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Habitat selection of free-ranging cattle in productive coniferous forests of south-eastern Norway

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ABSTRACT

Multiple use of communal forests requires informed management to balance divergent interests such as livestock grazing and timber production. In this study, we examined the habitat selection of free-ranging beef cattle in two vegetation-mapped communal forests of Norway's boreal zone. The two areas were 35 km apart, and they mainly differed regarding cattle stocking density, with one being below and the other above the livestock grazing capacity of the area. In total, 78 cows were fitted with global positioning system (GPS) collars during the summers 2015 to 2017. The collars were scheduled to take positions and measure activity at 5 and 10 min intervals. We applied generalized linear mixed models (GLMM) to describe the cows' selection of vegetation types, forest cutting classes, topographical features and distance to roads with resource selection functions (RSF), by comparing use with availability. The most selected vegetation types were wide-spread summer farm meadows, followed by the dominant bilberry spruce forest. In productive forest, the cows selected for clearcuts younger than 15 years and used thinning and post-thinning stands less than expected. In accordance with the Ideal free distribution hypothesis, the cows were more likely to use low productive habitats in the area with high compared to the one with low stocking density. The preference for young forest stands was strongest when grazing as compared to resting and walking. During grazing, the cows also preferred pre-thinning stands older than 15 years and inclined patches, but avoided north-facing slopes. Preference for south-facing slopes was strongest when resting and for forest roads when traveling.

To reduce the pressure of cattle in forest regeneration stands, we suggest limiting stocking densities to the grazing capacity of forest pastures, using vegetation and forest maps as information to guide the distribution of cattle, and maintaining or even expanding the existing meadows of the summer farms.

1. Introduction

Communal forests are important areas for multiple use such as timber production, livestock grazing, hunting and tourism. Managing these areas while accounting for the diverging interests and economic benefits of both the forestry, cattle industry and game hunting is challenging (Adams, 1975; Mitchell et al., 1982). Since the 1950s, the boreal forests of Scandinavia are mainly managed by clearcutting and other silvicultural practices, such as scarification, restocking and thinning, in order to increase timber production (Aasetre and Bele, 2009). The clearcuts are important areas for forest regeneration, but they also serve as important grazing areas for livestock and wild herbivores (Bjor and Graffer, 1963; Larsson and Rekdal, 2000; Edenius et al., 2002).

Because of the podsolization process, the soil layer of coniferous forests is generally nutrient poor and acidic (Strand, 1997). However, clearcutting changes the amount of light reaching the ground and contributes to the production of raw humus in the ground layer, which then becomes suitable for species such as heather, lichens, mosses, grasses, perennials, and young deciduous trees. Although these species are considered as weeds by the forestry industry because they outcompete the slow-growing coniferous seedlings (Östlund et al., 1997), they are an important food source for grazing livestock and wild herbivores (Larsson and Rekdal, 2000; Edenius et al., 2002). Resource provision on young forest stands is considered an important cause for the high productivity of the Scandinavian moose (Alces alces) population, together with age- and sex-specific harvest regulations (Lavsund et al., 2003). To what extent these temporally available resource patches in the boreal forest lead to competition or facilitation between domestic and wild herbivores depends on diet overlap and population densities of the involved species as well as plant productivity (Dorn, 1970; Mysterud, 2000). Grazing cattle can be used to control weeds in regeneration areas (Adams, 1975; Popay and Field, 1996) because they don't browse on coniferous trees (Lewis, 1980). However, several studies report increased frequency of damaged young trees in areas with grazing cattle (Bjor and Graffer, 1963; McLean and Clark, 1980; Hjeljord et al., 2014). In a Norwegian study, Hjeljord et al. (2014) found the levels of spruce damage in forest regeneration areas to be positively related to the cattle's use of the area, but damages were found

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at both high and low cattle stocking densities. The cattle of that study were not feeding on the trees, but the damages were mainly caused by trampling or bedding. Knowledge about cattle habitat selection at different behavioural states, such as grazing, travelling and resting, can guide the use of preventive measures for limiting the damages on young trees, e.g. by restricting the animals' area use or changing the procedures of seedling planting.

Habitat use by free-ranging livestock has been studied in several parts of the world with the purpose of informing management and promoting resource conservation (Kie and Boroski, 1996; Launchbaugh and Howery, 2005; Kaufmann et al., 2013a). Generally, cattle prefer habitats with high biomass production (Putfarken et al., 2008; Kaufmann et al., 2013b), and grass species are particularly preferred (Gordon, 1989). Bjor and Graffer (1963) studied dairy cattle grazing in the coniferous forests of Norway and found summer farm meadows to be preferred over habitats dominated by bilberry (*Vaccinium myrtillus*) and wavy hair grass (*Avenella flexuosa*). The forage production of the coniferous forests is considered as very low compared to grasslands. Hansen et al. (2009) estimated the average biomass production of the ground layer of bilberry and meadows spruce forest to 630 kg and 2000 kg dry matter ha^{-1}, respectively. In addition, terrain characteristics such as slope and distance to water influence habitat selection of cattle (Ganskopp and Bohnert, 2009; Henkin et al., 2012; Bailey et al., 2015). Roads are important in rough terrain and fragmented areas (Williams, 1954; Workman and Hooper, 1968) but not in easily travelled terrain (Roath and Krueger, 1982; Kaufmann et al., 2013b).

The ideal free distribution theory predicts that due to resource competition, animals at high stocking densities select for lower quality habitats than animals at low density (Fretwell and Lucas, 1969). Higher densities of large herbivores leads to an increased competition for resources which in turn may influence habitat selection at both large and small scale (Senft et al., 1987; Cornelissen and Vulink, 2015). Cattle, sheep and horses grazing at high stocking density are likely to use habitats with lower biomass production and lower quality forage (Hart et al., 1991; Mobæk et al., 2009; van Beest et al., 2014; Schoenbaum et al., 2017).

The aim of this study was to assess habitat selection of free ranging cattle in coniferous forests by studying (1) the selection of various vegetation types and forest stands by cattle grazing in two areas, one of high and the other of low stocking density, and (2) the selection of different forest stands while resting, grazing and travelling. We predicted that cows would prefer open grass-rich habitat patches (Gordon, 1989) close to easily travelled forest roads and slopes with the richest light supplies, facing south or west (Bailey et al., 1996). We expected the importance of these habitat factors to vary with the behavioural state of the animals (Mobæk et al., 2009; Schneider et al., 2013).

2. Materials and methods

2.1. Study area and animals

In Norway, only 3% of the land area is cultivated land, and the farmers' right to exploit communal areas as additional grazing areas is regulated by several laws (Ministry of Agriculture and Food, 1975, 1993). We monitored free-ranging cows in two common land areas located in southeastern Norway, in Hedmark County (60° N, 11° E). The cows were continuous grazing in two areas 35 km apart from each other, in Stange – Romedal Almenning (SRA, 150 km^2) in the summers of 2015–2017 and in Furnes – Vang Almenning (FVA, 100 km^2) in the summers of 2016 and 2017 (Fig. 1). The elevation ranged 300–600 m.a.s.l. in SRA and 600–700 m.a.s.l. in FVA. The bedrock in both areas is dominated by various acidic and nutrient-poor gneiss and granite rock with local touches of easy weathering gabbro which provided habitat patches of richer vegetation (Rekdal and Angelhoff, 2016). The average air temperature for the period June-September in the three study years was 13.2°, 14.6° and 13.2 °C, and precipitation during the four summer months was 75, 48 and 88 mm in 2015, 2016 and 2017, respectively (Norwegian Meteorological Institute, 2018).

Both study areas were dominated by bilberry-spruce forest (Table 1) (Rekdal, 2010, 2017). In mature forest stands, the shading effects of Norway spruce (*Picea abies*) favoured shade-tolerant bilberry (*Vaccinium myrtillus*) on the ground layer. Timber harvest in this vegetation type generated clearcuts characterized by low plant diversity, with wavy hair grass (*Avenella flexuosa)* covering up to 80% of the area. Scots pine (*Pinus sylvestris*) and heather of cowberries (*Vaccinium vitis-idaea*) were prevalent in areas of nutrient-poor soil. These pine forests were considered as areas of very low pasture value (Larsson and Rekdal, 2000). Small abandoned summer farms were widespread in the forests, and a network of forest roads built for timber transportation and public use fragmented the study areas.

We monitored adult lactating and dry cows of beef cattle breeds dominated by Charolais, Hereford and crossbreeds, from four and five farms in SRA and FVA, respectively. Cows from the same farm were turned out at the same site and time and considered as one herd. The number of animals varied greatly among the herds, from seven up to 98 cows of different age and reproductive status. The grazing period varied among the herds from 80 to 120 days (late May to early September). The grazing capacity of the study areas was estimated based on vegetation maps made in 2010 and 2017 for FVA and SRA, respectively (Rekdal, 2010, 2017). Mapped vegetation types are grouped into the three foraging classes (Table 1); Less Good (LG, 0.05 − 0.08 beef cows ha^{-1}), Good (G, 0.08 − 0.12 beef cows ha^{-1}) and Very Good (VG, 0.12–0.17 beef cows ha^{-1}) based on the approximately grazing value for cattle (Larsson and Rekdal, 2000). The distribution of the three foraging classes in SRA and FVA was 21% and 29% LG, 76% and 67% G, and 2% and 4% VG, respectively (Rekdal, 2010, 2017). Our study areas roamed 0.04 (SRA) and 0.16 (FVA) cows per hectare, which represented 38% and 148% of the area's grazing capacity, respectively. Hence, we considered SRA and FVA to be stocked at Low and High density, respectively.

2.2. GPS collars, location and activity data

Each year, we used 18 Tellus Medium plus GPS collars with a GSM link for remote data transfer, and 13 Tellus Basic GPS collars (Tellus, Followit AB, Lindesberg, Sweden) without remote data link. The number of GPS collars varied among years because of technical failures or collar losses during the grazing season (Table 2). All GPS collars had a built-in two-axis accelerometer for measuring neck movement. The GPS collars recorded positions at 5-minute intervals in 2015 and 2017. In 2016, we programmed all Basic collars and seven GSM collars of SRA to take positions at 10-minute intervals during the night resting period, to save battery and increase the monitoring period in areas with less satellite and GSM coverage. We performed a stationary test of position accuracy, by placing 7 GPS collars for 24 h at different slopes and canopy covers in SRA. The estimated average deviation from the position mean of these collars was 9.9 m ± 9.4 (SD). We downloaded the data directly from the GPS collars after the grazing season and loaded positions into R version 3.4.4 (R Core Team, 2018). To eliminate location errors, we used a screening method developed by Bjørneraas et al. (2010) which removes locations more than 20 km from the previous position, as well as locations differing by > 2 km from an average moving window of 21 positions. Furthermore, we considered all positions forming a spike in the movement trajectory as error positions and removed all spikes with outgoing and incoming speed exceeding 1500 m/h and the turning angle being between 166° and 194°. In total, the GPS collars registered 1 694 560 cow positions during the three grazing summers, and the average percentage of GPS success (ratio of post-screening to programmed positions) was 98.2% during the 5–10 min positioning attempts.

Systematic observations of GPS-collared cows in summer 2015 allowed us to calibrate the data of the built-in activity sensors based on

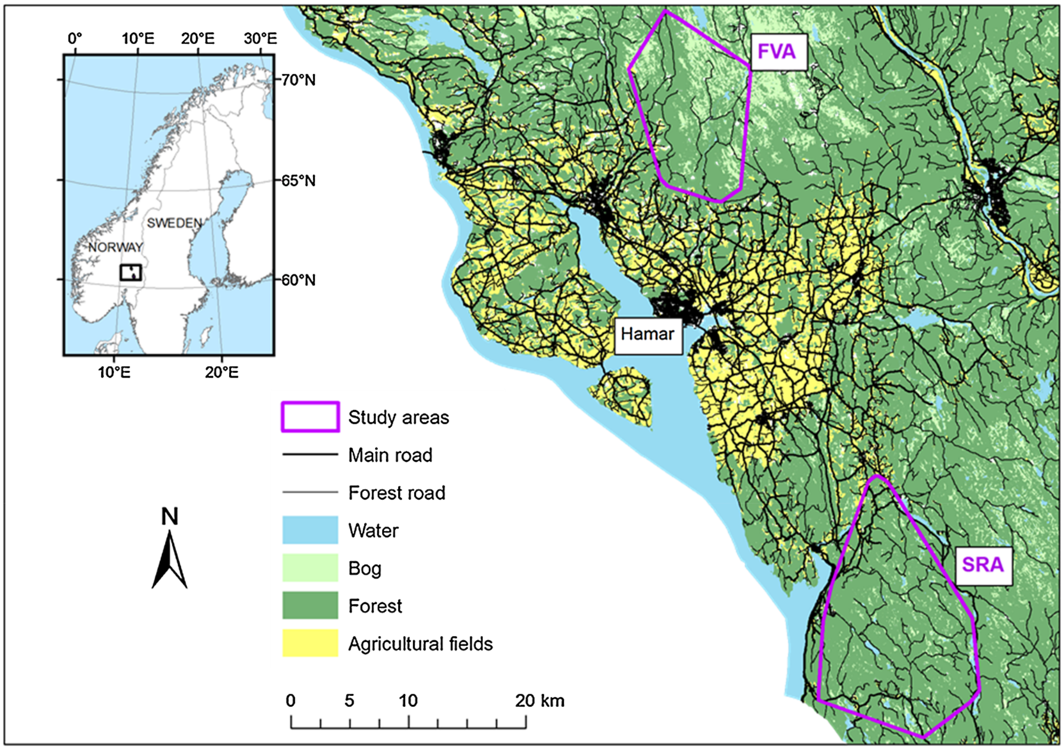

Fig. 1. Location of the study areas in Furnes/Vang almenninger (FVA) in 2016 and 2017 and Stange/Romedal almenninger (SRA) from 2015 to 2017 in south-eastern Norway.

Table 1
Distribution of vegetation types (%) (Rekdal, 2010, 2017), proportion of cow positions located in these vegetation types for the two study areas SRA (Stange and Romedal almenninger) and FVA (Furnes and Vang almenninger) and, grouping of vegetation types into the three foraging classes; Less Good (LG), Good (G) and Very Good (VG) based cattle feeding value (Rekdal, 2010; 2017).

	SRA		FVA		
Vegetation types	Cover	Cow positions	Cover	Cow positions	Foraging classification
Lichen and heather pine forest	13.2	3.1	21.6	5.0	LG
Bilberry pine forest	17.2	13.2	0.0	0.0	LG
Bilberry spruce forest	58.0	65.6	44.4	69.9	G
Meadow spruce forest	1.8	3.9	4.0	10.3	VG
Meadows	0.7	10.4	0.8	9.3	VG
Bogs and non-productive areas	2.0	1.4	14.5	0.9	LG
Other forests[a]	7.1	2.4	14.7	4.6	LG

[a] Bog and swamp forests.

Table 2
Distribution (%) of random points (reflecting availability) and GPS positions (reflecting use) in the regrouped cutting classes (New-Class) of pine and spruce forest for the study areas SRA and FVA in south-eastern Norway. The cutting classes are defined as 2.1 = Forest in regeneration 0–15 years after timber harvesting, 2.2 = Forest in regeneration older than 15 years, 3 = Young production forest in thinning stage, 4.5 = production forest in harvesting stage and old-growth forest.

New-Class	SRA		FVA	
	Random	Used	Random	Used
2.1	15.7	46.1	14.3	44.5
2.2	14.4	10.0	15.5	18.7
3	31.6	20.4	42.1	22.8
4.5	38.3	23.5	28.1	14.0

neck movement and distance moved between positions (Tofastrud et al., 2018). By following the method described by Ungar et al. (2005), we used a classification model to assign all 5-minute positions of the 52 study animals carrying Medium plus GPS collars to one of these activity categories: Resting (inactive or ruminating while lying or standing, low neck and locomotion activity), Grazing (high neck and low or intermediate locomotion activity) and Walking (high neck and locomotion activity). The global time budget showed that the cows spent 63 ± 0.5% of the time Resting, 34 ± 0.5% Grazing and 3 ± 0.2% Walking (Tofastrud et al., 2018).

2.3. Resource mapping

We created the following layers in ArcGIS 10.6 (Esri, 2017):

Vegetation layer: We created polygon layers based on the information from the vegetation maps. We retained all vegetation types of the coniferous forest. We considered summer farm meadows to be of great importance for grazing cattle and retained these areas as one distinctive class despite of the small total surface (Table 1). In order to restrict the number of small-scaled or less used vegetation types, we merged bogs and non-productive areas into a "bogs and non-productive areas" group, and all swamp and bogs forests into "other forests".

Forestry layer: We used information from the forestry plan services Allma (Allma - Allskog Mjøsen Skog og AT Plan, 2017) by permission of the management of the respective communal areas to create polygon layers of cutting classes and forest stand age, based on the number of years after timber harvesting (Table 1). The Norwegian stand classification of productive forest consists of five cutting classes: (1) Clearcuts before regeneration, (2) young forest stands, (3) early production forest in the thinning stage, (4) mature production forest, and (5) old-growth forest (Allma - Allskog Mjøsen Skog og AT Plan, 2017). We regrouped these cutting classes into four classes (New-Class) to better describe the light supply to the forest ground and thereby the grazing value as a function of tree height and density. Bjor and Graffer (1963) found that productive forests lost importance for grazing livestock 12–15 years after timber harvesting. Therefore, we combined cutting class 1 with class 2-stands younger than 15 years into a new class 2.1, cutting class 2-stands older than 15 years as 2.2, cutting class 3 remained unchanged and cutting classes 4 and 5 were combined into new class 4.5 (Table 2).

Topography and road layer: We created topographical raster layers describing elevation, slope and aspect at 25 m resolution, based on the official digital elevation model of the Norwegian Mapping Authorities. Aspect was classified into the four cardinal directions, north, east, south, and west, in addition to flat when slope = 0°. We created a raster layer of Euclidean distances to roads by using the Spatial Analyst tool in ArcGIS.

We imported all resource layers into R 3.4.4 (R Core Team, 2018) for further statistical analysis.

2.4. Resource selection function (RSF) models

Since the spatial scale of our study was at the habitat type level, i.e. Johnson's (1980) third order, we compared used positions to those available inside each study animal's home range, following the design III approach in resource selection modelling (Manly et al., 2002). We created 100% minimum convex polygons (MCP) including all positions per animal and year, to delineate 78 individual home ranges. We preferred 100% MCP over 95% MCP or probabilistic methods due to the temporally dense positioning (5 or 10 min) and the removal of outliers during the screening process, see chapter 2.2. Within each home range, we created random points equal to the number of cow positions. We then joined the resource layers to used positions and random points to describe used and available habitat. We used generalized linear mixed models (GLMMs) with a binary response (1 = used, 0 = random points) using the *lme4* package (Bates et al., 2015) in R. We checked the fixed predictors (resources variables) for collinearity using Pearson correlation coefficients and included only predictors at $r_s < 0.6$. We nested individual cow within herd as a random effect to control for temporal autocorrelation, uneven sample sizes and the lack of independence between individual cows within herds (Gillies et al., 2006). We standardized all continuous covariates from 0 to 1 in order to compare the strength of selection among these covariates and achieve a better model performance.

We modelled habitat selection of free ranging cows in relation to: (1) vegetation classes (categorical with six levels) and the abiotic factors: distance to roads (continuous), slope (continuous), elevation (continuous) and aspect (five-level categorical, including the four cardinal directions and flat terrain), by one model for each study area hereafter named vegetation models. (2) Forest classes (by creating New-Class combining forest stand and age) and the same abiotic factors as above, by one model for each study area hereafter named forest models. (3) Same as 2), but one model per behavioural state Grazing, Walking and Resting.

For model selection, we started with the full models including all covariates and used Bayesian information criteria (BIC) (Burnham and Anderson, 1998) to find the best among competing models (Tables 3–5). We conducted a lasso variable selection (Tibshirani, 1996) and cross-validation on the fixed components of our models including all covariates (see: Supplementary material for lasso plot of vegetation models).

We tested the predictive ability of our models by calculating the Brier score (Fenlon et al., 2018) for each subset in a 10-folds cross-validation procedure. We present the Brier score for each model in Tables 3–5.

3. Results

Overall, the generalized linear mixed models including all covariates had the strongest support. We found high differences in the ΔBIC value between the best-ranked and second best-ranked model for all habitat selection models and chose to report the fully saturated models (Tables 3–5). The lasso method agreed with the BIC in selection of the best-ranked models (see: Supplementary material for lasso plot of vegetation models). We found the strongest support for candidate models including both biotic (vegetation and New-Class) and abiotic (distance to roads, slope and aspects) covariates and chose the most complex models for investigation of ecologically important covariates on habitat selection (Aho et al., 2014).

3.1. Habitat selection of cattle in relation to vegetation classes and abiotic factors of the coniferous forest

The vegetation models were based on 1 067 305 and 627 255 positions located inside the area with mapped vegetation of SRA and FVA, respectively (Table 1). The best-ranked vegetation models explaining the probability of habitat use included vegetation class, distance to roads, slope, elevation and aspect as predictors (Fig. 2, Table 3). The cows spent about two third of their time in the bilberry spruce forest, the most common vegetation type with 58.0% and 44.4% of the total area in SRA and FVA, respectively (Table 1). The summer farm meadows were the most preferred vegetation type, covering only 0.7% and 0.8% of the areas and holding 10.5% and 9.4% of all positions in SRA and FVA, respectively (Table 1). In addition to summer farm meadows and bilberry spruce forests, cows in FVA used deciduous/swamp forests and lichen pine forests more than cows in SRA (Fig. 2). Open bogs were the least selected vegetation type in FVA (Table 1, reference value in Fig. 2). In SRA, cows selected for areas close to roads, while roads did not really relate to habitat use in FVA (Fig. 2). They selected in both areas for low elevations and slightly for flat areas (Fig. 2). Areas facing south were preferred most in both study areas, while areas facing north in SRA and east in FVA were preferred least (Fig. 2). The cross-validated Brier score for the vegetation models of RSA (BS = 0.085) and FVA (BS = 0.102) indicates a relatively good predictive ability (Table 3).

3.2. Habitat selection of cattle in relation to forest classes of the productive forest

A total of 1 219 716 GPS positions (74.0%) were located in areas of productive coniferous forests, because of the difference in study years between the study areas the proportion of positions was higher in SRA (57.5%) compared to FVA (42.5%). The best-ranked forest models for SRA and FVA were the full models including the variables New-Class (regrouped cutting classes), distance to roads, slope, elevation and aspect (Fig. 3). The cows highly preferred stands logged less than 15 years ago (i.e., New-Class 2.1). These stands covered 17.5% and 14.3% of the forested areas and hosted 46.1% and 44.5% of all cow positions in SRA and FVA, respectively (Table 2). We also found a strong preference for forest of cutting class 2 older than 15 years (i.e., New-Class 2.2) for cows at high stocking density in FVA, with 18.7% of the positions located in stands that covered 15.5% of the area. In SRA however, all stands other than New-Class 2.1 were used less than expected (Table 2). Similar to the vegetation models, the forest models showed decreasing probability of use with increasing elevation in both study areas. Cows preferred forested areas close to roads in SRA, and slightly avoided

Table 3
Model selection results of four a-priori models of habitat selection for free-ranging cattle in areas of low (SRA) and, high stocking density (FVA) in southeastern Norway. The models include the covariates vegetation class, direction of aspect and the standardized values of distance to roads, slope and elevation. The table shows the ranking of candidate models, the number of parameters in the model (K), Bayesian information criterion (BIC) estimates, differences in the BIC (ΔBIC) and Brier Score. Cow ID and herd was nested as a random intercept for all models.

	Veg class	Dist road sd	Slope sd	Elev sd	Aspect dir	K	BIC	ΔBIC	Brier score
mod_SRA1	x	x	x	x	x	14	2,165,136	0	0.085
mod_SRA4	x	x				9	2,209,934	44,797	0.088
mod_SRA3	x	x	x			11	2,203,605	38,469	0.091
mod_SRA2	x	x	x	x		12	2,197,356	32,219	0.107
mod_FVA1	x	x	x	x	x	14	1,417,636	0	0.102
mod_FVA4	x	x				8	1,455,899	38,263	0.103
mod_FVA3	x	x	x			9	1,455,788	38,153	0.136
mod_FVA2	x	x	x	x		10	1,422,633	4997	0.139

Table 4
Model selection results of four a-proiri models of habitat selection for free-ranging cattle in areas of low (SRA) and, high stocking density (FVA) in southeastern Norway. The models include the covariates New forest class (regrouped cutting classes), direction of aspect and the standardized values of distance to roads, slope and elevation. The table shows the ranking of candidate models, the number of parameters in the model (K), Bayesian information criterion (BIC) estimates, differences in the BIC (ΔBIC) and Brier Score. Cow ID and herd was nested as a random intercept for all models.

	N. forest class	Dist road sd	Slope sd	Elev sd	Aspect dir	K	BIC	ΔBIC	Brier score
mod_SRA1	x	x	x	x	x	13	1,822,341	0	0.153
mod_SRA4	x	x				7	1,852,532	30,191	0.154
mod_SRA3	x	x	x			8	1,851,374	29,034	0.159
mod_SRA2	x	x	x	x		9	1,843,462	21,121	0.170
mod_FVA1	x	x	x	x	x	13	1,193,075	0	0.140
mod_FVA2	x	x				7	1,226,813	33,738	0.144
mod_FVA3	x	x	x			8	1,222,918	29,843	0.166
mod_FVA4	x	x	x	x		9	1,199,316	6241	0.170

Table 5
Model selection results of four a-priory models of habitat selection for free-ranging cattle while performing resting (Rest), grazing (Graz) and walking (Walk) in SRA and, FVA in southeastern Norway. The models include the covariates New forest class (regrouped cutting classes), direction of aspect and the standardized values of distance to roads, slope and elevation. The table shows the ranking of candidate models, the number of parameters in the model (K), Bayesian information criterion (BIC) estimates, differences in the BIC (ΔBIC) and Brier Score. Cow ID and herd was nested as a random intercept for all models.

	N. forest class	Dist road sd	Slope sd	Elev sd	Aspect dir	K	BIC	ΔBIC	Brier score
Rest_mod1	x	x	x	x	x	13	1,444,133	0	0.111
Rest_mod4	x	x				6	1,470,842	26,709	0.113
Rest_mod3	x	x	x			7	1,469,155	25,022	0.123
Rest_mod2	x	x	x	x		8	1,456,082	11,950	0.132
Graz_mod1	x	x	x	x	x	13	718,423	0	0.216
Graz_mod4	x	x				6	731,814	13,391	0.216
Graz_mod3	x	x	x			8	731,824	13,400	0. 230
Graz_mod2	x	x	x	x		7	721,834	3411	0.234
Walk_mod1	x	x	x	x	x	13	83,717	0	0.101
Walk_mod2	x	x	x	x		9	83,886	169	0.104
Walk_mod3	x	x	x			8	84,241	524	0.109
Walk_mod4	x	x				7	84,509	792	0.111

those areas in FVA (Fig. 3). The most preferred aspects were west in SRA and south in FVA, while the least preferred aspects were east in SRA and north in FVA (Fig. 3). The cross-validated Brier score for the forest models of RSA (BS = 0.153) and FVA (BS = 0.140) indicates a relatively good predictive ability (Table 4).

3.3. Habitat selection of cattle at different behavioural states

In total, monitoring of 52 cows fitted with Medium plus GPS collars resulted in 1 229 493 observations of cow activity. All positions were located in areas of productive forest and classified as Resting (62.1%), Grazing (34.1%) and Walking (3.8%). The best-ranked models included the same fixed effects as the forest models (Table 5). Cows selected strongest for clearcuts younger than 15 years (New-Class 2.1) in all behavioural states, but their selection for these forests stands was 1.6 and 2.5 times stronger while grazing than while resting or walking, respectively (Fig. 4). They preferred young forest stands < 15 years while Grazing, less so while walking and least while Resting. Stands in the thinning stage (New-Class 3) were selected more than mature forest stands (New-Class 4.5) while Grazing and Walking, but less while Resting (Fig. 4). The cows were more likely to stay closer to roads while Walking rather than Grazing and Resting, and the distribution of positions located closer than 5 m to roads was 4.9%, 6.0% and 25.4% for Resting, Grazing and Walking, respectively. Probability of use was slightly positively related with slope while Grazing, but negatively while Resting or Walking (Fig. 4). Selection for south-facing slopes was strongest during Resting, while avoidance of north-facing slopes was strongest during Grazing (Fig. 4). The cross-validated Brier score of the behavioural states models, resting (BS = 0.111), grazing (BS = 0.216) and walking (BS = 0.111) indicates a relatively good predictive ability (Table 5).

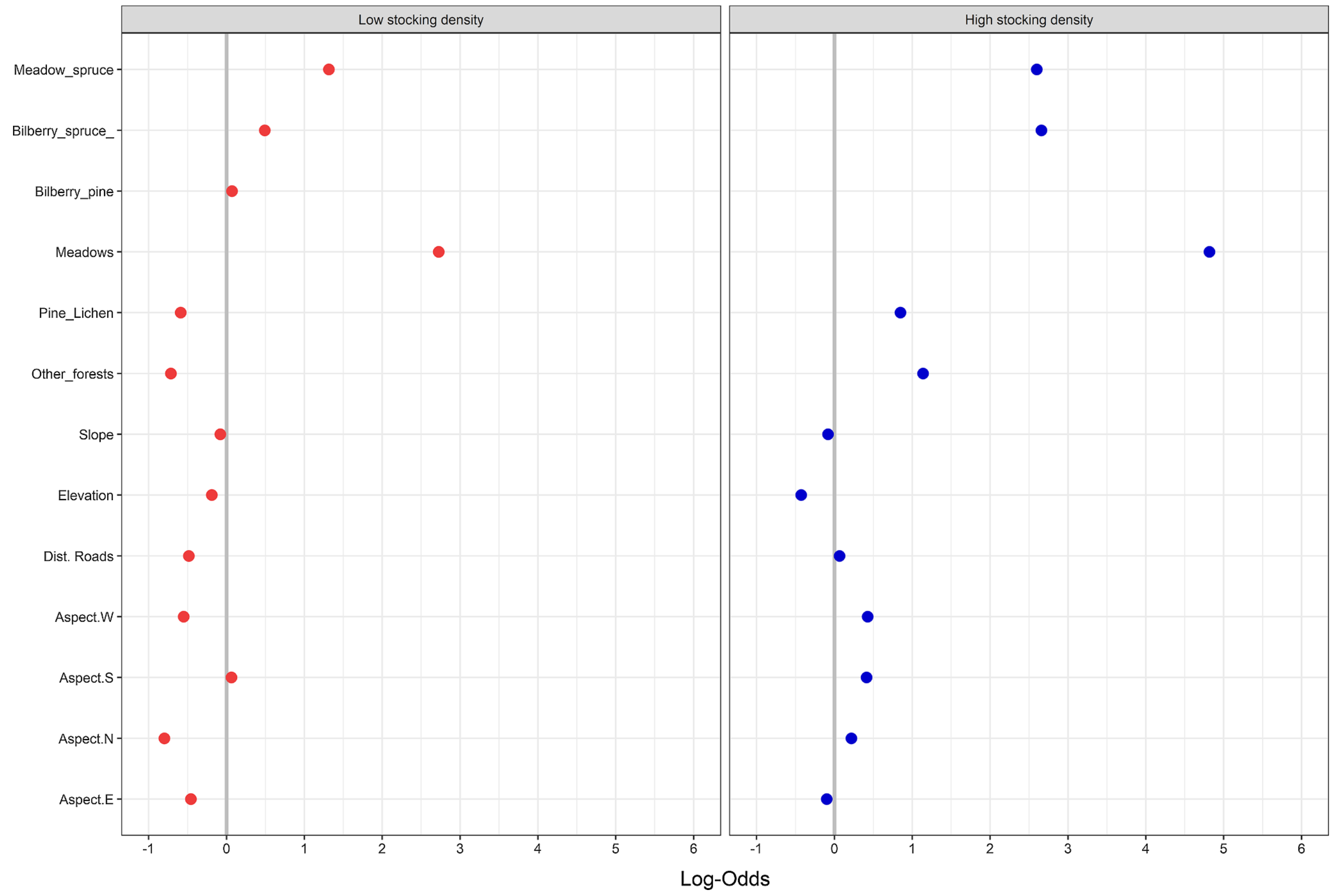

Fig. 2. Parameter estimates (log-odds) from vegetation models of free ranging cows during summer in boreal forest of southeastern Norway, at low (SRA) and high (FVA) stocking density. The log-odds of the vegetation types and aspects refer to bogs/non-productive and flat areas, respectively. The log-odds of the continuous scaled covariates slope, elevation and distance to road indicate the importance and direction of the relationship between selection and the covariate. The 95% confidence intervals of the log-odds were small and therefore only partly visible.

4. Discussion

The free-ranging cows preferred the summer farm meadows and young forest stands (≤15 years old) (Fig. 3) of primarily the bilberry spruce forest (Fig. 2). Although we did not measure the biomass of the different vegetation types, the classification system based on vegetation mapping (Rekdal, 2010, 2017), pointed out summer farm meadows as the most productive vegetation type, followed by bilberry spruce forest, and pine and swamp forests as well as bogs as the areas with lowest forage production for livestock. We consider the summer farm meadows and young forest stands as crucial for maximizing food intake of livestock in coniferous forests which are characterized by a ground floor dominated by heather or bare ground as a result of nutrient-poor soils and tree shading (Larsson and Rekdal, 2000). In a previous Norwegian study, Bjor and Graffer (1963) found that grazing cattle preferred open grasslands, although the use of this habitat decreased throughout the grazing season. Correspondingly, the cattle increased their time spent in areas dominated by *Vaccinium myrtillus* (bilberry heather) and *Avenella flexuosa* (wavy hair grass) during the summer.

Assuming appropriate stocking densities, grazing herbivores have the potential to maintain the nutritive value of forage plants by grazing the young regrowth on earlier grazed sites (Wallis De Vries, 1996), and they therefore maintain a strong preference for grazing in forest openings and clearcuts (Bjor and Graffer, 1963). However, if stocking density is high, competition for resources on those habitat patches may lead to an increased use of suboptimal habitats, according to the ideal free distribution hypothesis (Fretwell and Lucas, 1969). Our study design with only two study areas that differ not only in stocking density, but also in elevation, cattle release dates and other factors, does not allow for testing the impact of stocking density on cattle habitat selection. We can only speculate that the observed stronger selection for the nutrient poor pine and swamp forests and young forest stands older than 15 years in the high stocking density area FVA as compared to the low stocking density area SRA may be a result of increased resource competition. Wet areas are often dominated by plant species of low nutritional value like *Cyperaceae* spp. (sedges and rushes) and *Deschampsia caespitosa* (tufted hairgrass) (Garmo, 1986), which are avoided by free-ranging cattle as long as the dry areas offer the cows sufficient forage (Hessle et al., 2008).

In a study performed in the boreal forest of southeastern Norway, Herfindal et al. (2017) found low levels of interspecific interactions between cattle and moose. The dietary overlap between moose and livestock is considered low (Dorn, 1970), as moose are browsers (Mysterud, 2000) while cattle prefer grass and herbs (Gordon, 1989). Nevertheless, livestock has shown to reduce the foraging potential of the moose caused by changes in the amount and composition of forage, or by avoidance of areas grazed by domestic herbivores (Wam and Herfindal, 2018). In our study, cattle grazing in the area with high stocking density showed an increased use of habitats with higher tree densities and swamp forests in addition to the clearcuts. High densities of grazing cattle may therefore result in higher levels of interactions between cattle and moose, thus affecting moose fitness and an increased risk of disease transmission (Martin et al., 2011).

The forest industry is dependent on a network of forest roads and trails for timber harvesters. The cows in our study used these trails as important travel routes between clearcuts. We assume that this is the

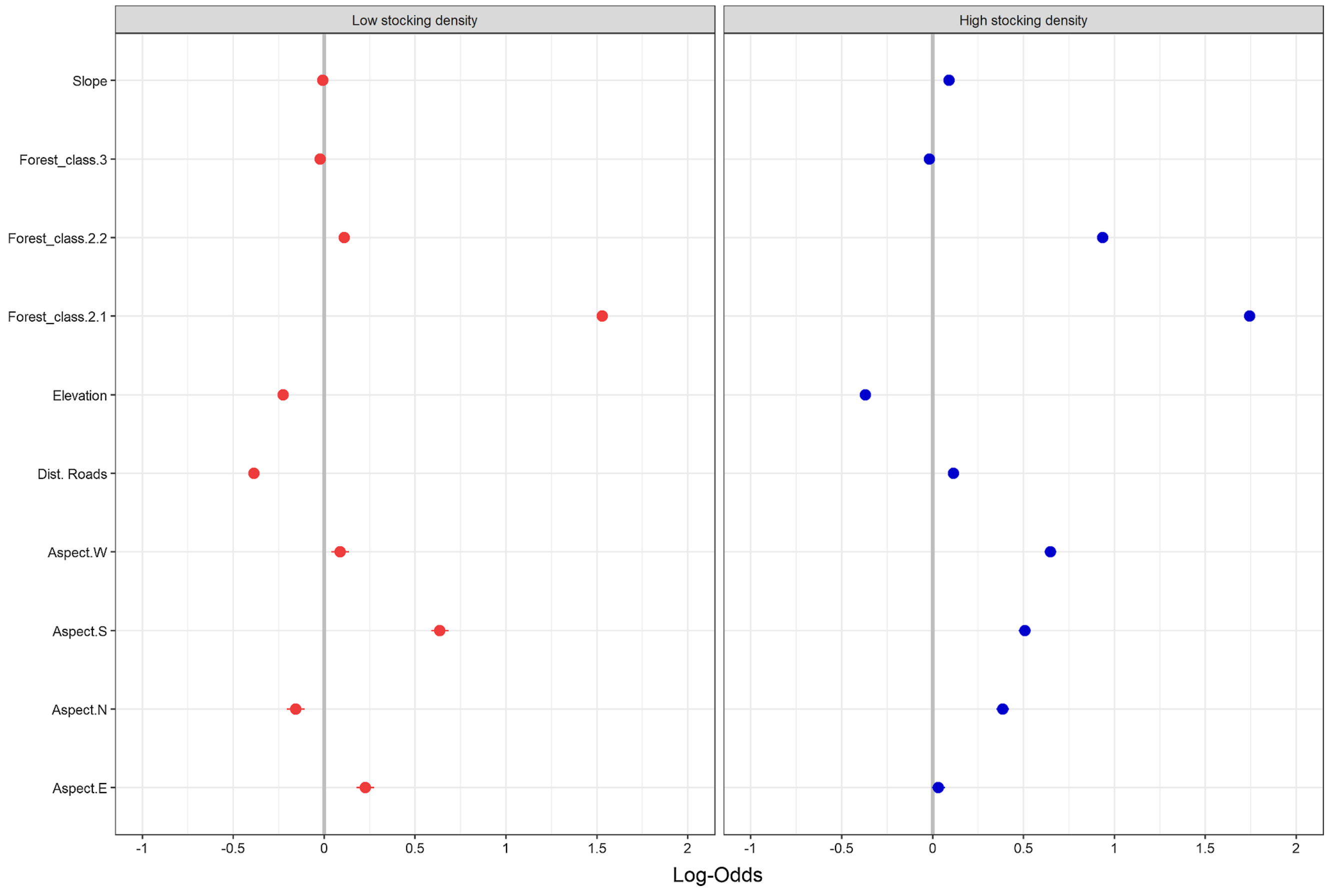

Fig. 3. Parameter estimates (log-odds) from forest models of free ranging cows in productive forests stands, at low (SRA) and high (FVA) stocking density. The log-odds of the forest classes and aspects refer to forest class 4.5 (mature and old growth forest) and flat areas, respectively. The log-odds of the continuous scaled covariates slope, elevation and distance to road indicate the importance and direction of the relationship between selection and the covariate. The 95% confidence intervals of the log-odds were small and therefore only partly visible.

most energy-saving way of travelling in the rough terrain with dense understory vegetation. Travelling made up only 3% of the cows' daily time budget, whereas resting made up approximately two third and grazing one third of their time (Tofastrud et al., 2018). When analysing habitat selection independently from the behaviour, we saw that cows in the low stocking density area SRA kept close to roads at all times, whereas they instead selected for areas further away from roads in the high stocking density area FVA. We assume that this difference may also be explained by the Ideal free distribution hypothesis: cows at high density must travel further away from the easy travelled forest roads to find optimal grazing sites. Roath and Krueger (1982) found logging roads to be an important factor for cattle distribution. In a study performed in the foothills of the Rocky Mountains, Kaufmann et al. (2013b) found cattle to avoid forest roads.

Animals react to heat stress by reducing their activity and seeking shelter in cooler habitats. Hahn (1999) observed that cattle reduced their activity when air temperatures exceeded 25 °C. Other studies showed that cattle preferred canopy cover in dense forest as shelter in warm periods (Miller and Krueger, 1976; Putfarken et al., 2008; Larson-Praplan et al., 2015). In Norway, Bjor and Graffer (1963) reported that cows stayed inside dense coniferous forest and performed less grazing activity during periods of heavy rain, heat and insect swarming. Although more than half of the forested areas in our study consisted of grown-up forest stands of cutting class ≥3, only 29.4% of all positions were located within these stands. This proportion was similar for Resting, Walking and Grazing. Cows rather preferred open areas for resting in our study. Heat stress may not have been an important factor here. On only 19 days during the three study summers, the maximum temperature exceeded 25 °C (Norwegian Meteorological Institute, 2018).

Previous studies have reported topography to be of importance for cattle distribution (Kaufmann et al., 2017). Inclined stands of bilberry forest have been suggested as good pastures as a result of high levels of leaching water in the upper soil layers (Rekdal and Angelhoff, 2016). Kaufmann et al. (2013b) reported slope to be the main abiotic factor of cattle habitat use. Bailey et al. (1996) stated that steep slopes were less used by cattle, and Ganskopp and Vavra (1987) showed that cattle preferred grazing in flat areas and avoided slopes exceeding 20%. In our study, slope had low importance for cattle habitat selection. Cows however preferred areas of low elevation, and they preferred slopes with the greatest access to light facing south- and west, over north- and east-facing slopes. We assume that this is a result of a more favourable microclimate for plant productivity.

Distance to water is considered as important for determining vegetation utilization by cattle (Pinchak et al., 1991; Putfarken et al., 2008; Kaufmann et al., 2017) but was not taken into account in our study since water was readily available in small ponds, streams and bogs in both study areas.

5. Conclusion

The strong preference of cattle for the small patches of summer farm meadows and young forest regeneration stands of the bilberry spruce forest indicates that these human-made habitat patches strongly improved grazing opportunities for cattle. While the summer farm meadows were originally established for livestock grazing in the previous

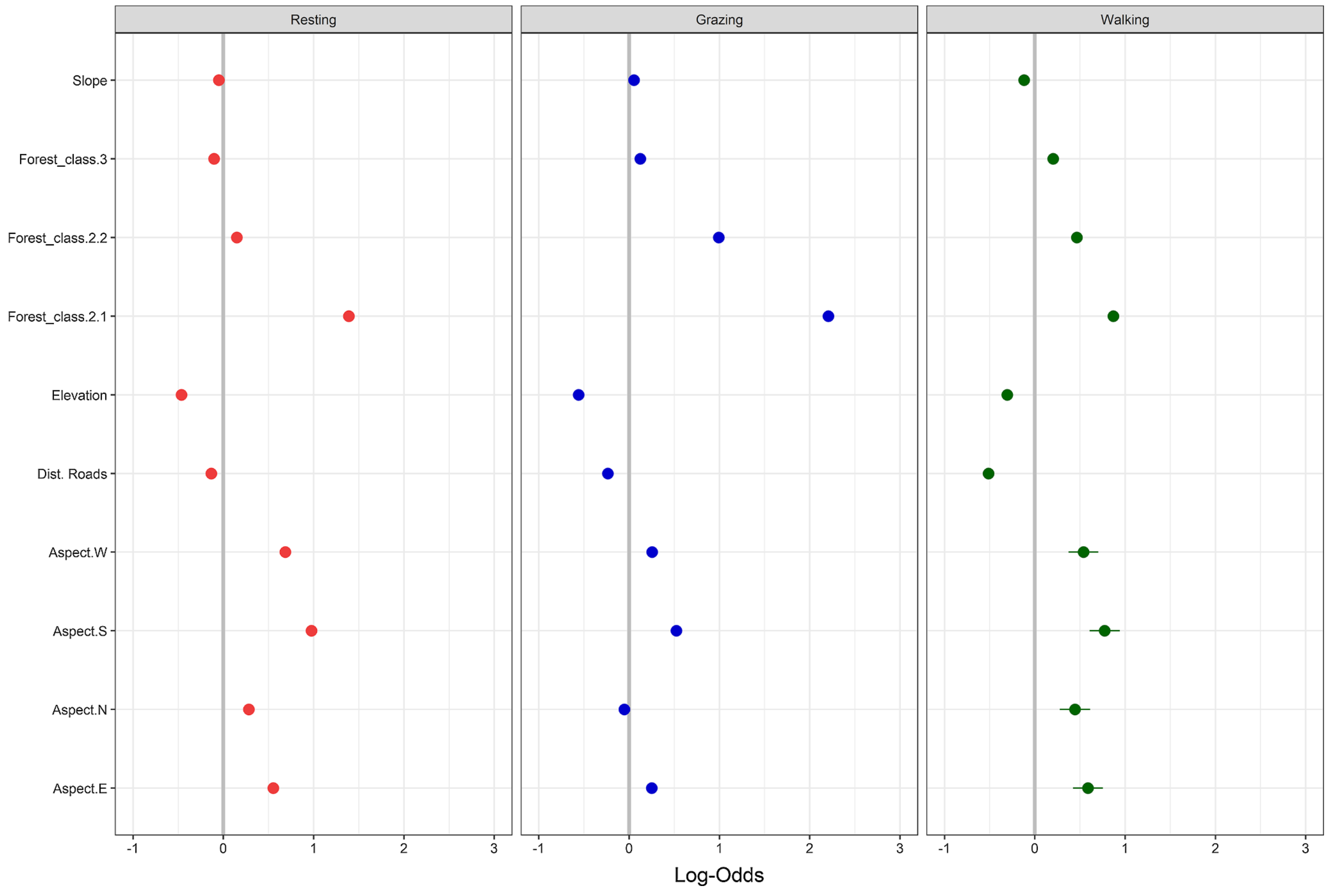

Fig. 4. Parameter estimates (log-odds) from activity models of cows in productive forests stands, during Resting, Grazing and Walking. The log-odds of the forest classes and aspects refer to forest class 4.5 (mature and old-growth forest) and flat areas, respectively. The log-odds of the continuous scaled covariates slope, elevation and distance to road indicate the importance and direction of the relationship between selection and the covariate. The 95% confidence intervals of the log-odds were small and therefore only partly visible.

centuries, the clearcuts are a mere result of timber harvesting. Food provision to domestic and wild ungulates is therefore a side effect on these young forest stands, with potential negative (e.g. trampling) and positive (e.g. weeding) impacts on forest regeneration. To trade-off potential impacts of livestock grazing on forest regeneration and maintain foraging opportunities of wild herbivores, managers of communal forests, farmers and wildlife managers should cooperate in order to adapt stocking densities and the distribution of cows in the communal areas based on vegetation and forestry maps. To provide more quality forage for livestock and reduce potential negative impacts on young forest stands, we propose to improve the feeding capacity of existing summer farm meadows by weeding, drainage and fertilization.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.01.014.

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