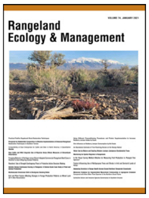
Rangeland Ecology & Management 93 (2024) 15–23

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: www.elsevier.com/locate/rama



Original Research

A Grazer in a Browser's Habitat: Resource Selection of Foraging Cattle in Productive Boreal Forest[☆]

Mélanie Spedener[1,*], Morten Tofastrud[2], Gunnar Austrheim[3], Barbara Zimmermann[1]

[1] *Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Department of Forestry and Wildlife Management, Inland Norway University of Applied Sciences, Koppang, Norway*
[2] *Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Department of Agricultural Sciences, Inland Norway University of Applied Sciences, Hamar, Norway*
[3] *Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, Trondheim NO-7491 Norway*

ARTICLE INFO

Article history:
Received 14 June 2023
Revised 18 September 2023
Accepted 19 December 2023

Key Words:
Beef cattle
Feeding ecology
Picea abies
Resource selection
Silvopastoralism

ABSTRACT

In Norway, cattle *(Bos taurus)* are released to large areas of boreal forest for summer grazing. To determine to what degree this practice challenges timber production and wildlife management, we need a better understanding of basic cattle ecology. What do cattle, typical grazers, feed on in a habitat typically used by browsers? We determined cattle's resource use and selection at three scales: habitat and microhabitat selection when foraging and diet selection. Boreal forest is dominated by grass-poor habitats, and despite their strong selection for grass-rich habitats, cows spent a lot of time in suboptimal habitats, like old bilberry *(Vaccinium myrtillus)* spruce *(Picea abies)* forest. However, they managed to find grass-rich habitat patches within those, selecting for patches with bentgrass (*Agrostis* spp.). Graminoids, mainly wavy hair-grass (*Avenella* spp.), tussock grass (*Deschampsia*), and true sedges (*Carex* spp.), made up the biggest part of the fecal samples. Woody plants, mainly willow (*Salix* spp.), *Vaccinium* spp., pine (*Pinus* spp.), and birch (*Betula* spp.), made up 9.4% ± 4.7% of the samples, a value lower than reported for other forest grazing cattle. Cattle avoided woody plants in their diet and selected for graminoids. They preferred deciduous over coniferous species. At these low stocking densities, the cows were grazers in this browser's habitat. Moreover, they selected rather on habitat and patch scale than for individual plants within a given habitat patch, considered typical for a grazer. Their grass-rich diet indicates little overlap with the diet of local wild ungulates, which are mostly browsers. Their aversion of spruce and selection for graminoids and deciduous trees indicates low conflict risk for browsing damages and even a beneficial weeding effect on trees planted for timber production.

Introduction

In Norway, cattle roam free in productive forest, where the main objective of the landowner is timber production from coniferous tree species. To mitigate potential conflicts between stakeholder interests, clarification is needed on the extent to which these cattle damage trees. Moreover, knowledge on the cattle's diet selection will increase our understanding of interactions between livestock and wild ungulates, which is needed to optimize wildlife management in areas with free-ranging cattle.

Ungulates are often characterized by their diet and placed along a gradient from strictly grazing to strictly browsing. Grazing is typically referred to as foraging on herbaceous monocots (hereafter referred to as graminoids), including true grasses (Poaceae), sedges (Cyperaceae) and rushes (Juncaceae), and browsing as foraging on woody and nonwoody dicotyledonous plants (Janis 2008), i.e., herbs, forbs, and leaves and twigs of woody plants (Clauss et al. 2008) (hereafter referred to as browse). The difference between graminoids and browse are seen in cell structure, plant chemistry, plant architecture, and plant dispersion (Shipley 1999), and browsers and grazers show morphological, physiological, and behavioral adaptations to efficiently extract the nutrients from the diet consumed (Shipley 1999; Gordon 2003; Clauss et al. 2008).

In the boreal forest in Norway, three wild cervid species can be found: moose *(Alces alces)* and roe deer *(Capreolus capreolus)*, both browsers, and red deer *(Cervus elaphus)*, an intermediate feeder between a browser and a grazer (Austrheim et al. 2011). Addition-

---

[☆] The study was funded by the Norwegian Agricultural Agency (NO) (15/18102-3) and the County governor of Hedmark (NO) (2015/3581, 2021/2595).

[*] Correspondence: Mélanie Spedener, Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Dept of Forestry and Wildlife Management, Inland Norway University of Applied Sciences, Koppang, Norway. +47 62 43 07 72

E-mail address: melanie.spedener@inn.no (M. Spedener).

https://doi.org/10.1016/j.rama.2023.12.004

ally, sheep *(Ovis aries)* and cattle *(Bos taurus)*, both typical grazers, utilize these forests during summer. Due to the population growth of large carnivores during the past decades (Chapron et al. 2014), fewer sheep are released for forest grazing (Aune-Lundberg and Munsterhjelm 2021), while the number of cattle has slightly increased (Statistics Norway 2023). On the one hand, cattle have been suggested as a more predator-resistant alternative to sheep (Zimmermann et al. 2003). On the other hand, to reduce beef import, cattle husbandry has moved from small-bodied dairy cattle that were kept partly on summer farms and the close surroundings in forests, to heavy beef cattle that are released into large areas of productive forest (Tofastrud et al. 2020).

The utilization of forests as summer rangeland is a long-standing tradition in Norway but has changed during the past century. Between 1949 and 1999, cattle densities decreased, while cervid densities increased dramatically (Austrheim et al. 2011; Speed et al. 2019). Forestry has changed from selective logging to clear-cutting practices, with higher stem densities and a mosaic of monocultural, even-aged forest stands (Nygaard & Øyen 2020), resulting in forests favorable for browsers due to high concentrations of browse, especially Scots pine *(Pinus sylvestris)*, rowan *(Sorbus aucuparia)*, aspen *(Populus tremula)*, birch (*Betula* spp.), and willow (*Salix* spp.), on young forest stands (Larsson and Rekdal 2000; Wam et al. 2010; Bjørneraas et al. 2011; Kolstad et al. 2018).

Studies on cattle grazing in boreal forest in Norway show that on a larger scale, foraging cattle selected for meadows, meadow spruce forest, bilberry spruce forest, and young forests (Tofastrud et al. 2019). On a smaller scale, foraging cattle selected for grass-rich habitat patches (Spedener et al. 2019). We wanted to add diet composition and selection to this picture, as well as the role of different plant genera. Therefore, we investigated resource use (independent of availability) and resource selection (what they used in relation to the availability) of adult beef cattle at three scales: habitat (vegetation type), microhabitat (plant groups and genera at foraging position), and diet (plant groups and genera in fecal samples).

We expected to find browse in the cattle's diet, but we did not know how much, based on highly varying results from previous studies of cattle in browser habitats, such as in boreal forest in Norway (around 10% in fecal samples) (Wam and Herfindal 2020), Mediterranean forest in Spain (up to 89% in fecal samples) (Bartolomé et al. 2011), heathlands in Spain (up to 15% in fecal samples) (Ferreira et al. 2013), pastures with hedges in Belgium (up to 19.3% of their time) (Vandermeulen 2017), and semi-arid sub-Saharan rangelands in Senegal (up to 84.2% of their foraging time) (Moleele 1998). We expected cattle to select for browse with high digestibility (i.e., we expect them to forage more on herbs than on woody plants, and, as found in Popp and Scheibe [2013], more on deciduous than on coniferous trees). However, we expected cattle, being specialized grazers, to select for grass-rich habitats and a grass-rich diet. These expectations were underpinned by two Norwegian studies. Lunnan and Todnem (2011) described bentgrass (*Agrostis* spp.), wavy hair-grass (*Avenella* spp.), tussock grass (*Deschampsia* spp.), and festuce (*Festuca* spp.) as important forage for grazers in mountainous areas in Norway. More specifically, Wam and Herfindal (2020) reported tussock grass, wavy hair-grass, and true sedges (*Carex* spp.) as main plant genera in fecal samples of cattle in boreal forest.

Material and Methods

Study area and animals

The study area was located in southeastern Norway and consisted of the two geographically distinct communal lands Furnes/Vang (FVA) and Stange/Romedal (SRA) (Fig. 1), and the data were collected from 2015 to 2017. The climate in the study area is continental with cold winters, warm summers, and a short growing season. FVA is about 120 km^2 with the elevation ranging from 600 to 700 (m.a.s.l.). Around 40% of this area is covered by spruce forest, 20% by Scots pine forest, and 40% by wetland (Rekdal 2010). SRA is about 150 km^2 with the elevation ranging from 300 to 450 m.a.s.l. Around 60% of this area is covered by spruce forest, 30% by pine forest, and 10% by wetland (Rekdal 2017). Cattle and sheep grazed in the area from late May to early September and the cattle densities during the grazing season were 0.04 (SRA) and 0.16 (FVA) cows per hectare. The sheep density was on average 0.125 sheep per ha. The cattle were suckler cows of various beef cattle breeds (Charolais, Hereford, Limousin, Simmental, and crossbreeds), accompanied by their calf. Each year, 18 cows were equipped with Global Positioning System (GPS) collars programmed to take positions and activity measures every 5 min throughout the entire grazing season (Tellus GPS medium plus, Followit Sweden AB, Lindesberg, Sweden). The GPS collars included a Global System for Mobile communications (GSM) download option, and positioning and activity data were available in real time through an Internet-based positioning portal called Followit Geo, located at http://geo.followit.se/. On the basis of the combination of accelerometer and GPS data, we identified the cows' behavioral states using the classification tree created by Tofastrud et al. (2018). Based on behavioral observations of 18 collared cows in the field a classification tree was created, that classified the collar data into Foraging, Low (resting behaviors), and High (other active behaviors other than foraging) activity with an accuracy of 79.4%. A detailed account of the methods and results is given in Tofastrud et al. (2018).

Data collection

Vegetation types at foraging cattle positions

For all GPS-recorded foraging positions ($n = 6827$), we extracted the vegetation types from vegetation maps (Fremstad 1997; Rekdal 2010, 2017), using the QGIS software. We removed all observations in "cropland" ($n = 34$), as cattle were not supposed to be on the crop fields. We also removed all observations in "human infrastructures" (roads, cabins, gravel pits) ($n = 175$). We did not want to include foraging on roadside vegetation or cabin gardens in this paper but instead focus on foraging within the forest. In order to restrict the number of small-scaled or less used vegetation types, we merged all deciduous forests and swamps into "deciduous and swamp forests" and bog, fens, and marshes into "unforested wetland."

Plant groups and genera at foraging cattle positions

For the 18 GPS-collared cows, we visited an average of 2 foraging positions per cow, resulting in 36 positions in total. We visited the position 12–24 h after the cow had departed. This was soon enough to find fresh tracks and late enough to avoid disturbance. At these positions ($n = 36$), we sampled the ground cover composition on plots of radius 1.78 m (10 m^2). Beef cows have a length of 2–2.5 m, so we assumed that they impact an area of about 10 m^2 when standing and grazing. We estimated the plot percentage covered by the functional plant groups woody plants, herbs, graminoids, "other vegetation," and "no vegetation." Woody plants included all trees, bushes, and shrubs under 2-m height. Taller plants were considered out of range for cattle. "Other vegetation" consisted of mosses, lichens, ferns, and horsetails. Examples of "no vegetation" are barren ground and stones. Only the vegetation groups were included in the diet selection analysis in this paper. Moreover, we placed five frames of 40 × 40 cm on each plot (one in the center and four at the periphery in each cardinal direction) and recorded presence/absence for all genera of woody

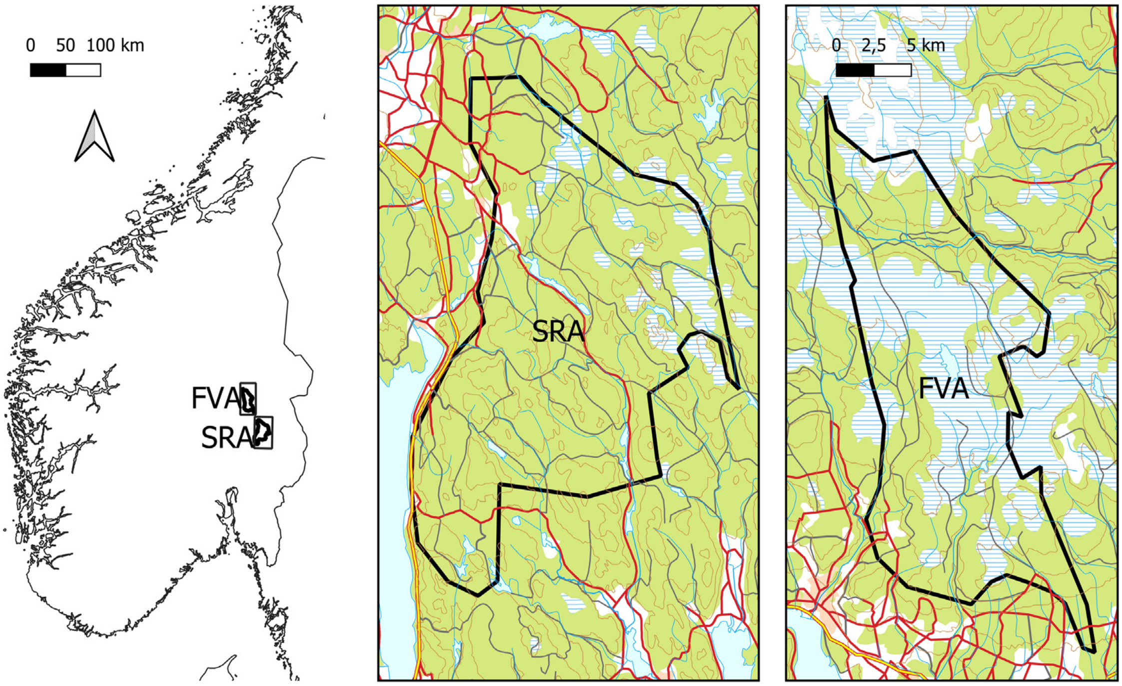


Figure 1. Map of the communal lands Furnes/Vang (FVA) and Stange/Romedal (SRA) in southeastern Norway, consisting mainly of productive boreal forest, where beef cattle range free during summer. In this study we study forage habitat and diet selection of these cattle. where we studied forage habitat and diet selection of free-ranging beef cattle in the productive boreal forest.

plants, herbs, and graminoids. This resulted in a number between zero and five per genus per plot.

Plant groups and genera in fecal samples

In 2016, fecal samples were collected from 38 cows in the study area. Thirty-six samples were collected in FVA, and 38 samples in SRA, resulting in 72 samples. The goal was to get two samples per cow, one in early summer (1 of June–10 of July) and one in late summer (1 August–15 of September). The samples were collected right after the cow had defecated, put in plastic bags, and stored in the freezer at about −18°C. In a next step the samples were prepared for microhistological analyses (see Johnson et al. 1983), which were carried out the same way and by the same person as in (Wam and Hjeljord 2010). Under a microscope, all fragments intersecting a 1 mm wide line along 40 mm long transects were examined. The transects were placed 3 mm apart. A minimum of 200 fragments were identified on each slide. The fragments were identified at least to functional plant group level and to genus level where possible. A challenge using this method is the fact that highly digestible plants like leaves from deciduous trees and herbs tend to be underestimated (Vavra and Holechek 1980).

Data analyses

Habitat selection when foraging

To determine cattle habitat selection when foraging, we compared vegetation types at cattle positions (used vegetation types) to random points within the cattle grazing area (available vegetation types). The cattle grazing area was defined as the area used by the cows and determined by creating a concave hull (allow holes, threshold = 0.5) in QGIS, one for each area. In these polygons, we created as many random points as there were cattle positions ($n = 9916$ in SRA, $n = 6991$ in FVA) and extracted vegetation type from the vegetation maps. We then removed all those used positions where cows were either resting or walking and kept only the foraging positions ($n = 3143$ in SRA, $n = 3684$ in FVA). We modeled the probability of use (binary response variable with 1 for used and 0 for control plots) in response to the vegetation type at each position, using GLMs of the binomial family with a logit link function. This corresponds to the probability functions RSPF introduced by Manly et al. (2007). We compared the model with vegetation type as fixed effect to the null model without any fixed effects. We selected the best model based on the Akaike Information Criterion corrected for small sample sizes (AICc [Burnham and Anderson 2002]) using the "model.sel" function within the MuMIn library (Barton 2022). Among the best models within ΔAICc < 2, we picked the most parsimonious one. The DHARMa package (Hartig 2022) was used to assess the goodness of fit of the final model by inspecting simulated quantile residuals against the predicted values. These analyses were done in R, version 4.1.2 (R Core Team 2021) with an RStudio interface version 1.3.1073 (RStudio Team 2015), using the R package "lme4" (Bates et al. 2015).

Microhabitat selection when foraging

To determine microhabitat selection of cattle when foraging, we compared the vegetation at cattle foraging positions (used, $n = 36$) with those on control plots (unused, $n = 144$), following a matched case-control study design. There were four control plots for each used plot, at 50-m distance from the used plot in each cardinal direction (Spedener et al. 2019). We sampled the vegetation on the control plots in the same way as in the used plots (see earlier). We modeled the probability of use (binary response variable with 1 for used and 0 for control plots) in response to the vegetation on each plot, using GLMMs of the binomial family with a logit link function. This corresponds to the probability functions RSPF introduced by Manly et al. (2007). The same type of model as in Spedener et al. (2019) was used, on a new data set and with the plant group graminoids replaced by either families or genera of graminoids. This resulted in two sets of models: one with graminoid families as response variables and one with graminoids genera as response variables. We excluded genera that occurred on $<$ 10% of the plots from these analyses. These models were compared with

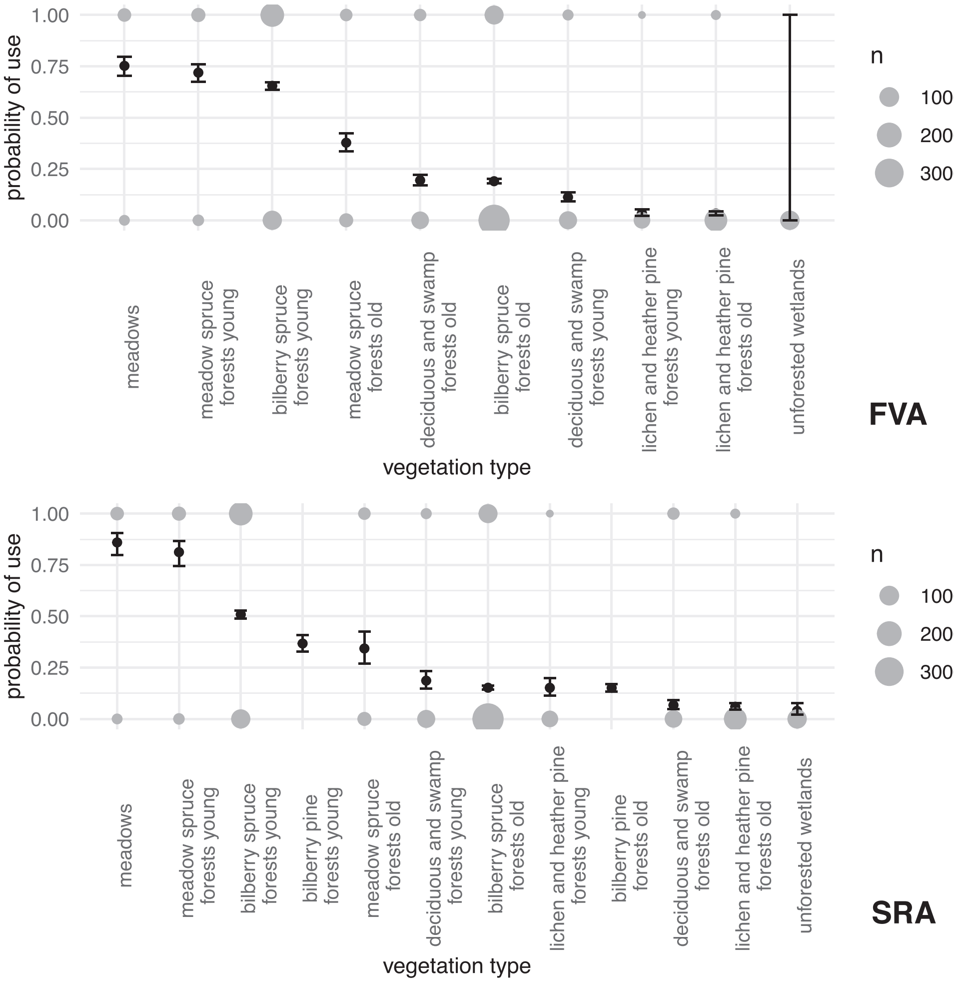


Figure 2. In black model predictions (mean and 95% prediction intervals) for the models describing foraging cattle's probability of site use in relation to vegetation type for the study areas communal lands Furnes/Vang (FVA) and Stange/Romedal (SRA). In gray are the observed data, on which the models are fitted. Forests under 15 yr are assumed to have an open canopy and are called young. Forests over 15 yr are assumed to have a closed canopy and are called old.

a null model without any fixed effects and to models with herbs and woody plants as fixed effects. We accounted for the dependency structure in our data and changing availability between positions by including habitat patch ID as random intercept in all models. In each model series, we selected the best model based on the Akaike Information Criterion corrected for small sample sizes (AICc [Burnham and Anderson 2002]) using the "model.sel" function within the MuMIn library (Barton 2022). Among the best models within Δ AICc < 2, we picked the most parsimonious one. The DHARMa package (Hartig 2022) was used to assess the goodness of fit of the final model by inspecting simulated quantile residuals against the predicted values. These analyses were done in R, version 4.1.2 (R Core Team 2021) with an RStudio interface version 1.3.1073 (RStudio Team 2015), using the R package "lme4" (Bates et al. 2015).

Diet selection within foraging patch

To determine cattle diet selection, we compared the plants found in fecal samples (used, $n = 74$) to the vegetation growing at foraging cattle positions (available, $n = 36$). We assumed that the cattle providing our fecal samples had been foraging on sites comparable with the ones we visited in the field. First, we investigated cows' selection for or against plant groups, modeling the probability of use for each plot using logistic regression. We used the same type of model as in Spedener et al. (2019), applying an isometric log-ratio transformation of the spurious anticorrelated composition data (Hron et al. 2012; Mair 2015). However, we did not include any random effect in the model this time, as availability was not defined separately for each observation of resource use. These analyses were done in R, using the R packages "robCompositions" and "lme4". Our sample sizes were too small to run diet selection analyses on genus level.

Results

Habitat use when foraging

Of all 6 827 GPS-recorded foraging positions, most (31.9%) were in bilberry spruce forest (Fig. 2). The other most used vegetation types were bilberry pine forest (6.6%), meadows (2.1%), and meadow spruce forest under 15 yr (1.9%).

Habitat selection when foraging

The models including vegetation type as fixed effect had a better model fit than the null models, both in FVA (ΔAICc = 4 194.18) and SRA (ΔAICc = 2 142.18). In both study areas, the cows strongly selected for meadows and young meadow spruce forests, as the probability of use of positions in this vegetation type was far above 0.5 (see Fig. 2). In both study areas, they strongly selected against deciduous and swamp forests, old bilberry spruce forest and lichen

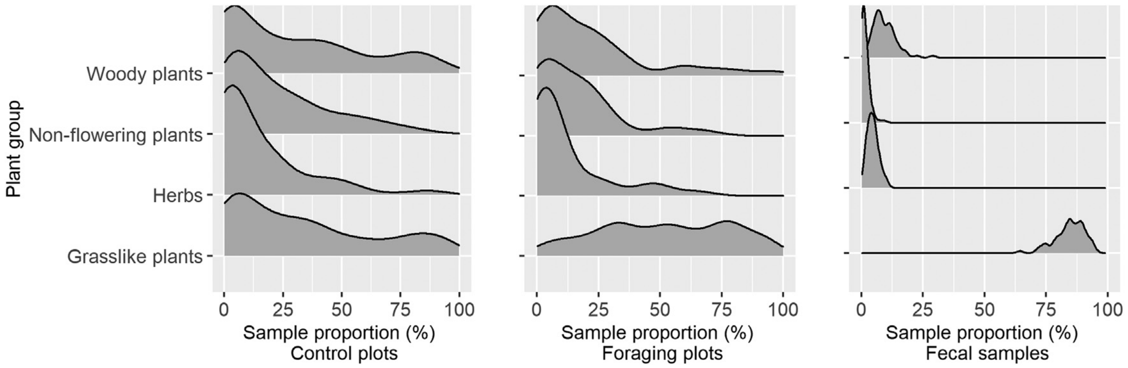


Figure 3. Ridge plots of the distribution of percentage cover per plant group across vegetation sampled on control plots (panel to the left), vegetation sampled on foraging cattle plots (panel in the middle), and fecal samples (panel to the right). The groups add up to 100%.

Table 1
List of the linear regression models fitted to investigate foraging cattle's microhabitat selection based on the vegetation sampled on foraging cattle positions and control plots, showing the fixed effects included, AICc, and ΔAICc. All models included *Habitat patch ID* as random effect.

Model	Fixed effects	AICc	ΔAICc
M2a	/	**163.5**	**1.09**
M2b	Juncaceae	164.6	2.22
M2c	Cyperaceae	164.3	1.85
M2d	Poaceae	162.4	0.00
M2e	Herbs	165.4	3.03
M2f	Woody plants	165.1	2.65
M3a	/	163.5	2.09
M3b	***Agrostis* spp.**	**161.4**	**0.00**
M3c	*Deschampsia* spp.	164.9	3.47
M3d	*Festuca* spp.	165.5	4.10
M3e	*Avenella* spp.	163.4	2.00
M3f	*Luzula* spp.	161.7	0.32
M3g	*Carex* spp.	164.3	2.85
M3h	Herbs	165.4	4.03
M3i	Woody plants	165.1	3.65

and heather pine forests (see Fig. 2). Cows in FVA selected for bilberry spruce forest, which was used according to its availability in SRA. Cows in SRA selected against bilberry pine forests and unforested wetlands, vegetation types that were rare or absent in FVA (see Fig. 2).

Microhabitat use when foraging

The average vegetation at a foraging cattle position consisted of 51.7% ± 26.7% graminoids, 11.5% ± 16.4% herbs, 21.8% ± 23.7% woody plants and 15.0% ± 16.6% of "other vegetation" (Fig. 3, panel in the middle). The most common herb genera were May lily (*Maianthemum* spp.), wood sorrel (*Oxalis* spp.), buttercup (*Ranunculus* spp.) and loosestrife *(Lysimachia* spp.*)* (Table 2). All three families of graminoids were present, with Poaceae as the most common. The most common genera of graminoids were wavy hair-grass, bentgrass, tussock grass, true sedges, and woodrush (*Luzula* spp.). The most common genus in the data was a woody plant, *Vaccinium spec,* including species such as bilberry (Vaccinium myrtillus), bog bilberry (Vaccinium uliginosum), and lingonberry (Vaccinium vitis-idaea). Other common genera of woody plants were spruce, birch, and raspberry (Rubus idaeus).

Microhabitat selection when foraging

In the first model series at plant family level, the null model performed best (Table 1). Thus, cattle did not select for graminoids at family level. In the second model series at plant genus level, the best model included bentgrass (see Table 1). Bentgrass was positively correlated with the probability of use by cattle (coefficient estimate = 0.25, 90% confidence interval: 0.05–0.44).

Diet based on fecal samples

An average fecal sample consisted of 84.6% ± 6.0% of graminoids, 4.6% ± 2.2% of herbs, 9.4% ±4.7% of woody plants and 1.3% ± 1.5% of "other vegetation" (Fig. 3, panel to the right). Herbs were not identified to genus level. Only two families of graminoids were found (Table 2). The most common genera of graminoids were wavy hair-grass, tussock grass, true sedges, Poaceae that could not be determined to genus level and festuca. The most common genera of woody plants were willow, *Vaccinium,* pine, and birch (see Table 2).

Diet selection within foraging patch

Fecal samples contained a higher proportion of graminoids (coefficient estimate = 2.95, 90% confidence interval: 1.45–4.99) and woody plants (1.25, 0.44–2.22), a lower proportion of "other vegetation" (−1.76, −2.41 to −1.23), and a similar proportion of herbs (−0.18, −0.99 to 0.58) compared with the field layer vegetation on the foraging plots.

Discussion

We investigated the feeding ecology of cattle, a typical grazer, released to productive boreal forests, a typical browser's habitat. The results confirm our expectations that cattle select for grass-rich habitats, such as productive and young forest stands on a large scale, and for grass-rich patches on a small scale. We did find browse in the cattle's diet, even though woody plants only made up 9.4% ± 4.7% of the fecal samples. This corresponds with values from a cattle diet study by (Wam and Herfindal 2020), in Norwegian boreal forest, but is far below the values reported in studies on cattle diet from a broad range of forest habitats (Moleele 1998; Bartolomé et al. 2011; Ferreira et al. 2013; Vandermeulen 2017). In those habitats, the foraging value of the tree species might be higher and the availability of graminoids lower. In the Mediterranean forests in Spain, for example, where woody plants made up 89% of the fecal samples, the main tree species were the deciduous oak (*Quercus* sp.) and beech (*Fagus* sp.). Even though the cows in our study foraged on woody plants, they did not select for it. Woody plants in the field layer did not affect their microhabitat selection. Furthermore, the overall proportion of woody plants in the fecal samples was higher than in the sampled vegetation. However, we should keep in mind that the proportion of herbs in

Table 2
Number of plant genus observations in fecal samples, vegetation samples at foraging cattle positions, and vegetation samples at control positions.

	Plant fragments per fecal sample (mean ± standard deviation)	Number of frames with plant occurrence per foraging site (mean ± standard deviation)
Woody plants		
Alnus spp.[1]	0.00 (± 0.00)	0.00 (± 0.00)
Betula spp.[2]	1.13 (± 1.20)	0.69 (± 1.19)
Calluna spp.	0.53 (± 0.80)	0.00 (± 0.00)
Empetrum spp.	0.00 (± 0.00)	0.00 (± 0.00)
Juniperus spp.	0.00 (± 0.02)	0.00 (± 0.00)
Picea spp.	0.01 (± 0.06)	1.56 (± 1.44)
Pinus spp.	1.29 (± 1.41)	0.25 (± 0.73)
Populus spp.[2]	0.00 (± 0.00)	0.06 (± 0.3)
Rubus spp.[2]	0.00 (± 0.00)	0.83 (± 1.23)
Salix spp.[2]	3.53 (± 2.50)	0.28 (± 0.88)
Sorbus spp.[2]	0.02 (± 0.07)	0.22 (± 0.59)
Vaccinium spp.[2]	2.86 (± 3.02)	2.08 (± 2.06)
Herbs	4.57 (± 2.18)	
Alchemilla spp.[2]		0.03 (± 0.17)
Chamerion spp.		0.11 (± 0.32)
Cirsium spp.		0.14 (± 0.68)
Filipendula spp.		0.14 (± 0.68)
Fragaria spp.		0.03 (± 0.17)
Galium spp.		0.03 (± 0.17)
Geranium spp.		0.11 (± 0.40)
Impatiens spp.		0.03 (± 0.17)
Linnea spp.		0.06 (± 0.23)
Lysimachia spp.		0.22 (± 0.48)
Maianthemum spp.		0.39 (± 0.99)
Melampyrum spp.[2]		0.03 (± 0.17)
Oxalis spp.		0.31 (± 0.71)
Pedicularis spp.		0.00 (± 0.00)
Potentilla spp.		0.03 (± 0.17)
Ranunculus spp.[2]		0.25 (± 0.84)
Rumex spp.[2]		0.17 (± 0.61)
Stellaria spp.		0.00 (± 0.00)
Trifolium spp.		0.11 (± 0.40)
Urtica spp.		0.03 (± 0.17)
Veronica spp.		0.14 (± 0.35)
Viola spp.		0.19 (± 0.52)
Graminoids		
Carex spp.[2]	11.11 (± 7.24)	1.08 (± 1.56)
Other Cyperaceae	0.26 (± 0.69)	0.00 (± 0.00)
Juncus spp.	0.00 (± 0.00)	0.03 (± 0.17)
Luzula spp.[1]	0.00 (± 0.00)	0.61 (± 1.08)
Agrostis spp.[2]	1.58 (± 0.88)	1.44 (± 1.81)
Alopercurus spp.	0.02 (± 0.06)	0.00 (± 0.00)
Anthoxanthum spp.[2]	0.05 (± 0.14)	0.00 (± 0.00)
Avenella spp.[2]	26.54 (± 14.10)	1.75 (± 1.79)
Calamagrostis spp.[2]	0.06 (± 0.13)	0.11 (± 0.40)
Deschampsia spp.[2]	25.91 (± 10.82)	1.31 (± 1.60)
Festuca spp.[2]	8.33 (± 3.13)	0.22 (± 0.59)
Molinia spp.[2]	0.80 (± 1.96)	0.00 (± 0.00)
Nardus spp.[1]	0.05 (± 0.20)	0.00 (± 0.00)
Phleum spp.	0.17 (± 0.29)	0.00 (± 0.00)
Poa spp.[2]	1.14 (± 1.12)	0.00 (± 0.00)
Other Poaceae	8.63 (± 3.80)	0.00 (± 0.00

[1] and [2] indicate low and high grazing values, respectively (Bjor and Graffer 1963; Larsson and Rekdal 2000).

the diet are typically underestimated using microhistological analyses of fecal samples. As the proportions of herbs, woody plants, and graminoids are correlated, an underestimation of herbs leads to an overestimation of woody plants and graminoids. This is why we cannot be sure if the high proportion of woody plants in our fecal samples is due to high intact of woody plants or a result of methodological bias. Another thing we must keep in mind is that we only assessed trees under 2 m height, as we assumed higher trees to be out of reach for cattle. This might be a weak assumption, as cattle might have a larger forage reach or forage on low hanging branches of higher trees. We expected cattle to prefer herbs over woody plants, but we do not know if they did as neither herbs nor woody plants were selected at microhabitat level, and the high digestibility of herbs is known to cause underrepresentation of this group in fecal samples (Vavra and Holechek 1980). Based on Popp and Scheibe (2013), we expected the cattle to prefer deciduous over coniferous trees. Indeed, we found a much higher proportion of deciduous than coniferous trees in the fecal samples, even though the forests are dominated by coniferous trees. We therefore conclude that our cows did prefer deciduous over coniferous trees.

The woody plant genera common heather (*Calluna* spp.) and juniper (*Juniperus* spp.) and the grasslike plant genera foxtail grass (*Alopecurus* spp.), vernal grass (*Anthoxanthum* spp.), moor grass (*Molinia* spp.), matgrass (*Nardus* spp.), timothy (*Phleum* spp.), and meadow grass (*Poa* spp.) were found in fecal samples but missing on the sampled plots. This can be explained by small sample sizes and a high proportion of rare species in the sampled vegetation. As (Chao and Shen 2003) have pointed out, biological communities tend to have a large number of species with relatively small abundances and when selecting a random sample of individuals and classifying each individual according to species identity, some rare species may not be discovered. Consequently, we were not able to do analyses for the diet selection on genus level. However, we could see some clear patterns in the data. For example, we did not find any spruce in the fecal samples, even though spruce is the most common plant in these forests. This left us with the conclusion that the cows avoided this species in their diet. The cows' aversion to spruce is not surprising, as even roe deer, the most common feeder of spruce, is reported to forage on spruce only during winter when other forage is scarce (Bergquist et al. 2003). We did find woody species such as willow, birch, rowan, and *Vaccinium* in the fecal samples. These plants are reported as forage for cattle in various sources (Hejcman et al. 2016; Vandermeulen et al. 2018; Wam and Herfindal 2020). In addition, willow has a long history of being used for cattle winter fodder in Iceland (Hejcman et al. 2016) and a recent study from Australia suggested the use of willow as forage supplement during droughts (Moore et al. 2003). When comparing the use of fresh and dried foliage, we must keep in mind that plants dried and stored for fodder lose volatile secondary compounds and could thus be more palatable (Bhat et al. 2013). On the other hand, drying foliage of certain woody species has shown to reduce their fodder quality (Vandermeulen et al. 2018). Surprisingly, raspberry was missing in the fecal samples. Again, digestibility varies between plants and will affect the proportions of plant remains in the feces. For example, raspberry leaves are softer and more digestible than pine needles, potentially masking a selection for *Rubus* and an aversion toward pine in our data. We would expect an aversion toward pine and argue that cows only forage on them by coincidence, as shown in Pearson et al. (1982). In their study in pine forests in Louisiana, pine was represented by some needles in cattle diets and considered foraging bycatch.

The cows preferred graminoids. We knew from before that they were selecting for grass-rich patches on microhabitat scale (Spedener et al. 2019), but we did not know what kind of graminoids was driving their selection. The findings of this study show that the cows did not select on graminoid family level and that they only selected for the genus bentgrass. The analyses of the fecal samples showed that the cows foraged mainly on wavy hair-grass, tussock grass, true sedges, and festuce. The surprisingly low proportion of bentgrass in the fecal samples can be partly explained by the high digestibility of bentgrass (Todnem and Lunnan 2014). Lunnan and Todnem (2011) described bentgrass, wavy hair-grass, tussock grass, and festuce as important forage for grazers in mountainous areas in Norway, and according to our findings, these are the most important forage for cattle in the forest as well. Moreover, the absence of Juncaceae in the fecal samples in this study is in accordance with the low occurrence of Juncaceae that has been previously reported in cattle diet composition in coniferous forest in California (Kie and Boroski 1996). The high proportion of true sedges in the fecal samples could indicate that the cows in our study did not have access to the most preferred feeding plants and had to switch over to a less optimal feeding resource (i.e., true sedges).

The boreal forest is dominated by grass-poor habitats, and despite their strong selection for grass-rich habitats on a large spatial scale, the cows spent a lot of time in suboptimal vegetation types, such as old bilberry spruce forest. However, they managed to find grass-rich habitat patches and keep a grass-rich diet in those grass-poor vegetation types. Moreover, it seems like they rather selected on habitat patch scale than for individual plants within a given habitat patch, which is considered typical for a grazer (Gordon 2003). This indicates that, for the observed stocking densities of about 2.5 cows per km^2 and 12.5 sheep per km^2, productive boreal forest is an adequate summer range for cattle, a typical grazer. This is supported by a previous study on weight gain of our study animals, which showed differences between breeds and study areas and indicated that it is possible to achieve acceptable weight gains for cattle grazing coniferous forest by finding breeds suitable for these extensive areas and stocking at moderate densities (Tofastrud et al. 2020).

We did not include the factors sex, age, and type of cattle in our analyses, three factors that are well known to influence cattle resource selection while foraging (Braghieri et al. 2011; Napolitano et al. 2011; Pauler et al. 2020). The animals in this study were all the same sex (females) and age (adults). Moreover, they were all beef cattle, which we assumed not to differ much when it comes to nutrient and energy requirements. All cattle in this study are part of breeding programs that emphasize high production and therefore differ considerably from the primitive, local, and semi-wild breeds used in the studies referred to at the beginning of this paragraph. Weaknesses of this study are the small sample sizes and the fact that we were not able to include the important factors seasonality and year-to-year variation in plant availability, growth stage, and chemistry (Vandermeulen 2017; Tofastrud et al. 2019). We did, however, account for the scale dependency of the selection process and defined availability in relation to the observations of resource use. This, combined with the use of animal-born accelerometers to identify cattle behavior, makes this cattle diet study unique. Of course, larger data sets than the ones available for this study are recommended.

The cows' avoidance of spruce indicates a low risk for browsing damage on trees planted for timber production in the study area because the main objective of local forestry practices is spruce timber production. Whether or not cattle damage spruce saplings by trampling and bedding still needs to be assessed, though. On the basis of this study, cattle might even be beneficial to forestry because they select for graminoids and forage on willow, plants that spruce saplings are competing with for light, water, and nutrients. Such a "weeding effect" to the benefit of coniferous tree saplings has been reported in earlier studies (Adams 1975). Moreover, there seems to be little diet overlap between cattle and wild browsers but potentially some overlap with the intermediate feeders (Gordon and Illius 1989; Hofmann 1989). These findings are in accordance with Wam and Herfindal (2018), who concluded that moose are not affected by livestock through direct food competition, although indirectly through altered food availability.

Implementation

The grazer in a browser's habitat still foraged like a true grazer. Therefore, we believe that the cattle foraging in our study pose a minor risk to Norway spruce planted for timber production and compete to a low degree for food resources with wild ungulates. In conclusion, cattle summer grazing can be considered an adequate way of utilizing the scarce and scattered grazing resources in productive boreal forest.

Declaration of authorship

MS, MT, and BZ formulated the idea; MS, MT, and BZ developed methodology; MS and MT conducted fieldwork; MS performed statistical analyses; MS drafted the manuscript; and MT, GA, and BZ gave editorial advice.

Statements and Declarations

Conflicts of interest: No potential conflict of interest was reported by the authors.

Ethics approval: All applicable institutional and national guidelines for the care and use of animals were followed.

Availability of data and material: The data are available in the supplementary material (Spedener_et_al_cattle_diet_selection_data.zip)

Acknowledgments

We would like to thank the cattle owners and the managers of the communal lands in Furnes/Vang and Stange/Romedal for their goodwill and cooperation in the implementation of this study; the students Jack Räisänen, Lisa Dickel, Ole Henrik Møllevold, and Steve Ehlen for carrying out fieldwork; Barbro Kristina Dahlberg for the microhistological analyses of the fecal samples; Karen Marie Mathisen for input on the analyses; and Hilde Karine Wam and two anonymous reviewers for their comments and suggestions that considerably improved this manuscript.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2023.12.004.

References

Adams, S.N., 1975. Sheep and cattle grazing in forests: a review. Journal of Applied Ecology 143–152.

Aune-Lundberg, L., Munsterhjelm, N., Fjellstad, W.J., Dramstad, W., 2021. Beitedyras geografi. 4. https://nibio.brage.unit.no/nibio-xmlui/handle/11250/2824968.

Austrheim, G., Solberg, E.J., Mysterud, A., 2011. Spatio-temporal variation in large herbivore pressure in Norway during 1949-1999: has decreased grazing by livestock been countered by increased browsing by cervids? Wildlife Biology 17 (3), 286–298.

Bartolomé, J., Plaixats, J., Piedrafita, J., Fina, M., Adrobau, E., Aixàs, A., Bonet, M., Grau, J., Polo, L., 2011. Foraging behavior of Alberes cattle in a Mediterranean Forest Ecosystem. Rangeland Ecology & Management 64 (3), 319–324.

Barton, K., 2022. MuMIn: Multi-Model Inference (1.46.0) [Programvare] Available at:. https://CRAN.R-project.org/package=MuMIn Accessed 04.01.2024.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using {lme4}. Journal of Statistical Software 67 (1), 1–48.

Bergquist, J., Bergström, R., Zakharenka, A., 2003. Responses of young Norway spruce *(Picea abies)* to winter browsing by roe deer *(Capreolus capreolus)*: effects on height growth and stem morphology. Scandinavian Journal of Forest Research 18 (4), 368–376.

Bhat, T.K., Kannan, A., Singh, B., Sharma, O.P., 2013. Value addition of feed and fodder by alleviating the antinutritional effects of tannins. Agricultural Research 2 (3), 189–206.

Bjor, K., Graffer, H., 1963. Beiteundersøkelser på skogsmark: investigation on grazing in woodland. Mariendals Boktrykkeri.

Bjørneraas, K., Solberg, E.J., Herfindal, I., Van Moorter, B., Rolandsen, C.M., Tremblay, J.-P., Skarpe, C., Sæther, B.-E., Eriksen, R., Astrup, R., 2011. Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. Wildlife Biology 17 (1), 44–54.

Braghieri, A., Pacelli, C., Girolami, A., Napolitano, F., 2011. Time budget, social and ingestive behaviours expressed by native beef cows in Mediterranean conditions. Livestock Science 141 (1), 47–52.

Burnham, K.P., Anderson, D.R., 2002. Avoiding pitfalls when using information-theoretic methods. The Journal of Wildlife Management 66 (3), 912–918.

Chao, A., Shen, T.-J., 2003. Nonparametric estimation of Shannon's index of diversity when there are unseen species in sample. Environmental and Ecological Statistics 10 (4), 429–443.

Chapron, G., Kaczensky, P., Linnell, J.D., Von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346 (6216), 1517–1519.

Clauss, M., Kaiser, T., Hummel, J., 2008. The morphophysiological adaptations of browsing and grazing mammals. The ecology of browsing and grazing. Springer, New York, NY, USA, pp. s.47–s.88.

Ferreira, L., Celaya, R., Benavides, R., Jáuregui, B., García, U., Santos, A.S., Rosa García, R., Rodrigues, M., Osoro, K., 2013. Foraging behaviour of domestic herbivore species grazing on heathlands associated with improved pasture areas. Livestock Science 155, 373–383.

Fremstad, E., 1997. Vegetasjonstyper i Norge. NINANIKU Stiftelsen for naturforskning og kulturminneforskning. https://brage.nina.no/nina-xmlui/handle/11250/2837231.

Gordon, 2003. Browsing and grazing ruminants: are they different beasts? Forest Ecology and Management 181, 13–21.

Gordon, I.J., Illius, A.W., 1989. Resource partitioning by ungulates on the Isle of Rhum. Oecologia 79 (3), 383–389.

Hartig, F., 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi_Level/Mixed) Regression Models (version 0.4.5) [Programvare] Available at:. https://CRAN.R-project.org/package=DHARMa Accessed ....

Hejcman, M., Hejcmanová, P., Pavlů, V., Thorhallsdottir, A.G., 2016. Forage quality of leaf fodder from the main woody species in Iceland and its potential use for livestock in the past and present. Grass and Forage Science 71 (4), 649–658.

Hofmann, R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78 (4), 443–457.

Hron, K., Filzmoser, P., Thompson, K., 2012. Linear regression with compositional explanatory variables. Journal of Applied Statistics 39 (5), 1115–1128.

Janis, C., 2008. An evolutionary history of browsing and grazing ungulates. The ecology of browsing and grazing. Springer, New York, NY, USA, pp. s.21–s.45.

Johnson, M.K., Wofford, H., Pearson, H.A., 1983. Microhistological techniques for food habits analysis. US Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, LA, USA Research paper SO-199.

Kie, J.G., Boroski, B.B., 1996. Cattle distribution, habitats, and diets in the Sierra Nevada of California. Rangeland Ecology & Management/Journal of Range Management Archives 49 (6), 482–488.

Kolstad, A., Austrheim, G., Solberg, E.J., De Vriendt, L., Speed, J.D., 2018. Pervasive moose browsing in boreal forests alters successional trajectories by severely suppressing keystone species. Ecosphere 9 (10), e02458.

Larsson, J.Y., Rekdal, Y., 2000. Husdyrbeite i barskog. NIJOS-Rapport.

Lunnan, T., Todnem, J., 2011. Forage quality of native grasses in mountain pastures of southern Norway. Grassland farming and land management systems in mountainous regions. In: Proceedings of the 16th Symposium of the European Grassland Federation, Gumpenstein, Austria, pp. 568–570 29-31 August, 2011.

Mair, E., 2015. Generalized linear models with compositional data [thesis, Wien] Available at:. https://repositum.tuwien.at/handle/20.500.12708/4997 .

Manly, B.F.L., McDonald, L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2007. Resource selection by animals: statistical design and analysis for field studies. Springer Science & Business Media, Berlin, Germany.

Moleele, N.M., 1998. Encroacher woody plant browse as feed for cattle. Cattle diet composition for three seasons at Olifants Drift, southeast Botswana. Journal of Arid Environments 40 (3), 255–268.

Moore, K.M., Barry, T.N., Cameron, P.N., Lopez-Villalobos, N., Cameron, D.J., 2003. Willow (*Salix* sp.) as a supplement for grazing cattle under drought conditions. Animal Feed Science and Technology 104 (1), 1–11.

Napolitano, F., Girolami, A., Pacelli, C., Braghieri, A., 2011. Activity budgets and forage selection of Podolian cattle, a semiwild bovine breed. ISRN Zoology 2011, 1–8.

Nygaard, P.H., Øyen, H., 2020. Skogshistorisk tilbakeblikk med vekt på utviklingen av bestandsskogbruket i Norge. NIBIO Rapport 6 (45), 34.

Pauler, C.M., Isselstein, J., Suter, M., Berard, J., Braunbeck, T., Schneider, M.K., Stevens, C., 2020. Choosy grazers: influence of plant traits on forage selection by three cattle breeds. Functional Ecology 34 (5), 980–992.

Pearson, H.A., Grelen, H.E., Epps, E.A., Johnson, M.K., Blakewood, B.W., 1982. Botanical Composition and Nutritive Value of Cattle Diets on Southern Pine Range [Research Paper]. 2024-01-04. https://www.srs.fs.usda.gov/pubs/rp/rp_so178.pdf.

Popp, A., Scheibe, K.-M., 2013. The importance of groves for cattle in semi-open pastures. Agriculture (Basel) 3 (1), 147–156.

R Core Team, 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Available at: https://www.R-project.org/. Accessed on 04.01.2024.

Rekdal, Y., 2010. Vegetasjon og beite i Furnes, Vang og Løten almenninger. Rapport fra vegetasjonskartlegging i kommunene Ringsaker, Hamar og Løten (13/2010; fra Skog og Landskap, p. 82). Norsk institutt for skog og landskap. https://nibio.brage.unit.no/nibio-xmlui/handle/11250/2469118.

Rekdal, Y., 2017. Vegetasjon og beite i deler av Romedal-og Stange almennninger (3/24; p. 59). NIBIO. https://nibio.brage.unit.no/nibio-xmlui/handle/11250/2436720.

RStudio Team, 2015. RStudio: Integrated Development Environment for R. RStudio, Inc Accessed 04.01.2024. Available at: https://www.rstudio.com. Accessed on 04.01.2024.

Shipley, L.A., 1999. Grazers and browsers: how digestive morphology affects diet selection. Grazing Behavior of Livestock and Wildlife 70, 20–27.

Spedener, M., Tofastrud, M., Devineau, O., Zimmermann, B., 2019. Microhabitat selection of free-ranging beef cattle in south-boreal forest. Applied Animal Behaviour Science 213, 33–39.

Speed, J.D.M., Austrheim, G., Kolstad, A.L., Solberg, E.J., 2019. Long-term changes in northern large herbivore communities reveal differential rewilding rates in space and time. PLoS ONE 14 (5), e0217166.

SSB, 2023. 12660: Livestock grazing on outfield pastures (M) 1995 - 2022. Statbank Norway. SSB. Available at: https://www.ssb.no/system/. Accessed on 04.01.2024.

Todnem, J., Lunnan, T., 2014. Utmarksbeite, fôrkvalitet til sau. Bioforsk Rapport.

Tofastrud, M., Devineau, O., Zimmermann, B., 2019. Habitat selection of free-ranging cattle in productive coniferous forests of south-eastern Norway. Forest Ecology and Management 437, 1–9.

Tofastrud, M., Hegnes, H., Devineau, O., Zimmermann, B., 2018. Activity patterns of free-ranging beef cattle in Norway. Acta Agriculturae Scandinavica, Section A—Animal Science 1–9.

Tofastrud, M., Hessle, A., Rekdal, Y., Zimmermann, B., 2020. Weight gain of free-ranging beef cattle grazing in the boreal forest of south-eastern Norway. Livestock Science 233, 103955.

Vandermeulen, S., 2017. Trees and shrubs influence the behaviour of grazing cattle and rumen fermentation. University of Liège, Liège, Belgium, p. 165 [thesis].

Vandermeulen, S., Ramírez-Restrepo, C., Beckers, Y., Claessens, H., Bindelle, J., 2018. Agroforestry for ruminants: a review of trees and shrubs as fodder in silvopastoral temperate and tropical production systems. Animal Production Science 58.

Vavra, M., Holechek, J.L., 1980. Factors influencing microhistological analysis of herbivore diets. Journal of Range Management 33 (5), 371.

Wam, H.K., Hjeljord, O., 2010. Moose Summer Diet From Feces and Field Surveys: A Comparative Study. Rangeland Ecology & Management 63 (3), 387–395. doi:10.2111/REM-D-09-00039.1.

Wam, H.K., Hjeljord, O., Solberg, E.J., 2010. Differential forage use makes carrying capacity equivocal on ranges of Scandinavian moose *(Alces alces)*. Canadian Journal of Zoology 88 (12), 1179–1191.

Wam, H.K., Herfindal, I., 2018. Subtle foodscape displacement of a native ungulate by free-ranging livestock in a forest agroecosystem. Ecosphere 9 (6), e02280.

Wam, H.K., Herfindal, I., 2020. Matvalg hos sau og storfe på skogsbeite NIBIO Rapport.

Zimmermann, B., Wabakken, P., Dötterer, M., 2003. Brown bear-livestock conflicts in a bear conservation zone in Norway: are cattle a good alternative to sheep? Ursus 72–83.