



An experimental assessment of biomass loss due to red deer (*Cervus elaphus* L.) grazing on agricultural grass meadows in Norway

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Abstract

In Europe, over a third of the agricultural area is grass meadows used for livestock grazing and fodder production. Grass meadows provide a food source for wild ungulates causing human-wildlife conflicts due to forage removal. Few experimental studies have quantified biomass loss with enough replicates to determine how surrounding environments influence level of biomass removal. Using an enclosure experiment on 57 grassland meadows over five years at the northwest coast of Norway covering 10 650 km², we quantified biomass removal by red deer (*Cervus elaphus* L.) and how environmental factors impacted biomass loss (Study 1). Furthermore, we examined development of biomass loss and crude protein concentration in five fields throughout the growing season (Study 2). The average predicted biomass loss to red deer grazing was 16% for the first harvest, and 7.3% for the second harvest (Study 1). Biomass loss increased with red deer density from 0% at the lowest density (0.6 red deer harvested/km²) to 31% at the highest density (4 red deer harvested/km²). Biomass loss increased from 12% to 32.8% as terrain ruggedness index (TRI) rose from 2.1 to 7.1. Absolute biomass loss increased towards time of grass harvest (Study 2). Crude protein concentration was higher in unfenced plots during the period before first harvest, but not between first and second harvest (Study 2). The quantification of biomass removal at a large spatial scale over several years in this study provides a better understanding of factors causing variation in losses.

Keywords Enclosure experiment · Grazing damages · Farmland · Human-wildlife conflict · Density effects

Introduction

Human-wildlife conflicts are common at the border of natural environments where wildlife forage on agricultural fields, leading to reduced harvests and economic loss for farmers (Hegel et al. 2009; Walter et al. 2010; Skonhøft et al. 2013). Understanding the impact of wildlife on agriculture is vital for managing wildlife populations. In Europe, over a third of the agricultural area is grasslands, primarily used for livestock grazing and fodder production. For wildlife, agricultural grasslands provide seasonally abundant high-quality forage and can be important at high population densities or during seasonal periods when availability of alternative food resources are naturally limited (Zweifel-Schielly et al. 2012; Mysterud et al. 2023). The grazing pressure from wildlife on agricultural fields varies over time and across spatial scales (Hjerermann et al. 2024). Knowledge of factors driving variation in wildlife grazing and its impact on crop yield and quality will aid in understanding where to target mitigation efforts and reduce human-wildlife conflicts.

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Red deer (*Cervus elaphus* L.) populations have increased significantly over the past half-century in Europe, largely due to changes in population management and land use practices (Milner et al. 2006; Linnell et al. 2020; van Beeck Calkoen et al. 2023). As a mixed feeder, red deer has a diverse diet, however, grass species are a main part of the diet during most of the year (Gebert and Verheyden-Tixier 2001; Spitzer et al. 2020). Agricultural grass meadows represent attractive, high-quality habitats for red deer and are heavily utilized in many parts of its range (Trdan and Vidrih 2008; Marchiori et al. 2012; Corgatelli et al. 2019). Choice of feeding patches is determined by both the quality and quantity of available food resources (Langvatn and Hanley 1993), and red deer has been shown to select actively managed and frequently renewed meadows because of higher crop quality (Lande et al. 2014). On the other hand, foraging on meadows involves lack of shelter which entitles a trade-off with predator avoidance behavior (Godvik et al. 2009). Selection of agricultural grass meadows as feeding sites will thus depend on different attributes in terms of the surrounding environment and quality and quantity of the forage. Studies have shown that red deer space use, habitat selection and behavior is dependent on spatial surroundings like distance to roads (Frid and Dill 2002) and topographical variability (Meisingset et al. 2022). Further, red deer are found to favor agricultural grass meadow sites near forest edges (Månsson et al. 2021) and to use more time feeding at high quality fields (Langvatn and Hanley 1993).

Ungulates can significantly reduce biomass of grass harvest (Carpio et al. 2020; Widén et al. 2023), but variation in the surrounding natural habitat and meadow crop quality cause the grazing pressure to differentiate between fields. There are several studies on biomass loss at agricultural meadows identifying significant losses from red deer in Europe. In Slovenia there have been documented biomass losses of 50%, 48% and 52% in single years (Trdan and Vidrih 2008; Trdan et al. 2024). In Italy, a study with data from three years found a 15–20% loss at the first harvest and a 25–40% loss at second harvest (Marchiori et al. 2012), while a single year study documented a 14% biomass loss to red deer grazing at second harvest (Corgatelli et al. 2019). All studies where enclosure experiments with fenced/unfenced designs, covering three (Trdan and Vidrih 2008; Trdan et al. 2024), four (Marchiori et al. 2012) and 24 fields (Corgatelli et al. 2019). However, none of these studies covered a large area over several years where seasonal and annual variation of biomass were quantified simultaneously. Previous investigations also lack quantitative estimates on the impact of relevant environmental factors. However, studies on biomass loss to red deer grazing suggests higher absolute biomass loss in years with high biomass (Marchiori et al. 2012; Trdan et al. 2024) and increased biomass loss in

areas with higher red deer population density (Corgatelli et al. 2019). In addition, studies following temporal changes in biomass loss and protein content of grass on agricultural grass meadows over one season have found indications of quite stable biomass loss and lower protein concentration in grazed meadows compared to ungrazed (Jarque-Bascuñana et al. 2022; Trdan et al. 2024). The sizable reductions in biomass found in earlier studies highlight the need for knowledge to understand drivers behind red deer grazing pressure distribution on larger spatial scales as well as the severity of biomass loss across years.

We here present and analyze data from two enclosure experiments to quantify temporal and spatial patterns of biomass loss to red deer grazing in Norway. In Study 1, we followed 57 meadows with fenced and unfenced plots (hereafter treatment) for one to five years from 2019 to 2023. Specifically, we tested (1) how red deer grazing in terms of biomass loss varies across years, between seasonal harvests, at grasslands of different renewal ages and with distance to coast, predicting higher biomass loss at first seasonal harvest in absolute dry matter, but lower in percentage loss (P1a), higher losses in years with high biomass (P1b), at younger meadows (P1c) and at meadows close to the coast (P1d). (2) We further tested how population density of red deer affects biomass loss, predicting increased biomass loss with higher population density (P2). Lastly, (3) we tested how the local surrounding landscape in terms of proportion of forest cover, proximity to roads and topographic variability in the vicinity of the meadow affected biomass loss, predicting higher pressure with increasing forest cover, lower pressure in proximity to roads and in areas with higher topographic variability (P3). In study 1, we measured biomass loss at each meadow only once before each harvest, and we had no measure of forage quality that may follow a different temporal trajectory than forage quantity (Van Soest 1994). Therefore, in study 2, we used the same experimental design in five meadows but followed the temporal vegetation development and biomass loss in detail by frequently sampling before first and second harvest in 1996. We aimed to answer, (4) how biomass loss and crude protein level develop throughout the growing season under high grazing pressure. Our baseline prediction was a stable level of biomass loss (P4a) and a lower protein concentration in fenced plots (P4b).

Materials and methods

Study area

The study area was in the western part of Norway, in the counties of Møre & Romsdal and Trøndelag (Fig. 1). The

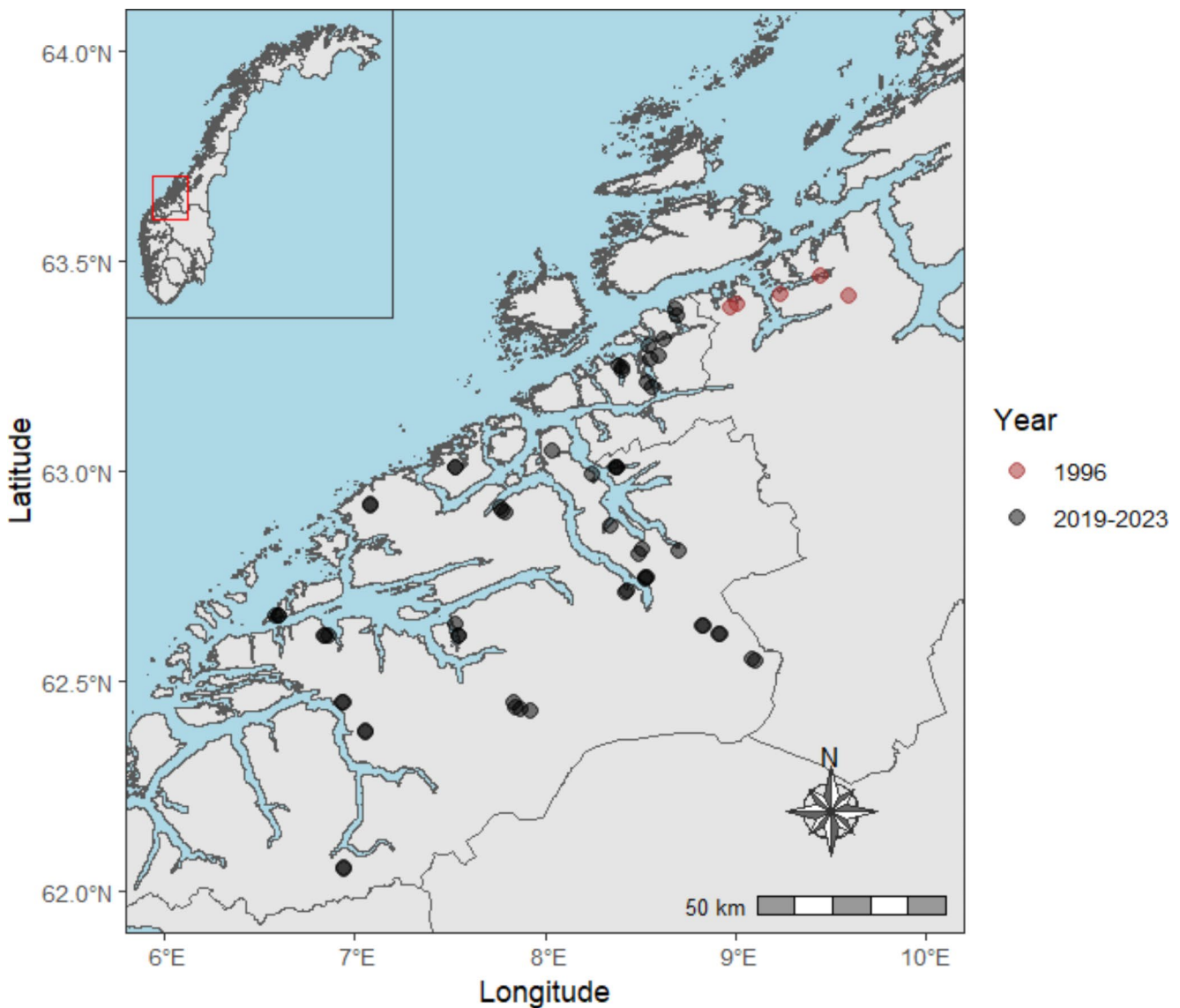


Fig. 1 The study area with the locations of each meadow for 1996 (study 2) and 2019–2023 (study 1)

meadows are located both at the coast and further inland, with ten meadows located on three islands. The landscape is characterized by fjords, rivers, high mountains, steep hills, and valleys, creating a diverse topography. The area has a temperate oceanic climate with mild winters and cool summers. Further inland and northwards, there is generally a decrease in both precipitation and temperature, and snow depth during winter tends to increase along the same gradients. From 2019 to 2023, the mean temperature in January was 0.7 °C (SD=2.18 °C) and the mean precipitation was 138 mm (SD=54.4 mm). Average temperatures in the summer months were 14.6 °C (SD=1.2 °C) for June and 14.8 °C (SD=1.46 °C) in July and the mean precipitation was 80 mm (SD=28.8 mm) for June and 135 mm (SD=67.8 mm) for July. Notably, 2022 experienced significantly higher rainfall with 124 mm in June and 245 mm in

July. For 1996 (Fig. 1), the temperature was 4 °C in January and 12 °C for June and July. The precipitation was 11 mm in January, and 152 mm and 130 mm for June and July, respectively. The natural forests in this area are mainly south and middle boreal, which is a mix of deciduous and coniferous trees (Moen and Odland 1998) and covered 28.6% of the land area in 2023 (Tenge 2016). The coniferous component consists primarily of Scots pine (*Pinus sylvestris* L.) and planted Norway spruce (*Picea abies* L.), while the deciduous component consists mainly of birches (*Betula* spp.) and alder (*Alnus incana* L.). The understory vegetation is dominated by bilberry (*Vaccinium myrtillus* L.) and different grass species. In 2023 the other main landcover classes were mountainous area (23%) and open mainland (31.5%, Tenge 2016).

Agricultural areas are mostly located in the flatter and more nutrient-rich areas along the valley bottoms and covered 4.3% of the land area in 2023. The agricultural production consists of mostly grass meadows and pastures, where grass is harvested for winter fodder or grazed seasonally by cattle or sheep. The most common cultivated grass species include timothy (*Phleum pratense* L.), blue grass (*Poa pratensis* L.), meadow fescue (*Festuca pratensis* L.), and perennial ryegrass (*Lolium perenne* L.). Public roads are predominantly situated along valley bottoms and in flatter areas, often in the agricultural landscape (Meisingset et al. 2013). There were 1036 farmers with 134,551 sheep and 637 farmers with 19,014 dairy cows in 2020 in Møre og Romsdal county (Statistics Norway 2023).

The study area has an overall high red deer population density with 0.6–4.0 deer shot/km² (roughly similar to a population of ~2.4–16.0 deer per km²) from 2019 to 2023 for the municipalities in Møre & Romsdal and 1.0–1.2 deer shot/km² (roughly similar to ~4.0–4.8 deer per km²) in 1996 for the municipalities in Trøndelag. Roe deer (*Capreolus capreolus* L.), moose (*Alces alces* L.) and different species of geese (*Anserini* spp.) may occasionally also be found grazing on agricultural land. Compared to red deer, these species are present at much lower population densities in our study areas. Therefore, we assume that these species did not add significant grazing pressure.

Experimental design of study 1

An enclosure experiment with fenced plots on 57 grass meadows of sizes from 0.28 ha to 27.25 ha (mean = 4.45 ha, SD = 4.97 ha) was conducted during 2019–2023 in Møre & Romsdal, Norway (Fig. 1). The study covered 13 municipalities and the total area as a Minimum Convex Polygon around our study sites was 10 656 km². The aim was to determine the influence of red deer grazing on grass biomass yield in contrasting surrounding conditions in terms of forest cover, human disturbance and topography in close proximity to the grazing sites during the growing season. Meadows were selected in collaboration with farmers who volunteered for the study via the farmers advisory service organization in the region. The farmers participating provided from one to four meadows and all proposed meadows were included in the study. At each meadow, we randomly selected one site to be fenced with three two-meter-long and two-meter-high iron fences forming a triangle (mesh size 10 × 10 cm, Fig. 2). Fences were installed right after snowmelt before the first year of grass sampling, after installment fences remained at the site until the meadow was removed from the experiment. We avoided meadow edges and areas where the soil and meadow condition were different compared to the main part of the meadow. Fences remained

closed throughout the growing seasons for the duration of the study and was removed during harvest. At harvest, three grass samples from 0.1 m² squares were collected inside the fenced area and from three random locations outside the fence. The grass samples were collected with Stihl HSA 26, a battery-operated harvester and cut at 8–10 cm above ground, which is comparable to what is used by farmers during grass harvesting. Samples were then placed in Skurup Evf 890 cabinets and dried for 48 h at a temperature of 60 °C. Before and after drying, the samples were weighed to obtain the dry matter biomass, and the mass was converted to a harvest equal from 1000 m². Harvests were between June 6th and June 24th for the first harvest, from July 31st to August 22nd for the second harvest. Each meadow was followed for a median of 2 years, with an average of 2.24 years. The mean meadow sampled each year was 24.2, but 2019 had only two meadows for first harvest and four for second harvest. The total sample size in study 1 was 1398 samples, where 699 were from fenced plots and 699 from unfenced plots distributed over the 57 meadows across five years (Table 1).

Environmental variables in study 1

We retrieved selected environmental variables expected to have an impact on biomass production and biomass loss due to deer grazing.

Meadow age. The age of each meadow, i.e., time since renewal, was retrieved from the farmers and categorized into three age classes: new (<3 years since last renewal, samples = 354), intermediate (renewed 3–9 years ago, samples = 702), and old (>9 years since last renewal, samples = 342). Some meadows were followed for several years, and thus age category changes. At renewal, farmers plow and sow new grass species using grass seed mixes dominated by timothy, perennial ryegrass and meadow fescue. All meadows were fertilized two times a year using animal manure and artificial fertilizers. The normal fertilization regime before first harvest in the study area is 3000 kg animal manure and 42–45 kg Yara complete fertilizer 25-2-6, which gives 10.5–11.0 kg Nitrogen, 0.7 kg phosphorus and 2.7 kg potassium per 1000 m². After first harvest, fertilization is normally at 2000 kg animal manure, supplied with 20–25 kg YaraBela OPTI-NS 27-0-0, which have about 6 kg Nitrogen. Fertilization is however somewhat specific at each meadow to meet local fields soil requirements.

Population density index. A well-established red deer density index was retrieved by accessing the number of harvested/shot red deer each year at the municipality level and dividing it by the available area that qualifies as red deer habitat (Mysterud et al. 2007). Red deer habitat is defined as the sum of the area in a municipality that is expected to



Fig. 2 The experimental setup on the grass meadows in study 1. Note that the picture is taken early in the growing season (19th of May 2021)

Table 1 Number of plots each year and harvest for unfenced and fenced plots in Møre & Romsdal, Norway, comprising dataset 1 (numbers in brackets are excluded data due to irregularities, see statistical analysis)

| Year | Harvest 1 | | Harvest 2 | | Total |
|-------|-----------|----------|-----------|----------|-----------|
| | Unfenced | Fenced | Unfenced | Fenced | |
| 2019 | 2 | 2 | 4 (1) | 4 (1) | 12 (2) |
| 2020 | 22 (2) | 22 (2) | 22 (1) | 22 (1) | 88 (6) |
| 2021 | 40 (3) | 40 (3) | 37 (2) | 37 (2) | 154 (10) |
| 2022 | 31(9) | 31 (9) | 29 (6) | 29 (6) | 120 (30) |
| 2023 | 24 (15) | 24 (15) | 22 (13) | 22 (13) | 92 (56) |
| Total | 119 (29) | 119 (29) | 114 (23) | 114 (23) | 466 (104) |

be frequently used by red deer, which typically is the summarized area of all habitat-types excluding open mountain, water edges and human infrastructure.

Site specific landscape characteristics. The elevation and the terrain ruggedness index (TRI) were retrieved from a digital terrain model managed by the Norwegian Mapping Authority with a resolution of 10×10 m. TRI is an index calculated from the amount of elevation difference between adjacent cells of a digital elevation model. A flat terrain will get a low TRI score around one, while a more topographical varied and rugged terrain will get a higher TRI. The

elevation of the site was set to the elevation of the raster that matched the location of the fenced plot. TRI was calculated for an area with 100 m and 500 m radius surrounding the fenced plot, giving each 10×10 m square in the circle a TRI score. The value used in analysis was the average TRI for the entire circle surrounding the plot. The size of the respective field (m²), the distances (m) to the nearest coastline, as well as the proportion of forest cover, roads and buildings within a 100 m and 500 m radius from the plot center were extracted from the FKB-AR5 land cover map (1:5000 scale) from The Norwegian Institute of Bio-economy Research (Tenge 2016). The proportion of forest cover, roads and buildings were converted to percentage of the total area in the circle surrounding the fenced plot.

Experimental design of study 2

An enclosure experiment with fenced plots on five grass meadows was conducted in 1996 in Trøndelag, Norway (Fig. 1), with the aim to determine the influence of red deer on the temporal development of biomass loss and protein concentration throughout the growing season. The meadows

were selected in areas known to have a high grazing pressure based on knowledge obtained from farmers. Meadows were fertilized with 21–24 kg of nitrogen, 1–4 kg of phosphorus and 14–20 kg of potassium per 1000 m². The total sample size resulted in 468 grass samples, 234 in fenced plots and 234 in unfenced plots. On each meadow, two areas of 50 m² were fenced with two-meter-high mesh fence (mesh size 10 × 10 cm) in spring right after snowmelt. Sites for enclosures on the meadows were placed on as equal and homogeneous areas as possible, taking soil type, moisture and edge effects into account. We had no red deer entering the enclosures during the experiment. In addition, a surrounding control area of 3000 m² was selected based on the same principles. The meadow size varied from 3.77 ha to 10.74 ha (mean = 6.07 ha, SD = 2.8 ha). The fences were only removed during the two harvests. Grass samples were collected six times before harvest 1 with an interval of approximately 14 days, with the first samples collected in the middle of May. Sampling before harvest 2 started three weeks after harvest 1 and samples were collected three to five times with an interval of approximately 14 days before second harvest. At each sampling, five randomly placed squares of 0.1 m² were cut for biomass measurements and crude protein analysis in both fenced and unfenced sites. Each grass sample was divided into two, one sample was kept in a plastic bag and then dried in a Skurup dryer for 48 h at 100 °C to measure dry mass, and the other was kept in a plastic bag and then dried for 48 h at 40 °C for analysis of protein content (Mould and Robbins 1981). Before drying, the samples used for the protein analysis were cut into one, two or three parts depending on the length of the grass. With grass length below 15 cm the entire sample was treated as one. At lengths between 15 and 30 cm, the top third was used as one sample and the bottom 2/3 as another sample. When grass length exceeded 30 cm, the grass was divided into three equal parts. After drying, all parts were grinded with a mechanic grinder before further analysis. The protein calculation was performed after the Kjeldahl-method and the protein concentration is given in percentage of the total weight of the dried grass sample. For grass lengths > 15 cm, only the top part was used to estimate protein percentage difference between fenced and unfenced plots, since we assume that this part of the grass is accessible for red deer.

Statistical analysis

The statistical analyses were performed in R, version 4.3.1 (Team 2023). Due to irregularities in the experimental setup regarding fences, data from some harvests were excluded ($n = 52$) from the analysis in study 1. The irregularities were introduction of grazing cattle on the meadow during the study period, water flooding of the meadow which moved

the fence, fence not properly closed, fences not covering the entire growing season, fences not placed back at same location after first harvest and unequal fertilized treatment of fenced/unfenced plots. Before fitting a model investigating factors affecting dry matter biomass, we first tested for correlation among the candidate spatial covariates influencing grazing pressure: elevation, distance to coast, proportion of forest cover, roads and buildings (Table S1). Distance to coast and elevation were highly correlated ($r = 0.7$) and distance to coast was selected over elevation as an explanatory variable because of lower Akaike Information Criterion (AIC) when comparing simple models to explain difference in dry matter biomass loss to red deer grazing between meadows. To identify possible nonlinear relationships, we plotted simple gam plots from the “mgcv” package with dry matter weight as response and all covariates as predictors (Wood 2017). We then checked for nonlinear relationship for each covariate one by one, with $k = 5$. TRI, red deer density index at municipality level and proportion of forest with both 100 m and 500 m radius were included as second order polynomial in the global model. A linear mixed-effect model with gaussian error structure from the lme4 package (Bates et al. 2014) was used to fit a global model with dry matter biomass as response and including all remaining spatial variables as well as the variables treatment, harvest (first or second), year (categorical) and red deer density index (Table S2). All the possible explanatory variables were also fitted as a two-way interaction with treatment and including a three-way interaction between the factorial variables harvest, year and treatment. To avoid large differences in scales among different variables, all covariates were rescaled centering on 0 by subtracting the mean and dividing by the standard deviation using the base R scale function. Ten meadows (15% of the data) were located on islands. Using the biserial.cor function from the ltm package (Rizopoulos 2007), we found a correlation between island and red deer density ($r = 0.61$), but not with any other spatial covariate. We could therefore not use island as an independent categorical variable together with density of red deer in the analysis. We used red deer density in the model selection, and present predicted values from island versus mainland in the figure from an alternative model including island as a factor instead of red deer density. Meadow ID was treated as a random variable to account for repeated measurements. We ran stepwise backwards model by using the drop1 function in the lme4 package (Bates et al. 2014), which removes predictors and looks at change in the deviance when the term is dropped. We repeated this step until it did not improve the model further. We then selected the simplest model within $\Delta 2$ AIC of the model with the lowest AIC-value. The model residuals were investigated using diagnostic plots to ensure model assumptions were met. Finally, we tested for spatial

autocorrelation with a DHARMA Moran's test for distance-based autocorrelation which proved no correlation with a p -value of 0.63.

To analyze how grazing pressure developed during the growing season (study 2) we fitted two separate generalized linear mixed-effect models with gaussian error structure using the lme4 package in R (Bates et al. 2014) with dry matter weight per 1000 m² and percentage crude protein between fenced and unfenced plots as response. As there were multiple observations before each harvest in one model, we replaced date with days before harvest as a predictor variable. Fields were harvested at the end of June for first harvest and end of August for second harvest, and harvest date was therefore set at first of July for first harvest and first of September for second harvest. Treatment (fenced/unfenced) and harvest number (first or second) were treated as categorical variables. Days before harvest was included as a second order polynomial to identify a potential non-linear relationship with the response, and was fitted in interaction with treatment to investigate how grazing pressure and protein concentration developed throughout the season in fenced and unfenced plots. Meadow ID ($n=5$) was included as random variable. Finally, we did a spatial autocorrelation test, and the model residuals were investigated using diagnostic plots to ensure model assumptions were met. The spatial autocorrelation test showed no autocorrelation for neither test, but model assumptions were not met for model

predicting dry matter weight. This was resolved by switching to a gamma error structure with a logarithmic link. We ran stepwise backwards model selection for both models by using the drop1 function in the lme4 package (Bates et al. 2014), which removes predictors and looks at change in the deviance when the term is dropped. We repeated this step until it did not improve the model further and then selected the simplest model within $\Delta 2$ AIC of the model with the lowest AIC-value.

Results

In study 1, there were seven models within $\Delta 2$ AIC and the simplest model had 1.01 higher AIC compared to the best model for predicting dry matter weight in kg per 1000 m² (Table S2). The selected model had a marginal R^2 of 0.38 and a conditional R^2 of 0.51 and included year, TRI (squared, 100 m radius), red deer density index (squared), proportion of roads (500 m), and treatment (fenced/not fenced) as well as the interaction between treatment and the remaining variables except year, and the interaction between year and harvest (Table 2, Table S2). Age class of meadow (since renewal), distance to coast, proportion of forest (100 m and 500 m), proportion of buildings (100 m and 500 m), TRI (500 m), proportion of roads (100 m radius) as well as most interaction terms did not enter the most parsimonious

Table 2 Parameter estimates, standard error, t-value and significance level (p) from the final generalized linear mixed-effects model explaining variation in dry matter biomass (kg/1000 m²) harvested from agricultural grass meadows in Norway. Reference levels for categorical variables: Fenced = yes, year = 2023, Harvest = first harvest. TRI = terrain ruggedness index. TRI and red deer density index was rescaled by mean-centering and dividing by the standard deviation

| Predictors | Estimates | std. Error | t-value | p |
|----------------------------------------------------------------------------------|-----------|------------|---------|--------|
| Intercept | 478.466 | 13.661 | 35.024 | <0.001 |
| Fenced [No] | -95.097 | 8.276 | -11.491 | <0.001 |
| Year [2019] | 68.838 | 37.072 | 1.857 | 0.064 |
| Year [2020] | 122.310 | 15.280 | 8.004 | <0.001 |
| Year [2021] | 89.842 | 13.514 | 6.648 | <0.001 |
| Year [2022] | -6.490 | 12.838 | -0.505 | 0.613 |
| Harvest [2] | -123.940 | 14.673 | -8.447 | <0.001 |
| TRI [1st degree] | 289.122 | 366.220 | 0.789 | 0.430 |
| TRI [2nd degree] | 568.308 | 354.171 | 1.605 | 0.109 |
| Proportion of roads | 28.197 | 8.605 | 3.277 | 0.001 |
| Red deer density index (shot/km ²) | 308.819 | 332.781 | 0.928 | 0.354 |
| Red deer density index (shot/km ²) [2nd degree] | -643.160 | 232.157 | -2.770 | 0.006 |
| Fenced [No] \times Harvest [2] | 57.644 | 11.842 | 4.868 | <0.001 |
| Fenced [No] \times TRI [1st degree] | -943.590 | 221.767 | -4.255 | <0.001 |
| Fenced [No] \times TRI [2nd degree] | -639.103 | 221.195 | -2.889 | 0.004 |
| Fenced [No] \times Red deer density index (shot/km ²) | -1258.992 | 221.154 | -5.693 | <0.001 |
| Fenced [No] \times Red deer density index (shot/km ²) [2nd degree] | 342.051 | 221.865 | 1.542 | 0.123 |
| Year [2019] \times Harvest [2] | -66.988 | 44.416 | -1.508 | 0.132 |
| Year [2020] \times Harvest [2] | -90.315 | 19.104 | -4.727 | <0.001 |
| Year [2021] \times Harvest [2] | -7.592 | 16.969 | -0.447 | 0.655 |
| Year [2022] \times Harvest [2] | -68.072 | 17.831 | -3.818 | <0.001 |

model (Table S2). We found large variation in harvested dry matter biomass between years, and between first and second harvest within years (Fig. 3). When including island/mainland as a factor instead of red deer density, the model predicted significant higher biomass loss to red deer grazing on islands compared to mainland (101 kg per 1000 m², Fig. 3, Table S5). The model predicted an average dry matter biomass loss to grazing of 16% (84.4 kg per 1000 m²) for the first harvest, and 7.3% (26.7 kg per 1000 m²) for the second harvest. In total this equals a yearly loss of 12.4% (111.1 kg per 1000 m²) per year. The data from the meadows displayed a large variation in biomass loss between sites, ranging from zero difference between fenced and unfenced plots to a maximum of 508 kg for one season, which also gave the highest percentage loss of 54.4%.

Biomass harvest varied significantly between years, but the lack of interaction with treatment indicated that harvest loss due to red deer grazing was relatively constant between years and not dependent on overall biomass production. The first harvest gave higher biomass in all years compared to the second harvest. The interaction between harvest and treatment predicted higher absolute biomass loss (57.6 kg per 1000 m²) from grazing at first harvest (Table 2). The most important spatial covariate explaining difference in dry matter biomass between fenced and unfenced plots was the red deer density index at municipality level. The predicted dry matter biomass loss increased non-linearly from no predicted damage at the lowest red deer density (0.6 red deer shot/km²) to 31.3% (110.3 kg) at the highest density

(4.0 red deer shot/km², Fig. a). An increasing TRI significantly impacted biomass loss. Biomass loss to red deer decreased from 14.2% (67.8 kg) at the lowest TRI (0.41) to 12% (54.5 kg) at 2.13 TRI, and then increased more rapidly to 32.8% (169.1 kg) at the highest TRI (7.1, Fig. b).

In study 2, the final model explaining dry matter biomass had a marginal R² of 0.78 and a conditional R² of 0.78. The model included days before harvest, days before harvest squared, fenced, harvest, and the interaction days before harvest squared and harvest (Table 3). The Δ AIC between the best model and the second-best model were 1.09 for model predicting dry matter weight and 2.4 for model predicting protein concentration (Table 3, Table 4, Table S3, Table S4). Fenced plots had 30% higher dry matter biomass compared to unfenced plots both at first and second harvest (Fig. a and b; Table 3). The predicted absolute loss in biomass (kg) increased towards time of harvest and differed with 247.8 kg and 125.4 kg/1000 m² between fenced and unfenced plots at first and second harvest, respectively (Fig. 5a and b). The final model predicting protein concentration had a marginal R² of 0.39 and a conditional R² of 0.45 and included days before harvest, days before harvest squared, fenced, harvest, and the interaction between days before harvest and harvest, as well as the interaction between days before harvest squared and Harvest (Table 4, Table S4). Crude protein concentration increased during the early growing season before progressively decreasing towards the first harvest. The model predicted that crude protein concentration was significantly higher (2%) in unfenced compared to fenced

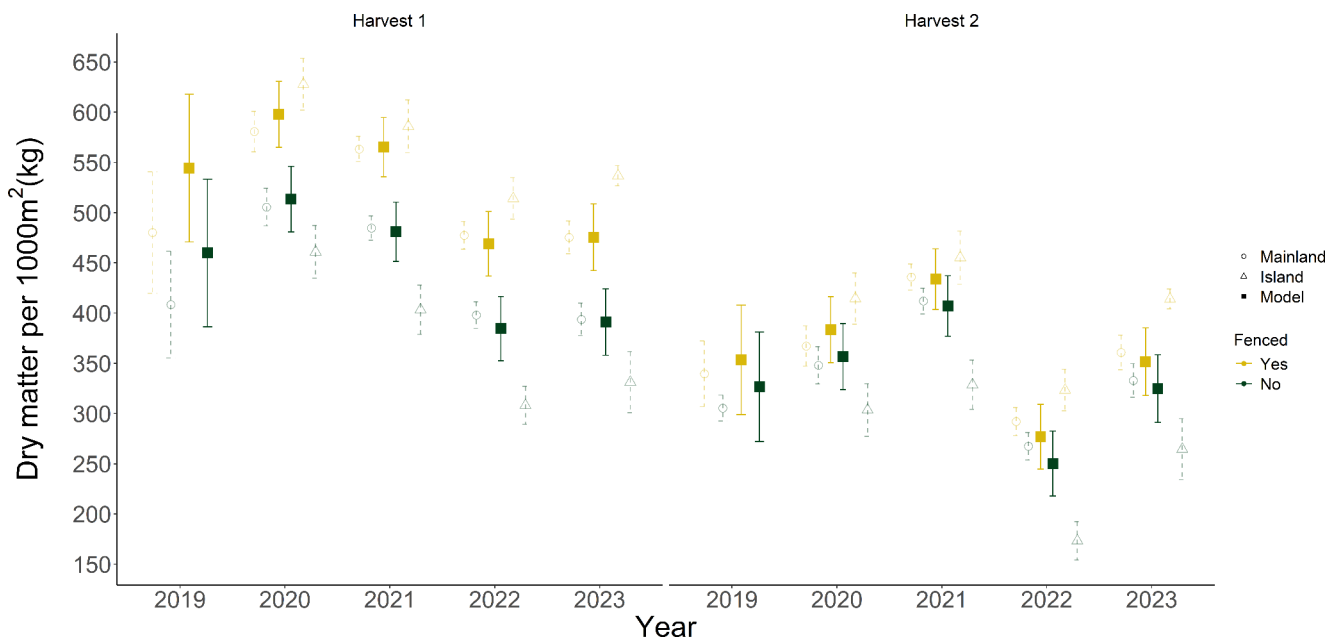


Fig. 3 Predicted values of dry matter (kg) per 1000 m² per year with 95% confidence intervals for fenced (yellow) and unfenced (green) sampling locations at the first and second harvest on agricultural grass meadows in Norway. The predictions are based on the selected gener-

alized linear mixed-effects model (Table 2, squares) and the alternative model with island as a factor variable (circles and triangles, Table S5). Predictions are made for the mean of the remaining predictor variables included in the model

Table 3 Parameter estimates, standard error, t-value and significance level (*p*) from a generalized linear mixed-effects model explaining development of dry matter biomass (kg) per 1000 m² at agricultural grass meadows in Norway as a function of days before seasonal harvest. Reference levels for categorical variables: Fenced = yes, Harvest = first harvest

| Predictor | Estimate | SE | t-value | <i>p</i> |
|------------------------------------------------|----------|--------|---------|----------|
| Intercept | 1073.12 | 87.725 | 85.365 | < 0.001 |
| Days before harvest [1st degree] | 0.952 | 0.006 | -8.278 | < 0.001 |
| Fenced [No] | 0.769 | 0.030 | -6.733 | < 0.001 |
| Days before harvest [2nd degree] | 1.000 | 0.000 | -4.082 | < 0.001 |
| Harvest [2] | 0.506 | 0.044 | -7.892 | < 0.001 |
| Days before harvest [1st degree] × Harvest [2] | 1.016 | 0.005 | 3.445 | < 0.001 |

Table 4 Parameter estimates, standard error, t-value and significance level (*p*) from a generalized linear mixed-effects model explaining development of protein concentration (%) in grass at agricultural grass meadows in Norway as a function of days before harvest. Reference levels for categorical variables: Fenced = yes, Harvest = first harvest

| Predictor | Estimate | SE | t-value | <i>p</i> |
|------------------------------------------------|----------|-------|---------|----------|
| Intercept | 11.510 | 1.003 | 11.478 | < 0.001 |
| Days before harvest [1st degree] | 0.948 | 0.077 | 12.340 | < 0.001 |
| Fenced [No] | 2.018 | 0.500 | 4.035 | < 0.001 |
| Days before harvest [2nd degree] | -0.017 | 0.002 | -10.750 | < 0.001 |
| Harvest [2] | 5.962 | 1.321 | 4.512 | < 0.001 |
| Fenced [No] × Harvest [2] | -1.719 | 0.784 | -2.193 | 0.029 |
| Days before harvest [1st degree] × Harvest [2] | -1.067 | 0.166 | -6.434 | < 0.001 |
| Days before harvest [2nd degree] × Harvest [2] | 0.033 | 0.005 | 6.780 | < 0.001 |

plots at time of first harvest for harvest 1 (Fig. c). Treatment did not affect crude protein concentration between the first and second harvest (Fig. 5d).

Discussion

The growing populations of red deer across Europe makes knowledge of biomass loss on grass meadows important for wildlife management. The spatial and temporal distribution of red deer grazing affects the balance between the benefits from retaining high densities against the costs in terms of harvest loss for farmers. We used an experimental design to quantify biomass loss to red deer grazing across a large spatial scale (10 656 km²) and over time (2019–2023) and found that red deer reduced biomass by an average of 11.2% (97.4 kg per 1000 m²) per year. In our study, biomass production varied markedly between years (Fig.). However, even though the biomass production varied across years and between harvests within years, the mean loss to red deer grazing was surprisingly constant around 11%. We found that red deer density index at municipality level was the most important factor influencing biomass loss among the covariates included in this study, and that topography modified the biomass loss. Our study suggests that population control could be an important measure to mitigate biomass loss. In addition, wildlife and agricultural management should be aware of the spatial attributes, like the local topography in our case, of each grass meadow when considering where to

prioritize measures to reduce biomass loss from grazing by red deer.

Seasonal and spatial variation in percent biomass loss

Our study shows a uniformly distributed loss of total grass biomass on farmland due to red deer grazing across years and between first and second harvest, despite that dry matter harvest yield varied substantially between years and harvest. Similar studies in Europe have documented large variation in biomass loss (14–50%) due to red deer grazing on agricultural grassland (Trdan and Vidrih 2008; Marchiori et al. 2012; Corgatelli et al. 2019; Trdan et al. 2024). These studies were, however, small-scale studies, covering only one or two years and fewer fields compared to our study. Our study also documents large variation in biomass loss across sites. This highlights that both temporal and spatial factors need to be taken into account when considering measures to prevent biomass loss caused by red deer grazing.

The availability and quality of forage differ between natural habitats and farmed areas throughout the growing season. When forage abundance is high in natural and forested habitats, red deer use open areas like agricultural meadows to a lower extent (Albon and Langvatn 1992; Godvik et al. 2009). Plant growth peaks later in the season in forested habitats, which may explain our results showing an overall reduced biomass loss at the second harvest compared to the first harvest. In addition, variation in plant quality may

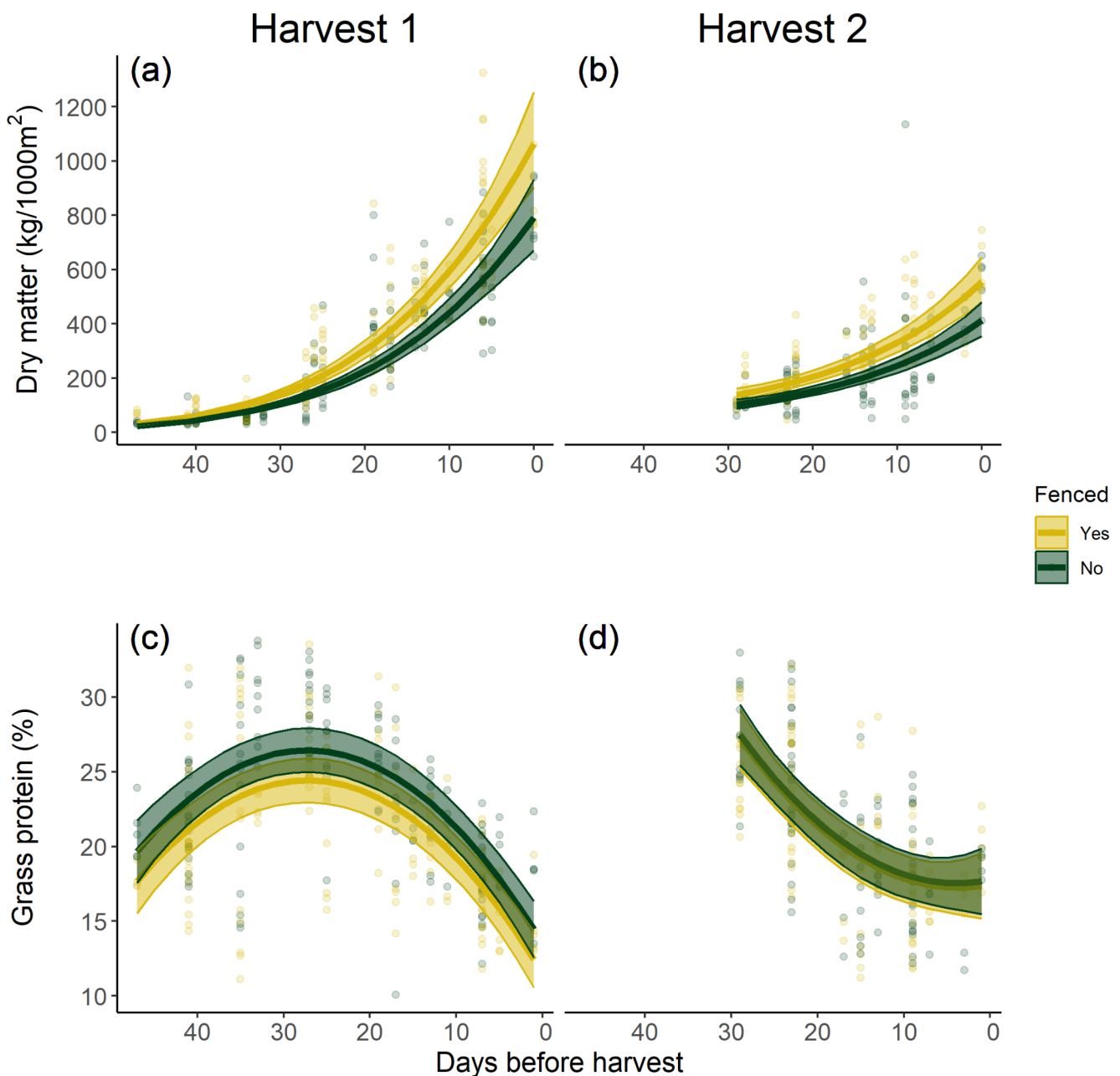


Fig. 5 Predicted values of development in dry matter biomass (kg/1000 m²; **a** and **b**) and crude protein concentration (%; **c** and **d**) in relation to days before the first and second harvest within fenced (yellow) and

unfenced (green) sites on agricultural grass meadows in Norway. The predicted lines and shaded 95% CI are based on a generalized linear mixed-effects model, and points are residuals

vary across years, and differently between natural habitats and farmed area. However, the overall loss was fairly stable from year-to-year despite marked variation in annual plant growth.

Grass species react to grazing by initializing regrowth and increasing their production of tillers (McNaughton 1983). Frequent re-grazing keeps the grass at an early phenological state, with higher protein concentration compared to undisturbed grass (Hebblewhite and Merrill 2008). Similar to a study in Slovenia (Trdan et al. 2024), the crude

protein concentration in the grass in our study was higher in unfenced compared to fenced plots before first harvest. This indicates that grazing might have a positive effect on grass quality. The impact was stable throughout the time before harvest with no change in the difference in crude protein concentration when approaching time of harvest compared to earlier in the growing season. Since grazing kept the protein concentration at higher levels, it mitigates part of the actual loss of feeding units (balance between nutritional value and absolute dry matter) at first harvest. In agricultural

terms a feeding unit is defined as the balance between nutritional value and absolute dry matter in kg where one unit is set to the value of 1 kg of barley with 14% water (Rekdal and Angeloff 2021). However, the overall biomass loss was so high, it is unlikely that the higher protein concentration fully compensated for the biomass loss in terms of feeding units.

Population density and grazing pressure

Population density of red deer was the strongest predictor for biomass loss in our study, and biomass loss increased by 31% from the lowest to the highest density (shot deer/km²). Several studies show that high red deer populations cause significant grazing damages when present at high densities (Bleier et al. 2012; Widén et al. 2023; Trdan et al. 2024) and that red deer grazing increase with population density (Hjermann et al. 2024). Our study have a considerable range in population density allowing us to estimate the effect on biomass loss. The meadows with the highest densities were located on islands (Fig. 4a). The link between grazing pressure on farmland and red deer population density is affected by processes at both the individual and population level. Higher density means more individuals potentially grazing on farmland. Further, higher population density could increase the competition for resources in natural habitats which might also influence both the number of deer grazing on agricultural meadows as well as the time spent grazing (Rosenzweig 1981). Density dependence may force individuals to take higher risks when foraging to fulfil their energy requirements (Merrill et al. 2020), causing more red deer to select agricultural meadows as foraging sites. In northern Italy, red deer damage to maize crops and dry matter biomass loss on meadows was significant only at high densities (Corgatelli et al. 2019). Density dependent foraging on farmland was also found for wild boar (*Sus scrofa*) in Sweden (Augustsson et al. 2024). Population reduction would likely be a measure that could lower biomass losses at broader scales. This might, on the other hand, be challenging to achieve, since both hunters and many landowners benefit from retaining high red deer densities (Olausson and Mysterud 2012). Compensation for red deer grazing damage could be an alternative conflict mitigation strategy, but currently farmers in Norway are not entitled to economic compensation of losses to wildlife.

Context and risk perception

Foraging behavior in many animal species is significantly constrained by risk perception since individuals often must navigate between habitats that rarely offer both high-quality forage and adequate cover (Sih 1980; Brown 1992;

Mysterud and Ims 1998; Piper 2011). We found increased biomass loss for meadows where the surrounding area was characterized by a high degree of topographical variation. Terrain ruggedness index and biomass loss showed a positive nonlinear relationship which suggests that there is a threshold for how rugged the terrain must be before the red deer gets a sense of cover from the topography. Other studies have used an anti-predator behavior framework to explain red deer use of grass meadows in relation to distance to forest, roads, and buildings (Månsson et al. 2021). Given the scarcity of natural predators in our study areas, hunting is the primary fear effect (Lone et al. 2015; Meisingset et al. 2022) and a significant proportion of red deer are shot on agricultural farmland (Rivrud et al. 2014). Red deer's antipredator responses could therefore restrict their use of open habitats, but we found no marked effect of proximity to human disturbance like roads. Our results suggest that the surrounding environment only in terms of topography affected grazing pressure of red deer and point to a limited role of using fear effects to mitigate grazing damages in our study area. However, our study did not directly quantify human presence and activity, only human infrastructure.

Grazing pressure and land use

We predicted that the age since renewal of the meadow would impact the grazing pressure since recently renewed meadows contain more energy rich grass species than intermediate and older meadows (Andueza et al. 2010). GPS-studies have shown that red deer select younger grass meadows when given a choice (Lande et al. 2014), and a correlative study of broad scale grazing pressure by red deer in Norway found a similar pattern (Hjermann et al. 2024). Surprisingly, we found no support for this in our experimental study. Previously, timothy has been commonly used in seed mixes in the study area due to its high nutritional value (Hall and Stout 1999; Andueza et al. 2010) and digestibility (Thorvaldsson 1992). Some farmers in our study area reported that they had changed away from a timothy dominated seed mixture to a mixture with more perennial ryegrass, which may have lowered the effect of meadow age. Perennial ryegrass is more resistant to grazing and a change in seed mixture to reduce grazing was suggested to mitigate geese grazing damages (Tombre et al. 2024). It is possible that choice of seed mixture could affect the biomass removal due to red deer grazing. We did, however, not obtain detailed information of seed mixtures at every meadow, and there is uncertainty if the effect of seed mixture would be prominent when comparing meadows at such a large scale as in our study.

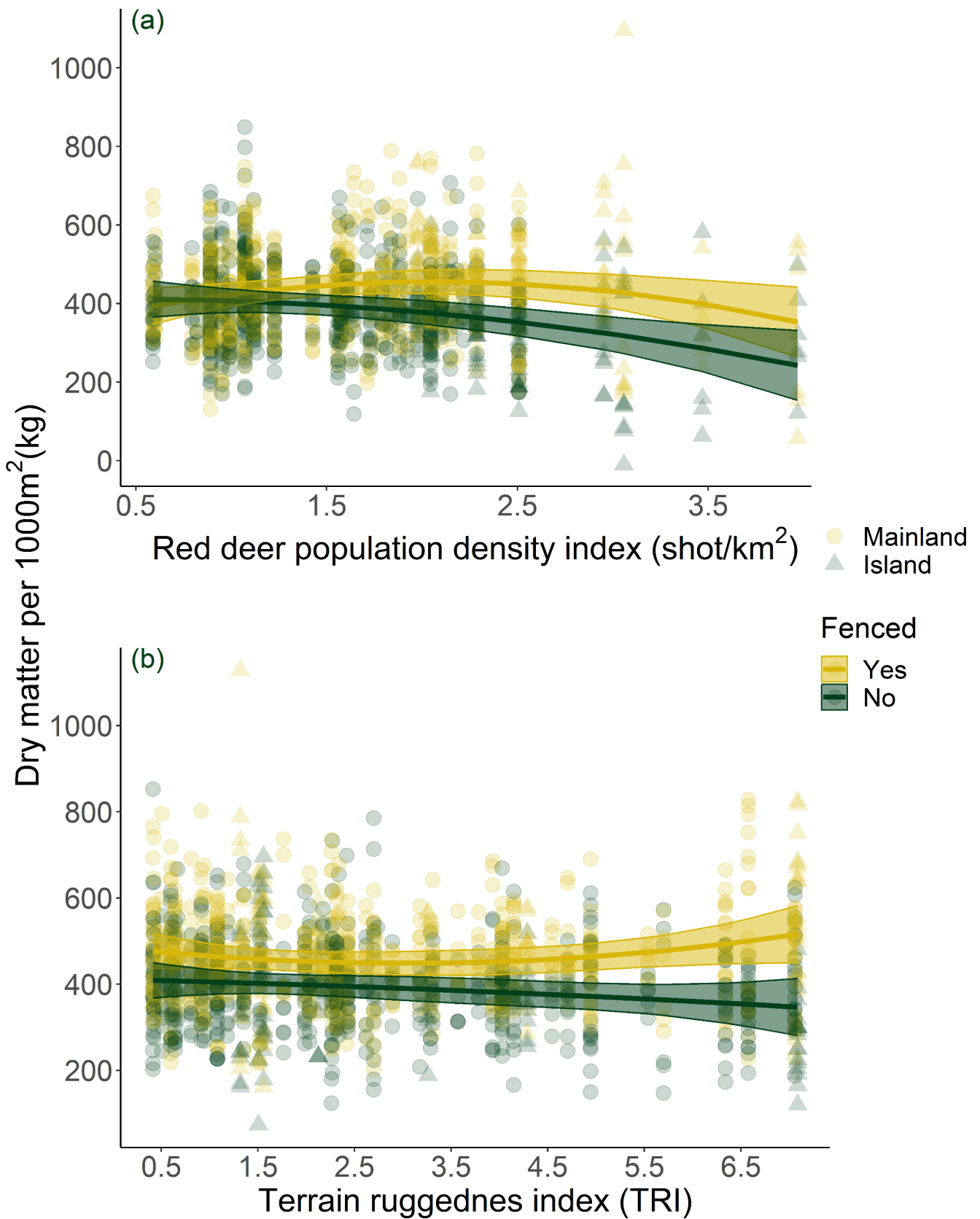


Fig. 4 Predicted changes in dry matter biomass (kg) per 1000 m² for fenced and unfenced plots in relation to (a), red deer density index and (b) terrain ruggedness index on agricultural grass meadows in Norway based on the selected generalized linear mixed effects-model. The

shaded areas depict the 95% CI of the predicted lines, and the points are residuals. Predictions are made for the mean of the remaining continuous predictor variables included in the model, and for the reference levels for the categorical variables (see Table 2)

Management implications

Grasslands are important and diverse ecosystems in Europe (Pellaton et al. 2022). In some areas with conservation of grasslands as a primary objective, red deer grazing has replaced earlier land uses and are considered important for grassland biodiversity (Riesch et al. 2019, 2020) and ecosystems (Riesch et al. 2022). In our system with agricultural grasslands, red deer grazing is a concern and important management topic due to loss of fodder for livestock and hence the farmers economy (Hjermann et al. 2024). Studies quantifying biomass loss to red deer grazing on a large spatial scale focusing on agricultural grasslands and fodder production are scarce. We showed that red deer density was the primary factor driving biomass loss at agricultural meadows at broad scale across several years. One relevant management measure to mitigate grazing by red deer on agricultural grassland is thus to control population density. However, the higher protein concentration at sites exposed to grazing may mitigate some of the total loss in terms of feeding units. Further, agricultural management and future studies should try to spatially segregate use of seed mixture (prioritize timothy in open, flat meadows) to gain knowledge of the strongest drivers of grazing pressure distribution. Further studies that examine the biomass loss to red deer when using different seed mixtures at fields with different spatial attributes would provide more knowledge of the drivers behind grazing pressure distribution.

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Author contributions EU wrote the first draft of the paper. EU did the statistical analysis under supervision of IMR and ELM. ELM, GRF, VV and PT organized and conducted the field work. AM was PI on the AgriDeer project. All authors provided comments to subsequent drafts and approved the final version.

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Data availability The data from this study will be available at <https://dataverse.no/dataverse/nibio> with a unique doi.

Declarations

Ethical approval Not applicable. This research did not involve animals or human participants. No approval of research ethics committees was

required for this study.

Conflict of interest We declare no conflict of interest.

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References

- Rekdal Y, Angeloff M (2021) Arealrekneskap i utmark. Utmarksbeite-ressursgrunnlag og beitebruk. NIBIO-rapport;7(208) 2021 <https://hdl.handle.net/11250/2837610>
- Albon SD, Langvatn R (1992) Plant phenology and the benefits of Migration in a Temperate Ungulate. *Oikos* 65:502–513. <https://doi.org/10.2307/3545568>
- Andueza D, Cruz P, Farruggia A et al (2010) Nutritive value of two meadows and relationships with some vegetation traits. *Grass Forage Sci* 65:325–334. <https://doi.org/10.1111/j.1365-2494.2010.00750.x>
- Augustsson E, Kim H, Andrén H et al (2024) Density-dependent dinner: wild boar overuse agricultural land at high densities. *Eur J Wildl Res* 70. <https://doi.org/10.1007/s10344-024-01766-7>
- Bates D, Mächler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:14065823
- Bleier N, Lehoczki R, Újváry D et al (2012) Relationships between wild ungulates density and crop damage in Hungary. *Acta Theriol (Warsz)* 57:351–359. <https://doi.org/10.1007/s13364-012-0082-0>
- Brown JS (1992) Patch use under predation risk: I. models and predictions. *Ann Zool Fennici* 29:301–309
- Carpio AJ, Apollonio M, Acevedo P (2020) Wild ungulate overabundance in Europe: contexts, causes, monitoring and management recommendations. *Mamm Rev* 1–14. <https://doi.org/10.1111/ma.12221>
- Corgatelli G, Mattiello S, Colombini S, Crovetto GM (2019) Impact of red deer (*Cervus elaphus*) on forage crops in a protected area. *Agric Syst* 169:41–48. <https://doi.org/10.1016/j.agry.2018.11.009>
- Frid A, Dill L (2002) Human-caused disturbance stimuli as a form of predation risk. *Ecol Soc* 6. <https://doi.org/10.5751/es-00404-060111>
- Gebert C, Verheyden-Tixier H (2001) Variations of diet composition of red deer (*Cervus elaphus* L.) in Europe. *Mamm Rev* 31:189–201. <https://doi.org/10.1111/j.1365-2907.2001.00090.x>
- Godvik IMR, Loe LE, Vik JO et al (2009) Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* 90:699–710. <https://doi.org/10.1890/08-0576.1>
- Hall MH, Stout RC (1999) Deer damage to alfalfa and mixtures with timothy or orchardgrass. *Rangel Ecol Management/Journal Range Manage Archives* 52:515–518
- Hebblewhite M, Merrill E (2008) Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *J Appl Ecol* 45:834–844. <https://doi.org/10.1111/j.1365-2664.2008.01466.x>

- Hegel TM, Gates CC, Eslinger D (2009) The geography of conflict between elk and agricultural values in the Cypress Hills, Canada. *J Environ Manage* 90:222–235. <https://doi.org/10.1016/j.jenvma.2007.09.005>
- Hjermann TKS, Bilet NA, Rivrud IM et al (2024) Red deer grazing pressure on agricultural grass meadows from broad to local scale. *Wildlife Biol* e01312
- Jarque-Bascuñana L, Calleja JA, Ibañez M et al (2022) Grazing influences biomass production and protein content of alpine meadows. *Sci Total Environ*. <https://doi.org/10.1016/j.scitotenv.2021.15177> 1: 818:
- Lande US, Loe LE, Skjærli OJ et al (2014) The effect of agricultural land use practice on habitat selection of red deer. *Eur J Wildl Res* 60:69–76. <https://doi.org/10.1007/s10344-013-0751-6>
- Langvatn R, Hanley TA (1993) Feeding-patch choice by red deer in relation to foraging efficiency. *Oecologia* 95:164–170. <https://doi.org/10.1007/BF00323486>
- Linnell JDC, Cretois B, Nilsen EB et al (2020) The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. *Biol Conserv* 244:108500. <https://doi.org/10.1016/j.biocon.2020.108500>
- Lone K, Loe LE, Meisingset EL et al (2015) An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Anim Behav* 102:127–138. <https://doi.org/10.1016/j.anbehav.2015.01.012>
- Månsson J, Nilsson L, Felton AM, Jarnemo A (2021) Habitat and crop selection by red deer in two different landscape types. *Agric Ecosyst Environ* 318. <https://doi.org/10.1016/j.agee.2021.107483>
- Marchiori E, Sturaro E, Ramanzin M (2012) Wild red deer (*Cervus Elaphus* L.) grazing may seriously reduce forage production in mountain meadows. *Ital J Anim Sci* 11:47–53. <https://doi.org/10.4081/ijas.2012.e9>
- McNaughton SJ (1983) Compensatory plant growth as a response to Herbivory. *Oikos* 40:329–336. <https://doi.org/10.2307/3544305>
- Meisingset EL, Loe LE, Brekkum Ø et al (2013) Red deer habitat selection and movements in relation to roads. *J Wildl Manage* 77:181–191. <https://doi.org/10.1002/jwmg.469>
- Meisingset EL, Gusevik J, Skjørestad A et al (2022) Impacts of human disturbance on flight response and habitat use of red deer. *Ecosphere* 13. <https://doi.org/10.1002/ecs2.4281>
- Merrill E, Killen J, Pettit J et al (2020) Density-dependent foraging behaviors on sympatric winter ranges in a partially migratory elk population. *Front Ecol Evol* 8:269
- Milner JM, Bonenfant C, Mysterud A et al (2006) Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *J Appl Ecol* 43:721–734. <https://doi.org/10.1111/J.1365-2664.2006.01183.X>
- Moen A, Odland A (1998) Nasjonalatlas for Norge: vegetasjon. Statens kartverk
- Mould ED, Robbins CT (1981) Evaluation of detergent analysis in estimating nutritional value of browse. *J Wildl Manage* 45:937–947. <https://doi.org/10.2307/3808101>
- Mysterud A, Ims RA (1998) Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* 79:1435–1441. [https://doi.org/10.1890/0012-9658\(1998\)079\[1435:FRIHUA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[1435:FRIHUA]2.0.CO;2)
- Mysterud A, Meisingset EL, Veiberg V et al (2007) Monitoring Population Size of Red Deer *Cervus Elaphus*: An Evaluation of Two Types of Census Data from Norway. *Wildlife Biol* 13:285–298. [https://doi.org/10.2981/0909-6396\(2007\)13\[285:MPSORD\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2007)13[285:MPSORD]2.0.CO;2)
- Mysterud A, Langvatn R, Meisingset EL, Rivrud IM (2023) Agricultural grasslands buffer density effects in red deer populations. *J Wildl Manage* 87:1–14. <https://doi.org/10.1002/jwmg.22357>
- Olaussen JO, Mysterud A (2012) Red deer hunting-commercializing versus availability. *Eur J Wildl Res* 58:597–607. <https://doi.org/10.1007/s10344-012-0610-x>
- Pellaton R, Lellei-Kovács E, Báldi A (2022) Cultural ecosystem services in European grasslands: a systematic review of threats. *Ambio* 51:2462–2477
- Piper WH (2011) Making habitat selection more familiar: a review. *Behav Ecol Sociobiol* 65:1329–1351. <https://doi.org/10.1007/s00265-011-1195-1>
- Riesch F, Tonn B, Meißner M et al (2019) Grazing by wild red deer: management options for the conservation of semi-natural open habitats. *J Appl Ecol* 56:1311–1321
- Riesch F, Tonn B, Stroh HG et al (2020) Grazing by wild red deer maintains characteristic vegetation of semi-natural open habitats: evidence from a three-year exclusion experiment. *Appl Veg Sci* 23:522–538
- Riesch F, Wichelhaus A, Tonn B et al (2022) Grazing by wild red deer can mitigate nutrient enrichment in protected semi-natural open habitats. *Oecologia* 199:471–485
- Rivrud IM, Meisingset EL, Loe LE, Mysterud A (2014) Interaction effects between weather and space use on harvesting effort and patterns in red deer. *Ecol Evol* 4:4786–4797. <https://doi.org/10.1002/ece3.1318>
- Rizopoulos D (2007) Ltm: an R package for latent variable modeling and item response analysis. *J Stat Softw* 17:1–25
- Rosenzweig ML (1981) A theory of Habitat Selection. *Ecology* 62:327–335. <https://doi.org/10.2307/1936707>
- Sih A (1980) Optimal behavior: can foragers Balance two conflicting demands? *Sci* (1979) 210:1041–1043. <https://doi.org/10.1126/science.210.4473.1041>
- Skonhofs A, Veiberg V, Gauteplass A et al (2013) Balancing income and cost in red deer management. *J Environ Manage* 115:179–188. <https://doi.org/10.1016/j.jenvman.2012.11.006>
- Spitzer R, Felton A, Landman M et al (2020) Fifty years of European ungulate dietary studies: a synthesis. *Oikos* 129:1668–1680. <https://doi.org/10.1111/oik.07435>
- Statistics Norway (2023) 11507: Husdyr, etter husdyrslag (F) 1969–2023. <https://www.ssb.no/statbank/table/11507/>. Accessed 1 Oct 2024
- Team RC (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Tenge IM (2016) Arealressurskart AR5
- Thorvaldsson G (1992) The Effect of temperature on growth, Development and Nitrogen in Shoots and roots in Timothy (*Phleum pratense* L.), tested in Growth Chambers. *Acta Agric Scand B Soil Plant Sci* 42:158–163. <https://doi.org/10.1080/09064719209417971>
- Tombre IM, Renna R, Dalmannsdottir S et al (2024) Gressproduksjon I et landskap med gress. Er det noen bærekraftige løsninger?
- Trdan S, Vidrih M (2008) Quantifying the damage of red deer (*Cervus elaphus*) grazing on grassland production in southeastern Slovenia. *Eur J Wildl Res* 54:138–141. <https://doi.org/10.1007/s10344-007-0106-2>
- Trdan S, Laznik Ž, Sinkovič T et al (2024) Quantitative and qualitative yield loss caused by red deer (*Cervus elaphus* L.) grazing on permanent organic grasslands. *Acta Agric Scand B Soil Plant Sci* 74. <https://doi.org/10.1080/09064710.2024.2321847>
- van Beeck Calkoen STS, Kuijper DPJ, Apollonio M et al (2023) Numerical top-down effects on red deer (*Cervus elaphus*) are mainly shaped by humans rather than large carnivores across Europe. *J Appl Ecol* 60:2625–2635. <https://doi.org/10.1111/1365-2664.14526>
- Van Soest PJ (1994) Nutritional ecology of the ruminant. Cornell University Press

- Walter WD, Lavelle MJ, Fischer JW et al (2010) Management of damage by elk (*Cervus elaphus*) in North America: a review. *Wildl Res* 37:630–646. <https://doi.org/10.1071/WR10021>
- Widén A, Cromsigt JPGM, Dressel S et al (2023) Direct and indirect effects of food, fear and management on crop damage by ungulates. *Ecol Solutions Evid* 4. <https://doi.org/10.1002/2688-8319.12266>
- Wood SN (2017) Generalized additive models: an introduction with R. Chapman and Hall/CRC
- Zweifel-Schielly B, Leuenberger Y, Kreuzer M, Suter W (2012) A herbivore's food landscape: seasonal dynamics and nutritional implications of diet selection by a red deer population in contrasting Alpine habitats. *J Zool* 286:68–80. <https://doi.org/10.1111/j.1469-7998.2011.00853.x>

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