BioOne COMPLETE

Spatial patterns of accumulated browsing and its relevance for management of red deer Cervus elaphus

Authors: Mysterud, Atle, Askilsrud, Harald, Loe, Leif Egil, and Veiberg, Vebjørn

Source: Wildlife Biology, 16(2) : 162-172

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/09-043

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Wildl. Biol. 16: 162-172 (2010)
DOI: 10.2981/09-043
© Wildlife Biology, NKV
www.wildlifebiology.com

Original article

Spatial patterns of accumulated browsing and its relevance for management of red deer *Cervus elaphus*

Atle Mysterud, Harald Askilsrud, Leif Egil Loe & Vebjørn Veiberg

The substantial increase of deer populations in Europe and North America in recent decades has led to concerns regarding the long-term sustainability of current management from an ecosystem perspective. Key questions to be answered are how herbivore density relates to available resource levels, e.g. food availability and browsing pressure, and how this relation should be monitored and included in management. In Norway, the harvest of red deer *Cervus elaphus* has increased from 1,479 to 35,700 during 1960-2008. Current monitoring programmes focus on deer body mass and number of seen deer rather than on the state of the vegetation communities. In our study, we quantify browsing frequency on common shrubs and trees in two municipalities, Gloppen and Flora, in the county of Sogn and Fjordane, Norway, to document current browsing pressure levels and to evaluate the potential of using browsing frequency of indicator species as a tool in the monitoring of red deer populations. We found that several species were heavily browsed (median browsing frequency > 60%). Due to their wide availability, we analysed the spatial patterns of accumulated browsing of the highly selected rowan *Sorbus aucuparia* compared to the less selected bilberry *Vaccinium myrtillus* and birch *Betula* sp. We predicted less spatial variation in browsing frequency of the highly selected rowan. However, we found that the best model predicting browsing on rowan (forest type, habitat productivity, canopy cover, aspect, slope and distance to arable land) based on habitat variables was more complicated than for birch (habitat productivity and altitude) and bilberry (forest type, habitat productivity, altitude and distance from the coast). This suggests large spatial variation in browsing frequency of rowan even though the average browsing frequency of rowan was higher than for bilberry and birch. Browsing frequency for all species was positively correlated with faeces counts, but only bilberry showed additional correlation with red deer (harvest) density at the local management unit scale. Due to its wide distribution and promising link to local red deer density, bilberry stands out as the most promising species to monitor among winter browse species. However, browsing frequency on different species was not always correlated. It remains to be determined to which extent browsing on bilberry can be used as an indicator for the browsing pressure on the whole vegetation community. The documentation of high browsing frequencies clearly suggests that further focus on these issues is warranted.

Key words: Cervus elaphus, density dependence, ecosystem management, monitoring, red deer, sustainability, ungulates

Atle Mysterud, Harald Askilsrud & Leif Egil Loe, Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway - e-mail addresses: atle.mysterud@bio.uio.no (Atle Mysterud); harala@student.matnat.uio.no (Harald Askilsrud); l.e.loe@bio.uio.no (Leif Egil Loe)
Vebjørn Veiberg, Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway, and Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway - e-mail: vebjorn.veiberg@nina.no

Corresponding author: Atle Mysterud

Received 12 May 2009, accepted 2 December 2009

Associate Editor: Glenn Iason

Many deer populations in Europe and North America have increased substantially in numbers over the last decades (Gill 1990, McShea & Underwood 1997). The long-term sustainability of the current situation with many high-density populations has been questioned from an ecosystem perspective (deCalesta & Stout 1997, deCalesta 1997). There is increasing concern for the impact of heavy browsing

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

and grazing on ecosystem function (Côté et al. 2004, Gordon et al. 2004, Mysterud 2006). Management goals have expanded from considering only the hunted ungulates to a broader focus including the entire ecosystem. In most cases, it remains unclear how high the grazing pressure is and what level of grazing pressure the ecosystem can sustain (but see Persson et al. 2005). A criticism of monitoring practices is that they often are directed and measured without consideration of multiple trophic levels (Mysterud 2006). Such information is missing since current management, at least in Scandinavia, typically focus on either direct measures of abundance such as 'seen deer' schemes (e.g. Ericsson & Wallin 1999, Mysterud et al. 2007), or measures of individual performance such as body mass (Morellet et al. 2007). This tradition derives from the common goal in ungulate management to maintain a stable harvest number and/or fitness or specific traits on a population level (e.g. fecundity, body mass and antler size) rather than focussing on the entire ecosystem.

Though selective harvesting influence the distribution of performance traits (Bischof et al. 2008), the most important causal factor seems to be population density. In recent years, we have achieved a good understanding of how the sequential effects of increasing densities affect reproduction and survival in large vertebrates (Gaillard et al. 2000, Eberhardt 2002). However, density typically has no clear meaning without considering resource levels (i.e. carrying capacity; Van Horne 1983), and the effects of depleted food resources on animal performance may be lagged in time (Noy-Meir 1975). A concern is therefore that resilience of food resources may be slow (Tanentzap et al. 2009). Monitoring vegetation rather than animal performance may be important if there is multiple aims in management or if the time lag between heavy browsing and density dependent responses in ungulate condition is long. We therefore need to quantify grazing pressure directly on the plants, and determine how this relates to either abundance or animal performance.

Grazing (or browsing) pressure can be defined in several ways. Often, it is expressed as herbivores' offtake per unit available biomass (e.g. weight or number of shoots) over time and space (Scarnecchia & Kohtmann 1982, Hörnberg 2001). A useful field approach is to look at the grazing frequency, i.e. the proportion of individual plants (or shoots) eaten over a given time period (Holechek et al. 1999, Evju et al. 2006). Highly selected plants are expected to have a high grazing frequency irrespective of density, whereas intermediate to low quality forage is expected to be rarely grazed at low density but increasingly grazed with increasing population density relative to resource levels (Choquenot 1991). Intermediate quality forage may therefore prove particularly useful for monitoring (Mysterud 2006), however, this assumption has rarely been tested in field studies. A study of grazing (or browsing) frequency of plant species with differing quality as forage can be a useful approach for studying the condition of available forage as a whole (Månsson 2009). However, browsing frequency for a given plant species not only relates to herbivore diet preference and population density (Choquenot 1991, Kausrud et al. 2006), but also to habitat selection and the composition of the plant community (Palmer et al. 2003).

In Norway, the harvest of red deer *Cervus elaphus* has increased from 1,479 in 1960 to 35,700 in 2008 (Statistics Norway 2009). The harvest in the county of Sogn and Fjordane alone made up 11,280 red deer in 2008. Reported negative density effects include increased age at first reproduction (Langvatn et al. 2004, Mysterud et al. 2009) and decreased body weight (Mysterud et al. 2001). In our study, we quantify the spatial patterns of browsing frequency of winter forage plants (browse species) of red deer in Sogn and Fjordane, Norway, at the end of winter. Our aim was two-fold: 1) to quantify patterns of browsing pressures on several browse species and relate this to earlier knowledge about browsing and long-term sustainability of forage production, and 2) to evaluate whether such surveys could be used in monitoring red deer populations, and subsequently led to a recommendation about which plant species could be targeted as suitable indicator species for overall browsing pressure to be monitored. We predict that spatial variation in local density (or habitat use) causes browsing frequency to differ among plants of low, intermediate and high nutritive value. Specifically, we expect lower spatial variation in browsing frequency in highly selected species compared to less selected species. Therefore, we expect intermediately selected plants to indicate changes in browsing pressure and red deer density better than highly selected forage species. An additional criterion to be useful for monitoring is abundance and a wide distribution range, and preferably clear variation between local management units if they differ in population density.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Additionally, since red deer show an extensive use of agricultural pastures (Godvik et al. 2009), we predicted higher browsing frequencies closer to pastures. We also predict browsing levels to vary with habitat type (e.g. forest type, altitude, slope and canopy cover) due to either higher access to other food plants, variation in plant quality, or because cover also plays a role for habitat selection.

Methods

Study area

Our data derive from two municipalities, Gloppen and Flora, in the county of Sogn and Fjordane on the southwestern coast of Norway (Fig. 1). Flora is a coastal municipality, whereas Gloppen is more of an inland municipality east of Flora. The topography is characterised by steep slopes, divided by narrow valleys and fiords, and it generally gets steeper inland towards the main mountain range. The forest is dominated by either Scots pine *Pinus sylvestris*, alder *Alnus incana* or birch, while planted Norway spruce *Picea abies* dominate locally. Common undergrowth species are juniper *Juniperus communis*, bilberry *Vaccinium myrtillus*, heather *Calluna vulgaris* and grasses and herbs. Agriculture is widespread in the flatter lowlands, and the arable land is mainly cultivated to pastures and meadows for grass production. The mean temperature varies between 1.6°C in February and 13.4°C in August on the mainland parts of Flora, and from -0.5°C in February to 14.2°C in July in Gloppen. The mean annual precipitation in Flora varies from 1,985 mm at the Florø station to 3,520 mm at the Grøndalen station, and in Gloppen from 1,260 mm at the

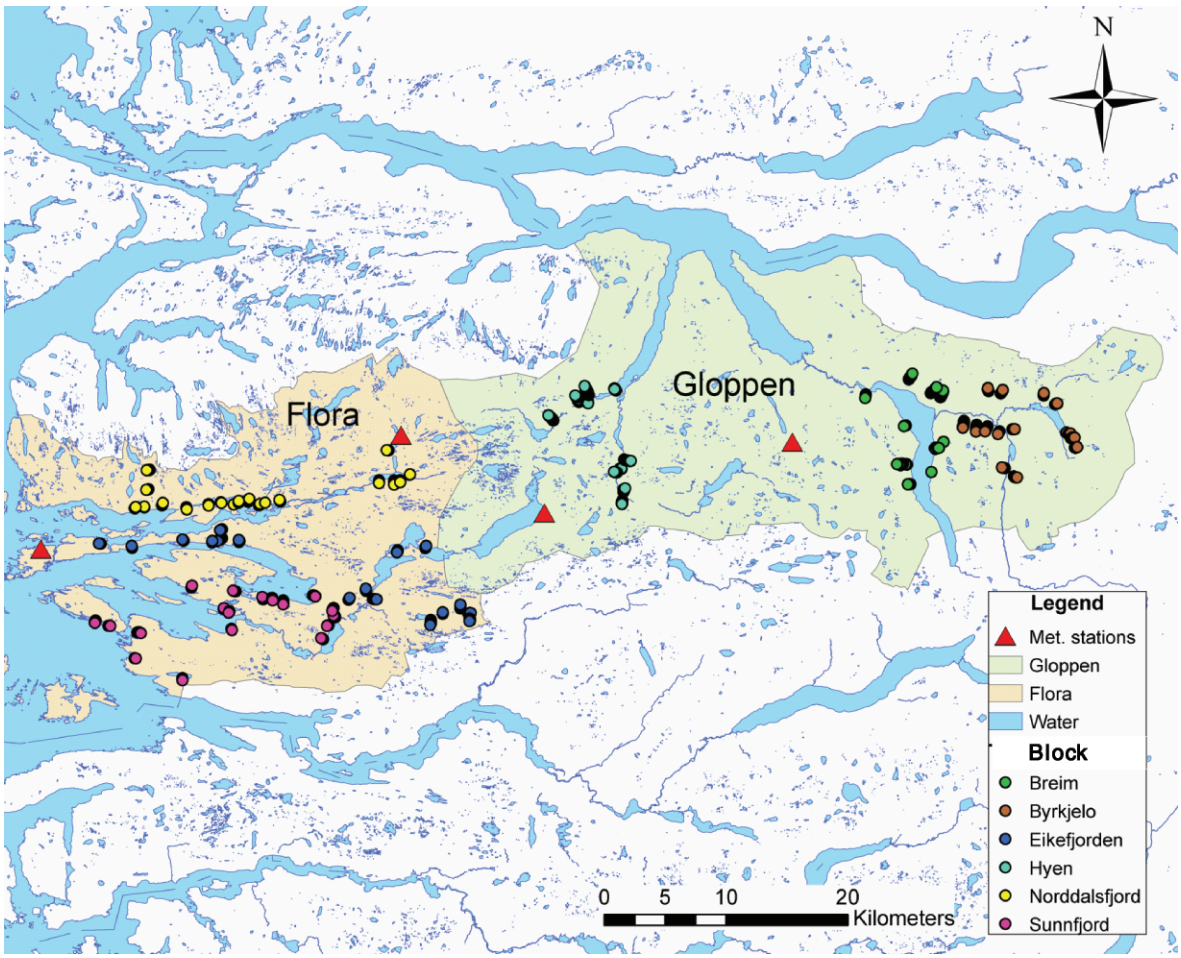


Figure 1. Location of meteorological stations, blocks and transects conducted in the municipalities of Gloppen and Flora in the county of Sogn and Fjordane, Norway. Each transect is marked by a dot, and dots in the same colour refer to a specific block.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Sandane station to 2,760 mm at the Eimhjellen station (see Fig. 1). In these areas, there are virtually no moose *Alces alces* or roe deer *Capreolus capreolus*, but during summer, some areas are grazed by sheep *Ovis aries* or cattle *Bos taurus*.

Sampling design

Our field work was carried out during 10-30 April 2006 in Gloppen and 13 April - 3 May 2007 in Flora, in the county of Sogn and Fjordane, Norway. We used a block-wise randomised sampling design with three blocks in each of the two municipalities (see Fig. 1). The block was a region within the municipality chosen partly by knowledge of main habitat types important for red deer distribution and partly to form a unit possible to cover within a day of sampling. The transect location was chosen as follows. First, a random block (among the three for a given municipality) was chosen; then a random 1-km^2 square within the block, and finally transects were randomly placed from valley bottoms to higher altitude perpendicular to the steepest elevation. Because of practical reasons (roads are generally situated along fiords or valley bottoms), we drew a random starting point for transects from along the roads. Along transects, plots were randomly distributed every 20-50 m (mean: 35 m) until either 500 m a.s.l., a hill top was reached, or until it was too dangerous to continue due to steep terrain. The length of transects thus differed depending on local topography.

We surveyed a total of 532 plots (all positioned by the aid of GPS) from 83 transects. Every plot was a circle with a radius of 3.99 m (50 m^2). The numbers of browsed and unbrowsed shoots were counted within 2 m from ground level. The definition of shoot was somewhat arbitrary, about what a deer could clip in one bite, i.e. very small subdivisions of shoots were not counted. This was done for all specimens inside the plot area for rowan *Sorbus aucuparia*, pine, juniper, spruce, aspen *Populus tremula*, sallow *Salix caprea* and other *Salix* sp., whereas for the tree species birch, alder, bird cherry *Prunus padus*, hazel *Corylus avellana*, oak *Quercus robur* and holly *Ilex aquifolium*, only a single tree nearest to the middle of the plot was examined partly due to high abundance locally. Due to occasional very high abundance of dwarf shrubs (bilberry, heather, bog bilberry *Vaccinium uliginosum* and cowberry *Vaccinium vitis-idaea*) within a plot, measurements were carried out within a 50×50 cm frame placed over the closest dwarf shrub to the centre of the plot. In addition to counting browsed and available shoots, the following habitat variables potentially important to red deer were recorded in the field:

- Canopy cover (in %) using a spherical densiometer (Lemmon 1956);
- Aspect (four classes: North, East, South and West);
- Slope (in °) using a compass with a clinometer;
- Altitude (in m);
- Number of red deer pellet groups/plot (from current winter; older pellets were clearly degraded).

We used a GIS-based map provided by the Norwegian Forest and Landscape Institute for habitat variables (e.g. Godvik et al. 2009) to assign information on the following habitat variables at every plot:

- Forest type (three classes: pine forest, deciduous forest and mixed forest). To be classified as forest, there should be at least six trees above 5 m per 1,000 m^2. Pine forest has at least 50% of the area covered with pine trees, mixed forest 20-50% coniferous trees, and deciduous forest has $< 20\%$ coniferous trees;
- Habitat productivity (three classes based on soil properties: very high, high and normal to low);
- Distance to the coast (in m);
- Distance to arable land (in m).

In Norway, hunting quotas are allocated to local management units ('vald') consisting of smaller or larger congregations of landowners. Administrative borders were provided by the municipality for 23 local management units together with harvest statistics. We used the number of red deer harvested per km^2 of deer habitat in 2006 as an index of local population density (*cf.* Mysterud et al. 2001, Mysterud et al. 2007). The red deer habitat (termed qualifying area) is defined in management as all forested areas and bogs below the forest line. All sampling plots were located within the area covered by these units.

Statistical analyses

When ranking overall selection, we calculated availability of each plant species as frequency of occurrence (i.e. the number of plots where the species occurred divided by the total number of plots). The further detailed analysis was based on browsed shoots out of total number of shoots in a

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

plot per species. Since we calculated browsing as a frequency, logistic regression seems like the first choice of model type. However, due to the assumed strong dependency between shoots (i.e. if one shoot is eaten, it is more likely that another is also eaten from the same plant), instead, we used linear models with browsing frequency as the response variable. We (arcsin-sqrt) transformed browsing frequency to obtain normality and to obtain residuals with constant variance, which was checked by plotting the residuals. There was no strong correlation between total number of shoots available and browsing frequency (birch: $r = -0.087$, bilberry: $r = 0.075$ and rowan: $r = 0.153$), suggesting that functional responses do not need to be incorporated in the analyses. We weighted each observation (proportion of browsed shoots) with number of shoots available, i.e. so that an estimate of proportion of browsed shoots based on one out of 10 available shoots is given less weight than one based on 100 available shoots.

We first ran a simple model with only species as a factor. Based on this model, we targeted rowan, bilberry and birch as candidates for detailed analyses because: 1) they differ in mean browsing frequency (high for rowan, intermediate for bilberry and birch), and 2) they are abundant and widespread throughout the study area. We analysed browsing frequency for the three focal species with three independent sets of covariates. We tested whether there was spatial variation in browsing frequency related to:

1) Administrative units (municipality, block, local management unit). We treated 'block' as a management unit, though this was only part of our sampling design and designated several local management units. Note that municipality also contains a potential year effect, since sampling was done in separate years in each municipality (see above).
2) Direct measures of red deer habitat use were number of pellet groups or density at the local management unit ('vald') scale. The number of faecal pellet groups within each plot will reflect the amount of time deer spent at the exact location shortly before browsing was estimated. The number of deer shot per local management unit is, on the other hand, a proxy for density on a larger scale during the autumn hunting season (which we assume correlates with winter density). We were particularly interested in the residual effect of density at local management unit scale after accounting for the number of pellets. We ln-transformed number of pellet groups before analysis and added 1 to each value to avoid ln-transforming 0.
3) Biological factors describing habitat (forest type, habitat productivity, canopy cover, aspect, slope, altitude, distance from arable land and distance from the coast). Distances from arable land and from the coast were ln-transformed, and we added 1 to each value to avoid ln-transforming 0.

The best model was found through selection based on the AIC criterion (Burnham & Anderson 2002), and we used manual selection with both backward (starting with full model and removing terms) and forward (adding terms to the null model) approaches to assess the robustness. All statistical analyses were performed using R (R Development Core Team 2008).

Results

Browsing frequency and availability at the plant species level

The model with only plant species as the explanatory variable explained 37% of the variation in browsing frequency (Fig. 2). As expected, the highly palatable aspen, rowan, sallow and other willow *Salix* sp. were among the most selected species. Common plant species such as bilberry and birch were found to be intermediately selected. Bilberry is by far the most available species and was present in 77.8% of the plots. Rowan availability was 21.4%, while the availability of birch was 40.0%.

Spatial variation and administrative factors

Explanatory variables in the best models differed among the three focal species. For explaining variation in bilberry browsing with the administrative factors, the local-scale management unit ('vald'; AIC = 344.164) performed better than block (AIC = 383.720) and the coarse municipality scale (AIC = 386.608). Spatial variation was slightly more coarse-scaled for birch (i.e. municipality: AIC = 161.599; block: AIC = 158.460; local management unit: AIC = 163.289) and rowan (i.e. municipality: AIC = 235.976; block: AIC = 212.436; local management unit: AIC = 213.215). For both these species, 'block' was included in the best model, although only

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

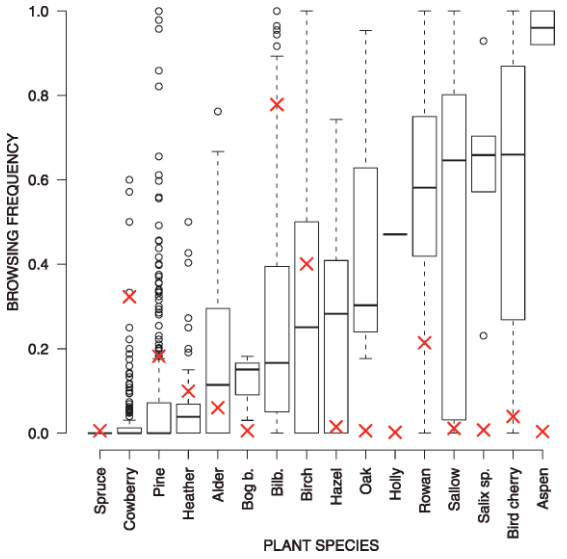


Figure 2. Overall red deer browsing frequency of the plant species encountered at the southwestern coast of Norway. Boxplots; the thick solid line is median; box upper and lower limits are first and third quartile; open circles are outliers. Red crosses indicate overall availability, and the abbreviations Bog b. = Bog bilberry and Bilb = bilberry.

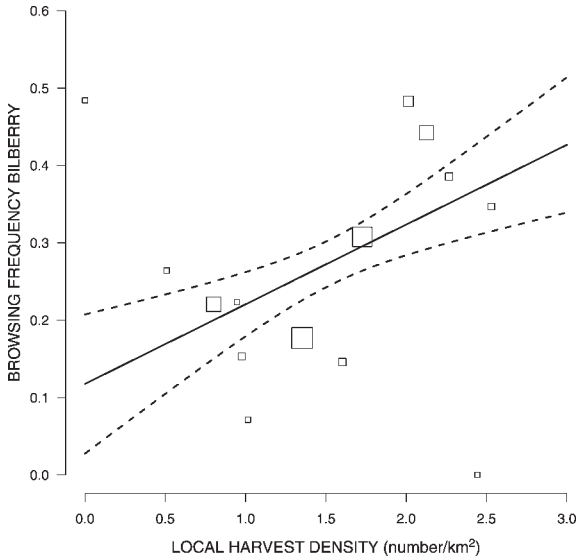


Figure 3. Relationship between red deer browsing frequency (browsed shoots/available shoots) on bilberry and local (harvest) density on the southwestern coast of Norway.

marginally better than local management unit for rowan. Best models explained 21.1, 28.8 and 11.1% of the variation in browsing frequency of bilberry, birch and rowan, respectively.

Spatial variation, red deer area use and density

We then related browsing frequency to red deer area use (pellet counts) and population density (harvest numbers). The best model for birch (pellet group: AIC = 209.455; local density: AIC = 211.923; both: AIC = 211.291) and rowan (pellet group: AIC = 232.915; local density: AIC = 233.665; both: AIC = 233.061) included only number of pellet groups. This implies that the browsing pressure was partly explained by the presence of deer on the exact location during the winter of the measurements. The best model for bilberry included both number of pellet groups and local density (pellet group: AIC = 372.890; local density: AIC = 380.502; both: AIC = 362.136; Table 1 and Fig. 3). Best models explained 10.4, 13.6 and 14.3% in bilberry, birch and rowan, respectively.

Spatial variation and habitat variables

The best model including habitat variables explained 22.8% of the variation in browsing frequency of rowan, 13.7% of bilberry and 18.8% of birch. The best model of browsing frequency on rowan was a more complicated model than for bilberry and in particular for birch (Table 2). Habitat productivity was included in the models

Table 1. Best models using direct indices of local (harvest) density and use assessed from faecal pellet counts to explain browsing frequency of red deer in Norway on rowan, bilberry and birch.

Parameters	Estimate	SE	t	P
Rowan				
Intercept	0.9053	0.0209	43.339	< 0.001
Ln (Number of Pellet groups +1)	0.0789	0.0397	1.989	0.048
Bilberry				
Intercept	0.2746	0.0482	5.693	< 0.001
Local deer harvest density	0.1347	0.0296	4.558	< 0.001
Ln (Number of pellet groups +1)	0.1122	0.0313	3.588	< 0.001
Birch				
Intercept	0.4651	0.0331	14.070	< 0.001
Ln (Number of pellet groups +1)	0.0711	0.0453	1.570	0.118

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 2. Best models using habitat variables to explain browsing frequency of red deer in Norway on rowan, bilberry and birch. Estimates for factors are given as contrasts relative to a baseline level (as indicated).

Parameters	Estimate	SE	t	P
Rowan				
Intercept	0.5729	0.1307	4.384	< 0.001
Forest type (Pine vs mixed)	0.0659	0.0688	0.958	0.339
Forest type (Deciduous vs mixed)	0.1143	0.0503	2.270	0.024
Habitat productivity (high vs normal/low)	-0.1138	0.0476	-2.391	0.018
Habitat productivity (very high vs normal/low)	0.0182	0.0642	0.283	0.777
Canopy cover	0.0020	0.0011	1.869	0.063
Aspect (North vs east)	-0.0285	0.0480	-0.593	0.554
Aspect (South vs east)	-0.0293	0.0622	-0.470	0.639
Aspect (West vs east)	-0.2907	0.0733	-3.966	< 0.001
Slope	-0.0042	0.0017	-2.440	0.015
Ln (Distance to arable land +1)	0.0688	0.0201	3.417	0.001
Bilberry				
Intercept	0.8217	0.1091	7.530	< 0.001
Forest type (Pine vs mixed)	-0.2304	0.0485	-4.752	< 0.001
Forest type (Deciduous vs mixed)	-0.0577	0.0453	-1.274	0.204
Habitat productivity (high vs normal/low)	-0.1230	0.0408	-3.011	0.003
Habitat productivity (very high vs normal/low)	-0.0649	0.0594	-1.091	0.276
Altitude	0.0004	0.0002	1.979	0.049
Distance from coast	-0.0324	0.0161	-2.009	0.045
Birch				
Intercept	0.6572	0.0577	11.391	< 0.001
Habitat productivity (high vs normal/low)	0.1970	0.0577	3.417	0.001
Habitat productivity (very high vs normal/low)	0.1398	0.0666	2.100	0.037
Altitude	-0.0011	0.0002	-5.262	< 0.001

of all species. Browsing levels for both bilberry and rowan were lowest in the intermediate productivity class, and equal to or higher at both high and normal/low productivity habitats. Forest type was also included for bilberry and rowan, but the direction of estimates was not consistent among the species. Our hypothesis of higher browsing frequency closer to agricultural pastures was not supported. This parameter was only included in the rowan model, and browsing decreased rather than increased close to pastures. This result was dependent on inclusion of a few strong outliers; there was no marked pattern related to distance from agricultural pastures when excluding these. For birch, a contrasting pattern emerged with only habitat productivity and altitude included (see Table 2). Our observations during the field work suggested a marked difference between browsing frequency on ordinary shoots and root shoots (likely of much higher quality), which we were unable to control for in later analysis. For all three species, adding the term from the best model of management unit (to the best model with habitat covariates) resulted in largely improved models ($\Delta AIC > 2$), suggesting that variation among blocks for rowan and birch and local management units for bilberry was not due to habitat variables alone. The prediction that the high quality forage rowan should show less spatial variation was therefore not supported.

Discussion

Our main aims were to quantify the browsing pressure on common shrubs and trees, identify potential indicator species suitable for monitoring, and evaluate whether such surveys would be useful for the local deer management. Monitoring of forage availability and browsing frequency may be a useful addition to monitoring body mass or population density, since both represent a measure of the resource abundance and the impact from the present deer population. To be useful for monitoring, it is important that plant species are fairly widely available. In particular bilberry, but also rowan and birch filled this criterion in our study areas (see Fig.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

2). Also, it may be useful to include species of differing quality, or at least to include species of intermediate preference, so that a variable browsing frequency depending on population density relative to resource levels are expected. Highly preferred species are often less abundant (Månsson et al. 2007b, Månsson 2009), and are not predicted to show large variation in browsing frequency. Browsing frequency of intermediately preferred species is on the other hand expected to vary depending on population density relative to resource levels. Due to its wide distribution, and the relationship between spatial variation in browsing frequency and red deer density, bilberry stands out as the most promising species to monitor. Bilberry is also frequently eaten by other large herbivores such as roe deer and moose (Cederlund et al. 1980) and to some extent by domestic sheep (Kausrud et al. 2006). It is therefore potentially more widely applicable. However, our study represents a short-term study of spatial variation in browsing frequency. The level of browsing on bilberry is known to depend on snow depth (Mysterud & Østbye 1995, Månsson 2009). Snow depths were shallow in the coastal study areas that we considered, and might not be equally useful in all areas or during winters with more snow cover.

Monitoring vegetation or animals - a question of time lags and main diet

Monitoring programmes often depend on a small number of indicators and may fail to consider the full complexity of the ecological system (Dale & Beyeler 2001). However, what will be gained by an addition of monitoring bilberry browsing? The optimal monitoring method depends on estimation accuracy, management objectives and financial constraints (Yoccoz et al. 2001, Rönnegård et al. 2008). The current monitoring programme of cervids in Norway focuses on direct measures of abundance ('seen deer') and on individual performance (body mass and reproduction). The advantage of using the state of the vegetation community, rather than the animal performance in monitoring, is that it does not contain the lags present between the heavy browsing and density-dependent responses on ungulate condition. We may need either browsing surveys as an additional tool, or we need a link between the indices already used in monitoring and the state of the vegetation community. For example in moose management, surveys of browsing frequency on pine is commonly conducted in Sweden (the Äbin method; available at: http://www.svo.se/minskog/templates/svo_se_vanlig.asp?id=7619), and it is increasingly used also in Norway (Solbraa 2004). For typical browsers like moose which rely on trees as their main diet, time lags are typically expected to be stronger than for herbivores relying on more short-lived and tolerant grasses. The red deer is classified as a mixed feeder, and rely much more on graze than browse (Hofmann 1989, Gebert & Verheyden-Tixier 2001). Particularly during snow free periods in winters (fairly common along the west coast of Norway) and in spring (when the green-up on arable land precedes the green-up on outlying fields and forested areas), red deer are more likely to feed on agricultural pastures and in other areas with grass than in forested areas. Bilberry is likely not a dominant food plant in their diet. It is therefore unclear whether red deer browsing on bilberry reflects overall condition of the vegetation community. Clearly, to quantify grazing frequency in vegetation, surveys are indeed more difficult for grazers and mixed feeders than for browsers, as bite marks are more difficult to observe and last shorter for grasses than for browse (Evju et al. 2006).

Habitat and spatial variation in browsing

Spatial scale may be important in browsing surveys (Edenius et al. 2002, Månsson et al. 2007a, Månsson 2009), and utilisation of various species may differ from region to region at coarse scales (Gebert & Verheyden-Tixier 2001). In addition, we also found evidence of more local variation. Forest type was included in the best models describing variation in browsing frequency for bilberry and rowan. The direction of estimates was on the other hand not consistent among the species. This suggests that spatial differences in habitat characteristics may be related to forage quality, which subsequently affects the browsing frequency. Such relations may be challenging to control for if the aim is to monitor the whole vegetation community with a few indices. It is more likely that monitoring of browsing frequency at the same locations over time is a more feasible option, even though natural succession will cause a gradual change in vegetation characteristics represented at each plot in forest ecosystems. Birch was browsed more frequently than expected (Ahlén 1965). This was likely due to the heavy browsing on root shoots, whereas ordinary shoots were less frequently browsed. Spatial differences in the occurrence of root shoots may explain the contrasting patterns found for this species. Observations suggest that agricultural areas may be very impor-

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

tant for red deer in winter, spring and autumn (Godvik et al. 2009), and may serve as attractive areas with increased browsing levels in nearby natural habitat types. However, contrary to our predictions, browsing frequency in areas near farmland was not higher. This may suggest that deer do not shelter in the closest edge vegetation (which would presumably lead to intensified browsing), but move further away from pastures in periods when they are not used.

Browsing pressure and plant community structure

Selective feeding by ungulates can both increase and decrease the abundance of palatable plant species, depending on location, grazing frequency, ecological history and environmental relations (see review in Augustine & McNaughton 1998). Highly selected species are the first to respond to effects of grazing unless they are highly tolerant (Mysterud 2006). It remains to be determined whether the reported browsing frequency in Sogn and Fjordane, Norway, has had a measurable effect on the plant community, since little is known about the resilience of our ecosystems regarding to high browsing pressure (see Tanentzap et al. 2009 for a recent account in New Zealand). A North American review of grass dominated ecosystems concluded, that on average heavy grazing (when preferred species do not maintain themselves) was 57% utilisation of primary forage plants, moderate grazing (preferred species can maintain themselves, but do not improve production) was 43%, and light grazing was 32% utilisation (preferred species maximise their herbage producing ability; Holechek et al. 1999). Motivated by the financial returns following favourable practices, knowledge regarding grazing tolerance and stocking rate on rangeland as well as on cultivated grazing land has been widely studied. Equivalent knowledge regarding browsing tolerance and species-specific consequences of various browsing levels has to a much lesser extent been investigated for relevant species of browse. The rowan and several less abundant species experience a heavy browsing pressure in our study areas, but there is currently no information regarding the consequences on species abundance and production. Browsing by red deer has a strong, negative influence on bilberry size, abundance and fruit set (Hegland et al. 2006), and controlled experiments have shown that bilberry may need more than five years to totally recover from severe clipping (Tolvanen et al. 1994). Though negative consequences related to severe browsing can be documented for specific species, our study clearly highlights the challenges related to the use of browsing-related monitoring indices in a heterogeneous landscape. Just as annual variation in snow cover will influence both the availability of food resources and the spatial distribution of animals, choice of monitoring species, and plot location may equally influence the findings.

Conclusion

With the current rapid increase in red deer numbers, better knowledge regarding deer impact on biodiversity and ecosystem function is clearly needed. Managers should look beyond 'seen deer' schemes and consider a broader ecosystem perspective when setting harvest quotas. The documented high browsing levels on several winter forage plants in our study indicates that previously reported declines in body mass is at least partly an indication of negative feedback from the resource base. We recommend therefore taking reported declines in body mass more seriously and consider reducing population density. Reducing density would involve applying a precautionary principle in management, as we have not come to the point where we can more precisely determine how much a given red deer density affects plant community changes and ecosystem function.

Acknowledgements - we are grateful to Ragnar Aaserud for field assistance, to Harald Kjær, Gloppen, and Magnus Frøyen, Flora, for help with obtaining maps over local management units and local hunting statistics, and to Glenn Iason, Johan Månsson and one anonymous referee for very helpful comments to a previous draft. Our study was funded by the Research Council of Norway ('Natur og næring'-program; project no. 179370/I10).

References

Ahlén, I. 1965: Studies on the red deer, *Cervus elaphus* L., in Scandinavia. - Swedish Wildlife Research 3: 177-376.

Augustine, D.J. & McNaughton, S.J. 1998: Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. - Journal of Wildlife Management 62: 1165-1183.

Bischof, R., Mysterud, A. & Swenson, J.E. 2008: Should hunting mortality mimic the patterns of natural mortality? - Biology Letters 4: 307-310.

Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference. A practical information-

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

theoretic approach. - Springer, New York, New York, USA, 488 pp.
Cederlund, G., Ljungqvist, H., Markgren, G. & Stålfelt, F. 1980: Foods of moose and roe deer at Grimsö in central Sweden - results of rumen content analysis. - Swedish Wildlife Research 11: 167-247.
Choquenot, D. 1991: Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. - Ecology 72: 805-813.
Côté, S.D., Rooney, T.P., Trembley, J.-P., Dussault, C. & Waller, D.M. 2004: Ecological impacts of deer overabundance. - Annual Review of Ecology and Systematics 35: 113-147.
Dale, V.H. & Beyeler, S.C. 2001: Challenges in the development and use of ecological indicators. - Ecological Indicators 1: 3-10.
deCalesta, D.S. 1997: Deer and ecosystem management. - In: McShea, W.J., Underwood, H.B. & Rappole, J.H. (Eds.); The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington D.C., USA, pp. 267-279.
deCalesta, D.S. & Stout, S.L. 1997: Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. - Wildlife Society Bulletin 25: 252-258.
Eberhardt, L.L. 2002: A paradigm for population analysis of long-lived vertebrates. - Ecology 83: 2841-2854.
Edenius, L., Ericsson, G. & Näslund, P. 2002: Selectivity by moose vs the spatial distribution of aspen: a natural experiment. - Ecography 25: 289-294.
Ericsson, G. & Wallin, K. 1999: Hunter observations as an index of moose *Alces alces* population parameters. - Wildlife Biology 5(3): 177-185.
Evju, M., Mysterud, A., Austrheim, G. & Økland, R.H. 2006: Selecting herb species and traits as indicators of sheep grazing pressure in a Norwegian alpine habitat. - Ecoscience 13: 459-468.
Gaillard, J-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. 2000: Temporal variation in fitness components and population dynamics of large herbivores. - Annual Review of Ecology and Systematics 31: 367-393.
Gebert, C. & Verheyden-Tixier, H. 2001: Variations in diet composition of red deer (*Cervus elaphus* L.) in Europe. - Mammal Review 31: 189-201.
Gill, R. 1990: Monitoring the status of European and North American cervids. - The Global Environment Monitoring System Information Series No. 8, United Nations Environment Programme, Nairobi, Kenya, 277 pp.
Godvik, I.M.R., Loe, L.E., Vik, J.O., Veiberg, V., Langvatn, R. & Mysterud, A. 2009: Temporal scales, trade-offs and functional responses in habitat selection of red deer. - Ecology 90: 699-710.
Gordon, I.J., Hester, A.J. & Festa-Bianchet, M. 2004: The management of wild large herbivores to meet economic, conservation and environmental objectives. - Journal of Applied Ecology 41: 1021-1031.
Hegland, S.J., Rydgren, K. & Seldal, T. 2006: The response of *Vaccinium myrtillus* to variations in grazing intensity in a Scandinavian pine forest on the island of Svanøy. - Canadian Journal of Botany 83: 1638-1644.
Hofmann, R.R. 1989: Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. - Oecologia 78: 443-457.
Holechek, J.L., Gomez, H., Molinar, F. & Galt, D. 1999: Grazing studies: What we've learned. - Rangelands 21: 12-16.
Hörnberg, S. 2001: The relationship between moose (*Alces alces*) browsing utilisation and the occurrence of different forage species in Sweden. - Forest Ecology and Management 149: 91-102.
Kausrud, K., Mysterud, A., Rekdal, Y., Holand, Ø & Austrheim, G. 2006: Density-dependent foraging behaviour of sheep on alpine pastures: effects of scale. - Journal of Zoology (London) 270: 63-71.
Langvatn, R., Mysterud, A., Stenseth, N.C. & Yoccoz, N.G. 2004: Timing and synchrony of ovulation in red deer constrained by short northern summers. - American Naturalist 163: 763-772.
Lemmon, P.E. 1956: A spherical densiometer for estimating forest overstory density. - Forest Science 2: 314-320.
Månsson, J. 2009: Environmental variation and moose *Alces alces* density as determinants of spatio-temporal heterogeneity in browsing. - Ecography 32: 601-612.
Månsson, J., Andrén, H., Pehrson, Å & Bergström, R. 2007a: Moose browsing and forage availability: a scale-dependent relationship? - Canadian Journal of Zoology 85: 372-380.
Månsson, J., Kalén, C., Kjellander, P., Andrén, H. & Smith, H. 2007b: Quantitative estimates of tree species selectivity by moose (*Alces alces*) in a forest landscape. - Scandinavian Journal of Forest Research 22: 407-414.
McShea, W.J. & Underwood, H.B. 1997: The science of overabundance. Deer ecology and population management. - Smithsonian Institution Press, Washington, D.C., USA, 402 pp.
Morellet, N., Gaillard, J-M., Hewison, A.J.M., Ballon, P., Boscardin, T., Duncan, P., Klein, F. & Maillard, D. 2007: Indicators of ecological change: new tools for managing populations of large herbivores. - Journal of Applied Ecology 44: 634-643.
Mysterud, A. 2006: The concept of overgrazing and its role in management of large herbivores. - Wildlife Biology 12(2): 129-141.
Mysterud, A., Meisingset, E.L., Veiberg, V., Langvatn, R., Solberg, E.J., Loe, L.E. & Stenseth, N.C. 2007: Monitoring population size of red deer *Cervus elaphus*: an evaluation of two types of census data from Norway. - Wildlife Biology 13(3): 285-298.
Mysterud, A. & Østbye, E. 1995: Roe deer *Capreolus capreolus* feeding on yew *Taxus baccata* in relation to bilberry *Vaccinium myrtillus* density and snow depth. - Wildlife Biology 1(4): 249-253.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Mysterud, A., Yoccoz, N.G. & Langvatn, R. 2009: Maturation trends in red deer females over 39 years in heavily harvested populations. - Journal of Animal Ecology 78: 595-599.

Mysterud, A., Yoccoz, N.G., Stenseth, N.C. & Langvatn, R. 2001: The effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. - Proceedings of the Royal Society of London, Series B 268: 911-919.

Noy-Meir, I. 1975: Stability of grazing systems: an application of predator-prey graphs. - Journal of Ecology 63: 459-481.

Palmer, S.C.F., Hester, A.J., Elston, D.A., Gordon, I.J. & Hartley, S.E. 2003: The perils of having tasty neighbors: grazing impacts of large herbivores at vegetation boundaries. - Ecology 84: 2877-2890.

Persson, I-L., Danell, K. & Bergström, R. 2005: Different moose densities and accompanied changes in tree morphology and browse production. - Ecological Applications 15: 1296-1305.

R Development Core Team. 2008: R: A language and environment for statistical computing. - R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www-r-project.org/ (Last accessed on 24.03.2010).

Rönnegård, L., Sand, H., Andrén, H., Månsson, J. & Pehrson, Å 2008: Evaluation of four methods used to estimate population density of moose *Alces alces*. - Wildlife Biology 14(3): 358-371.

Scarnecchia, D.L. & Kohtmann, M.M. 1982: A dynamic approach to grazing management terminology. - Journal of Range Management 35: 262-264.

Solbraa, K. 2004: Veiledning i elgbeitetaksering. - Skogbrukets Kursinstitutt; Honne, Biri, 28 pp. (In Norwegian).

Statistics Norway. 2009: Official hunting statistics of Norway. - Statistics Norway, Oslo and Kongsvinger, Norway. Available at: http://www.ssb.no/jakt_fiske_en/ (Last accessed on 24.03.2010).

Tanentzap, A.J., Burrows, L.E., Lee, W.G., Nugent, G., Maxwell, J.M. & Coomes, D.A. 2009: Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. - Journal of Applied Ecology 46: 1064-1072.

Tolvanen, A., Laine, K., Pakonen, T., Saari, E. & Havas, P. 1994: Responses to harvesting intensity in a clonal dwarf shrub, the bilberry (*Vaccinium myrtillus* L.). - Vegetatio 110: 163-169.

Van Horne, B. 1983: Density as a misleading indicator of habitat quality. - Journal of Wildlife Management 47: 893-901.

Yoccoz, N.G., Nichols, J.D. & Boulinier, T. 2001: Monitoring of biological diversity in space and time. - Trends in Ecology and Evolution 16: 446-453.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use