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Master thesis

Spatial grazing patterns of red deer in agricultural meadows

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Abstract

The size of the Norwegian red deer population is historically high and typical of the trend seen over much of Europe. Dense populations may cause damage to agricultural crops, and crop yield is drastically decreased by red deer grazing in certain areas. We know that red deer select actively managed meadows, i.e., frequently renewed by fertilisation and re-seeding, over other agricultural meadows. Despite its importance, information regarding spatial grazing patterns by red deer on agricultural meadows is limited. In this study, I aim to quantify how grazing on agricultural meadows by red deer varies across spatial scales in southwest Norway. I hypothesise that grazing on agricultural meadows is determined by three major effects: (H1) Factors affecting forage quality and availability in meadows relative to natural habitats, such as population density and seasonal change, (H2) meadow management, such as renewal of meadows, and (H3) perceived predation risk and human disturbance, such as distance to settlement and forest edge. Grazing levels were assessed across meadows in a hierarchical study design, and I analysed the data using a binary logistic regression that model absence of grazing and a beta regression that model the level of grazing given grazing occurred. This enabled me to quantify both variation among spatial hierarchical units and the mechanisms behind spatial grazing patterns. I found that the grazing variation was largest between meadows in the local area and smallest on broader scale. High red deer density areas received more grazing relative to low-density areas, more grazing occured when meadow grass was shorter, and early in summer relative to late, suggesting that red deer select meadows over natural habitat when the difference in quality and availability of forage are large enough. Newly refreshed meadows received more grazing than the older ones, implying that a large part of the local site effect was caused by meadow management. Evidence of trade-off effects also appeared important as spatial grazing patterns changed near roads, houses, and forests. Broad-scale variation in red deer density explained some of the variations in grazing. However, since the largest variation in grazing was found locally, population reduction at broad scales may not effectively lower damages. These results may affect the scale at which management should target mitigation efforts.

Contents

Introduction

Foraging behavior is defined as all the ways by which an organism finds and utilizes energy and nutrients (Stephens & Krebs, 1986). To maximize net energy gain, the animal should adopt a foraging strategy that provides the most resources for the lowest cost. Animal foraging behavior is therefore an important factor for growth, survival, and reproductive success. Animals' choice of certain habitats as foraging grounds instead of others hence affect the fitness of the forager. Resources that wild animals obtain from farmland is referred to as agricultural subsidies, an element contributing to the linkage between agricultural and natural ecosystems (Liu et al., 2007). Insight into how farmland and surrounding habitats affect wildlife is paramount in understanding wildlife population dynamics and predicting grazing patterns. It is important to understand how and why animals use certain habitats when designing effective management strategies, as this will further improve sustainability of wild animal populations and their interconnected ecosystems.

When choosing foraging habitat, animals will consider a wide range of factors (Belovsky, 1981; Westneat, 1994). The choice will often be a trade-off between potential energy gains and risks associated with a given habitat (Lima & Dill, 1990), and a cost relating to selecting habitat, e.g., the time and energy used to seek out habitat (Rosenzweig, 1981). The effect of such trade-offs for choices of foraging habitat may vary with season, weather condition, and time of day, in addition to the size, age, sex and daily activity of the animal (Beier & McCullough, 1990; Perez-Barberia & Gordon, 1999). Further, habitat selection is expected to be density-dependent (Rosenzweig, 1981). By assessing how quality of habitat is affected by competition in the area, animals can change their selection patterns, also affecting the density pattern in the population (Morris & MacEachern, 2010). Selection of habitat occurs in a hierarchical manner (Senft et al., 1987), and may be divided into four levels of selection (Johnson, 1980). The highest level can be defined as selection on the geographical or physical range of the species. Secondly, within this area, home range will be selected. Feeding site selected within the home range can be termed as the third level, and lastly, the animal chooses a certain forage to be eaten at the given site.

In the last 50 years red deer (*Cervus elaphus*) populations in Europe have increased markedly (Milner et al., 2006). This increase is likely due to changes in population management and land use practices. Selective hunting has been used to increase the relative reproductive value of populations (Milner et al., 2006), targeting young animals and adult males (Apollonio et al., 2010). While limited in natural habitats, high quality food is relatively abundant on agricultural land in specific seasons over most of red deer's range. However, more open farmland will cause increased exposure to human disturbance and predatory dangers. Synthetic fertilization has improved the quality of agricultural crops, which may attract and increase the number of red deer foraging on farmland (Mysterud et al., 2002; Zweifel-Schielly et al., 2012). Red deer select meadows over other types of farmlands, especially the ones that are managed actively and renewed frequently by fertilization and re-seeding (Lande et al., 2014). However, we lack estimates of how land use practices, such as meadow management and botanical composition, affect the variation of grazing on broad scales. Additionally, how large are these effects compared to other local effects or compared to landscape level drivers like topography and distance to the coast?

The size of the Norwegian red deer population is historically high and typical of the trend seen over much of Europe. A total of 49 301 red deer was shot during the hunting season 2022-2023 (Statistisk sentralbyrå, 2023). This is approximately a 500% harvest increase since the late 1980's. Big game hunting yield was estimated to 1 470 MNOK in 2018 (Andersen & Dervo, 2019). However, this is a double-edged sword, leading to many conflicts of interest. Dense populations of large ungulates will also have costly impact on both natural- and agricultural habitats. Sward from meadows is intended to be used as fodder for livestock and therefore a valuable product. Unfortunately, grazing by wild red deer can have severe effect on meadow production, reducing the quality and quantity of fodder (Marchiori et al., 2012; Trdan & Vidrih, 2008). In high density areas the intense foraging may have ecological as well as economic repercussions (Øpstad et al., 2022).

In this thesis, I quantify how grazing on agricultural meadows by red deer vary across various spatial scales across the south-west of Norway in the growing season of 2021. The study area was divided into a study grid containing spatial hierarchical levels, where each level contained unique meadow observations. This enabled me to quantify variation in grazing among spatial units and allow me to gain insight into what level forage habitat selection occurs. I measured within meadow and meadow characteristics, proximity to certain habitat types and broad scale drivers, assumed to be important mechanisms behind spatial grazing patterns.

An overview of main hypotheses and predictions are summarized in Table 1. I hypothesize that: H1) Grazing on agricultural meadows is determined by forage quality and availability relative to natural habitats. From H1, I predict increased grazing levels in areas with higher red deer population density, whereas I predict distance away from coast, higher elevation, and higher (more mature) grass to be associated with reduce grazing. I also predict that there will be more grazing early in the summer season relatively to late summer. H2)

Grazing is determined by quality of forage relative to other meadows available, essentially determined by meadow management. From H2, I predict a higher grazing on younger meadows, higher timothy presence, and higher cultivated grass-type presence, whereas higher wild grass-type presence is expected to be negatively correlated with grazing. H3) Grazing on agricultural crops is determined by perceived predation risk and human disturbance. From H3, I predict that increased distance to roads and houses will increase grazing, but increased distance to forest edge will decrease grazing.

Table 1: An overview of hypotheses (H), corresponding predictions (A-E) investigated, parameters used to measure the effect, argument, and reference. Referring to supported predictions as (S) and rejected predictions (R). Spatial level hierarchy explained in Observational design and Figure 3.

Hypotheses	Predictions	Parameters	Argument	Reference
H1. Grazing on agricultural meadows is determined by forage quality and availability infields relative to natural habitats.	**A.** Higher *red deer density* will increase grazing. (**S**)	Index for red deer population density (shot per km^2) on municipality level.	More animals lead to competition for natural forage, forcing more red deer onto agricultural farmland.	(Corgatelli et al., 2019)
	B. Further *distance away from coast* will decrease grazing. (**R**)	Distance (m) measured on meadow level.	Natural habitats have better quality foraging during summer further inland, therefore red deer will utilize less farmland.	(Albon & Langvatn, 1992)
	C. Higher *elevation* will decrease grazing. (**R**)	Elevation (m) measured on meadow level.	Higher elevation ranges have better quality forage during summer, therefore red deer utilize less farmland.	(Albon & Langvatn, 1992; Mysterud et al., 2017)
	D. More grazing in *early summer relative to late.* (**S**)	Early (May/June) vs. late (July) summer.	Natural habitats are selected when forage abundance is high (later in summer).	(Albon & Langvatn, 1992)
	E. Higher *grass height* will decrease grazing. (**S**)	Grass height (cm) measured on transect level.	Mature grass contain relatively less protein and more fibre than younger grass	(Østrem et al., 2015)
H2. Grazing on agricultural meadows is determined by meadow management.	**A.** *Younger meadows* will have more grazing. (**S**)	Meadow age (new, intermediate, and old).	Newer meadows contain more energy rich grass species.	(Andueza et al., 2010; Blaxter et al., 1961)
	B. More *timothy cover* will increase grazing. (**S**)	Area (%) covered by timothy measured on transect level.	Meadows with high quality forage, such as timothy, are more attractive.	(Langvatn & Hanley, 1993)
	C. More *high quality forage* will increase grazing. (**R**)	Area (%) covered by cultivated grass types measured at transect level.	Cultivated grass types are high in energy and easily digestible, thus more attractive.	(Langvatn & Hanley, 1993)
	D. More *low quality forage* will decrease grazing. (**R**)	Area (%) covered by grass types introduced from natural habitats measured at transect level.	Wild grass types are lower in energy and digestibility, thus less attractive.	(Langvatn & Hanley, 1993)
	E. More *plant cover* will increase grazing. (**R**)	Area (%) covered by plants measured at transect level.	Denser meadows contain more biomass, thus more attractive.	(Trudell & White, 1981)
H3. Grazing on agricultural meadows is determined by perceived predation risk and human disturbance.	**A.** Further *distance to roads* will increase grazing. (**S**)	Distance (m) to public roads measured at square level.	Mechanical activity act as threatening stimuli inducing antipredation response in red deer.	(Andersen et al., 1996; Frid & Dill, 2002)
	B. Further *distance* to *houses* will increase grazing. (**S**)	Distance (m) to houses measured at square level.	Human activity act as threatening stimuli inducing antipredation response in red deer.	(Frid & Dill, 2002; Meisingset et al., 2022)
	C. Further *distance* to *forest edge* will decrease grazing. (**S**)	Distance (m) to forest edge measured at square level.	Trees and shrubs act as cover and decrease perceived risk of predation.	(Månsson et al., 2021)

Material and methods

Study area

The study area is located in the counties of Møre & Romsdal and Trøndelag in the western part of Norway (Figure 1). Fjords, rivers, high mountains, steep hills, and valleys make for a topographical heterogenous landscape (Figure 2A). Generally, there is a decline in precipitation and temperature further inland and northwards, but with an increase in snow depth along the same gradients. Mean temperature is 14.8 °C in June and 18.0 °C in July 2021. Normal precipitation is 91.0 mm and 96.0 mm, in June and July 2021 respectively (Molde, Nøisomhed weather station, station id: SN62290). The natural forests are predominantly boreonemoral, a forest mixture between deciduous- and coniferous trees (Mysterud, 2000). The coniferous part is mainly made up of Scots pine (*Pinus sylvestis*) and planted Norway spruce (*Picea abies*), and the deciduous part is chiefly composed of birches (*Betula* spp.) and alder (*Alnus incana*). Agricultural production normally utilizes the flatter and more nutrient rich areas along valley bottoms. These are most commonly used for meadows and pastures producing grass harvested for winter fodder for livestock and/or are seasonally grazed. Timothy (*Phleum pratense*), blue grass (*Poa pratensis*), meadow fescue (*Schedonorus pratensis*) and perennial ryegrass (*Lolium perenne*) are some of the most commonly cultivated grass species.

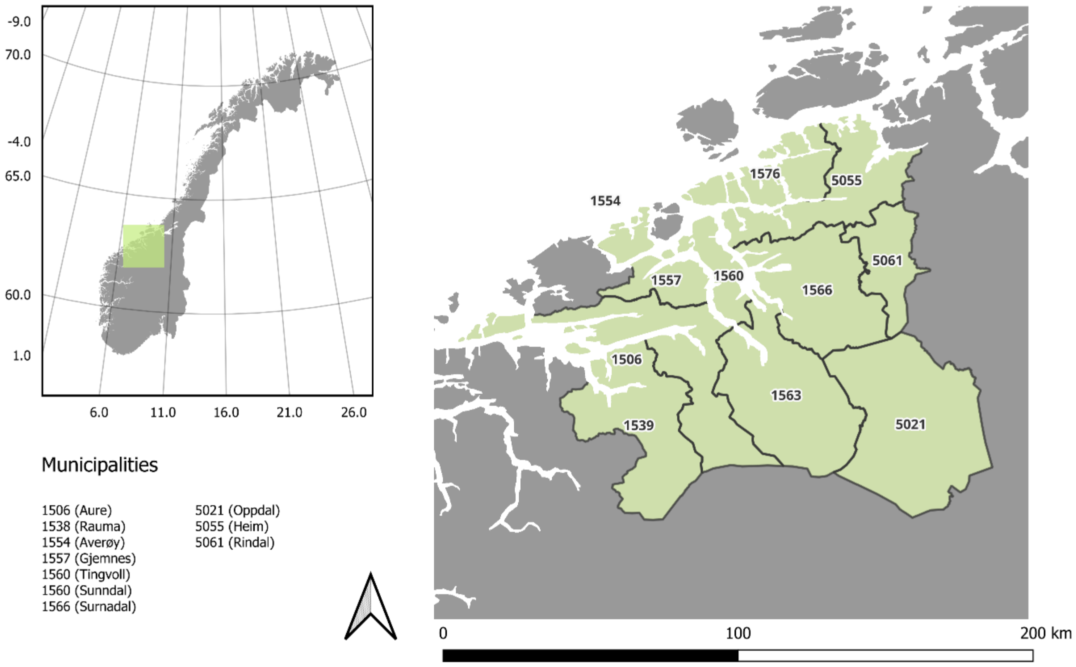

Figure 1: An overview of the study area in the western part of Norway. The specific municipalities included in the study area is highlighted in green. The map was produced in QGIS (QGIS Development Team, 2022). The background map was obtained from Norwegian Mapping Authority (Kartverket, 2015).

Observational design

This observational study had a nested design containing 6 hierarchical levels, originally distributed into: Block (10), site (20), meadow (60), transect (240), square (4800) and sub-squares (19200). Vegetation was botanized and measured from a total of 60 meadows, located within 11 municipalities. The areas were surveyed during two field periods: before 1. harvest: May (19th) – June (6th) 2021 and between 1. and 2. harvest: July (13th – 30th) 2021. Each field work period lasted about two weeks and consisted of two observers working in pairs. The first pair consisted of different people than the second. Due to the lengthy fjords and to limit travel time between observational destinations, an efficient route rather than a fully randomized route was used in order to visit all meadows before the respective harvests.

Blocks divided the research area into a grid composed of A, B, C, D x 1, 2, 3, 4, 5 in order to get a representative sampling of the area (red grid in Figure 3). Within each block, there were two sites randomly allocated. Each site was a triplet of three meadows (red dots in Figure 3). In the study area, there were pre-established areas where grazing damage was measured using exclosures (blue triangles in Figure 3, and Figure 2A, n = 10). These were included as one meadow in a site, while the two remaining were drawn at random to assess their local representativeness. For every meadow, we delineated two transects moving alongside each other. These were fairly straight lines that we drew up manually when visiting during the field work. A transect consisted of 20 squares 5 m apart (using our step length). The squares were delimited using a standard botanical metal frame measuring 50x50 cm (Figure 4). Within the metal frame there were 4 sub-squares, made up of horizontal and vertical thin rope, which made it easier to assess the vegetation. Here we botanized vegetation and measured grazing quantity and degree, explained further below.

Figure 2: Photos taken on two different meadows. A) Left: Illustration of the typical topographically heterogeneous landscape of Møre & Romsdal Norway. B) Right: An exclosure used to measure grazing damage as part of another study in the AgriDeer-project.

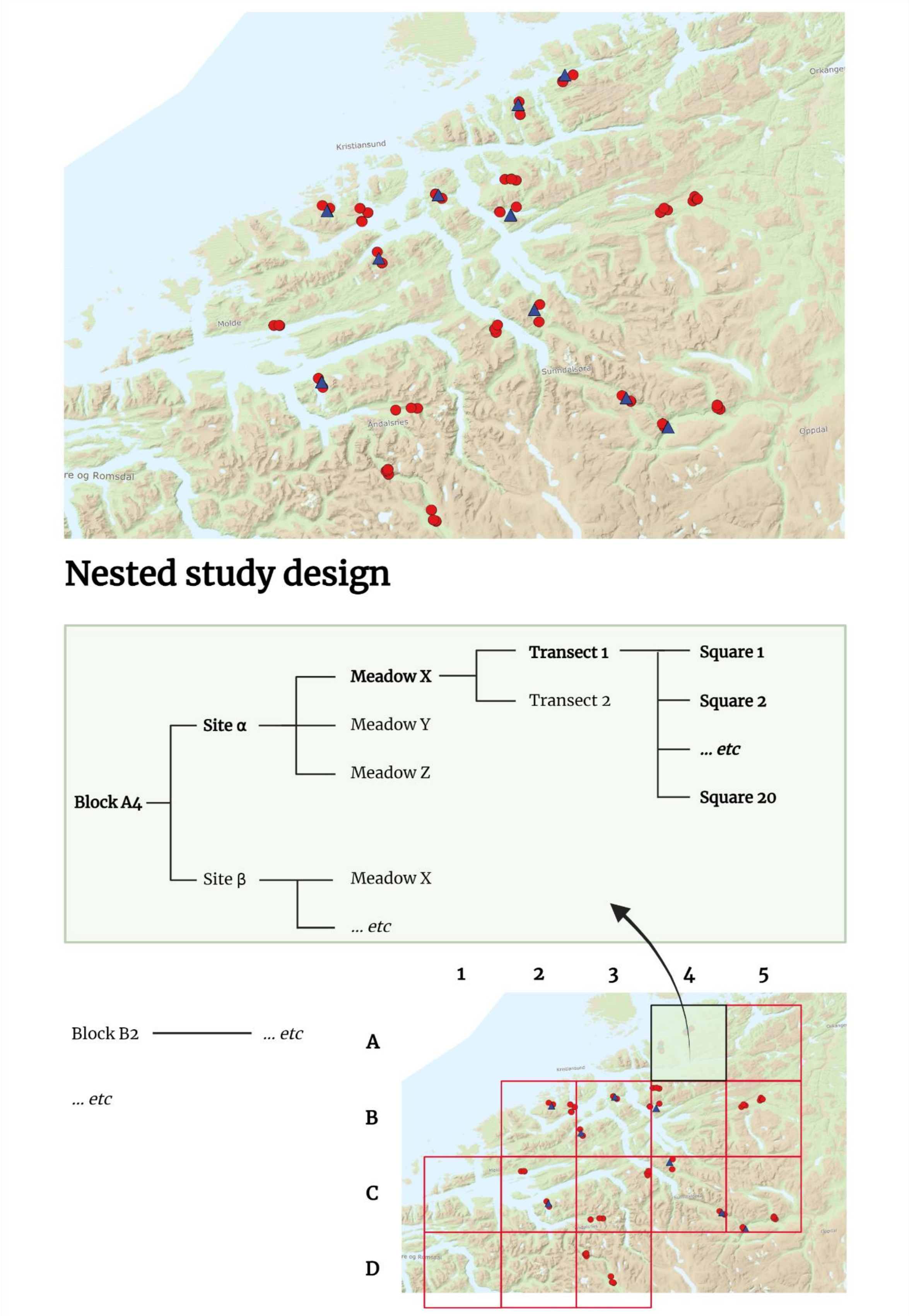

Figure 3: An overview of the study area and a schematic representation of the nested study design. Meadows are presented as red dots. Blue rectangles present the pre-established meadows that measures crop damage using exclosures. Red boxes display the study grid referred to as "blocks", and a triplet of three meadows in close vicinity of each other is referred to as "sites". The background map was obtained from Norwegian Mapping Authority (Kartverket, 2015).

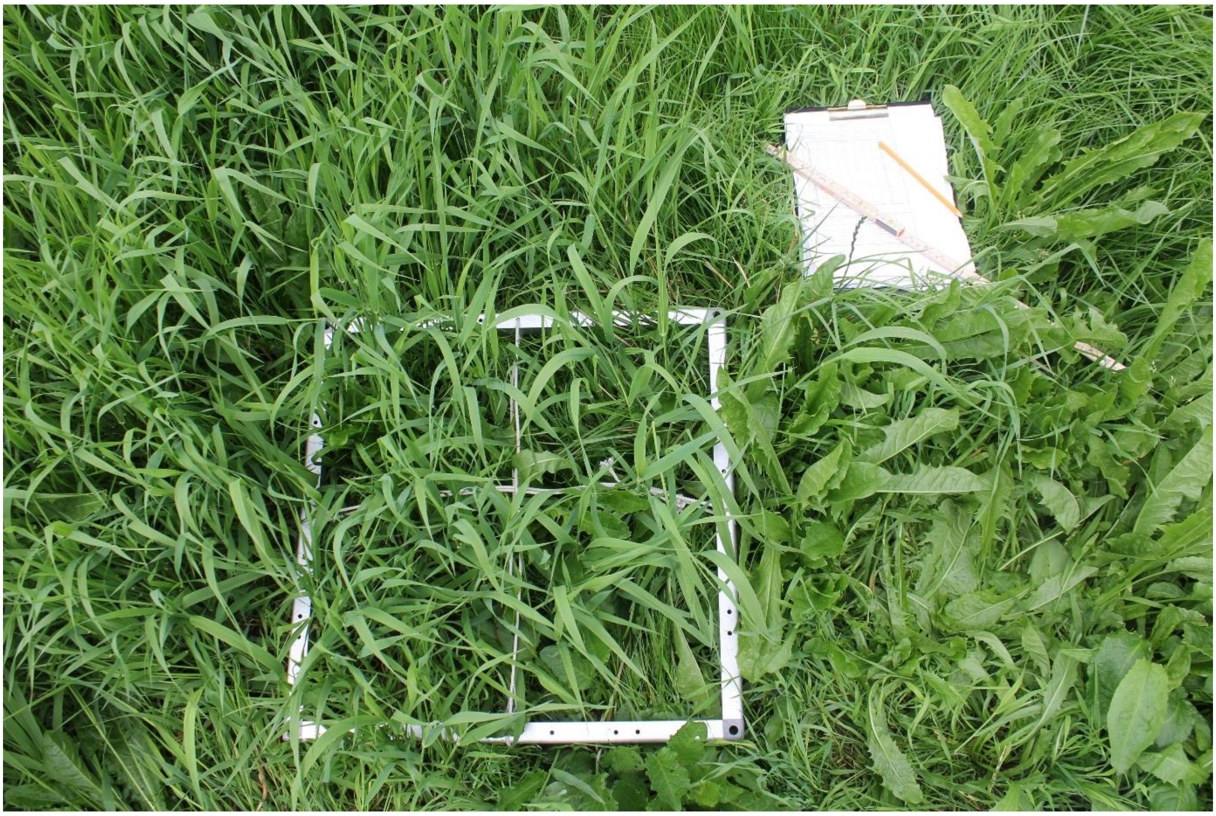

Figure 4: One of the observational points in a meadow. The botanical frame is lying in the grass ready for use (bottom centre). Water resistant paper attached to a clipboard used to write down results (upper right) with a meterstick and a pen resting on top.

To ensure a randomized starting point at every meadow, we followed three rules. 1) We used a computer to randomly assign a starting point at the meadow edge. 2) From this point, the fieldworkers walked a random interval between 30 – 70 m to determine the transect starting point. When encountering smaller plots, where it wasn't possible to obtain this distance, the fieldworkers divided the steps in half. 3) If the size of the meadow allowed it, the first and second transect would ideally be 30-70 meters apart. Because of these rules, the exact position of the squares examined before the first harvest would differ from the ones before the second harvest. We avoided the meadow edge by staying minimum 10 m from the edges, because the meadow along forest edges is often affected by shading and unlikely to be representative for the larger area.

Data collection

Grass and meadow data was measured according to details given (Table 2). Grazing quantity, grazing degree (illustrated in Figure 5), and GPS-coordinates were measured for every square (method adapted from Thorvaldsen & Rivedal, 2014). Seeded cover consisted of 7 plant types common in seed mixtures: Timothy, cat grass (*Dactylis glomerata*), perennial ryegrass, white clover (*Trifolium repens*), red clover (*Trifolium pratense*), blue grass and meadow fescue. The botanical variables gathered were grass height and plant, wild grass, seeded and timothy cover, measured on square 1, 4, 8, 14, and 20 of each transect. This was intended to give a fair estimate of the meadow's botanical composition while ensuring sampling efficiency. Variables like field worker, date and time of day were also noted. Ten meadows had to be replaced because the original meadow for different reasons was unavailable (e.g., used for other purposes than harvesting grass such as livestock or grain production). In other cases, the harvest had already been carried out. Because of this, five meadows were replaced with a neighbouring meadow in both periods, whilst the other five were replaced in only one of the periods. The replacements were undisturbed but similar meadows in proximity to the original ones. On three different occasions, no other alternative meadows was nearby, and the meadows had to be disregarded. These three were all part of the observations scheduled before the 2nd harvest.

Table 2: A detailed explanation of how the botanical variables were measured at each meadow. 'Wild grass cover' refers to the cover of wild grass species which are not commonly cultivated by farmers, and most likely have been introduced from natural areas. 'Seeded cover' refers to the cover of plant species which are commonly cultivated by farmers. There is no single variable for the non-grass vegetation cover, but it is integrated with the 'Plant cover' variable. Thus, if 'Wild grass cover' and 'Seeded cover' does not equal 'Plant cover' it means that the remaining vegetation is made up of wild non-grass vegetation.

Variables	**Definition**
Grazing quantity	Number of grazing incidents in every sub-square, measured on 4 levels. 0 is no observed grazing; 1 is 1-3 grazing instances, 2 is 4-6 grazing instances, 3 is 7+ grazing instances.
Grazing degree	The mean grazing degree in every sub-square, measured on 4 levels. 0 is no observed grazing degree; 1 is light grazing - only the tip of the grass blade/plant leaf is grazed upon; 2 is intermediate grazing – about half the blade/leaf is grazed; 3 is heavy grazing – roughly the whole blade/leaf is grazed.
Plant cover	Part of the ground covered with vegetation (0-100%), rounding up to the closes 5%.
Wild grass cover	Part of the ground covered with wild grass species (0-100%), rounding up to the closes 5%.
Seeded cover	Part of the ground covered with seeded vegetation (0-100%), rounding up to the closes 5%.
Timothy cover	Part of the ground covered with timothy (0-100%), rounding up to the closes 5%.
Grass height	Mean grass height (cm), measured using the tallest crop from every sub-square and dividing by 4, only using integers.

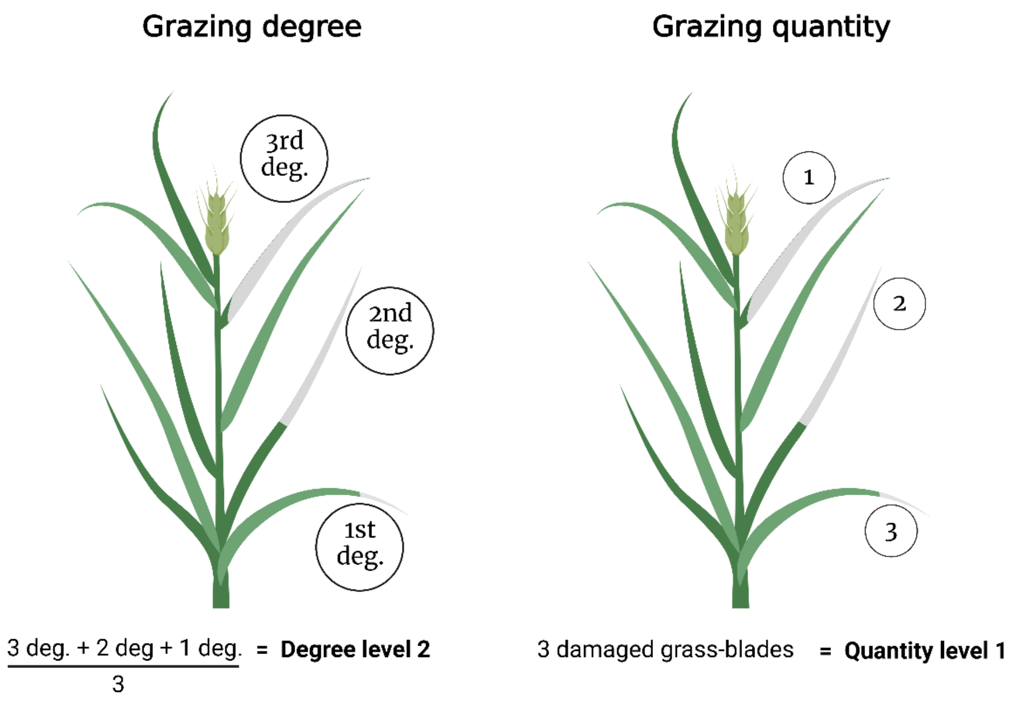

Figure 5: Illustrating an example of how grazing degree and grazing quantity were determined on grass. Detailed explanation is found in Table 2.

Covariates

Additional covariates were also added to the dataset. Because of the strong effect plant composition has on nutritional value, we expect the meadow age (i.e., the time since last renewal of the field) to have an effect on grazing (Andueza et al., 2010). This information was obtained by interviewing the respective landowners/farmers. It was later sorted into three categories: “New” are meadows that had been renewed within the last 1-3 years, “intermediate” was renewed between 4-8 years ago, and the “old” category was more than 9 years since last renewal. Age had to be disregarded in the instances where meadows were replaced (≈ 11% of data), arranging these occurrences into an “unknown” group. An index for red deer population density was calculated by using official harvesting data (Statistisk sentralbyrå, 2021). This was done by dividing the number of harvested animals from the hunting season of 2020 with the size (km^2) of the qualifying area (i.e., what has been deemed to be red deer habitat) for each municipality. This index for population density has been widely used in other studies and accounts for about 15-20% of the population size (Mysterud et al., 2001.). The variables elevation, distance to coast, roads, and buildings were all extracted using the GPS-coordinates, gathered during the fieldwork, with rasterized, digital topographical maps from the Norwegian Mapping Authority (Kartverket). This enabled the retrieval of measurements from every observational location. Elevation was measured in meters above sea level (resolution 50x50 m), distance to coast was measured in meters from demarcated line, distance to roads measures the distance from the closest public road, and closest distance to buildings. Distance to forest edge was extracted from AR5 land cover maps from The Norwegian Institute of Bioeconomy Research (NIBIO). I derived the mean of elevation and distance to coast on meadow level, whilst distance to roads, buildings and forest edge remained unchanged using all observational locations to exhibit in-field variation.

Statistical analysis

The analysis was done using the statistical programming language R version 4.2.2 (R Core Team, 2022). Data from one transect and the associated data was removed from the dataset as a result of GPS error. The removal of this transect and the three disregarded meadows from field period before the second harvest, reduced the total data to 4660 individual squares of observation. Grazing quantity and grazing degree, were averaged across each square, giving a value for the entire botanical frame as a whole, instead of one value from each sub-square. Further, I rescaled it from count data (0, 1, 2, 3) to a distribution of values from 0-1. These variables were zero-inflated. I calculated the mean of the botanical variables (4/20 squares per transect), thus gaining values on all observational points (20/20 squares per transect).

I wanted to quantify the variation within and between the random structures block, site, meadow, and transect. The R package ‘lme4’ was used to find out what random structure explains the data best (Bates et al., 2015). I first compared intercept only linear mixed-effect models including these random terms and assessed the model fit using the Akaike Information Criterion (AIC). The best random structure was used when fitting the full model. Before fitting models with fixed effects, I investigated the correlation between the potential predictors. I used the R package ‘corrplot’ to estimate correlation between numerical fixed effect parameters (Wei & Simko, 2021). Parameters that had a moderate or high correlation ($r > 0.6$ or $r < -0.6$) were not entered in the same model, and I later retained the parameter with the least correlation towards other variables (Akoglu, 2018). The R package ‘mgcv’ was used to assess non-linear relationships using generalized additive models (GAM, Wood, 2011). Depending on the form of the non-linearity, an appropriate polynomial was then used in the parametric modelling. Because of the large number of zeros in the response variables, I used a beta distributed mixed-effect model with zero inflation to analyse variation in grazing quantity and degree. The R package ‘glmmTMB’ was used to fit the model (Brooks et al., 2017). The zero-inflated beta distribution can be divided into two models: A binary logistic regression model that model occurrences of zeros, and a beta regression model that model data between 0-1.

All fixed effect variables except population density, and the three categorical variables meadow age, harvest (before first/second) and exclosures were transformed, normalizing the data, and reducing skewedness, or scaling the values so that the data range would resemble that of the other variables interval. After correlated variables and non-linear parameters had been established, I made a model including candidate explanatory variables for the beta regression model. Those were red deer density (shot per km^2), distance to coast (m), harvest (categorical; before first/second), grass height (cm), meadow age (categorical; new/intermediate/old), timothy cover (%), plant cover (%), wild grass cover (%), distance to road (m), distance to houses (m), distance to forest edge (m) and exclosures (categorical; with/without). I used a backwards model selection procedure using likelihood ratio tests. The variable with the largest p-value was removed from the model. Model x was then compared to model x+1. If the p-value was insignificant (>0.05) the variable was removed, and model selection proceeded. If the p-value was significant (<0.05) the variable was retained, and the model was retained as the final model. The same candidate explanatory variables and selection procedure was used for the binary logistic regression-part of the model. From the final model, I extracted both the marginal and conditional R^2 to investigate how much of the variation in the response variable that can be explained by fixed effects and/or random effects as a whole. Furthermore, I investigated the effects of the fixed variables and the random variables individually by plotting their predicted effects on the response variable.

Results

The two measures of grazing, namely grazing degree and grazing quantity, that were candidates for response variables, were highly correlated (r = 0.935). Thus, I proceeded with one final model using only one of the grazing measures. The two response variables both measured presence and level of grazing. Grazing quantity was the easiest to determine because it only involved counting instances. Grazing degree may have been slightly more subjective and could pose difficulties when deciding between the three degrees (e.g., when does 1. degree turn into 2. degree). Therefore, grazing quantity was used as response in the final models investigating grazing level and absence. For the predictors, distance to coast and elevation were highly correlated (r = 0.823), and I retained distance to coast which had the overall lowest correlation to the other numerical parameters. Similarly, wild grass cover and seeded cover were negatively correlated (r = -0.651) and wild grass cover was retained. Population density of red deer had some negative correlation with distance to coast and elevation, but not higher than recommended for inclusion in the same model (<0.6; Figure 6). Non-linearity was inspected using GAM, but no strong non-linearity was found. For selection of random effects, the most parsimonious model based on AIC included block, site, meadow, and transect as random terms (ΔAIC = 2). The second best model added square as a random term. The random effects were fitted in a nested structure in the same order as listed above, due to the hierarchical design of the study.

Figure 6: An overview of the numerical fixed effects and their correlations. Plot was generated using the R package 'corrplot' (Wei & Simko, 2021). Correlation is sorted by number (-1 to 1) and shading (red to blue) as indicated by right side gradient. (log) = log transformed. (sqrt) = square root. (sc) = rescaled, by centring on the mean and dividing by the standard deviation.

Hierarchical levels of variation in grazing

When quantifying the variation explained by the nested random effects in the model, the variance was highest among meadows within sites, followed by sites within blocks, transects within meadows, and lowest among blocks (Table 3). Overall, the fixed effect explained 30 % of the variation in grazing quantity (marginal r-squared = 0.300), whereas both fixed- and random effects explained about 56 % of variation in grazing quantity (conditional r-squared = 0.564).

Table 3: Estimation of random effects from the best fitted zero-inflated model explaining the variation in grazing quantity by red deer.

Parameters	**Variance**	**Standard deviation**
Transect/Meadow/Site/Block	0.285	0.534
Meadow/Site/Block	0.668	0.817
Site/Block	0.327	0.572
Block	<0.001	<0.001

Analysis of level of grazing, given grazing occurred

The final beta regression model included the fixed effects distance to road, distance to forest, density of red deer, wild grass cover, meadow age, and harvest number (Table 4). Thus, grass height, timothy cover, plant cover, exclosures, distance to houses and distance to coast had no significant effect on grazing quantity and were not retained. More grazing by red deer (Figure 7) occurred on squares further away from roads (E), in municipalities with high red deer density (A), on transects with high wild grass cover (D), and on new relative to intermediate meadows (C). The model estimated a decrease in grazing quantity on squares further away from forest edges (F) and on a temporal scale, estimating less grazing before the second relative to before the first harvest (B).

Table 4: Estimation of fixed effect parameters and factors from the best fitted conditional model explaining grazing quantity by red deer. Model selection is explained in Statistical analysis*. SE = Standard Error. (log) = log transformed. Reference level for Meadow age is "intermediate" and reference level for harvest period is "first".*

Parameters	**Estimate**	**SE**	**Z-value**	**P-value**
Intercept	-2.185	0.560	-3.903	<0.001
(log) Distance to road (m)	0.119	0.051	2.343	0.019
(log) Distance to forest edge (m)	-0.104	0.049	-2.132	0.033
Density of red deer (shot per km^2)	0.845	0.199	4.248	<0.001
(log) Wild grass cover (%)	0.467	0.101	4.603	<0.001
Meadow age New vs Intermediate	1.081	0.266	4.069	<0.001
Meadow age Old vs Intermediate	0.363	0.238	1.529	0.126
Meadow age Unknown vs Intermediate	-0.051	0.250	-0.205	0.838
Before Second harvest vs First	-1.849	0.082	-22.571	<0.001

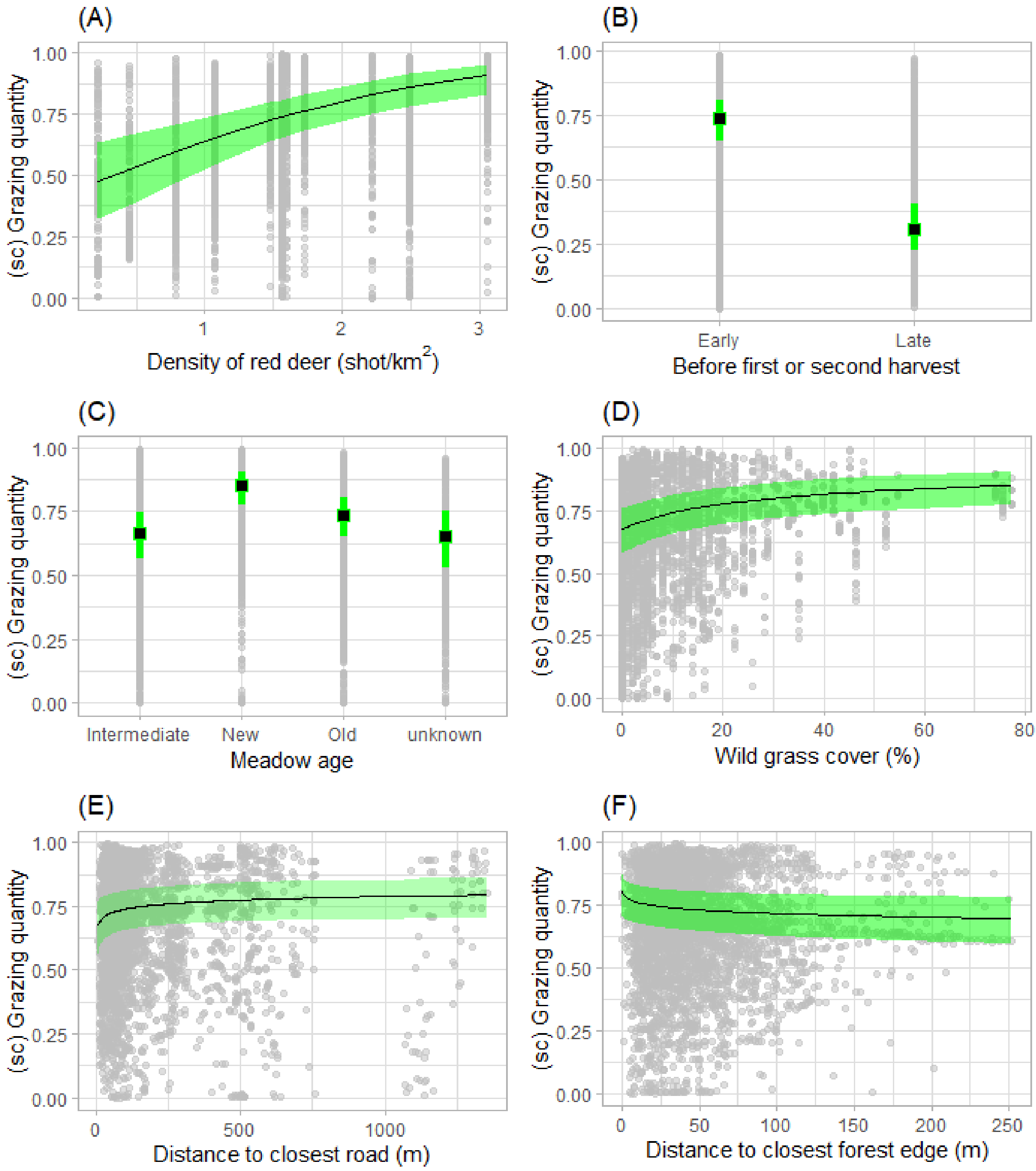

Figure 7: Plotted estimates of the predicted effect of all parameters and their residuals from the most parsimonious conditional model (A-F). Estimated response-effect on explanatory variable is expressed as a black line with a 95% confidence interval in green. Residuals are represented as grey dots. (sc) = scaled, to vary between 0-1.

Analysis of grazing absence

The final binary logistic regression model included the fixed effects distance to forest, distance to houses, density of red deer, timothy cover, plant cover, grass height, meadow age and harvest number (Table 5). Thus, distance to coast, distance to road, wild grass cover, exclosures had no significant effect on grazing quantity and were not retained. The probability of grazing quantity absence (Figure 8) increased on squares further away from forest edge (E), transect with higher grass height (C), as well as on the temporal scale, estimating higher probability of grazing absence before second harvest relative to before first (B). The probability of grazing absence decreased on squares further away from houses (D) and in municipalities with higher density of red deer (A).

Table 5: Estimates of fixed effect parameters and factors from the best fitted zero-inflated model explaining grazing quantity absence by red deer. SE = Standard Error. (log) = log transformed. (sqrt) = square root. (sc) = scaled, by centring on the mean and dividing by the standard deviation. Reference level for Meadow age is "intermediate" and reference level for harvest period is "first".

Parameters	**Estimate**	**SE**	**Z-value**	**P-value**
Intercept	2.074	1.123	1.846	0.065
(log) Distance to forest edge (m)	0.269	0.092	2.927	0.007
(log) Distance to houses (m)	-0.610	0.162	-3.761	<0.001
Density of red deer (shot per km^2)	-0.958	0.239	-4.005	<0.001
(sc) Grass height (%)	0.370	0.087	4.228	<0.001
Before second harvest vs First	3.315	0.110	30.111	<0.001

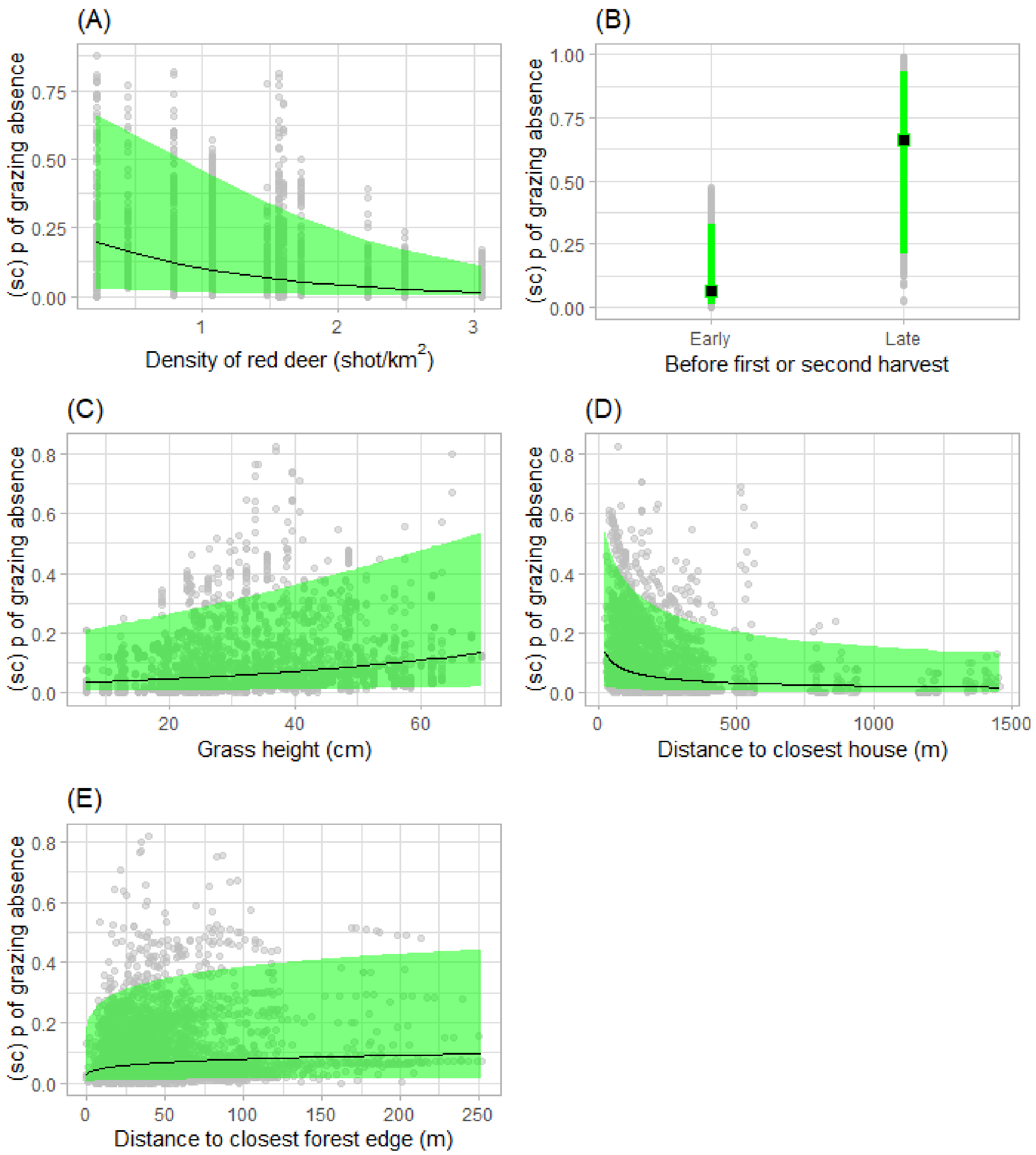

Figure 8: Plotted estimates of the predicted effect of all parameters and their residuals from the most parsimonious zero-inflated model (A-E). Estimated response-effect on explanatory variable is expressed as a black line with a 95 % confidence interval in green. Residuals are represented as grey dots. (sc) = scaled, to vary between 0-1.

Discussion

Increasing populations of deer in Europe are causing more damage to farmland. It is essential to study how wildlife uses agricultural farmland to understand red deer population dynamics and predict grazing damage. We know that red deer select meadows over other types of agricultural land (Lande et al., 2014). However, we do not know what factors determine the spatial pattern of grazing on meadows. In this study, I investigated how local and regional factors affect spatial grazing patterns on agricultural meadows during summer months. A change in the grazing response (grazing quantity) is either caused by a change in the number of red deer foraging or a change in the mean amount of grazing done by each individual red deer. For clearance grazing quantity is not able to measure economic grazing damage from red deer, only patterns of grazing. I used a model separating the analysis into the (1) absence of grazing and (2) the level of grazing given grazing occurred. The largest variation in grazing was found between meadows within sites rather than within meadows or at broader scales. These results may affect the scale at which management should target mitigation efforts.

Broad-scale variation in red deer grazing on meadows; density effects

The extent to which grazing can be predicted by population density is of particular interest to management, as this provides a solution to mitigation efforts through deer density reductions. Habitat selection is expected to be density dependent. (Morris & MacEachern, 2010; Rosenzweig, 1981). An overall hypothesis (H1) was that grazing on agricultural meadows is determined by forage quality and availability relative to natural habitats. From this general hypothesis, I made predictions regarding how red deer density and different spatial and temporal effects would potentially affect red deer grazing (Table 1). Increased population density of cervids will lead to competition and depletion of natural habitat, where the presumed consequence is a decline in vital rates (Fowler, 1987). However, natural habitat and agricultural land have coupled dynamics, as red deer use farmland as forage subsidies (Mysterud et al., 2023). I found that the probability of grazing absence decreased, and grazing levels increased with higher red deer density (H1A). Due to meadow subsidies fuelling red deer population growth, natural regulation of densities caused by competition forage will have less impact on population density. If red deer populations keep increasing, a larger portion of their diet will likely contain farmland subsidies, effectively buffering density effects. Therefore, more efficient harvest plans are needed to manage an increasing red deer population under such conditions. Otherwise, red deer might inflict even more damage on crops in the future.

Although municipality-level red deer density had a marked effect on grazing levels, this assumes homogeneity of animal distribution on a large spatial level and will not capture the local variation in the density of animals. Red deer density at the scale of the local management unit ("vald") has proven to be more reliable than on the municipality level (Mysterud et al., 2023). This scale might help uncover why variation in grazing is largest at the meadow level. Unfortunately, such data was unavailable for this study, it is also time-consuming to collect this type of fine-scale data, but it would be interesting to integrate it into later studies to explain local grazing patterns more accurately. Identifying both broad- and local-scale density effects on agricultural grasslands is valuable when reacting to damages inflicted by red deer. Overall, my results indicate that density reductions at a broad scale can mitigate grazing by red deer on agricultural meadows.

Broad-scale variation in red deer grazing on meadows; shift in availability and quality

The choice of feeding patch is a crucial concern to ruminant herbivores because most of their active time is spent foraging and ruminating (Bunnell & Gillingham, 1985). This choice determines the quality and the quantity of forage intake (Langvatn & Hanley, 1993). Ungulates will therefore select for feeding patches with high nutrient content (Hanley, 1997). When grass height increased, my data indicates that red deer were less interested in foraging, as the probability of grazing absence was higher in taller grass (H1E). This effect was expected as shorter grass is generally younger and will have lower fibre content and more protein than mature grass (Albon & Langvatn, 1992; Østrem et al., 2015). Because the biomass is greater in taller grass, there is arguably still an element of selection between young and mature grass, as other studies highlight (Lande et al., 2014). However, red deer may seriously impact the quantity of forage (Corgatelli et al., 2019; Marchiori et al., 2012; Trdan & Vidrih, 2008). Therefore, an alternative explanation to why I observed more grazing on shorter grass is that grazing reduce grass height. Although the alternative explanation is a plausible argument it seems unlikely considering the grass height measuring method used (Table 2), and red deer's tendency to select for fresh grass (Albon & Langvatn, 1992; Fryxell et al., 1988).

The availability and quality will differ between natural and meadow habitats throughout the summer. During summer months, forage will change in both habitat types, but the areas will exhibit different phenological development. Depending on the productivity throughout the growing season, meadows will be cut two or three times a year and will therefore have several peaks in forage quality (Thorvaldsen & Rivedal, 2014). Natural habitats will generally display a temporal lag in vegetation development relative to farmland. Peaks in natural forage will also depend on restricting growth factors like snow cover, access to light, and nutrients. Red deer will therefore utilize farmland more in the periods when the forage gain between farmland and natural habitats is at its largest.

Food quality in temperate climates is considered dynamic and highly seasonal (Trudell & White, 1981). Because of this, seasonal shifts in red deer forage habitat are expected. When investigating temporal effects, I found that grazing absence increased, and grazing levels decreased later in the summer relative to early (H1D). This temporal shift aligns with previous theory suggesting that large ungulates tend to follow the development of clear patches with newly sprung vegetation as it emerges from the snow cover, inviting animals up in the terrain and/or further inland from early to later on in the growing season (Skogland, 1984). As cervids display a vertical movement pattern from low-elevation winter range to high-elevation summer range, I assume that the grazing effect observed from season and grass maturity would translate to broad proxies of landscape, such as distance to coast and elevation. Inland areas with higher elevation are characterized by more variable topography, and I expected the natural habitat to have higher quality forage (Mysterud et al., 2001). However, elevation was not selected for the full model as it correlated with distance to coast, and distance to coast (H1B) was not a clear predictor of variation in red deer grazing on meadows.

When investigating the random structure, the lowest variation in level and probability of grazing presence was found between blocks. These areas (approximately 50 km^2) might be too large to observe spatial pattern in grazing, as it includes six different meadows that all could present a considerable variation in topography and surrounding habitat type. Rather than the spatial study grid represented as blocks, the study area could have been divided into valleys which might have been able to reflect the ecological system and the landscape's topography more accurately.

Local-scale variation in red deer grazing on meadows; management and quality

Herbivore food intake is determined by the forage quality (Blaxter et al., 1961). Depending on management, the availability and quality of food are likely to vary between meadows. Because the largest source of variation in grazing was found between meadows within sites, it should be evident that meadow management plays a vital role in determining grazing level (H2). I found that grazing levels are higher in new meadows than in intermediate ones (H2A). This difference in grazing levels is presumably because new meadows contain more energy and nutrient-dense forage (Andueza et al., 2010). The farmer's risk of losing yield when renewing meadows poses a dilemma. In order to supply quality fodder for cattle, the meadow should be renewed, but this investment might come at the expense of substantial grazing damage by red deer. One way to tackle this problem can be to reduce forage availability, which will be further discuss below.

When renewing meadows, seed mixes that include timothy are most commonly used. The nutritive value of timothy is high (Andueza et al., 2021; Hall & Stout, 1999), and suited as forage in temperate climates due to its digestibility (Thorvaldsson, 1992). Red deer and cattle also highly value it (Langvatn & Hanley, 1993; Lunnan, 2006). In heavy grazing areas, timothy decreases quickly due to its low tolerance to grazing. Strong selection by red deer towards newly refreshed meadows is well documented (Lande et al., 2014). This selection of meadows might explain why old meadows that have not been renewed for over nine years display no significant difference in grazing level or probability of absence compared to intermediate ones. The lack of measurable effect of timothy may be due to its quick depletion in areas with heavy grazing pressure, becoming rare and/or hard to detect.

My prediction regarding the effect of wild grass had the opposite effect than expected (H2D), as wild grass increased grazing levels. However, Red deer males commonly use low-quality meadows with high biomass in contrast to females that mainly select high-quality forage on new and intermediate meadows (Lande et al., 2014). The result could also have been affected by the misidentification of grass species. Before the first harvest, grass will frequently display flowers, which can be used as important identifiers for many species. After the first harvest, the same grass can be more challenging to identify and could become a source of error due to a lack of flowers. Coordination is critical in all types of scientific mapping when working in groups. If the group is more coordinated, there is less probability of errors. Coordination of the fieldworker's mapping method and species identification skill was also highly valued in this study. Nevertheless, it is hard to eliminate differentiation between fieldworkers entirely as they possess different botanical skill sets.

Local-scale variation in red deer grazing on meadows; potential gain and risk

Antipredator responses are adaptions to increase individual survival triggered by fear (Boissy, 1995). In many cases, wild animals will recognize humans as predators and human disturbance may provoke antipredatory responses in prey (Frid & Dill, 2002). Predation risk may limit individuals' utilization of high-quality habitats in prey populations (Festa-Bianchet, 1988). When using high disturbance areas, red deer will be more vigilant (Jayakody et al., 2008), and higher levels of vigilant behaviour will reduce the animals foraging rate (Fortin et al., 2004). Knowledge of how the benefit of forage and predation risk vary across habitats is critical in understanding the trade-offs associated with habitat selection (Kie, 1999). Large mammals will typically be faced with a trade-off where open landscapes yield good forage, whereas closed habitats present shelter against weather and predators (Godvik et al., 2009). The effect of disturbances and predation risk when red deer forage on meadows was consistent with all three predictions of (H3). I found higher grazing levels further away from roads (H3A), and the probability of grazing absence decreased further away from houses (H3B). These results display the same fear response affecting the spatial pattern of grazing. Although both roads and houses can exhibit human disturbance, the type of disturbance may differ, and consequently red deer reaction may change (Hodgetts et al., 1998). Proximity to habitats providing cover, such as forests, will also affect the agricultural land use by deer (Morrison et al., 2003). Distance further away from the forest has been shown to decrease the probability of red deer presence on farmland (Månsson et al., 2021). My results show that the probability of grazing absence decreased, and the level of grazing increased closer to the forest edge (H3C).

The location of meadows relative to human disturbance factors and forest cover are therefore affecting red deer grazing level. However, these factors might be more difficult to change though management. Nevertheless, knowledge of fear effects may be used actively in management (Cromsigt et al., 2013). In the case of mitigation efforts, reduction of forage availability due to fear effects might be an alternative strategy. This insight could be utilized by focusing the renewal of meadows located closer to disturbance and further away from the forest.

Conclusion

Spatial variation in red deer density, meadow management, and risk of predation are all important mechanisms affecting red deer grazing. At a broad scale, when more animals compete for natural habitats, it appeared to force red deer onto agricultural meadows. Thus, density of red deer increased grazing on meadows. It should be evident that managers can compensate these damages by increasing red deer harvesting rates on broad scales in high density areas. Temporal shifts in food availability and quality in natural relative to meadow habitat was likely the reason why less grazing was observed on taller grass and later in the season.

Variation in grazing was largest at the local scale, presented by meadows within sites. This spatial level should hence be the focal point of red deer management. Red deer grazing was higher on new compared to intermediate meadows, an effect likely caused by differences in forage-quality. The pattern of spatial grazing is also an outcome of trade-offs between availability and quality of forage versus predation risk. More grazing occur further away from habitat associated with human activity, and closer to forest habitat that provide cover protection. If possible, farmers should prioritize renewing meadows close to roads and houses and far from forests to mitigate grazing damage.

Populations control of deer is a topic of large concern in parts of Europe and North America due to the damage large populations of deer can inflict on agricultural farmland. My study highlights how broad and local factors affect red deer grazing on agricultural meadows across spatial and temporal scales. Management efforts should combine broad and local scale strategies when targeting mitigation to lower grazing damage.

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