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Agricultural grasslands buffer density effects in red deer populations

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Abstract

Population densities of several cervid species have increased in recent decades in North America and Europe, and cervids frequently eat and damage agricultural crops. Competition and depletion of natural food resources are the main mechanisms for the density-dependent decline in vital rates of large herbivores. The extent to which access to agricultural crops can buffer density effects in cervid populations, however, is unknown. Agricultural grasslands cover more than a third of the European agricultural area, and red deer (*Cervus elaphus*) use these grasslands in many European countries. Over the past few decades, such grasslands have been subject to management intensification (with renewal and fertilization) in some areas and abandonment (no longer being harvested) in other areas. We used generalized linear mixed-effects models to examine the development of body masses of red deer in Norway during a period of population density increase in 16 local management units with different availability of cultivated grasslands (0.87–6.44%) in a region with active management of grasslands (Tingvoll, $n = 5{,}780$, 2000–2019) and a region with ongoing abandonment (Hitra, $n = 10{,}598$, 2007–2020). There was a consistent decline in the body mass of red deer linked to increased population density in both regions. A higher proportion of agricultural grassland was linked to higher body mass and lower density effects in both sexes and across all age classes.

There is a link between body mass, survival, and reproduction. Therefore, the buffering of density effects of access to agricultural crops will fuel cervid population growth and lead to less natural regulation of abundance, making it more difficult to control dense cervid populations by harvesting.

KEYWORDS

agricultural subsidies, cervids, coupled natural-agricultural ecosystems, cultivated grasslands, population dynamics, red deer

Agricultural subsidies in an ecological setting refer to the resources that wild animals can gain from farmland and contribute to linkage between farmed and natural ecosystems (Gottschalk et al. 2007, Liu et al. 2007). Knowledge on how agriculture affects wildlife is important to understanding wildlife population dynamics and predicting, and potentially mitigating, grazing damage. Grasslands are a farming practice that cover more than a third of the European agricultural area (Andueza et al. 2010, Huyghe et al. 2014). Grasslands are dominated by perennial grasses and are used for harvesting of winter fodder and direct grazing by livestock but can have high biological diversity depending on land use intensity (Allan et al. 2014). Over the last century, changes in the use of grasslands have involved management intensification (renewal and fertilization) and abandonment (Bakker and Berendse 1999). Land use intensity has profound implications on grassland biodiversity (Allan et al. 2014, Scherreiks et al. 2022), and the resulting changes in plant composition and quality may affect the attractiveness to grazing wildlife (Lande et al. 2014).

A core issue in population ecology of large mammals is the quantification of the effects of density on growth, life history, and demography (Fowler 1987, Bonenfant et al. 2009). Density-dependent effects on body mass have been documented following increasing populations of cervids over the last half century. These include studies on white-tailed deer (*Odocoileus virginianus*; Keyser et al. 2005, Ayotte et al. 2019) and elk (*Cervus canadensis*; Stewart et al. 2005) in North America and red deer (*Cervus elaphus*; Mysterud et al. 2001*b*, Bonenfant et al. 2002, Rodriguez-Hidalgo et al. 2010, Putman et al. 2019) and roe deer (*Capreolus capreolus*; Pettorelli et al. 2001, Kjellander et al. 2006) in Europe. Competition and depletion of natural food resources are assumed to be the main mechanisms for the density-dependent decline in vital rates in cervid populations (Fowler 1987). The use of crops by large herbivores has typically been assessed from a damage perspective (Putman 1986, Putman and Moore 1998, Reimoser and Putman 2011, Corgatelli et al. 2019). There are few studies that have documented how deer performance indicators, such as body mass, vary according to land use and its intensity. Red deer use agricultural grasslands extensively in Italy (Corgatelli et al. 2019), Switzerland (Zweifel-Schielly et al. 2012), Sweden (Månsson et al. 2021), and Norway (Godvik et al. 2009, Lande et al. 2014). Red deer select meadows that are actively managed and renewed with re-seeding and fertilization (Lande et al. 2014). We have previously reported heavier red deer body mass on broad scales in municipalities with a higher proportion of grasslands in Norway (Mysterud et al. 2002). Whether access to agricultural grasslands can buffer the negative effects of population density on body mass, however, remains unknown.

In this study, we compared the body mass development of red deer in Norway during a period of population density increase in local management units with different availability of meadows (i.e., cultivated grasslands). Furthermore, we compared 2 regions with different recent agricultural management: one with meadows that is still being intensively managed (Tingvoll) and another with ongoing abandonment and a decrease in the proportion of grasslands being harvested (Hitra). We specifically tested whether the predicted negative effect of increasing population density on body mass was buffered by high access to grasslands and whether the effect was consistent for both sexes and across ages.

STUDY AREA

The 2 study regions were 2 municipalities situated on the west coast of Norway between 62°45′N and 63°40′N (Figure 1). The Tingvoll (337 km^2) municipality in Møre and Romsdal county is a peninsula with a varied topography mounting to elevations 1,176 m above sea level. The municipality of Hitra (569 km^2), Trøndelag county, is an island with a topography varying at smaller scales (max. elevation = 345 m above sea level). The 2 study areas are approximately 70 km apart and experience similar weather and climatic conditions. Mean temperature and precipitation for July is 14°C and 22 mm, respectively, and 4°C and 55 mm for January. Both areas have a mix of coniferous forest, mainly Scots pine (*Pinus sylvestris*) and some planted Norway spruce (*Picea abies*), and deciduous forest, birches (*Betula* spp.) and alder (*Alnus incana*).

Agricultural farmland in the form of grass meadows is interspersed with forest and typically at the lower elevations. The area of agricultural grasslands in active use on Hitra declined from 15.1 km^2 in 2007 to 11.7 km^2 in 2019, but it was stable between 19–20 km^2 in Tingvoll for 2000–2019 (Statistics Norway 2022). Each field of cultivated grasslands were small in both regions, typically ranging from 0.5–10 ha and scattered around but in different proportions of the total area among local management units (Table 1). There was no systematic fencing of grasslands, implying that they were usually readily available for red deer grazing (Godvik et al. 2009). There is no other agriculture in the area than the grasslands.

Red deer is the most abundant cervid species in both municipalities. Roe deer (*Capreolus capreolus*) occur in smaller numbers locally. There are occasionally moose (*Alces alces*) in Tingvoll but not on Hitra. The lynx (*Lynx lynx*) has become common since about 2015 in Tingvoll. During the study period, harvest of red deer increased from 847 in 2007 to 1,200 in 2020 on Hitra and from 335 in 2000 to 639 in 2019 for Tingvoll. In Norway, a local management unit is the legal entity for hunting management, typically consisting of several landowners (Meisingset et al. 2018). All local management units in this study have their own management plans for 3 to 5 years, with goals for population development and annual hunting quotas divided into sex and age classes (calves, yearlings, and adults ≥2 yr of age). The harvest season was from 10 September to 30 November or 23 December during 2007–2012 and from 1 September to 23 December during 2013–2020.

METHODS

Harvest and body mass data

We collected data on 12,606 harvested red deer across the island of Hitra from 2007 to 2020 and 6,430 deer in the mainland municipality of Tingvoll from 2000 to 2019. The local management units organized the data collection. All hunters reported information about the sex, body mass, and location (local management unit) of all deer shot during the hunting season. Hunters then returned the jawbones to the management units for aging. Managers organize age assessment of collected jawbones. Calves and yearlings were aged from tooth eruption patterns and adults by counting annuli in the cementum of the first incisor (Veiberg et al. 2020). Body mass is dressed mass (i.e., live mass minus head, skin, viscera, bleedable blood, and metapodials) and was obtained with 1-kg accuracy and weighed within 24 hours after shooting (Langvatn 1977). We removed the data that did not contain sex, age, or accurate body mass or data with missing information on location. We removed data from 1 small local management unit in Hitra and from 2 small units in Tingvoll because of their small sample size. We collected data from 8 local management units in each region and body mass (kg) from 10,598 red deer (5,293 calves and yearlings, 3,053 adult females, 2,252 adult males) in the final models for Hitra and 5,780 (3,552 calves and yearlings, 1,412 adult females, 816 adult males) for Tingvoll.

To calculate the index of population density, we divided the number of harvested deer for each local management unit by the qualifying area (i.e., what we determined to be red deer habitat; Mysterud et al. 2007). This

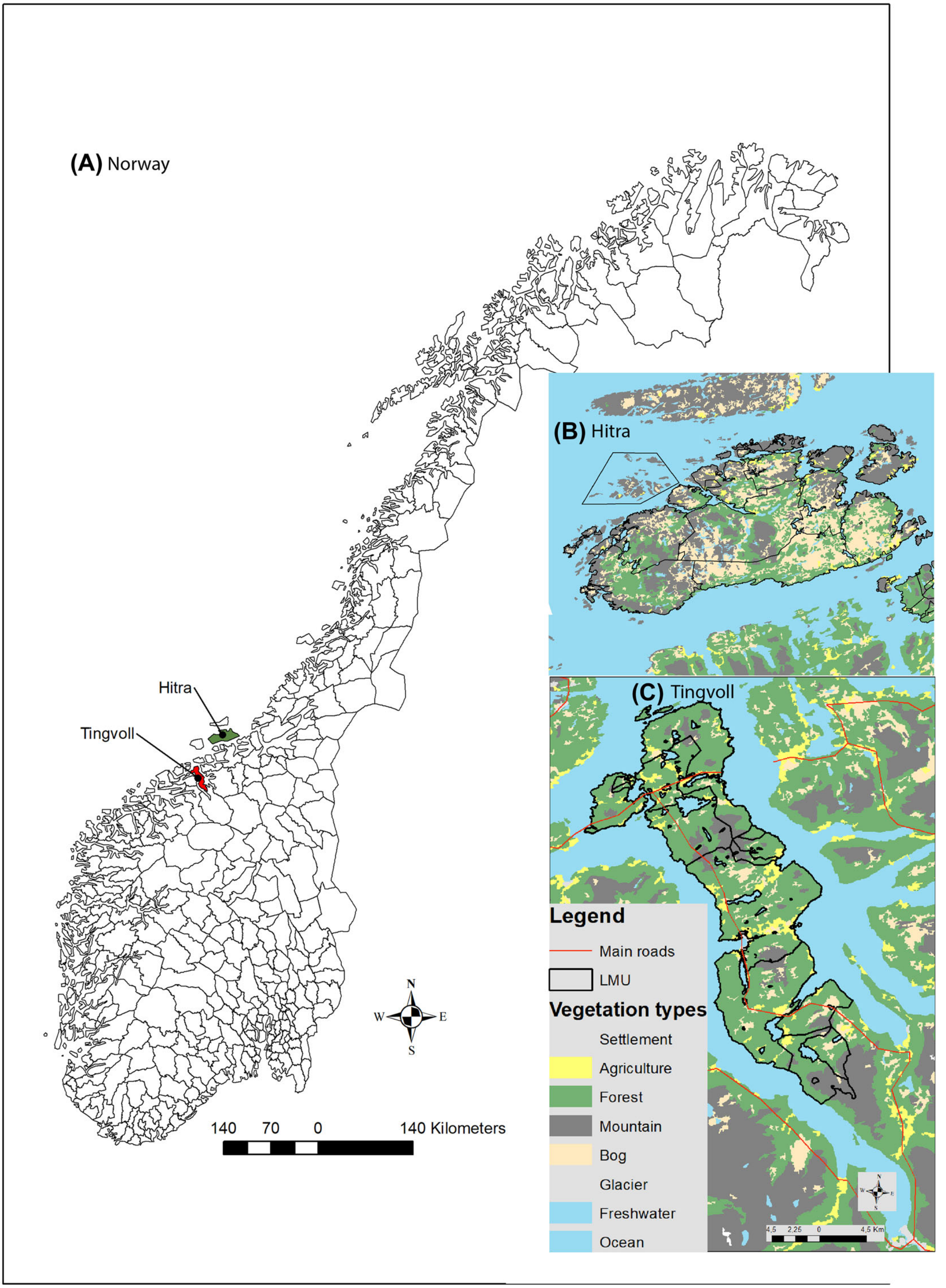

FIGURE 1 A) The 2 study regions for body mass development of red deer in Norway, 2000–2020, B) Hitra, and C) Tingvoll. The habitat composition of the local management units (LMU) differ in availability of agricultural grass meadows.

TABLE 1 An overview of the local management units, their proportion of meadows, range of population densities, and sample size of harvested red deer used in the analyses of Tingvoll and Hitra municipalities, Norway, 2000–2020.

Unit number	Area (km^2)	Fully grown meadow (%)	Agriculture (%)	Red deer density index (range), deer shot/km^2	Red deer sample size
Hitra					
5	74.9	1.04	1.50	1.30–1.73	1,775
15	38.9	3.17	4.23	1.77–2.67	593
18	44.4	3.53	5.76	2.00–3.60	631
26	151.2	2.99	3.96	1.29–2.31	1,260
63	64.9	4.33	5.95	2.36–4.40	2,296
64	114.2	1.60	1.92	0.83–1.46	900
66	185.9	0.87	1.03	1.76–2.34	1,784
69	10.8	1.50	2.13	0.73–1.16	1,359
Tingvoll					
1	28.7	3.41	4.05	0.73–1.75	437
2	61.1	3.24	4.46	0.75–1.82	900
4	82.7	5.96	7.24	0.54–2.60	1,629
5	30.0	2.05	2.9	0.83–2.67	683
6	19.5	6.44	8.06	3.14–5.23	770
7	18.9	5.86	7.43	2.01–3.84	451
20	46.9	2.86	3.66	0.98–1.92	683
22	17.4	3.07	3.58	1.09–2.12	227

index has been widely used in previous studies (Mysterud et al. 2001*b*). The red deer harvest density was 0.7–4.4 deer shot/km^2 in Hitra and 0.5–5.2 deer shot/km^2 in Tingvoll, which is approximately 15–20% of the population size.

Data on habitat composition and climate

Local management units were 10.8–185.9 km^2 on Hitra and 17.4–82.7 km^2 in Tingvoll (Table 1). We extracted the proportion of fully grown meadows and agriculture for each unit via overlay of land cover maps. The proportion of cultivated grasslands was 0.87–4.33% on Hitra and 2.05–6.44% in Tingvoll (Table 1). We included fully grown meadows and infield grazing areas, as the proportion of fully grown meadows was highly correlated with overall agricultural grasslands ($r = 0.992$ on Hitra, $r = 0.995$ in Tingvoll). We did not have the proportion of fully grown meadows as a time series for each unit. This area was stable in Tingvoll, while areas of fully grown meadows were in decline on Hitra.

We used the North Atlantic Oscillation (NAO) winter index (Dec–Mar) as a proxy for annual climate variation (Hurrell 1995). This index has a relationship with winter snow and early spring forage conditions, and notably affects red deer body mass (Mysterud et al. 2001*a*).

Statistical analysis

We used generalized linear mixed-effects models to analyze variation in body mass using library lme4 (Bates and Maechler 2009) in R version 4.0.3 (R Development Core Team 2019). We used generalized additive models using library mgcv to investigate if there were possible non-linear relationships between ordinal day and body mass and between age and body mass of males, which was included in the models (Wood 2006). We log-transformed the response variable, body mass (kg), to stabilize the variance. We considered age, sex, NAO, ordinal day, proportion of agricultural grasslands, and population density index as predictor variables. We included the interaction between the proportion of agricultural grasslands and population density index to investigate directly if access to farmland buffers the density effects (our focal hypothesis), and the third-order interaction term with age (age×population density×proportion of agriculture) to look for age-related patterns in buffer effects. We included the ordinal day (linear or second-order polynomial term) to account for any body mass change during the hunting season.

Females and males have different growth patterns, and there can be complicated interactions between age, sex, and ordinal day for adults owing to rutting in fall (Yoccoz et al. 2002). Therefore, we split the models into calves and yearlings, adult (≥2 yr old) females, and adult (≥2 yr old) males based on previous analysis of red deer body mass in Norway (Mysterud et al. 2001*b*, Yoccoz et al. 2002). We included an interaction between age (categorical) and sex in the model for calves and yearlings. For adult females, we used categories 2, 3, 4, 5, and ≥6 years old (Mysterud et al. 2001*b*), while for adult males, we considered polynomials up to the fifth order for age and restricted data to ages 2 to 10 years (as there were few males of older ages). For adult males, we considered higher order polynomial terms for ordinal day and interaction terms between age and ordinal day owing to age-specific patterns of body mass loss related to rutting activity (Yoccoz et al. 2002).

We standardized all continuous predictor variables, except age, by subtracting the mean and dividing it by the standard deviation, resulting in mean = 0 and standard deviation = 1, using the scale function in R. We fitted local management units as random intercepts. We used separate analyses for the 2 municipalities (Hitra and Tingvoll) to avoid overly complex models, and because the time periods differed among municipalities. We performed model selection by backward selection using Akaike's Information Criterion (AIC) and likelihood ratio tests, and tested whether the random term improved the model fit. We considered models with ΔAIC > 2 to be less parsimonious and used a threshold of $P < 0.05$ for likelihood ratio tests. The model selection results from AIC and likelihood ratio tests were consistent.

In the final models, we used standard diagnostic tools to assess patterns in the residuals, looked for influential values, and ensured that the model assumptions were met. In addition to using standard plots and tests, we also explored model fit using the library DHARMa in R (Hartig 2022). There were no strong patterns in the residuals. We also assessed correlations among predictor variables, which were acceptably low ($r < 0.6$), except for the population density and proportion of agricultural meadows for Hitra ($r = 0.74$). As these were our focal variables, we included the interaction in the models but discussed the results with moderate-to-strong correlation.

RESULTS

All the most parsimonious models included the proportion of agriculture, the population density, and their interaction term (Tables 2 and 3). There was evidence of a negative effect of population density and of a positive effect of access to agricultural grasslands, and the interaction term quantifies how much the negative effect of population density depended on how much agricultural land was available. That is, access to agricultural grasslands partly buffered the negative effect of population density (Figure 2; Appendix A, available in Supporting Information). As an example in numbers, the dressed body mass of a red deer calf in Tingvoll declined from 26.7 kg to 23.7 kg for a 3.5-fold density increase (from 0.75 to 2.6 shot/km^2) when 2.05% of the habitat was agricultural grasslands, while it declined only from 27.1 to 26.6 kg when 6.44% of the habitat was agricultural grasslands for the

TABLE 2 Parameter estimates from the most parsimonious models for body mass of red deer from Tingvoll, Norway, 2000–2019. All continuous predictor variables were standardized, except age.

Parameter	Estimate	SE	Lower 95% CL	Upper 95% CL
Calves and yearlings (n = 3,552)				
Intercept	3.182	0.011	3.160	3.204
Age category yearlings vs. calves	0.599	0.008	0.583	0.614
Sex (males vs. females)	0.082	0.008	0.067	0.098
NAO[a]	0.009	0.002	0.004	0.014
Ordinal date	2.816	0.173	2.477	3.155
Ordinal date^2	−1.440	0.170	−1.772	−1.108
Proportion of agriculture	0.030	0.010	0.010	0.049
Population density	−0.039	0.007	−0.053	−0.025
Age × sex (males vs. females)	0.057	0.011	0.035	0.079
Proportion of agriculture × population density	0.022	0.007	0.009	0.035
Adult females (n = 1,412)				
Intercept	3.946	0.010	3.926	3.966
Age category 3 yr vs. 2 yr	0.055	0.009	0.037	0.073
Age category 4 yr vs. 2 yr	0.097	0.010	0.077	0.116
Age category 5 yr vs. 2 yr	0.116	0.011	0.094	0.139
Age category ≥6 yr vs. 2 yr	0.157	0.007	0.143	0.172
Ordinal date	−0.496	0.109	−0.710	−0.282
Ordinal date^2	−0.554	0.108	−0.765	−0.343
Proportion of agriculture	0.024	0.009	0.006	0.042
Population density	−0.039	0.008	−0.054	−0.024
Proportion of agriculture × population density	0.029	0.007	0.015	0.042
Adult males (n = 816)				
Intercept	4.437	0.014	4.410	4.463
Age	4.359	0.144	4.076	4.641
Age^2	−2.006	0.142	−2.283	−1.728
Ordinal date	−2.246	0.143	−2.527	−1.965
Ordinal date^2	−0.197	0.142	−0.475	0.082
Proportion of agriculture	0.042	0.014	0.015	0.069
Population density	−0.055	0.011	−0.076	−0.033
Age × ordinal date	−28.834	4.340	−37.340	−20.328
Age^2 × ordinal date	9.562	4.469	0.803	18.322
Age × ordinal date^2	13.655	4.254	5.317	21.993

(Continues)

TABLE 2 (Continued)

Parameter	Estimate	SE	Lower 95% CL	Upper 95% CL
Age^2 × ordinal date^2	−5.992	4.387	−14.590	2.606
Proportion of agriculture × population density	0.019	0.010	0.000	0.039

[a]North Atlantic Oscillation winter index.

same density increase (Figure 2B). The third-order interaction term between age, population density, and proportion of agricultural grasslands did not enter the best models. That is, the interaction between population density and proportion of agriculture did not vary depending on age, and hence, there was no clear evidence of an age-dependent buffering effect. For Hitra, the population density and proportion of agricultural grasslands were correlated ($r = 0.74$) above the level recommended when assessing independent effects.

The most parsimonious model for calves and yearlings in both regions also included effects of sex, age category, NAO, ordinal day (linear and squared), and the interaction between sex and age category (Tables 2 and 3). Males were larger than females, and sex differences were larger for yearlings than for calves, as indicated by the interaction term between sex and age category. In Tingvoll, the mean dressed body mass of male calves was 26.9 kg, female calves were 24.8 kg, male yearlings were 51.8 kg, and female yearlings were 45.1 kg. On Hitra, the mean dressed body mass of male calves was 21.4 kg, female calves were 20.4 kg, male yearlings were 38.2 kg, and female yearlings were 34.4 kg. Body mass increased with increasing NAO, and there was a non-linear effect of ordinal day, in which an increase in body mass in the early part of the season was followed by a leveling off and a slight decrease in the later part of the season.

The most parsimonious model for adult females in both regions included the age category and ordinal day (linear and squared). An average adult female had a dressed mass of 61.5 kg in Tingvoll and 50.3 kg on Hitra. The most parsimonious model for adult males (aged 2–10 yr) in both regions included a squared term for age, ordinal day, and interactions up to a second-order polynomial term for both variables (Tables 2 and 3). The ordinal day effect quantified the body mass loss during the rutting season. The interaction term between age and ordinal day quantified how body mass loss during the rutting season depended on male age. For adults, the NAO was not retained in most parsimonious models. The average adult male had a dressed mass of 88.7 kg in Tingvoll and 67.0 kg on Hitra.

DISCUSSION

Our study showed that access to farmland can increase deer body mass and, importantly, it can also buffer the effects of increasing population density on body mass. Body mass mediates density effects on survival (Loison et al. 1999) and reproduction in red deer (Langvatn et al. 2004). The buffering of population density effects by agricultural subsidies therefore decreases deer population regulation and fuels further growth in the population if not strictly managed by harvest.

Farmlands can provide higher quality and abundance of forage to wildlife at specific times depending on the type of crop, and the use of farmland by cervids can be seasonally extensive (Reimoser and Putman 2011). At high population densities, our data indicated that red deer during fall were heavier after the main growing season, when they had more access to agricultural grasslands. This effect was consistent for calves, yearlings, adult females, and adult males in both the regions. For long-lived vertebrates, an initial sign of increased population density is reduced body mass of young individuals (Eberhardt 2002). In turn, there is a strong link between body mass and age at first reproduction (Langvatn et al. 2004) and juvenile winter survival (Loison et al. 1999) in red deer. Land use connected to livestock farming therefore leads to less dependence on natural forage by deer. Furthermore, forage in cultivated

TABLE 3 Parameter estimates from the most parsimonious models for body mass of red deer from Hitra, Norway, 2007–2020. All continuous predictor variables were standardized, except age.

Parameter	Estimate	SE	Lower 95% CL	Upper 95% CL
Calves and yearlings (n = 5,293)				
Intercept	3.003	0.025	2.954	3.052
Age category yearlings vs. calves	0.526	0.008	0.511	0.541
Sex (males vs. females)	0.050	0.008	0.034	0.065
NAO[a]	0.005	0.002	0.001	0.009
Ordinal date	2.811	0.201	2.417	3.205
Ordinal date^2	−0.594	0.199	−0.984	−0.205
Proportion of agriculture	0.068	0.027	0.014	0.121
Population density	−0.076	0.011	−0.097	−0.054
Age × sex (males vs. females)	0.055	0.011	0.034	0.076
Proportion of agriculture × population density	0.031	0.009	0.014	0.049
Adult females (n = 3,053)				
Intercept	3.769	0.014	3.741	3.797
Age category 3 yr vs. 2 yr	0.071	0.007	0.057	0.085
Age category 4 yr vs. 2 yr	0.100	0.009	0.082	0.117
Age category 5 yr vs. 2 yr	0.121	0.010	0.102	0.140
Age category ≥6 yr vs. 2 yr	0.150	0.006	0.138	0.163
Proportion of agriculture	0.040	0.015	0.011	0.070
Population density	−0.036	0.009	−0.053	−0.018
Ordinal date	−0.009	0.002	−0.014	−0.005
Proportion of agriculture × population density	0.018	0.007	0.004	0.032
Adult males (n = 2,252)				
Intercept	4.148	0.016	4.117	4.179
Age	7.801	0.193	7.423	8.179
Age^2	−3.652	0.187	−4.018	−3.285
Ordinal date	−1.928	0.191	−2.301	−1.554
Ordinal date^2	−0.159	0.191	−0.534	0.215
Proportion of agriculture	0.064	0.017	0.030	0.098
Population density	−0.057	0.013	−0.082	−0.032
Age × ordinal date	−86.374	9.365	−104.729	−68.018
Age^2 × ordinal date	18.878	9.322	0.606	37.150
Age × ordinal date^2	21.918	9.060	4.160	39.676
Age^2 × ordinal date^2	−3.857	8.959	−21.417	13.702
Proportion of agriculture × population density	0.029	0.010	0.010	0.049

[a]North Atlantic Oscillation winter index.

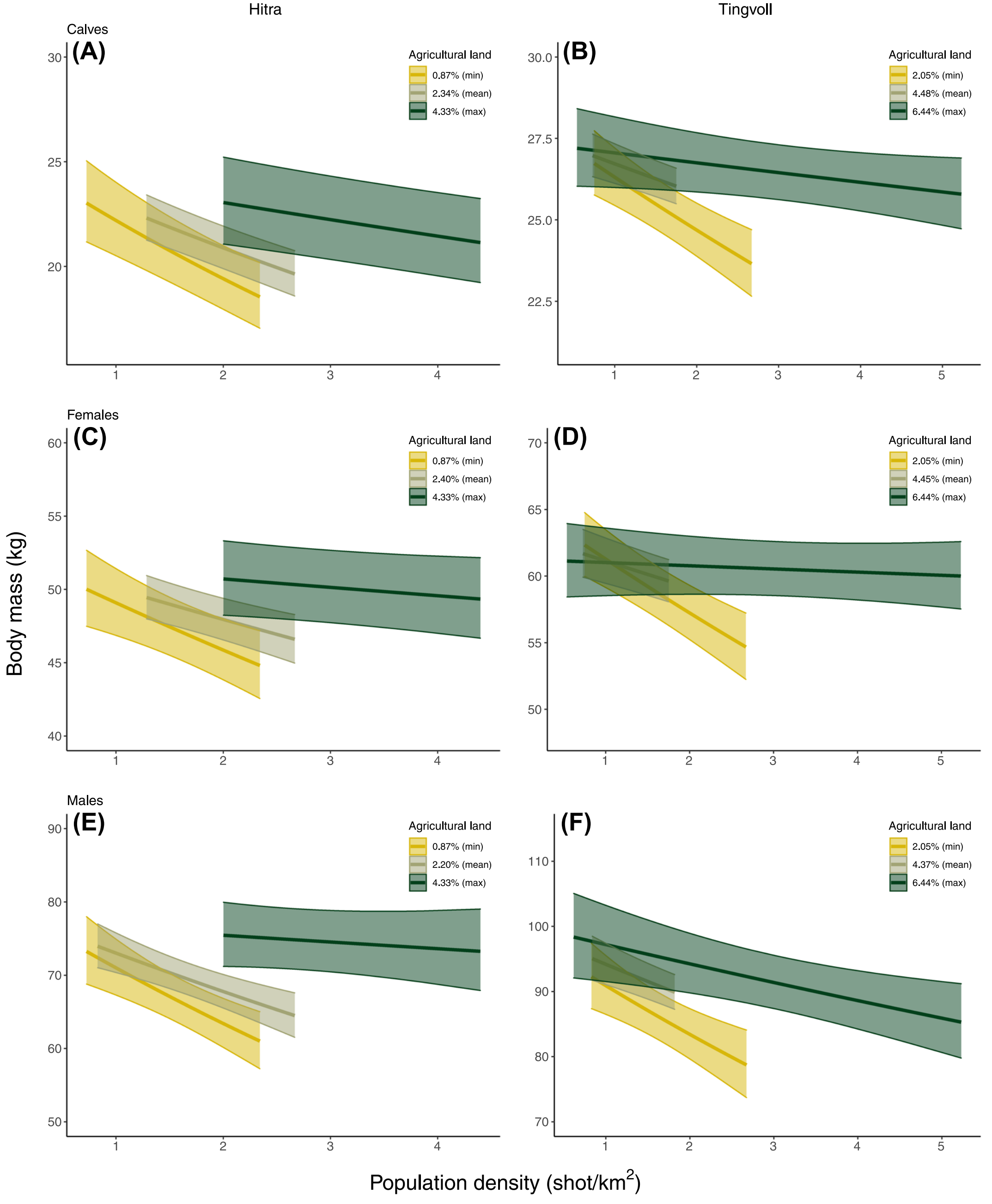

FIGURE 2 Body mass development of red deer as a function of population density and availability of agricultural grass meadows in Hitra and Tingvoll regions, Norway, 2000–2020. The lines are predicted means (95% CI) of body mass for variable levels of proportion of agricultural meadows (min. and max. observed) for calves on A) Hitra and in B) Tingvoll, adult females on C) Hitra and in D) Tingvoll, and adult males on E) Hitra and in F) Tingvoll.

grasslands at high deer densities are likely to be less depleted than in the forest, lowering the natural regulation of wild grazing animal populations. This provides a challenge for agricultural management, as dense wildlife populations may remove a high proportion of the annual biomass production: up to 60–70% in Norway (Meisingset et al. 1997, Meisingset and Krokstad 2000, Thorvaldsen and Rivedal 2014) and >50% in Italy (Corgatelli et al. 2019).

Our study highlights the important role of current land use on body mass. Plant composition strongly influences the nutritive value of meadows (Andueza et al. 2010). Fertilization typically increases dietary quality in ruminants but leads to a low diversity of plant communities (Bruinenberg et al. 2002). In Norway, actively used grasslands are fertilized annually and harvested 2–3 times during the growing season (Mysterud et al. 2012). A policy of renewing the meadows by mowing and re-seeding was implemented during 1986–1996 in Norway. From that point onwards, seed composition that included timothy (*Phleum pratense*) became the most used. The digestibility of timothy is high under cool summer temperatures (Thorvaldsson 1992, Thorvaldsson et al. 2007, Bertrand et al. 2008) and is typically used in northern Europe and eastern Canada (Piva et al. 2013). Timothy has a high nutritive value (Andueza et al. 2021) and is highly preferred by red deer (Langvatn and Hanley 1993) and other deer species (Hall and Stout 1999). Timothy is not tolerant to grazing, and the standing crop of timothy decreases quickly in areas of heavy grazing. Consequently, meadows that are not renewed have a decreasing amount of timothy, and red deer have a strong selection for newly renewed meadows (Lande et al. 2014). We observed that there is an ongoing abandonment of grasslands in Hitra, with 22.5% of grasslands out of active use. We also observed that access to agricultural meadows had buffering effects on population density on this island. In the future, further abandonment may negatively affect population productivity.

Agricultural fields are often monocultures, with mature crops being used as food for wildlife only for a short period before they are harvested. In contrast, grass meadows are dominated by perennial grasses that regrow quickly after harvesting if the conditions are good (Andueza et al. 2016). Hence, there will be some food available to grazers year-round, not only during the plant-growing season but also fairly quickly after harvest. We measured how access to meadows (cultivated grasslands) during summer affected body growth. Red deer continue to use meadows during winter (Godvik et al. 2009). Summer forage may typically determine the size and condition of individual deer, while winter range conditions may determine the carrying capacity of an area (Klein 1965). Most red deer females in our study areas were residents (Hitra: 100%, $n = 13$, Tingvoll: 71%, $n = 31$) within well-defined home ranges during the plant-growing season (Meisingset et al. 2011). During fall, the migratory part of the population with low access to meadows during summer moved into lowland winter ranges with more agriculture. Measurement of the effects of access to meadows during winter is more challenging because there is no harvest of red deer, and populations are mixed owing to migration. Therefore, we likely underestimated the full (annual) effects of access to agricultural grasslands.

MANAGEMENT IMPLICATIONS

The control of dense deer populations is a recurring challenge in large parts of North America and Europe. Increasing populations of red deer are causing increasing management conflicts due to agricultural damages in most core areas along the west coast of red deer range in Norway. We documented overall higher body condition and weaker density-dependent decline in body condition in areas with high access to agricultural grasslands. This can increase growth of the deer populations, and managers need to compensate for this by an increase in harvest rates to avoid overabundant deer populations.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

All data derive from deer incoming as part of ordinary and regulated hunting.

DATA AVAILABILITY STATEMENT

Data and code are available in Zenodo: https://doi.org/10.5281/zenodo.7270072 (Mysterud et al. 2022).

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