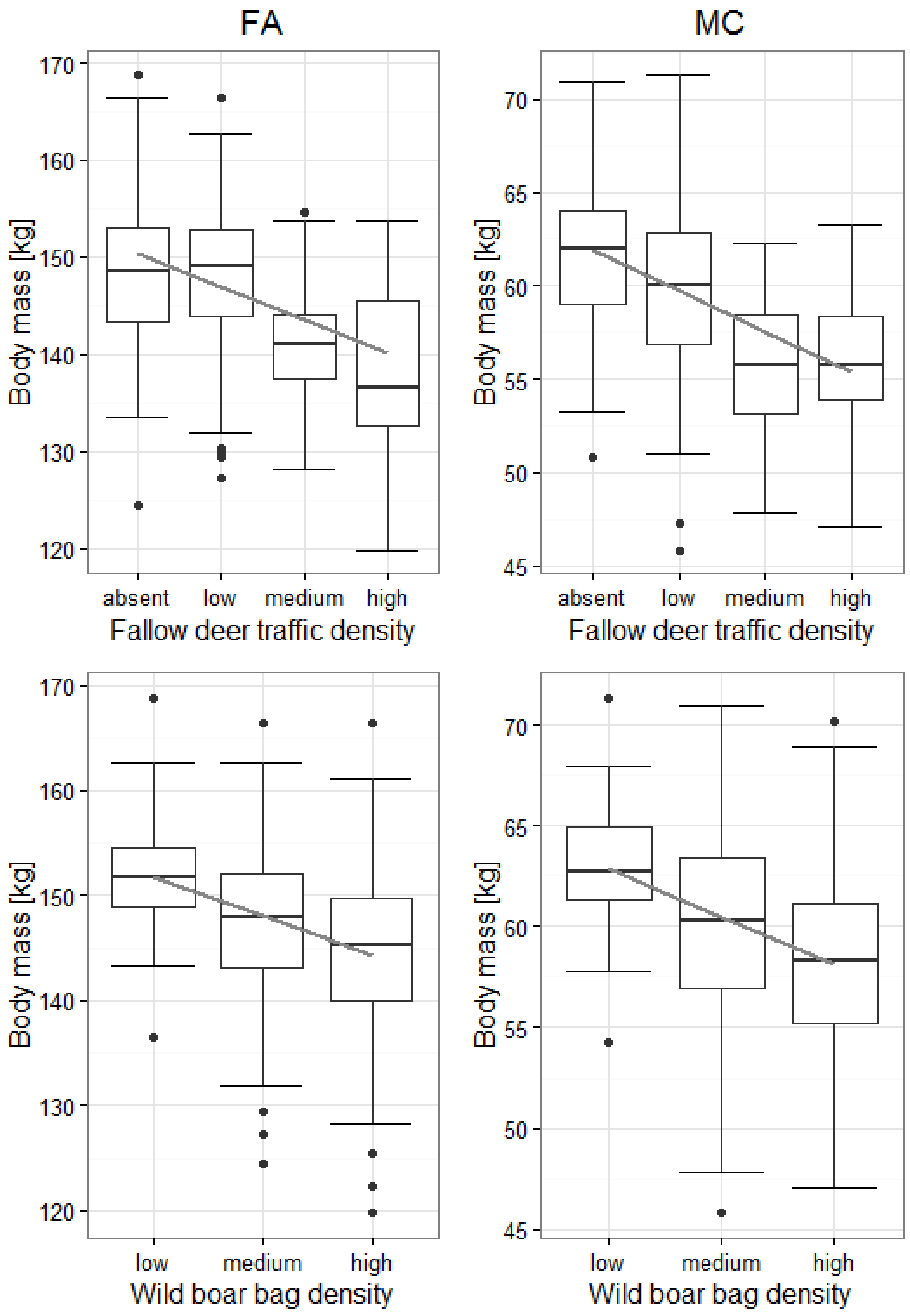


Figure 10. Relationship between body mass and wild boar and fallow deer density for female adult (FA) and male calf (MC) moose. Definitions of density categories are given in the Appendix (S2). Observe the different scales on the y-axes. Trend lines are shown in grey.

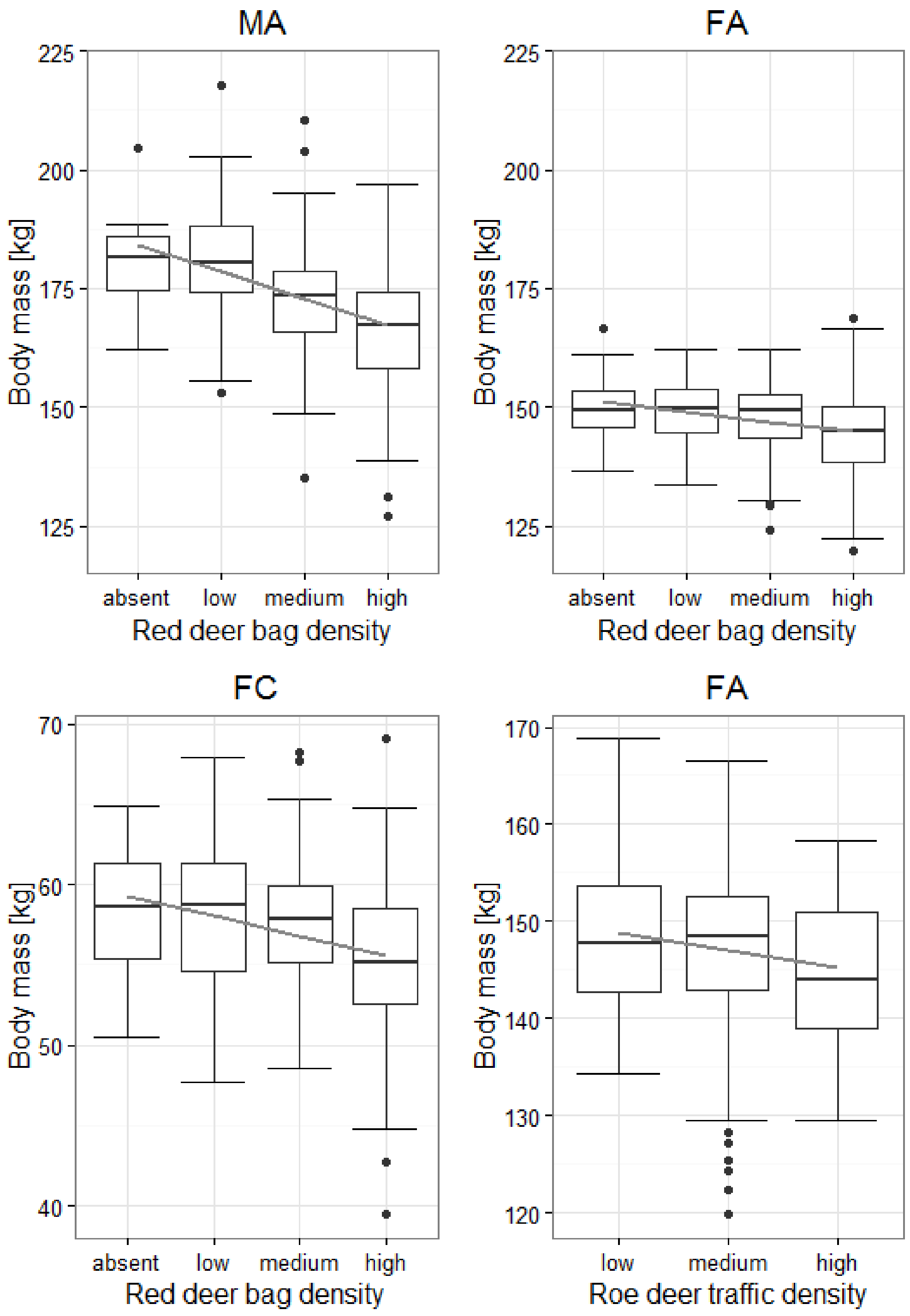


Figure 11. Relationship between body mass and red deer density for male adult (MA), female adult (FA) and female calf (FC) moose, as well as roe deer density for female adult (FA) moose. Definitions of density categories are given in the Appendix (S2). Observe the different scales on the y-axes in the second row. Trend lines are shown in grey.

Concerning the habitat variables, habitat diversity and most forest-related factors (forest age and composition, i.e. proportions of broad-leaved, mixed and coniferous forest) were not included in any of the selected models. Land use proportions were decisive for calf weights especially in the models for the North, but barely for adults. The proportion of artificial areas (i.e. mainly urban and industrial sites) in the North showed however a strong negative correlation with adult male mass up to a proportion of around 2 % and a weaker negative correlation thereafter (r^2 = 25 %), and a weak negative correlation with male calf mass (r^2 = 5 %). Agricultural and other open areas (pastures, grasslands) showed weak negative correlations with calf weights in the North if such areas occupied more than 8 % of the MMA (MC: r^2 = 6 %, FC: r^2 = 5 %; Figure 12). Wetlands showed comparable tendencies (MC: r^2 = 3 %, FC: r^2 = 4 %). A noticeable feature for female calves in the North was the presence of negative interaction of elevation and wetland. In the southern region, proportion of transitional habitats (wood-shrub, including young forests and clear-felled areas) was the single most important habitat feature for calves in the models (MC: r^2 = 24 %, FC: r^2 = 22 %). Calf weights increased up to a proportion of about 5 % of the MMA, whereupon they remained stable with increasing habitat proportions (max. 10 %, Figure 13).

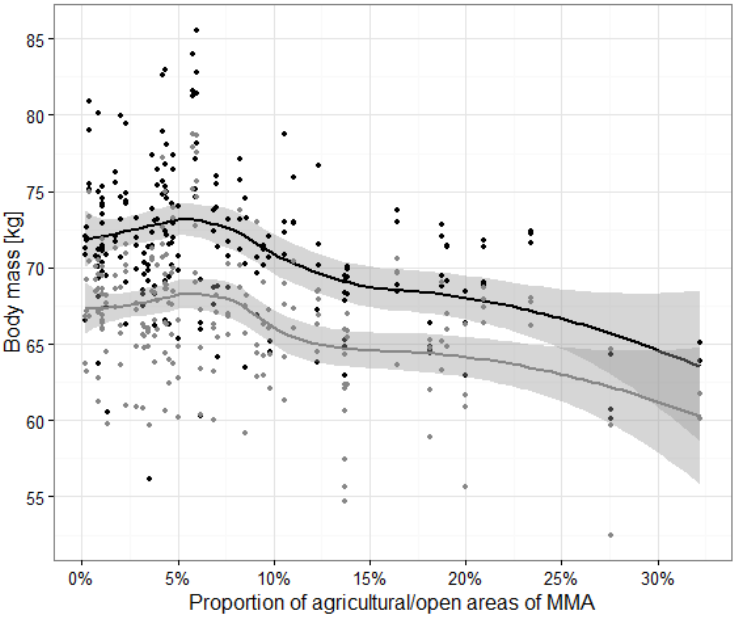


Figure 12. Relationship between body mass and proportion of agricultural/open areas of total MMA for moose calves in the northern region (black = male, grey = female calves). The curves are fitted using a LOESS function. The shaded areas show the standard errors.

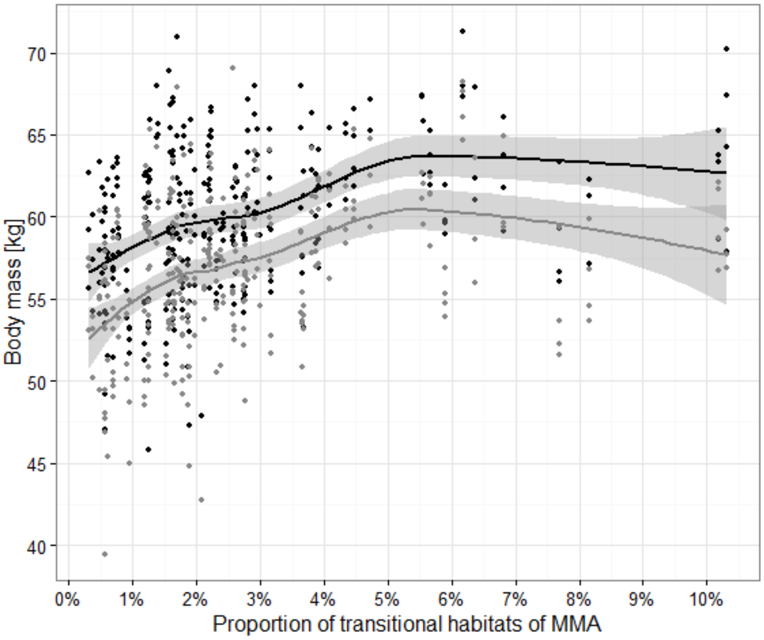


Figure 13. Relationship between body mass and proportion of transitional habitats of total MMA for moose calves in the southern region (black = male, grey = female calves). The curves are fitted using a LOESS function. The shaded areas show the standard errors.

Human disturbance was only relevant in the South and for male moose. Railway density had no visible effect on any age-class. Road density had a net positive effect on adult male condition in the model, with road densities between 0.35 and 0.40 km/km^2 being correlated with an increase in body mass (r^2 = 10 %, Figure 14). Human population density was negatively correlated with adult male mass (r^2 = 6 %). Unexpectedly, its net effect on male calf condition in the model was positive (r^2 = 11 %); however, this was probably due to few samples with densities beyond 0.6 persons/ha. Focusing on densities up to 0.6 persons/ha, moose weights first increased up to around 0.25 (MA, r^2 = 8 %) and 0.3 (MC, r^2 = 15 %) persons/ha, respectively, and continuously decreased thereafter.

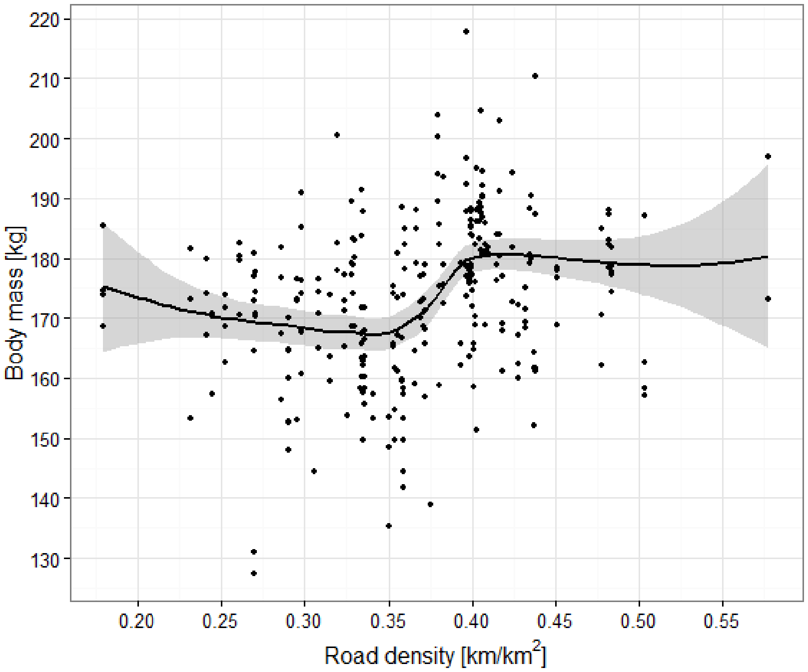


Figure 14. Relationship between body mass and road density for adult male moose in the southern region. The curve is fitted using a LOESS function. The shaded areas show the standard errors.

Relative importance of the factors

As apparent from above, different factors were important in predicting moose body mass in the northern and southern region. As a general trend, intraspecific factors (sex ratio) were only relevant in the North, while human disturbance was only significant in the models for the southern region. Concerning interspecific factors, species richness was relevant only in the North, while actual densities of other ungulate species were relevant in the South only. Abiotic factors such as habitat diversity and forest structure and especially climate (snow depth, temperature, vegetation period and seasonality) were hardly relevant. Differences in important factors were however larger between age-classes than regions and sexes: Generally, abiotic factors (latitude, elevation, precipitation) including habitat proportions were almost exclusively important for calves, while intraspecific factors, i.e. sex ratio, were kept only in the final models for adults. Interspecific factors also seemed to correlate with adult moose condition to a higher degree than with calf condition.

Relative importance of variables based on hierarchical partitioning varied between model groups (Figure 15). Most important for adult moose in the North were sex ratio and species richness, in the South densities of red deer (MA) and wild boar and fallow deer (FA), respectively. Calves showed higher yearly variation, apparent from the factor hunting year being of high importance in both regions. In the North, proportion of agricultural and other open areas was another important factor. In the South, elevation was important for both sexes, accompanied by latitude for females and wild boar density for males.

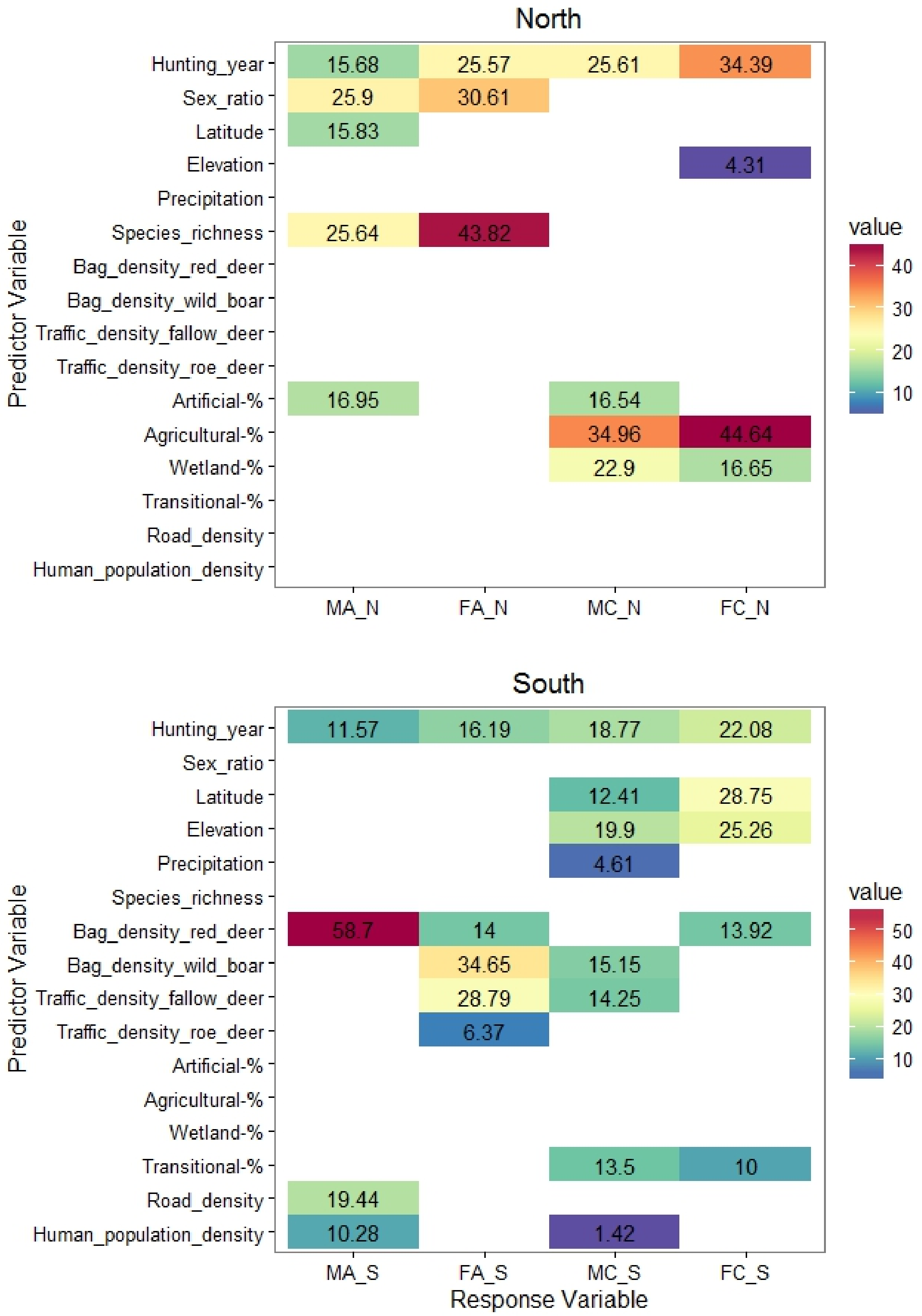


Figure 15. Variable importance, measured as the percentage (%) of total variance explained by each variable, estimated by hierarchical partitioning. Each "column" sums up to 100 % in total.

Discussion

In this study, I show that the factors predicting moose body mass in Sweden differ between age-classes, sexes and regions as follows: **(1)** Apart from sex and age-class, sex ratio (male:female) was the single most important intraspecific factor for adult moose weight in the North. **(2)** "Stationary" abiotic factors, i.e. latitude and elevation, were important predictors of calf weight in the South, whereas climate played a subordinate role in all groups. **(3)** Interspecific factors applied mainly to adult moose – increasing ungulate species richness was correlated with lower weights in the North, while increasing actual densities showed negative trends with body mass in the South. Tendencies varied with the ungulate species in question – adult male mass was negatively correlated with higher red deer densities, while adult female weights showed negative trends with all four other ungulate species (red deer, fallow deer, roe deer, wild boar). Calf weights were negatively correlated to a lesser extent with red deer (female calves) and fallow deer and wild boar densities (male calves), respectively. **(4)** Habitat factors applied mainly to calves – areal proportions of artificial sites, agricultural areas and wetlands were important negative factors predicting calf weights in the North, while the proportion of transitional forest (young forest and clear-felled areas) was positively correlated with weights in the South. **(5)** Human disturbance was relevant only in the South, with human population density being negatively correlated with male moose mass of both age-classes, whereas road density showed unexpected positive tendencies on adult male weight. **(6)** The most important predictors of weight for adult moose were sex ratio and species richness in the North and different species densities in the South. For calves, year and proportion of agricultural areas were most important in the North. In the South, elevation was an important predictor, as well as latitude and wild boar density for female and male calves, respectively.

Moose body mass

My results for adult male moose in the northern region agreed well with weights reported for male moose in Norway (190-240 kg, Nilsen and Solberg (2006); 204.6-268.9 kg, Garel et al. (2006)) and ranged below findings reported for adult males in northern Norway (ca 270 kg, Solberg et al. (2004)) and Sweden (214-262 kg, Sand et al. (1995)). Adult females are also slightly heavier in comparable studies from Norway (ca 190 kg in northern Norway, Solberg et al. (2004); 172.7-212.9 kg, Garel et al. (2006); ca 165-185 kg, Nilsen and Solberg (2006)) and Sweden (ca 180 kg, Sand (1996); 164-205 kg, Sand et al. (1995)). Sand et al. (1995) reported adult northern Swedish moose to be 15-20 % larger than southern moose – trends were similar but weaker in my study with 10 % and 12 % for adult male and female moose, respectively. Adult females are also in Norway heavier in northern than southern regions (south: 177.5±22.3 kg, north: 189.5±23.9 kg, Saether et al. (1996)) and consistently lighter than males (Sand et al., 1995; Solberg et al., 2004; Garel et al., 2006; Nilsen and Solberg, 2006). In line with my study, male calves are heavier than female calves in the literature (Cederlund et al., 1991; Ericsson et al., 2002). Calf weights in this study were similar to values from Sweden (male 70.0 kg, female 66.7 kg, Cederlund et al. (1991)) and Norway (male 66.93±6.08 kg, female 63.42±5.90 kg, Herfindal et al. (2006a); male 65.9±12.8 kg, female 61.8±12.1 kg, Herfindal et al. (2006b).

Factors I did not account for in my study were potential body mass variation during rut, having been observed for adult male moose (see e.g. Sand et al. (1995)), as well as the increase of body mass during moose lifetime. I was unable to account for the latter as carcass data were collected at the resolution of calves and adults only, with a negligible proportion of hunters determining age of the felled moose. Consideration of variation during the rut was traded for a larger sample size, assuming that including all moose shot during the entire hunting season would even out that phenomenon, also because I was interested in annual instead of seasonal trends in body mass. Both of these potential drawbacks apply mainly to adult (male) moose. Additionally, in Norway, harvested moose do not necessarily represent natural populations in their composition (Solberg et al., 2000), due to hunter selectivity for large/old males and avoidance to shoot fecund females with calves which may be heavier due to size-dependent fecundity (Saether and Heim, 1993; Sand et al., 1996). Consequently, body mass estimates for adult males may be overestimates and for adult females underestimates of the real populations (Nilsen and Solberg, 2006). Similar trends may have applied to the Swedish moose used in this study. However, hunter selectivity may be lower in Sweden than in Norway due to (a) an increasing focus on calf harvest with the aim to increase moose population quality (50 % of shot moose should be calves according to guidelines, SAHWM (2008)), restricting the hunters from shooting preferred large males, and (b) low moose densities especially in northern Sweden combined with a short season for most hunters (the majority of hunters are active mainly during the first week of the season), reducing the amount of shooting opportunities and along with that hunter selectivity (Solberg et al., 2000).

Effects of the single predictors

In all analysis groups, moose body mass showed a noticeable yearly variation, apparent from the high contribution of the variable "hunting year" to the total variance explained (approx. 11-34 %). Variations between years may be due to high adaptiveness of hunters in their shooting behaviour, as Swedish hunters try to adapt their harvest to changing conditions such as newly established wolf territories (Wikenros et al., 2015). As expected, between-year variation was even higher for calves than for adults, probably due to calves being highly affected by changing conditions between years (i.e. other conditions that were not captured by my included variables): According to the timing of birth hypothesis (Saether and Heim, 1993), calf weight variations may be closely related to individual differences in birth date due to rapidly changing food quality and quantity in the early northern summer. Calves born later may thus have lower weights than early-born ones (Kvalnes et al., 2016). Alternatively, varying abilities of mothers in raising their young may cause variations in calf weights (maternal effect hypothesis, Saether and Heim (1993)). Several authors have suggested cohort effects causing variance in moose weights (Forchhammer et al., 2001). As I did not have information on either birth date, experience of mothers or cohort performance, I was unable to test for these hypotheses. Likely, a combination of them was responsible for the observed annual variations.

The high conditional r^2 (i.e. the large amount of variance explained by the random factor MMA) shows that there existed even considerable variation between moose populations, i.e. local factors and preconditions were decisive for moose weight. Possible dynamics at smaller scales that I could not control for may include individual differences in foraging abilities and winter weight loss (range quality hypothesis, Saether and Heim (1993)). Unexplained variance in my models might be attributed to lacking precise knowledge on local habitat conditions and diets at a finer scale, such as available key forage species (Hjeljord and Histol, 1999), and possibly also to genetic structuring of moose populations which has recently been suggested as important in explaining body mass variance (Herfindal et al., 2014).

The lacking **density**-dependence of moose body mass in this study confirmed the hypothesis that Swedish moose populations are held well below their biological carrying capacity by active management, as several authors suggest that density-dependent effects only occur at high population densities (see Garel et al. (2006) for a review). Other studies have however found (weak) relationships between density and weight for adult moose in Scandinavia (Solberg and Sæther, 1994; Sand et al., 1995). In contrast, **sex ratio**, i.e. number of adult males per adult female moose, was significant for adult moose of both sexes in the northern region, where sex ratios also were more skewed than in the South. Adult males are facing a trade-off between growth and reproduction, and if sex ratio is low (i.e. there are fewer males available) earlier reproduction should be favoured, leaving less resources for growth and consequently leading to lower body mass (Solberg and Sæther, 1994). The importance of sex ratio for adult females was unexpected, but I suggest that females have to spend less time on searching for mates at higher sex ratios, allowing them to allocate more time to feeding, which may in turn lead to higher body mass. The relationship could also be inverted: Worse maternal condition (i.e. lower body mass) can lead to a lower proportion of male calves born (Mysterud et al., 2000), as energetic costs are assumed to be higher for rearing a son (Pavitt et al., 2016). According to the extrinsic modification hypothesis, even environmental conditions may affect (calf) sex ratios *in utero* by inducing changes in the mothers' condition during pregnancy, e.g. by nutritional stress (Weladji and Holand, 2003).

Adult male weights were positively correlated with **latitude** in the northern region as expected by Bergmann's rule (Bergmann, 1848; Sand et al., 1995) and different alternative explanations (Herfindal et al., 2006b). This observation did not apply to calf and adult female weight in the North, suggesting perhaps different selection pressures than for adult males. As weights were still higher in the northern region compared to the South, region alone may have accounted for the difference in these groups. For unknown reasons, calf body mass increased with latitude in the southern region except for the central part (57° 30' N to 58° 30' N) where the relationship was negative. The positive correlation of **elevation** and calf body mass up to a height of 250-300 m a.s.l. may be attributed to forage quality increasing with altitude (Mysterud et al., 2001a; Ericsson et al., 2002) and possibly also to lower human population densities at increasing elevations. Beyond 300 m, the negative effects of elevation seem to set in, with harsher conditions (snow depth, shorter growing season, etc) leading to lower body weights (Saether et al., 1996; Hjeljord and Histol, 1999; Ericsson et al., 2002). **Precipitation** can affect body mass indirectly by influencing plant growth, quality and availability (Sand et al., 1996; Lenart et al., 2002). Its positive correlation with male calf mass in the South up to an annual amount of around 800 mm could be attributed to these processes delivering increased forage, while more precipitation may relate to too wet conditions, e.g. affecting heat insulation of calves which may on the long term affect body weight. Other studies have found no (Cederlund et al., 1991) or no consistent (Hjeljord and Histol, 1999) effect of precipitation on body mass. **Temperature, snow depth** and **seasonality** seemed to play minor roles for moose body mass. The lacking correlation of body mass with snow depth was unexpected, but might have been due to my coarse temporal data resolution – authors using monthly instead of yearly means have found effects of both snow depth (Hjeljord and Histol, 1999) and temperature (Solberg and Sæther, 1994). In my study, including monthly means would however have increased the already high amount of potential variables at the expense of statistical power.

Interspecific factors were relevant in the models for all age-classes. According to Boer and Prins (1990), interspecific competition demands three conditions to be fulfilled, being overlap in habitat, overlap in consumed forage and limiting shared nutritional resources. As I did not have direct measurements of any of these components, my study thus cannot prove or disprove competition – however, it may show potential trends. The (from an evolutionary point of view) short study period of four years should however be kept in mind. The negative correlation of **species richness** and adult moose condition in the North could indicate increasing interactions. Three other ungulate species present were related to much lower moose weights than two species, and the difference between three and four other species was marginal, suggesting the existence of a threshold value for the effect on moose weight with the presence of three additional ungulate species. Latham (1999) describes that competition should be rare among sympatric species, as distinct resource partitioning resulted from past competition. Overlapping niches may however occur with introduced species that did not co-evolve with native ones (Latham, 1999) – this may be relevant for both introduced fallow deer and reintroduced wild boar in Sweden. Competition may also arise if the established community is disturbed in another way (Putman, 1996). Several studies have shown (potential) competition between the three deer species (see e.g. Putman (1996)), but interspecific studies involving moose are rare (but see Jedrzejewska et al. (1997) for an exception, showing that moose density in Eastern Europe is less correlated with other ungulates than other species). Moose size may be both an advantage and a disadvantage in competitive environments: Moose have exclusive access to food resources at browse heights which deer cannot reach (Nichols et al., 2015), but require also higher food intake due to their size, meaning that resources may easier become limiting (Gordon and Illius, 1989). In my study, other **ungulate densities** had significant negative correlations with moose weight in all age-classes. Bag density is correlated with actual density for deer and wild boar in Italy (Imperio et al., 2010) and time-delayed for moose in Norway (Ueno et al., 2014). My bag data may have a bias as reporting of ungulates other than moose and red deer is not mandatory in Sweden. Traffic accident density reduces this problem as every ungulate-vehicle collision has to be reported to the police, but traffic accidents are in turn also related to other factors than density, such as traffic volume, vehicle speed and road characteristics (Seiler, 2004). Ueno et al. (2014) have found accidents to be a poor density index, but propose its use to cross-check other indices. The correlation of densities with moose condition varied between ungulate species. Red deer (bag) density was negatively correlated with moose weight for all age-classes except male calves. Red deer have a large competitive potential due to their size and food niche as an intermediate feeder (Latham et al., 1999) and have been shown to displace roe deer, which have a similar feeding ecology as moose, in several studies (Petrak, 1993; Latham, 1999). Unexpectedly, increasing wild boar (bag) densities showed negative trends with female adult and male calf condition despite the different biology of wild boar compared to cervids (Focardi et al., 2015). Considering that wild boar often appear in large groups and have high impact on forbs and grasses by their rooting behaviour, general disturbance and food competition could potentially explain these findings. Roe deer avoiding wild boar feeding areas due to disturbance (Pellerin, 1993) support this hypothesis. Fallow deer (accident) densities were also negatively correlated with female adult and male calf weight, probably for similar reasons as wild boar. Fallow deer occur in large groups and occupy a broad food niche, making them effective competitors (Dolman and Waber, 2008). Several studies have found negative effects of fallow deer on roe deer, a species with a selective feeding behaviour comparable to moose (Focardi et al., 2006; Ferretti et al., 2008; Focardi et al., 2015). An alternative explanation for the observed negative trends of both wild boar and fallow deer on moose body mass could be lacking co-evolution (Latham, 1999), as both species are (re)introduced to Sweden. Finally, roe deer (traffic) densities showed the weakest negative trends with moose weight, only correlating with female adult moose mass. Although roe deer have a similar food niche as moose, they are considered even more selective and leave much food behind, diminishing their competitive potential. Additionally, they are small in size and appear in small groups. Roe deer may be rather displaced by other ungulates such as fallow deer than negatively affecting them (Focardi et al., 2015).

When it comes to habitat factors, **forest composition** (age and species) and **habitat diversity** were surprisingly unimportant for moose condition. Habitat diversity may already have been accounted for in the models by the different habitat proportions themselves. As the forest age map used in the analyses was dated from 2010, more recent clear-felled areas were not captured which may explain the non-importance of young forests in this study. However, this could potentially be important, considering the fact that at a given time, different forest age classes may be accessible to moose and their composition within moose home ranges may vary in space and time (Allen et al., 2016). This will require matching the harvest data with simultaneous estimates of available forest of different ages. Regarding forest composition, proportion of **transitional habitats** was the single most important forest variable for moose. Transitional habitats include wood-shrubs and clear-felled areas, thus important forage environments for moose (Bjorneraas et al., 2011). Other forest variables may be subordinate and therefore not show significant relationships with moose body mass. Transitional habitats were important for calves in the southern region, with proportions up to about 5 % of the MMA showing positive trends with body mass. Herfindal et al. (2006a) suggest that food quality is more important for moose body mass than quantity. Transitional habitats offer high-quality forage, and food requirements may be met with proportions of up to 5 %, with larger proportions not promoting moose condition additionally. Young forest stands are also selected by Norwegian moose (Bjorneraas et al., 2011). **Artificial areas** (i.e. mainly urban and industrial sites) were negatively correlated with male moose mass of both age-classes, but surprisingly only in the northern region. Moose may be more sensitive to artificial structures in the North as such areas are less widespread there compared to the South. Furthermore, infrastructure influence in the South may be captured by road and human population density instead (see further down). Sheremet'ev et al. (2011) have found Russian moose to be less affected by artificial habitats than other ungulates (roe deer and wild boar). **Agricultural and other open areas** and **wetlands** were important negative predictors of calf body mass in the North. In both sexes, negative trends of agricultural/open areas first set in after passing a threshold of around 8 %. The results suggest open non-forest areas to be generally unfavourable for calves, possibly due to little cover/protection or food availability (Allen and Singh, 2016). For unclear reasons, the negative interaction between elevation and wetland significantly improved the model for female calves in the North.

Road density was unexpectedly positively correlated with adult male moose body mass in the South. Foraging opportunities along roadsides and access to mineral salts (Grosman et al., 2011; Laurian et al., 2012) may outweigh the likely disturbance effects of roads. As there are more roads in productive areas, the observed trends could also be related to other reasons than the road itself. Measuring traffic density instead of road density could reduce that issue, but reliable measures for traffic density are rare. **Railway density** did not relate to moose weight, possibly due to the lower density of the railway network and many railways being fenced. **Human population density** was negatively correlated with male moose weight in the South beyond densities of 0.25 and 0.3 people/ha for adults and calves, respectively. Few studies exist on moose concerning human disturbance, but Sahlén (2016) has found positive relationships between moose cortisol levels and human infrastructure, and Neumann et al. (2010) suggest skiing to disturb Swedish moose at least on short-term. Long-term effects of human disturbance on moose condition can thus not be excluded.

Relative importance of the factors

Factors important for predicting moose body mass differed between **regions**, most certainly due to different premises in the two areas. Intraspecific factors (sex ratio) and species richness were only relevant in the North, a sparsely populated environment with low densities of other ungulate species. Human disturbance (road and human population density) and ungulate densities were relevant predictors only for moose living in the southern, more fragmented and densely populated, area. **Age-class** differences were apparent across regions, with intra- and interspecific factors being more important for adults, while climate and habitat variables were more relevant for calves. These findings agree with Solberg and Sæther (1994) who have found climate to be important mainly for calves and sex ratio for adults. Adult moose may be less affected by climate as they could be buffered against environmental fluctuations (Herfindal et al., 2006a). In contrast, Sand et al. (1995) have found climate to be more important in affecting adult moose weight than population density and habitat. Differences between **sexes** applied mainly to adult moose: Only males showed tendencies of sensitivity to infrastructure (artificial habitat, road density and human population density), while only females' body mass was negatively correlated with increasing densities of wild boar, fallow deer and roe deer. Even in calves, human factors (artificial habitat and human population density) were only relevant to males. Furthermore, calves of different sexes showed trends with densities of different ungulate species (males with wild boar and fallow deer, females with red deer) for yet unknown reasons. The reason for the observed higher sensitivities of males to humans and females to interspecific factors is unclear as well. One could speculate it to be an eco-evolutionary response to the persistence of male-biased hunting that has existed for long periods of time before a production-based harvest system was introduced in the early 1980s. On the other hand, female hunting is potentially more recent and density dependence may affect female condition first.

Looking more closely at the most important single variables per model, sex ratio and species richness were the most relevant factors for adults of both sexes in the North. Sex ratios have earlier been shown to be decisive for moose weight (Solberg and Sæther, 1994) and may have higher importance in the North as they are significantly more skewed there compared to the South. In the naturally species-poorer North which is still dominated by moose and roe deer in terms of ungulates, moose may be less adapted and consequently more sensitive to the presence of several ungulate species. In contrast, a main predictor for adult moose weight in the South was other ungulate densities. Red deer were the single most important factor in predicting male body mass, probably due to their high competitive potential (Latham et al., 1999). Female weights were mainly correlated with fallow deer and wild boar, two species that occur in large groups and have strong potential for food competition (Focardi et al., 2006). An important feature of ungulate life history is sexual segregation, meaning that male and female moose might experience very different habitat conditions throughout the year except during the rut (Ruckstuhl and Neuhaus, 2000; Singh et al., 2010). Therefore, it may not even be surprising that different factors are observed to correlate with male and female body condition differently in our North and South. Year and proportion of agricultural/open areas were most decisive for calves of both sexes in the North, suggesting higher dependence of calves on yearly changing environmental conditions as well as a possible need for habitats with protective cover. Male calf weight in the South was mainly correlated with elevation, year and wild boar density, female calf weight with latitude and elevation. Elevation had positive tendencies on calves of both sexes, probably due to higher altitudes offering quality forage and lower human disturbance, factors becoming relevant in the more fragmented and densely populated South. Latitude in the South may interact with more local distribution of habitat or human use of the landscape and population density.

Finally, body mass in the North was almost always predicted by fewer variables with high consistence in the main variables between age-classes. This observation agrees with Danell and Bergström (2010) who suggest that ecological relationships are generally more distinct in northern compared to southern Sweden.

Effect of data quality

Data used in the analyses were quality-checked before including them as variables. All datasets come however with their limitations and the differences in data quality may have affected the results of this study. The coarse age resolution of body mass data, differentiating only between calves and adults without accounting for actual age, could be a reason for the low amount of total variance explained by the selected models for adult moose. Fine-scaled climatic trends may not have been detected due to yearly mean values being used in the analyses in order to increase statistical power. Furthermore, varying monitoring efforts of other ungulate species than moose make it difficult to assess data reliability.

It would however not be straightforward to test how the data limitations affect the results. This work is a first attempt to unite many different datasets and make use of the enormous amount of free information available. Further studies are needed to evaluate data quality and develop improvements for the limitations of the different datasets.

Conclusion and implications for management

My results support that factors predicting moose body mass differ between regions, sex and age-classes. Additionally, considerable variation exists between populations and years. I suggest that climate change is decreasing predictability and thus increasing variation by creating complexity in food availability. Obviously, the observed tendencies are a product of current Swedish moose management strategies and human use of the landscape. Increasing moose quality is a continuous management goal in Sweden, and body mass a reliable indicator of such. According to my results, moose managers should try to improve moose sex ratio especially in the northern region, for instance by making efforts to save older males and focusing on calf harvest. My study also highlights the importance of other ungulates for moose condition and I therefore encourage the continuing development of a multispecies management approach. The current Swedish system is strongly moose-biased, but adjustments to other species are in progress, for instance visible in red deer management units being established in increasing parts of the country. To conclude, there is an ongoing urgent need of knowledge about multispecies interactions under Scandinavian conditions, making this an important topic for future research.

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Appendix S1

Supplementary methodology on data preparation

Geographical data

Administrative borders (counties, municipalities, districts/parishes) were obtained from the open database "Öppna data" by the Swedish National Land Survey (*Lantmäteriet*). In particular, I used the polygon layers with division into counties (AN) and municipalities (AK) of the GSD-Map of Sweden (1:1 million) in combination with a separate shapefile including the districts/parishes.

A shapefile with the current (hunting year 2015/16) borders of the moose management areas (MMAs) was obtained from the County Administration Board (CAB) in Jönköping. With the help of reports from MMA-meetings, I traced back changes in MMA borders until 2012/13 and created separate layers for each hunting year. Gotland and the two greatest Swedish lakes (Vänern and Vättern) were excluded from the layers as they have no relevance for moose.

In order to map distribution of other ungulates which are currently managed at the level of hunting parishes instead of MMAs, I compiled and revised a map with all hunting parish borders in Sweden in collaboration with the Swedish Association for Hunting and Wildlife Management (SAHWM, *Svenska Jägareförbundet*). Information on changes of parish borders during the study period was derived from publicly accessible protocols of annual member meetings of the hunting parishes in question.

Intraspecific variables

Moose sex ratio (number of adult males per adult female) and density were calculated from the publicly available "MooseObs" (*Älgobs*) data administered by the Swedish CAB. MooseObs is an accepted monitoring method which relies on hunters systematically counting all moose observations and the corresponding amount of observation hours during the first week of the moose hunting season (Ericsson and Kindberg, 2011). It results in observations per man-hour as an index for moose density. To improve reliability of the data, only estimates based on at least 5000 man-hours are considered.

I included two other density indicators as control data. Bag density, i.e. total amount of moose shot per 1000 ha, was calculated by summing all individual moose documented in the "moose data" database (www.algdata.se) by MMA per year and dividing the number by the area of each MMA. Traffic accident density was calculated by summing up the amount of GPS-points of vehicle collisions with moose recorded by the Swedish police per MMA per year and dividing that number by the total length of roads in the MMA. Railways were not corrected for in the calculation as accidents are far less common there than on roads. It is mandatory for each car driver in Sweden to report collisions with ungulates to the police, which is why the dataset is assumed to capture most vehicle collisions occurring in the country. Before performing density calculations, the coordinates obtained from the police were quality-checked, removing locations outside the country and distant from roads.

Abiotic variables

MMAs were divided into two regions, North and South, based on the geographical border *Limes Norrlandicus* (Figure 1). I georeferenced the border of the *Limes Norrlandicus* in ArcGIS and consequently assigned the MMAs to one of the two regions. MMAs intersecting the borderline were assigned to the region where their major area was located.

Latitude in decimal degrees was derived from the Y-coordinate of the centroid of each MMA, calculated in ArcGIS using the *Calculate Geometry* tool. Elevation (m a.s.l.) was obtained as a raster file with a cell size of 5 m from the Swedish National Land Survey. Length of the vegetation period, defined as accumulated day degrees higher than 5 °C (the limit above which grass grows) over the reference period 1960-1990, was derived from a shapefile with temperature isoclines obtained from the Swedish Meteorological and Hydrological Institute (SMHI).

Annual precipitation sums (mm) and average temperatures (°C) were also retrieved from SMHI. As SMHI provided values per calendar year and most moose are shot before the turn of the year, I assigned the SMHI data to the part of the hunting year before New Year (e.g. to the hunting year 2012/13, I assigned the weather data of the year 2012). I selected 95 weather stations across the country, joined the weather measurements to the coordinates of the corresponding weather station on the map and interpolated the weather data in ArcGIS using inverse distance weighted (IDW) interpolation to obtain a continuous raster layer of the climate variables.

Data on snow depth were also available from SMHI. As snow depth is expected to have a delayed effect on body mass, I decided to include snow depth of the winter previous to the kill of the moose (e.g. for the hunting year 2012/13, I included snow depth for the winter 2011/12). I selected 162 weather stations in Sweden and extracted daily snow depth measurements for September-May (corresponding to the months where snow was observed at least one weather station in the country). After having calculated annual mean values based on these, I interpolated snow depth as described above.

Seasonality was included as a measure of food availability. I retrieved the Dynamic Habitat Indices (DHI) data from the SILVIS Lab (http://silvis.forest.wisc.edu/dhi) and extracted the third layer in the raster stack, i.e. the coefficient of variation (CV) of productivity. As a measure of productivity, I chose the fraction of photosynthetically active radiation (fPAR) measured every 8 days from 2003-2014 at 1-km resolution (Andrew Allen, personal communication 2017-02-07).

Interspecific variables

Species richness was defined as the number of ungulate species other than moose present in the MMA. I based that variable on the occurrence of vehicle collisions with the species in question, as I assumed that traffic accidents capture presence faster than hunting statistics and furthermore at a higher spatial resolution, considering that accident data were obtained as GPS-points for the accident location while hunting statistics had been collected at hunting parish level. Data were corrected for discontinuity: From the point in time where the first accident with a certain species was recorded in a MMA, it was assumed that the species continued to be present until the end of the study period, even if the data included absences of vehicle collisions for other following years. This was assumed as extinction in a MMA after establishment was regarded as less likely than extension of the species' distribution range after establishment (consider e.g. the history of re-colonization of wild boar in Sweden).

Densities of the other ungulate species roe deer, red deer, fallow deer and wild boar were obtained from two different sources in order to have control data. Traffic accident density was calculated in the same way as for moose (see above). Bag density was calculated from the bag statistics for each species which I obtained from the SAHWM. The monitoring system is based on hunters on the level of hunting parishes voluntarily reporting their bag for each species to the database www.viltdata.se. Species numbers are then extrapolated from the area covered with reports to the whole hunting parish. I calculated bag density per 1000 ha by dividing extrapolated bag numbers by the size of the corresponding hunting parish. To transform the data to MMA level, I first converted the hunting parish shapefile with the bag density data to a raster file with the density values and a cell size of 1 ha and then used the ArcGIS tool *Zonal Statistics as Table* to calculate mean density values per MMA. This approach accounted for the different proportions of hunting parish areas overlapping with the MMA, i.e. weighted the different densities of the contributing hunting parishes by the area the parishes were contributing to the total area of the MMA.

Habitat variables

Land use proportions were obtained from the Corine Land Cover (CLC) data from 2012 provided by the European Environment Agency (EEA). I downloaded the raster file with 25 m resolution from http://land.copernicus.eu/pan-european/corine-land-cover/clc-2012 and converted it to a shapefile. Using the ArcGIS *Identity* tool, I calculated the areas of each landform in km^2 per MMA and exported them to Excel. The original 48 land use classes were summarized into 7 classes, being Artificial (urban areas and industrial sites), Agricultural/Open (agricultural areas and open areas such as grasslands and heathlands), Wetland (inland wetlands and salt marshes), Broad-leaved forest, Coniferous forest, Mixed forest (neither broad-leaved nor coniferous forest constitute more than 75 % of the crown cover) and Transitional habitat (including young forest and clear-felled areas) (Lantmäteriet, 2015). The categories "Sparsely vegetated habitats" and "Water" were excluded due to little occurrence (sparsely vegetated habitats) and unimportance for moose (water), respectively. For the analyses, I calculated the proportion of each of the 7 categories in percent of the total MMA.

Habitat diversity was calculated by Simpson's λ index (Simpson, 1949) with the following formula

$$\mathrm{S}\lambda = \sum_{i=0}^{n} p_i^2$$

where p_i equals the proportion of land use type i (Herfindal et al., 2014).

Forest age in years was extracted from the corresponding layer of the Forest Map (*Skogskarta*) produced by the Swedish University of Agricultural Sciences (SLU) in 2010 (www.slu.se/skogskarta). I transformed the layer from the older projection RT90 to SWEREF99 using the method *CUBIC* suitable for continuous data in ArcGIS.

Human variables

Human population size as a measure for human disturbance was obtained as estimates per municipality from Statistics Sweden (www.scb.se) for the 31st December of each year. Considering that most moose weights are collected before New Year, I assigned the estimates to the first part of each hunting year (e.g. the hunting year 2012/13 is assigned population data from the 31st December 2012). I calculated population densities by dividing each population count by the area of the corresponding municipality. In ArcGIS, I calculated the centroid of each municipality and assigned it the belonging population density per ha. I interpolated the population data using inverse distance weighted (IDW) interpolation to obtain a continuous raster layer of population densities across Sweden.

Road and railway density were included as a measure of the effect of roads and railways on moose weights. Based on the line layer with roads (VL) and the line layer with railways (JL) of the GSD-Map of Sweden (1:1 million) available through the Swedish National Land Survey (www.lantmateriet.se), I calculated the kilometres of roads and railways per square kilometre for each MMA using the *Kernel Density* tool in ArcGIS.

Appendix S2

Supplementary methodology on statistical analyses

Used R packages

For data editing in general, I used the R packages dplyr (Wickham and Francois, 2016) and tidyr (Wickham, 2017). For creating plots, I used the packages ggplot2 (Wickham and Chang, 2016) and lattice (Sarkar, 2017) in most cases. When checking for spatial autocorrelation, different packages were used for creating bubble plots and sample variograms (*bubble* and *variogram* function in the package gstat (Pebesma and Graeler, 2017), respectively) and spatial correlograms/Moran's I plots (*correlog* function in the ncf package (Bjornstad, 2016)). To calculate Moran's I Index, I applied the *Moran.I* function in the ape package (Paradis et al., 2017). For the principal component analysis (PCA), I used the packages FactoMineR (Husson et al., 2017), factoextra (Kassambara and Mundt, 2017) and corrplot (Wei and Simko, 2016). I conducted the linear discriminant analysis (LDA) using the ade4 package (Dray et al., 2017). Variance inflation factors were calculated using the packages car (Fox et al., 2016) and fmsb (Nakazawa, 2017). Hierarchical partitioning was conducted with the hier.part package (Walsh and Mac Nally, 2015) and model importance was calculated with the MuMIn package (Bartoń, 2015). Cross validation was implemented with the DAAG package (Maindonald and Braun, 2015) using the *CVlm* function for linear regression, and therefore excluding the random factor hunting year in this analysis.

Transformations of explanatory variables

The variables elevation and snow depth were square-root transformed (sqrt(x)) due to their right-skewed data distributions. Seasonality and human population density were log-transformed (log(x) as this improved their right-skewed distributions more than a square-root transformation, as apparent from the plotted histograms. All habitat proportions data were transformed with the arcsine square-root transformation asin(sqrt(x)), commonly used for proportion data (Hjeljord and Histol, 1999; McDonald, 2014).

Due to many zero values present, the continuous variables accident density and bag density for ungulate species other than moose were transformed into categorical variables. I divided them into four categories (absent, low, medium, high) based on data range. "Absent" was defined as a density of zero. For accident density, "low" included data values smaller than 25 % of the maximum value, "medium" 25-50 % and "high" values larger than 50 % of the maximum. Categorization differed slightly for bag density due to even more skewed data distribution. "Low" was defined as values smaller than the median, "medium" as values larger than the median but smaller than the 3rd quantile of the data, and "high" contained values larger than the 3rd quantile. The corresponding data ranges per species are shown below (Table S2.1).

Table S2.1. Data ranges for the ungulate density categories in number/1000 ha. The category "Absent" is always defined as a density of zero and therefore not included in the table. Indexes included in the models are indicated as bold.

Species	Source	Unit	Low	Medium	High
Red deer	Traffic accidents	accidents / km of road	< 0.017	0.017 –0.034	> 0.034

Red deer	**Bag statistics**	**individuals / 1000 ha**	**< 0.020**	**0.020 – 0.235**	**> 0.235**
Fallow deer	**Traffic accidents**	**accidents / km of road**	**< 0.084**	**0.084 –0.168**	**> 0.168**
Fallow deer	Bag statistics	individuals / 1000 ha	< 0.031	0.031 – 1.058	> 1.058
Roe deer	**Traffic accidents**	**accidents / km of road**	**< 0.386**	**0.386 – 0.771**	**> 0.771**
Roe deer	Bag statistics	individuals / 1000 ha	< 4.297	4.297 – 7.197	> 7.197
Wild boar	Traffic accidents	accidents / km of road	< 0.085	0.085 – 0.170	> 0.170
Wild boar	**Bag statistics**	**individuals / 1000 ha**	**< 2.474**	**2.474 – 8.382**	**> 8.382**

Appendix S3

Supplementary on results

Model parameters for each model group

Model parameters for the different groups are shown in the following tables (Table S3.1 – S3.8). In all tables, "Estimate" refers to the parameter estimate, "SE" is the standard error for the estimate, "DF" is the degrees of freedom, and "t-value" is the t test statistic and "p-value" a measure for the significance of the variable.

Table S3.1. Model parameters for the selected model for the group MA_N. Column headings are explained in the text above.

Variable	Estimate	SE	DF	t-value	p-value
Intercept	187.06	3.04	133	61.61	1.2×10^{-99}
Hunting year – 1314	5.68	2.17	133	2.62	0.010
Hunting year – 1415	9.30	2.14	133	4.35	2.7×10^{-5}
Hunting year – 1516	9.30	2.13	133	4.36	2.6×10^{-5}
Sex ratio	4.26	0.91	133	4.67	7.2×10^{-6}
Latitude	2.74	1.37	133	2.00	0.047
Species richness – 2	0.96	3.02	133	0.32	0.752
Species richness – 3	-7.33	3.30	54	-2.22	0.031
Species richness – 4	-3.92	4.45	54	-0.88	0.383
*arcsin(sqrt(*Artificial-%*))*	-3.49	1.02	133	-3.42	8.4×10^{-4}

Table S3.2. Model parameters for the selected model for the group MA_S. Column headings are explained in the text above.

Variable	Estimate	SE	DF	t-value	p-value
Intercept	184.45	2.83	193	65.06	3.1×10^{-133}
Hunting year – 1314	-5.20	1.58	193	-3.28	0.001
Hunting year – 1415	-3.54	1.58	193	-2.24	0.026
Hunting year – 1516	0.41	1.60	193	0.26	0.797
Red deer bag density – low	-5.04	2.65	193	-1.90	0.059
Red deer bag density – medium	-7.67	2.90	193	-2.64	0.009
Red deer bag density – high	-14.38	2.87	193	-5.01	1.2×10^{-6}
Road density	4.32	1.02	193	4.22	3.8×10^{-5}
*log(*Human population density*)*	-3.81	1.02	193	-3.73	2.5×10^{-4}

Table S3.3. Model parameters for the selected model for the group FA_N. Column headings are explained in the text above.

Variable	Estimate	SE	DF	t-value	p-value

Intercept	165.30	2.30	126	71.86	4.0×10^{-104}
Hunting year – 1314	4.57	1.63	126	2.81	0.006
Hunting year – 1415	6.23	1.61	126	3.87	1.8×10^{-4}
Hunting year – 1516	6.55	1.61	126	4.06	8.6×10^{-5}
Sex ratio	2.91	0.75	126	3.87	1.7×10^{-4}
Species richness – 2	-2.10	2.40	126	-0.88	0.383
Species richness – 3	-9.12	2.44	54	-3.73	4.6×10^{-4}
Species richness – 4	-10.23	3.64	54	-2.81	0.007

Table S3.4. Model parameters for the selected model for the group FA_S. Column headings are explained in the text above.

Variable	Estimate	SE	DF	t-value	p-value
Intercept	156.66	2.18	192	71.69	1.6×10^{-140}
Hunting year – 1314	-2.90	1.03	192	-2.80	0.006
Hunting year – 1415	-3.04	1.03	192	-2.95	0.004
Hunting year – 1516	1.22	1.05	192	1.17	0.245
Fallow deer traffic density – low	0.42	1.09	192	0.38	0.703
Fallow deer traffic density – medium	-4.23	2.24	192	-1.89	0.060
Fallow deer traffic density – high	-7.58	2.62	192	-2.89	0.004
Red deer bag density – low	-1.26	1.64	192	-0.77	0.444
Red deer bag density – medium	-2.69	1.85	192	-1.45	0.148
Red deer bag density – high	-4.56	1.89	192	-2.41	0.017
Roe deer traffic density – medium	-1.44	1.17	192	-1.23	0.220
Roe deer traffic density – high	-5.05	1.97	192	-2.56	0.011
Wild boar bag density – medium	-3.44	1.32	192	-2.61	0.010
Wild boar bag density – high	-5.41	1.46	192	-3.71	2.7×10^{-4}

Table S3.5. Model parameters for the selected model for the group MC_N. Column headings are explained in the text above.

Variable	Estimate	SE	DF	t-value	p-value
Intercept	70.04	0.58	141	121.31	1.7×10^{-144}
Hunting year – 1314	-0.24	0.50	141	-0.47	0.639
Hunting year – 1415	2.53	0.50	141	5.09	1.1×10^{-6}
Hunting year – 1516	2.35	0.49	141	4.76	4.8×10^{-6}
*arcsin(sqrt(*Artificial-%*))*	-2.05	0.48	141	-4.27	3.5×10^{-5}
*arcsin(sqrt(*Agricultural/open-%*))*	-1.29	0.45	141	-2.85	0.005
*arcsin(sqrt(*Wetland-%*))*	-2.19	0.56	141	-3.88	1.6×10^{-4}

Table S3.6. Model parameters for the selected model for the group MC_S. Column headings are explained in the text above.

Variable	Estimate	SE	DF	t-value	p-value
Intercept	64.27	0.77	214	83.54	2.4×10^{-165}
Hunting year – 1314	-5.52	0.63	214	-8.82	4.2×10^{-16}
Hunting year – 1415	-1.56	0.40	214	-3.94	1.1×10^{-4}
Hunting year – 1516	-1.19	0.42	214	-2.83	0.005
Latitude	1.58	0.39	214	4.03	8.2×10^{-5}
*sqrt(*Elevation*)*	2.48	0.47	214	5.31	2.9×10^{-7}
Precipitation	-1.02	0.33	214	-3.10	0.002
Fallow deer traffic density – low	-0.80	0.43	214	-1.84	0.067
Fallow deer traffic density – medium	-3.29	0.91	214	-3.61	3.8×10^{-4}
Fallow deer traffic density – high	-3.85	1.14	214	-3.37	8.9×10^{-4}
Wild boar bag density – medium	-1.50	0.58	214	-2.57	0.011
Wild boar bag density – high	-1.86	0.74	214	-2.50	0.013
*arcsin(sqrt(*Transitional-%*))*	1.18	0.36	214	3.26	0.001
*log(*Human population density*)*	1.01	0.41	214	2.46	0.015

Table S3.7. Model parameters for the selected model for the group FC_N. Column headings are explained in the text above.

Variable	Estimate	SE	DF	t-value	p-value
Intercept	66.11	0.69	138	95.85	3.8×10^{-128}
Hunting year – 1314	0.39	0.54	138	0.73	0.470
Hunting year – 1415	2.70	0.50	138	5.37	3.3×10^{-7}
Hunting year – 1516	2.07	0.51	138	4.04	9.0×10^{-5}
*sqrt(*Elevation*)*	1.12	0.54	138	2.09	0.038
*arcsin(sqrt(*Agricultural/open-%*))*	-0.82	0.46	138	-1.79	0.076
*arcsin(sqrt(*Wetland-%*))*	-1.44	0.55	138	-2.62	0.010
*sqrt(*Elevation*)* × *arcsin(sqrt(*Wetland-%*))*	-1.03	0.53	138	-1.95	0.053

Table S3.8. Model parameters for the selected model for the group FC_S. Column headings are explained in the text above.

Variable	Estimate	SE	DF	t-value	p-value
Intercept	59.93	0.83	206	71.82	8.7×10^{-148}
Hunting year – 1314	-3.96	0.41	206	-9.69	1.6×10^{-18}
Hunting year – 1415	-1.83	0.41	206	-4.48	1.3×10^{-5}
Hunting year – 1516	-1.02	0.41	206	-2.49	0.014

Latitude	2.26	0.39	206	5.83	2.2×10^{-8}
*sqrt(*Elevation*)*	1.96	0.41	206	4.74	4.5×10^{-6}
Red deer bag density – low	-0.83	0.76	206	-1.08	0.280
Red deer bag density – medium	-0.75	0.86	206	-0.86	0.389
Red deer bag density – high	-2.40	0.89	206	-2.68	0.008
*arcsin(sqrt(*Transitional-%*))*	0.70	0.36	206	1.97	0.050

Appendix S4

Supplementary figures

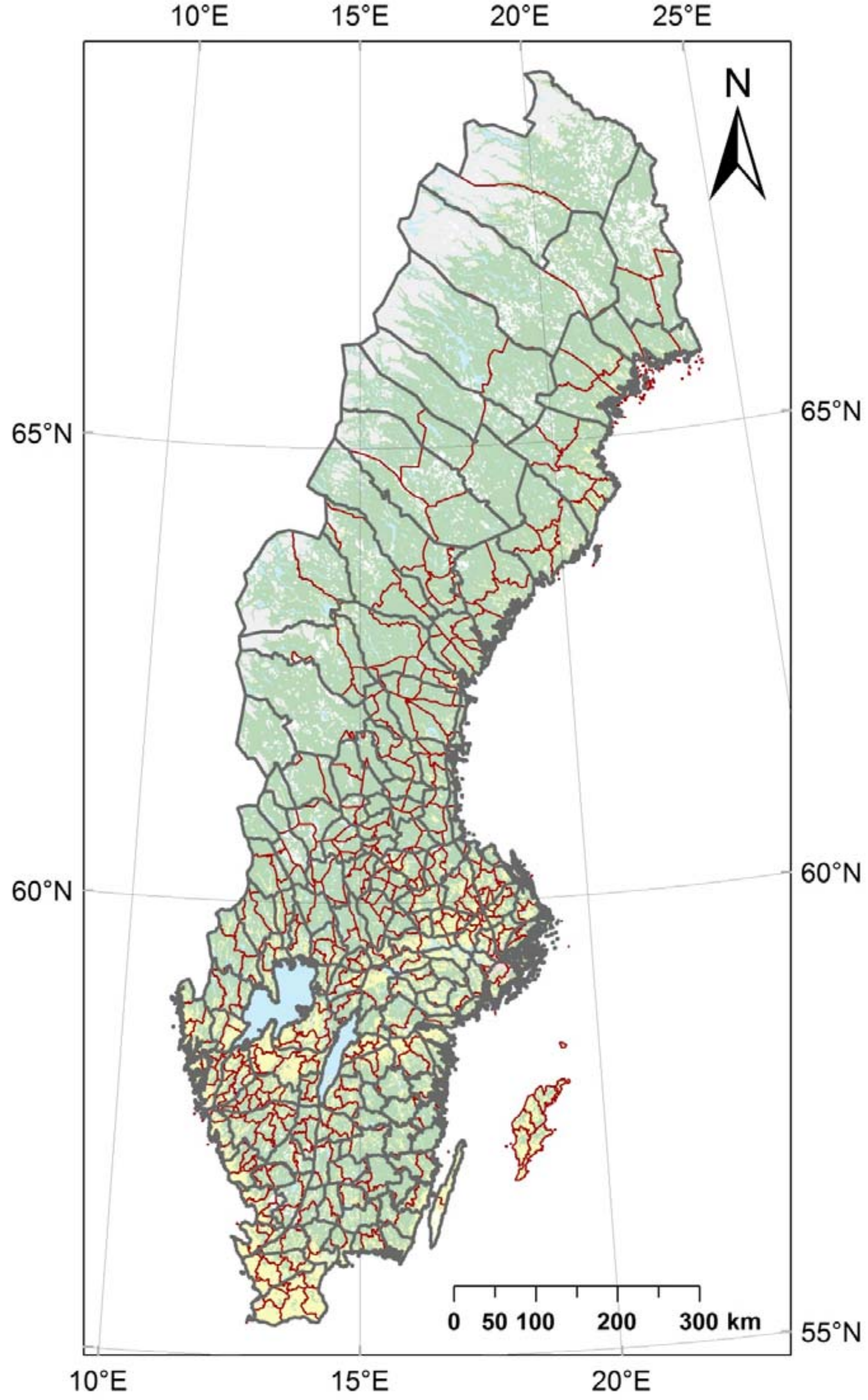

Figure S1. Map showing how moose management areas (MMA, effective 2015/16, grey lines) relate to hunting parishes (effective 2016, red lines).

SENASTE UTGIVNA NUMMER

2017:5	Land use changes and its consequences on moose habitat Författare: Ida Olofsson
2017:6	Micro habitat selection of herbivores in response to perceived predation risk and forage quality in Hluhluwe-iMfolozi game reserve Författare: Edvin Rapp
2017:7	Risky places and risky times: Vegetation cover and carnivore olfactory cues influence patch selection and antipredator behavior of African ungulates
2017:8	Tall trees survival in relation to bottom-up and top-down drivers in Hluhluwe-iMfolozi Park, South Africa Författare: Petter Madsen
2017:9	Prevalence of *Borrelia burgdorferi* sensu latu in rodents from two areas with varying wild ungulate densities in Southern Sweden Författare: Jimmy Nyman
2017:10	Remotely monitoring heart-rate and feeding behaviour of fish by using electronic sensor-tags Författare: Therese Arvén Norling
2017:11	Pride and prejudice – Extra-group paternity in lions and the effects of marker density on kinship and relatedness estimates Författare: Julia L. Jansson
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