Faculty of Applied Ecology and Agricultural Sciences

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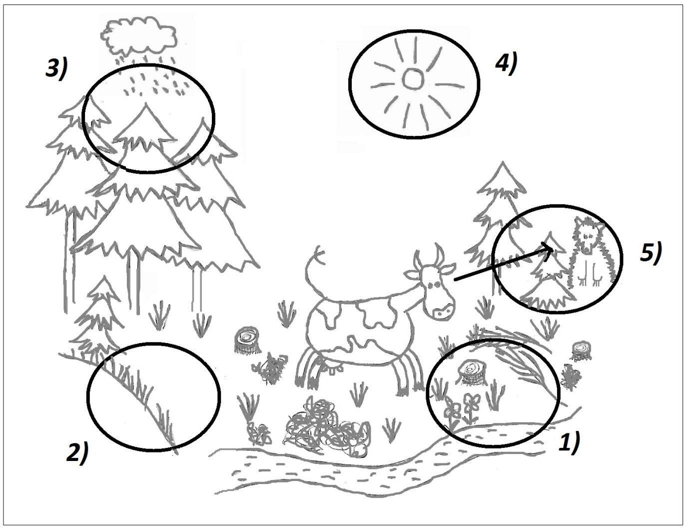
Master thesis

Micro habitat selection by beef cattle on summer pasture in boreal forest, south-eastern Norway



Master in Applied Ecology
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Abstract

Grazing systems are diverse. With a low percentage of the land area being suitable for agriculture, forest grazing is an important part of livestock husbandry in Norway. While many studied focus on the effects of forest grazing on forest, studies on the effects on cattle are less common. The goal of this study was to identify the factors influencing the microhabitat selection by grazing and resting beef cattle at summer pasture in boreal forest. 16 female adults cows were equipped with GPS collars and activity sensors during summer grazing in 2017 in Hedmark county, Norway. Positioning and activity data were used to identify grazing and resting positions. At these positions, habitat variables were recorded following a matched case-control sampling design. The data was analysed using generalized linear mixed models. The results show that grazing cattle's microhabitat selection is influenced by other factors than resting cattle's microhabitat selection. The probability of use by grazing cattle was positively correlated with the percentage of grasses in the ground cover only. The probability of use by resting cattle was positively correlated with the percentage of grasses in the ground cover and positively with canopy cover and negatively with incline. These findings increase our knowledge on habitat selection by cattle and can be applied to the management of common use forested lands and to the management of cattle on pastures.

Key words: beef cattle, boreal forest, *Bos taurus,* GLMM, matched case-control design, micro habitat selection

Sammendrag

Mangfoldet av beitesystemer er stort. Skogsbeite er en viktig del av den norske husdyrproduksjonen, siden bare en liten andel av landets areal eier seg for landbruk. Mens effektene av skogsbeite på skog har blitt undersøkt gjennom mange studier, effektene på storfe er undersøkt mindre. I vårt studie identifiserte vi faktorene som påvirker mikrohabitat valget av beitende og hvilende kjøtfe på sommerbeite i boreal barskog. 16 voksene kuer var utstyrt med GPS halsbånd og aktivitetssensorer i beitesesongen 2017 i Hedmark fylke, Norge. Basert på datene om posisjon og aktivitet identifiserte vi posisjoner for beite og hvil. Basert på et spesielt studie design, «matched case-control sampling design» på engelsk, samlet vi in dater om habitat variabler på disse posisjonene. Vi analyserte datene ved bruk av generaliserte lineare blannete modeller (GLMM). Resultatene våres viste at mikrohabitat valget av beitende storfe er påvirket av andere faktorere enn mikrohabitat valget av hvilende storfe. For beitende storfe, vi fant en positiv sammenheng mellom sannsynligheten for utnyttelse av dyret og andelen av gress i markvegetasjonen. For hvilende storfe, vi fant en positiv sammenheng mellom sannsynligheten for utnyttelse av dyret og andelen av gress i markvegetasjonen, en positive sammenheng mellom sannsynligheten for utnyttelse av dyret og kronedekningen og en negativ sammenheng mellom sannsynligheten of utnyttelse av dyret og hellingsgraden. Funnene våres øker kunnskapen om habitat valg av storfe og kan anvendes i forvaltning av almenninger og i forvaltningen av storfe på beite.

Nøkkelord: boreal barskog, *Bos taurus*, GLMM, kjøttfe, matched case-control design, mikrohabitat valg

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1. Introduction

Cows rule the world: In the year 2000, cattle and water buffaloes accounted for nearly two-third of the total live weight of domesticated animals, which are dominating the biosphere's vertebrate zoo mass (Smil 2014). Cattle grazing systems are diverse. Besides grass land pastures there are mountain, woodland and forest pastures. In Norway, with only a low percentage of the land area being suitable for agriculture, the utilization of non-agricultural land, in particular forest and mountain areas, as summer pastures is an important part of livestock husbandry. This practice has a long tradition of 5000-6000 years (Austrheim et al. 2008) and in 2016, more than 8 000 horses, 58 000 goats, 250 000 cattle and 2 000 000 sheep were released (Landbruksdirektoratet, 2018). In order to increase Norway's food self-sufficiency, the county governor of Hedmark aims for an increased beef meat production and thereby increased number of forest grazing beef cattle (Fylkesmannen i Hedmark 2014). While many studies have been carried out on the effects of forest grazing on the forest (Adams 1975; Mosquera-Losada, Riguerio & McAdam 2005; Hjeljord, Histol & Wam 2014), studies on the effects on the cattle are less common. We decided to study cattel's habitat selection. Bred to graze on open, flat, homogenous grass fields, how do they behave in a very heterogenous habitat with vertical and horizontal structure, uneven ground, a patchy distribution of food resources and sporadic visits of large carnivores?

Studies of habitat selection, "the process by which an animal chooses which habitat components to use" (Hall, Krausman & Morrison 1997), are a major part of ecology, which is the study of interactions between organisms and their environment. These studies are typically conduced by comparing used to available or to unused habitat (Manly 2002). Habitat availability is not generally uniform in nature, but varies with space and time. Arthur et al. (1996) presented a method allowing to account for these changes by defining availability separately for each observation of habitat use. Every observed location is paired with several potential locations that are locally available to but not used by the individual at a given time. Habitat selection has shown to be dependent on the studied animal's species, sex, age, perception of the environment, experience, social status, physical condition and behavioural activity as well as on the studie's temporal and spatial scale (Johnson 1980; Manly 2002; Mayor et al. 2009; Morrison, Marcot & Mannan 2006; Prima, Duchesne & Fortin 2017). Habitat selection by cattle in boreal forest has been studied in Canada, California (U.S.), Oregon (U.S.) and Sweden, at different temporal and spatial scales, focusing either on herds or on groups of individuals, specific or not on certain behaviours (Roath & Krueger 1982; Gillen, Krueger & Miller 1984; Kie & Boroski 1996; Walburger et al. 2009; Steyaert et al. 2011; Kaufmann et al. 2013, 2017).

In this study, we focused on micro habitat selection by female adult beef cattle, released on common use forested lands in four municipalities in south-eastern Norway during the grazing period 2017. The animals were equipped with GPS collars and activity sensors, allowing us to determine their position and behaviour. Since cattle have been shown to spend 90-95 % of their day grazing, ruminating and resting (Kilgour 2012), we decided to focus on grazing and resting cattle. The goal of this study was to identify the factors influencing their micro habitat selection, asking the question: "At that precise moment, why has the cow been grazing or resting right here and not over there?"

Cold stress in cattle has been observed at temperatures far below 0°C and during exposure to precipitation (Van laer et al. 2014). Heat stress in cattle has been observed at temperatures above 25 °C (Berman et al. 1985; Hahn 1999; Ominski et al. 2002). Accounting for possible uncertainty in these findings, we expect cattle to show heat avoidance behaviour at temperatures above 20 °C. The presence of the large carnivore species brown bear (*Ursus arctos*), wolf (*Canis lupus*), lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) has been reported and confirmed in the study area in 2017 (Rovbase, 2018).

Cattle are (1) foraging and resting on the ground, with a herbivores diet and no more body protection than their skin, (2) large and heavy animals, struggling to manoeuvre in steep terrain, (3) homeothermic animals, avoiding undercooling, (4) homeothermic animals, avoiding overheating and (5) prey animals, hiding away or watching out for predators. Hence we expect the factors (1) ground cover composition, (2) incline, (3) canopy cover in combination with rainfall, (4) sun exposure in combination with temperature and (5) visibility to influence their micro habitat selection (Figure 1). We expected the observed cattle to select (1) for different ground cover categories depending on their behaviour, (2) for low incline, (3) for high canopy cover given rainfall, (4) against sun exposure given an air temperature above 20 °C and (5) for either low or high visibility.

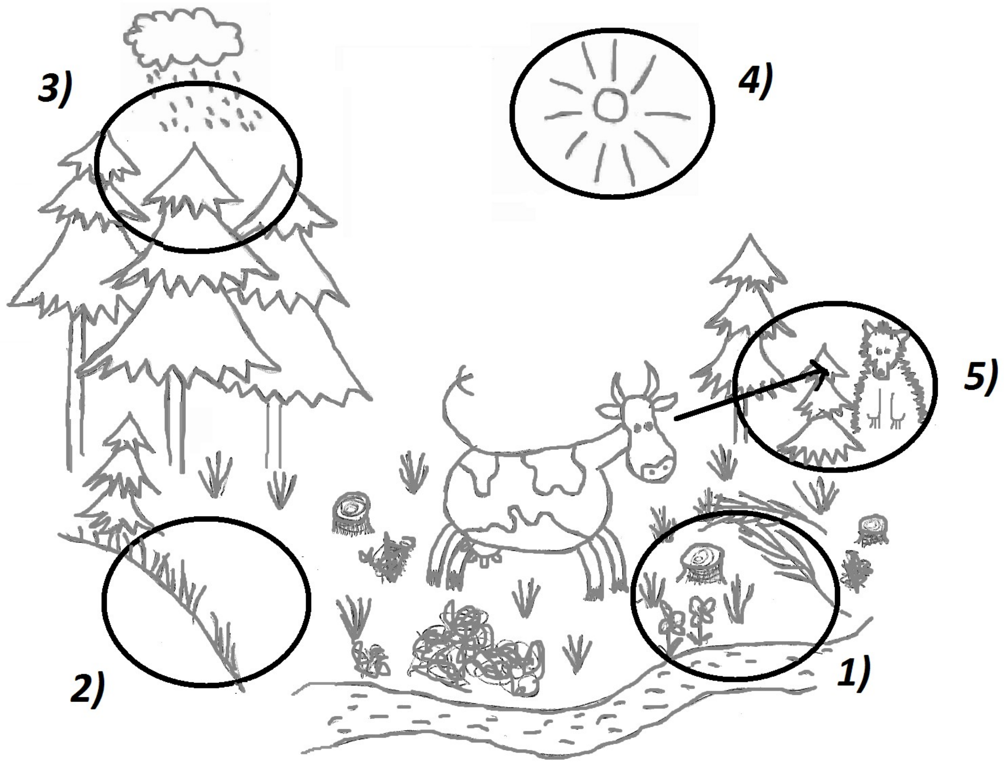


***Figure 1**: Factors considered in this study potentially influencing micro habitat selection by cattle: 1) ground cover composition, 2) incline, 3) canopy cover, 4) sun exposure and 5) visibility.*

2. Material and methods

2.1. Study area and period

The study area was located in Hedmark county in south-eastern Norway at 61° East and 11° North and consisted of the common use forested lands Furnes/Vang (FVA) and Stange/Romedal (SRA) (Figure 2). The climate in the study area is continental with cold winters and warm summers. Snow generally stays on the ground from late October until mid April, seasonality of climate and light conditions are strong and the growing season is short. The common use forested lands of FVA are about 120 km^2 large and located at an altitude ranging from 600 to 700 m.a.s.l.. Around 45 % of the area is covered by spruce forest, 20 % by pine forest and 35 % by wetland (M. Angeloff, personal communication). Around 380 cows and 1500 sheep were released for summer grazing in this area in 2017 (M. Tofasrud, personal communication). The common use forested lands of SRA are about 150 km^2 large and located at an altitude ranging from 300 to 450 m.a.s.l.. Around 60 % of the area is covered by spruce forest, 30 % by pine forest and 5 % by wetland (Rekdal 2017). Around 360 cows and 1200 sheep were released for summer grazing in this area in 2017 (M. Tofasrud, personal communication). We collected the data throughout the grazing period from the 28th of June and the 24th of August in 2017.

2.2. Weather stations

Since the closest weather stations of the Norwegian Meteorological Institute are situated in the valley, collecting data irrepresentative for the weather in our study area, we installed two weather stations with-in the study area. These WH-1080 weather stations (Clas Ohlson AB, Insjön, Sweden, 2010) recorded and stored air temperature (°C) and rainfall (mm/hour) at 5 minutes intervals. The first weather station was situated in FVA (60.959326° East, 11.0470266° North), around 4 m from the ground and thereby at 544 m.a.s.l. The second weather station was situated in SRA (60.5572488° East, 11.3442017° North), around 4 m from the ground and thereby at 481 m.a.s.l. (Figure 2). In SRA, during the study period, the temperature ranged from 2.6 °C to 25.4 °C, with an average of 13.4 °C and the hourly rainfall ranged from 0 mm to 11.1 mm, with an average of 0.11 mm. In FVA, during the study period, the temperature ranged from 2.9 °C to 28.6 °C, with an average of 13.0 °C and the hourly rainfall ranged from 0 mm to 25.2 mm, with an average of 0.11 mm.

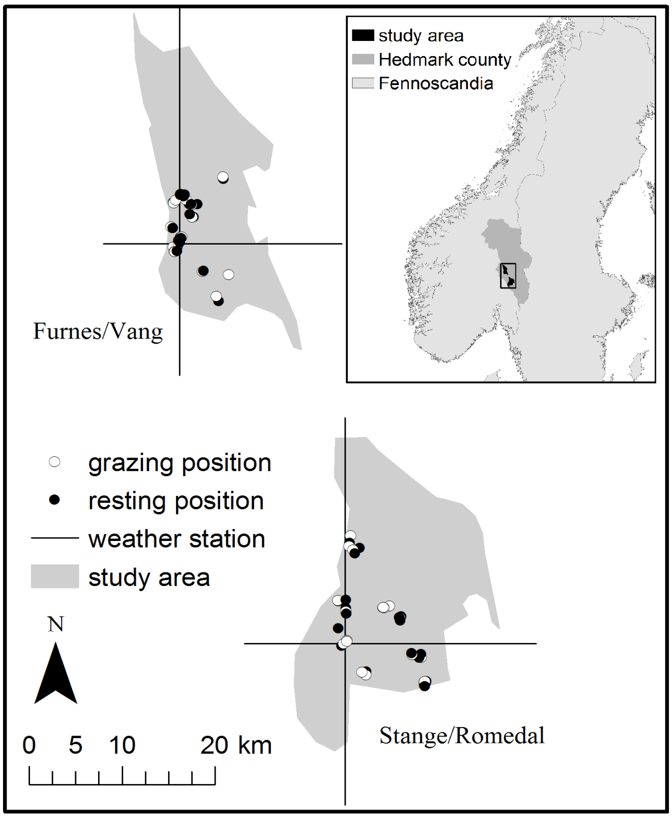


Figure 2*: Map of the study area. Common lands of Furnes/Vang (FVA) in the North and Stange/Romedal (SRA) in the South (grey shaded areas). Visited grazing positions (white points) and resting positions (black points) and installed weather stations (crossing of the lines).* Created in *ArcGIS 10.2.2 (ESRI 2011)*

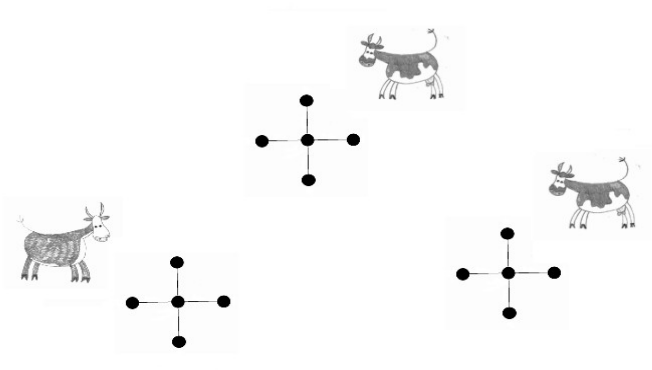


Figure 3: *Dependency structure in our data: Five plots per position and several positions per cow.*

2.3. Cattle

The study animals were 16 adult female cows (*Bos taurus*), 12 with and 4 without calf, from 11 different farms and of 5 different breeds, namely Charolais, Hereford, Aberdeen Angus, Simmental and Limousin and mixes between them. Our study complies with the Norwegian legislation on animal experimentation and animal welfare. We did not need any ethical approval from the authorities.

2.4. GPS collars and accelerometers

The animals were equipped with Followit Tellus Medium Plus (Followit Lindesberg Sweden AB, 2013) GPS collars with integrated dual-axis accelerometer. The GPS receivers were programmed to fix positions every 5 minutes. Time to Fix (TTF), that is the time for the GPS receiver to acquire satellite signals and calculate the position, was set to a maximum of 90 seconds. Within TTF, animal activity was recorded by the accelerometer. The sensitivity of the activity sensors was set to the highest level. We divided the measured activity values by TTF in order to obtain comparable values in the unit pulses per second. Positioning and activity data were sent per SMS to and were available through an internet based positioning portal, called Followit Geo™ and located at http:://geo.followit.se/.

2.5. Visited positions

Every morning before leaving for the field, we downloaded the positioning and activity data available for the previous 24 hours. Between the cows with available data, we randomly chose one, aiming for a balanced sample with three grazing and three resting positions per cow. Based on the downloaded data and an earlier study on the calibration of activity data (Tofasrud, unpublished), we identified grazing and resting sessions and chose representative positions from the middle of such sessions to visit in the field for data collection. To ensure high accuracy and precision, these positions had to be based on at least 4 satellites. Grazing sessions were identified by activity values above 3 pulses per second on both X and Y axis and distances < 100 m travelled between positions, whereas resting sessions were identified by activity values of 0 on both X and Y axis and no distance travelled over a period of several positions (Tofasrud, unpublished). Out in the field, we checked for signs of recent grazing or resting at the chosen positions. The few positions not showing any such signs were discarded from the pool of visited positions.

2.6. Sampling design and recorded variables

To account for spatio-temporal changes in the availability, we followed the matched case-control sampling approach introduced by Arthur et al. (1996), defining availability separately for each observation of habitat use. At each visited position we created five plots: the central plot, which the cow had been to, and four control plots. These control plots were placed to each cardinal direction, 50 m from the central plot (Figure 3). We considered the distance of 50 m short enough to represent availability on the microhabitat scale and large enough to account for inaccuracy in the GPS positions. If a plot was not accessible to the cattle, for example because it was in a fenced area, we discarded it from the sample. Following this rule, we discarded 4 control plots.

At each plot, we recorded the variables of interest (Figure 1). Some variables were recorded on the plot area, while others were recorded at the plot centre. Based on cattle's body size, we decided for a plot area of 10 m^2, which gave a plot radius of 1,78 m. On the plot area, we recorded *incline* and *ground cover* composition. *Incline*, defined as the mean of the absolute inclines in the four cardinal directions, was measured in percentage with a 1,78 m long stick and a clinometer. *Ground cover* was divided into predefined categories (Table 1) and the plot area belonging to each of these categories was measured in percentage by visual judgement. At each plot, the plot area belonging to these categories added up to 100 %. At the plot centre, we recorded *canopy cover*, *sun exposure* and *visibility*. *Canopy cover* was measured in percentage with the application HabitApp on a Samsung Galaxy Tab 10.1 ™ (Samsung Electronics, 2016) tablet. *Sun exposure*, defined as the absence of any cover between cow and sun, was measured by visual judgement, based on the position of the sun at the time the cow had been at the central plot of a given position, determined with the application CalcSun on a Samsung Galaxy Tab 10.1 ™ tablet. A value of 0 corresponded to night time or presence of trees and hills shading the cow and a value of 1 corresponded to day time and absence of any such trees and hills. *Visibility*, defined as the mean of the distances to the first obstacle at cattle eye level parallel to the ground in the four cardinal directions, was measured in meters with a measure tape.

***Table 1**: Predefined categories for ground cover and their definitions.*

Category	**Definition**
obstacles	Rocks, trees, water surfaces, etc., preveting a cow from standing or lying on this plot
dead_material	Bare ground, gravel, dead plant material, etc.
lichens_mosses	All lichen and moss species
herbs	All herbaceous plant species
shrubs	Woody species, including heather (*Erica* spec. and *Calluna* spec.), berries (*Rubus idaea* and *Vaccinium* spec.) and tree seedlings under 30 cm height
grasses	All graminoid species, including the families Poaceae, Cyperaceae and Juncaceae

2.7. Data analyses

The goal of this study was to model the *probability of use* by cattle at different plots according to their habitat characteristics measured in the field. Models predicting the *probability of use* have been termed resource selection probability functions (RSPF) and can be estimated using logistic regression (Manly 2002). Since we expected different factors to influence the microhabitat selection of cattle according to their behaviour, we decided to fit models for grazing and resting separately.
We explored and analysed our data in R, a Language and Environment for Statistical Computing, with the RStudio interface (RStudio Team 2016; R Core Team 2017), following the protocols by Zuur et al. (Zuur, Ieno & Elphick 2010; Zuur & Ieno 2016). Exploring the data through plots created with the R package ggplot2 (Wickham 2009), we encountered neither zero troubles in the response nor outliers in any variable. We encountered some collinearity problems related to the *ground cover* composition. Being part of the same composition, the categories of *ground cover* were positively correlated and should not be directly used in a regression model.

We followed an approach presentet by Hron, Filzmoser & Thompson (2012) based on the isometric logratio (ilr) transformation allowing to include all the categories of a composition in the same model. Since the interpretation of the parameter estimates demands caution and since the small sample sizes of our data did not allow us to include all the variables in the global models we decided to analyse the *ground cover* composition data separately. This allowed us to identify the categories effecting the *probability of use* by cattle and to include only these categories in the global models later on. For reasons described below, the models were generalized linear mixed models (GLMMs) of the binomial family and including position ID nested into cow ID as random effects. For the ilr-transformation, we used the R package compositions (van den Boogaart, Tolosana & Bren 2014). For the presentation of the model output, we computed the parameter estimates and their 95 % confidence intervals of the intercept and the first coordinate of the composition of each of the 6 regressions, using the R package lme4 (Bates et al. 2015). With this data, we created forest plots using the R package ggplot2. The categories for which the 95 % confidence interval of the parameter estimate of the corresponding coordinate did not include the value 0 were included in the global models later on.

We checked for collinearity among the remaining explanatory variables and, based on Pearson correlation coefficient ($|r| < 0.6$), they could all be included in the same model.

While figuring out the best way of modelling the expected interactions between *canopy cover* and *rainfall* and between *sun exposure* and *temperature*, we noticed that our data was inappropriate for this purpose. It had been raining on only 5 and the temperature had exceeded 20 °C on only 6 out of the 81 positions. Alternatively, we decided to include the variables *canopy cover* and *sun exposure*, but not *rainfall* nor *temperature* in the global models.

Data sampled following a matched case-control design can be analysed using conditional logistic regression (CLR), which has become a common tool in habitat selection studies (McLoughlin et al. 2010; Prima, Duchesne & Fortin 2017), or using generalized linear mixed models (GLMMs) of the binomial family, with the pairing variable included as random intercept. Parameter estimation using CLR relies on within-strata variability and can not be done for explanatory variables that only vary between strata (Kleinbaum & Klein 2002), e.g the cow ID at the different positions in my data. Parameter estimation using GLMMs, however, is not restricted in that way. By including additional random effects it is possible to account for unbalanced sample designs, spatial autocorrelation, variation in behaviour and selection among individuals and functional responses in selection (Gillies et al. 2006; Aarts et al. 2008; McLoughlin et al. 2010). In order to account for the dependency structure in our data (Figure 3), for changing availability between positions and for unbalanced sampling among cows, we decided for the GLMM approach with a varying intercept for *position ID* nested within *cow ID*. Besides these random effects, the global model included the fixed effects *incline* (continuous), *canopy cover* (continuous), *sun exposure* (binary), *visibility* (continuous) and its squared effect, and, based on the composition analyses, *grasses* (continuous), that is the percentage of grasses in the *ground cover* (Equation 1). The global model was the same for grazing and resting.

$$
\begin{aligned}
&P_{ijk} \sim Bin(\pi_{ijk}\,;1)\\
&logit(\pi_{iik}) \sim \alpha + \beta_1 * grasses_{iik} + \beta_2 * incline_{iik} + \beta_3 * canopycover_{iik}\\
&\qquad\qquad + \beta_4 * sunexposure_{ijk} + \beta_5 * visibility_{ijk} + \beta_6 * visibility^2 + b_i + b_{ij}\\
&b_i \sim N(0, \sigma^2_{cowID})\\
&b_{ij} \sim N(0, \sigma^2_{positionID})\\
&i = 1, \ldots, 17\\
&j = 2, \ldots, 9\\
&k = 4, 5
\end{aligned}
\tag{1}
$$

where P_{ijk} is the probability of use at the k^{th} plot at the j^{th} position of the i^{th} cow.

To improve the interpretability of the regression parameters, we centred and standardized the explanatory variables (Schielzeth 2010), using the R package standardize (Eager 2017). We fitted the model using the glmer function in the R package lme4.

We did model selection based on the second order Akaike Information Criterion (AICc), which is measuring both the fit and the complexity of the model and correcting for small sample sizes. We selected for the model with the lowest AICc value and considered models with a difference in AICc below 2 as equivalent. Among equivalent models, we chose the simplest one following the principle of parsimony. Since the random effects resulted from the study design, we only selected on the fixed effects. Due to the high number of candidate models, we used the automated model selection function dredge from the R package MuMIn (Barton 2017). Dredge generated models with all possible combinations of fixed effects included in the global model and ranked them according to their AICc value.

Model assumptions was based on plots generated with the R package DHMARMa (Hartig 2017). To determine homogeneity of variances, we plotted the scaled residuals versus the predicted values.

To determine normality of errors, we plotted the predicted versus the observed residuals. To determine independence of errors, we plotted the scaled residuals versus each variable in the model and versus each variable not in the model. We assessed the residuals for temporal dependency. To present the model output, we computed the parameter estimates and their 95 % confidence intervals of the variables included in the best model using the R package lme4 and created forest plots using the R package ggplot2. For model visualization, we plotted the predicted *probability of use*, that is its mean and 95 % confidence interval, and the observed presence against the variables included in the model. The variables included in the model but not shown in the graph were held constant at their mean.

3. Results

3.1. Sample sizes

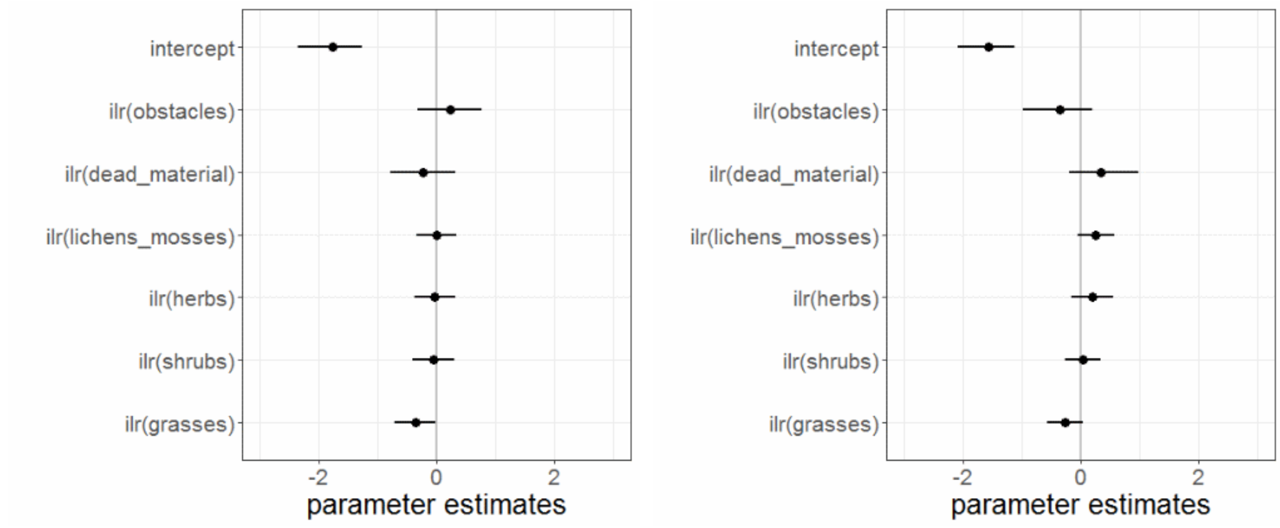
Since some collars were temporary out of GSM signal and send their positioning and activity data with a delay of some hours or days, our sample consisted of on unequal number of positions per cow. For grazing, the sample size was 178, that is 36 central and 142 control plots. For resting, the sample size was 223, that is 45 central and 178 control plots.

3.2. *Ground cover* composition analyses

The results of the *ground cover* composition analyses are presented in Figure 4. For both grazing and resting, only the 95 % confidence interval of the parameter estimate for the coordinate corresponding to the category *grasses* did not include the value 0. This means that, for both grazing and resting cattle, only the category *grasses* is correlated with *probability of use* by cattle. Therefore we decided to include only this *ground cover* category in the global models later on.

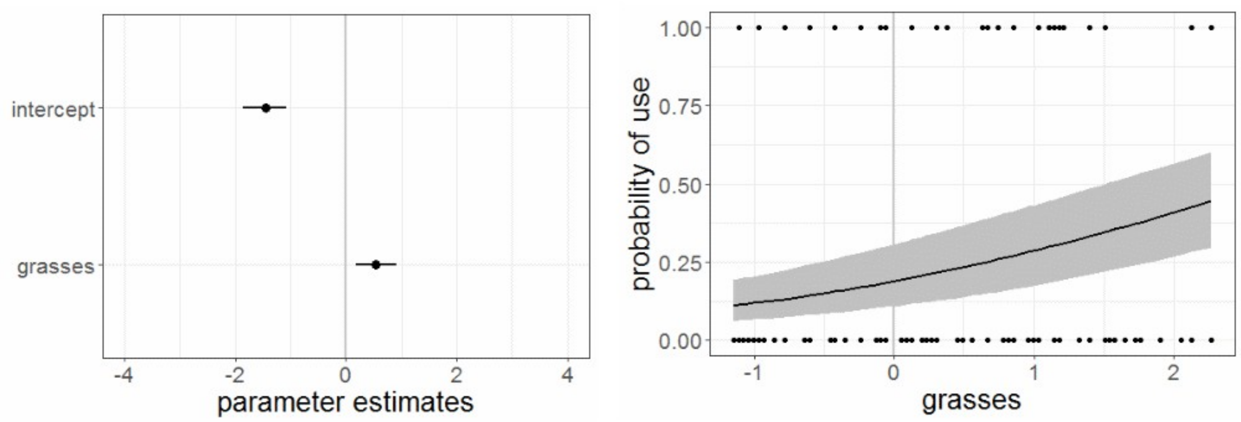
3.3. *Probability of use* by grazing cattle

Model mg1, our best model for explaining the variation in *probability of use* by grazing cattle, included the fixed effect *grasses* and the random effects *position ID* nested within *cow ID* (Table S1, Appendix S1). The variance of both random effects was 0. Model validation indicated no violations of the underlying assumptions. Model outcome and predictions for mg1 are presented in Figure 5. According to mg1, the linear predictor of the response was positively correlated with the variable *grasses*. Since the logistic function is monotonically increasing, this means that the response itself, that is *probability of use* by grazing cattle, was positively correlated with the variable *grasses.* Hence grazing cattle selected for a high percentage of grasses in the ground cover.



a) *b)*

***Figure 4**: Results, that is mean and 95 % confidence interval of the parameter estimates from regression of* probability of use *by a) grazing cattle and b) resting cattle on the ilr-transformed ground cover categories. It is important to emphasize that in each graph the results of six regression models are shown, because in each model we focus only on the estimation of the parameters corresponding to the first coordinate and the intercept.*

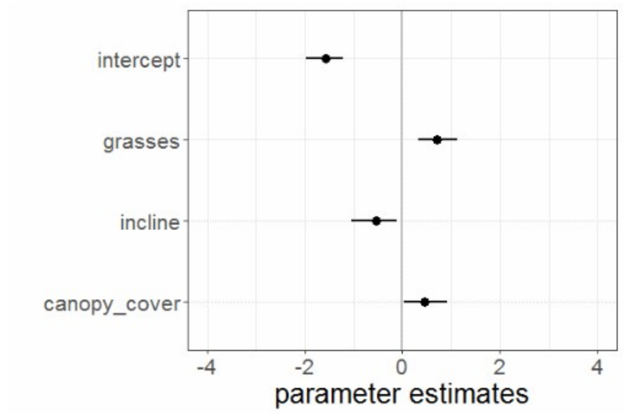


a) *b)*

***Figure 5**: Model output and predictions for our best grazing model: a) mean and 95 % confidence interval of the parameter estimates and b) predicted* probability of use *(line) with 95 % confidence interval (ribbon) and observed presence/absence (points) by grazing cattle against the standardized variable* grasses.

3.4. *Probability of use* by resting cattle

Model mr1, our best model for explaining the variation in *probability of use* by resting cattle, included the fixed effects *grasses*, *incline* and *canopy cover*, as well as the random effects *position ID* nested within *cow ID* (Table S2, Appendix S1). The variance of the random effects was 0. Model validation indicated no violations of the underlying assumptions. Model output and predictions for mr1 are presented in Figure 6. According to mr1, the linear predictor of the response is positively correlated with the variables *grasses* and *canopy cover* and negatively correlated with the variable *incline*. Since the logistic function is monotonically increasing, this means that the response itself, that is *probability of use* by resting cattle is positively correlated with the variables *grasses* and *canopy cover* and negatively correlated with the variable *incline*. Hence resting cattle selected for a high percentage of grasses in the ground cover, for high canopy cover and for low incline.



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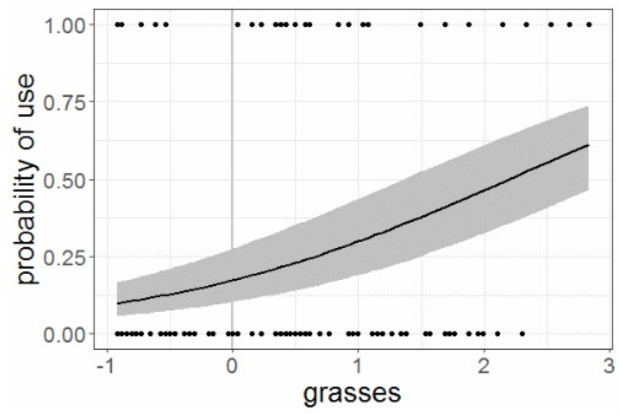
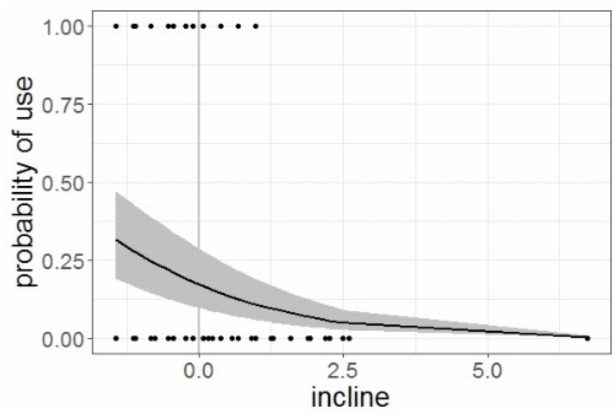
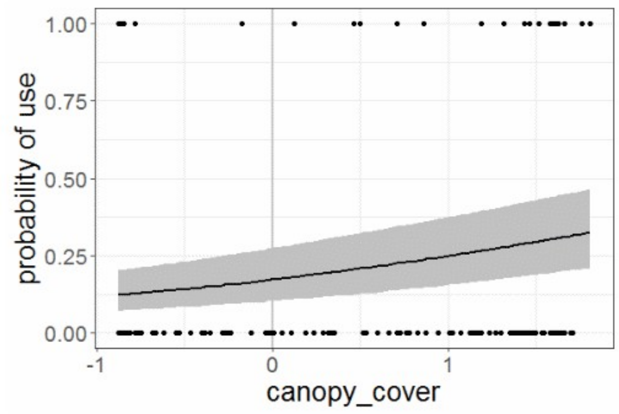


b)



c)



d)

Figure 6*: Model output and predictions for our best resting model: a) mean and 95 % confidence interval of the parameter estimates. Predicted* probability of use *(line) with 95 % confidence interval (ribbon) and observed presence/absence (points) by resting cattle against the standardized variable b)* incline, *c)* canopy cover *and d)* grasses*, with the remaining variables set at their mean.*

4. Discussion

In this study, we expected the factors (1) ground cover composition, (2) incline, (3) canopy cover in combination with rainfall, (4) sun exposure in combination with temperature and (5) visibility to influence micro habitat selection by cattle. According to the results, grazing cattle's microhabitat selection was influenced by the ground vegetation category grasses only, whereas resting cattle's microhabitat selection is influenced by grasses, incline and canopy cover.

Although we expected cattle to select for different ground cover categories depending on their behaviour, we found the same results for grazing and resting cattle. For both, we found that *grasses* was the only *ground cover* category correlated with *probability of use* and for both, this correlation was positive. Hence both grazing and resting cattle select for high percentage of grass in the ground cover. For grazing cattle, this is surprising, since they have been shown to forage not only on grasses, but on herbs, shrubs and trees as well (Holechek et al. 1982; Kie & Boroski 1996; Rutter 2006; Mandaluniz, Aldezabal & Oregui 2011; Bele, Johansen & Norderhaug 2015). For resting cattle, this is surprising as well, since grass is not the only comfortable ground cover category. For grazing cattle, explanations for our findings could be inappropriate measurement in covered plot area, not taking into account the vegetation's height and nutritial value, inappropriate definitions of the ground cover categories, including both edible and unedible species in the same category, or the relative importance of the category grasses in cattle's diet. For resting cattle, explanations for our findings could be inappropriate definitions of the ground cover categories, including both comfortable and uncomfortable species in the same category or the possible fact that cattle like to rest where they have been grazing before.

Although we predicted both grazing and resting cattle to select for low incline, we found that *incline* was negatively correlated with *probability of use* by resting cattle only. Explanations for our findings could be the fact that the process of a cow getting up from lying to standing position is far more ground support demanding (Dalgaard & Gjødesen 2010), than the process of moving around, once in standing position. The selection for low incline of free-ranging cattle in boreal forest, on various spatial scales and independent on their behaviour, has been shown in several studies (Gillen, Krueger & Miller 1984; Walburger et al. 2009; Kaufmann et al. 2013).

Since it has been raining at only 5 out of the 81 positions, we were not able to test the prediction on cattle's selection for canopy cover given rainfall. However, Bjor & Graffer (1963) and Vandenheede et al. (1995) found that cattle do seek shelter when it is raining. By including *canopy cover*, but not *rainfall* in the models, we found different results for grazing and resting cattle. For grazing cattle there was no and for resting cattle there was a positive correlation between *canopy cover* and *probability of use.* We could not find any explanation for this difference. The correlation observed for resting cattle could be a consequence of previous rainfall, a preventive measure to potential subsequent rainfall or not related to rainfall at all. Based on our data, rainfall at the moment the cow was resting at the position can be excluded as possible explanation. Canopy cover might be positively correlated with shelter from harassing insects. Insect are common in boreal forest during summer, are more common in wet, swampy areas than in dense forest stands and have been shown to influence habitat selection of cattle (Bjor & Graffer 1963). Further up in the mountains, insects have been shown to influence habitat selection of reindeer (*Rangifer tarandus*) (Skarin et al. 2004; Vistnes et al. 2008). Canopy cover might be negatively correlated with the accessibility of areas for cattle. Inaccessible areas like slash rich clear cuts or swampy areas with sinking ground often have a low tree density and thereby a low canopy cover. Another explanation could be that our cattle, kept in stables during many months of the year over generations, ended up habituated to and even actively selecting for high horizontal cover.

Since the temperature was above the threshold of 20 °C at only 6 out of the 81 positions, we were not able to test the prediction on cattle's selection for sun exposure given a high air temperature. However, cows have been shown to spend more time in shade on days with high ambient temperature and solar radiation (Bjor & Graffer 1963; Bennett, Finch & Holmes 1985; Schütz et al. 2009). By including *sun exposure*, but not *temperature* in the analyses, we could not find any correlation between *sun exposure* and *probability of use*, neither for grazing nor for resting cattle. Explanations for our findings could be the fact that cattle do not select against sun exposure when it is not hot. Nevertheless, this is only one of many possibilities, neither sustained, nor rejected by my data. It is possible that cows do choose for or against sun exposure, even at temperatures below 20 °C, but that my data is inappropriate to reflect any patterns. Reasons could be my definition of sun exposure, which does not take into account the presence of clouds or the low variation in sun exposure between the plots of each position.

Although we predicted cattle to select for either low or high visibility, we could not find any correlation between *visibility* and *probability of use*, neither for grazing nor for resting cattle. Explanations for our findings could be an inappropriate definition of visibility, not making any difference between visibility, "the property that provides sightlines, which allow an individual to visually detect predators" and concealment, "the property of cover that hides a prey animal from a predator" (Camp et al. 2013). Recording and including both visibility and concealment in the models could solve this problem. We might be wrong assuming that cows detect and are detected by predators by vision. Animals perceive their environment through multiple sensory faculties, including vision, hearing and olfactory (Phillips 2008), and a habitat's property in relation to animal cover and discovery should be based on all of those. Unfortunately, as human beings, we are not able to perceive and thereby measure from an animal's point of perception. Nevertheless, based on the wide hearing range of the cow bells, we can exclude vision as crucial sensory faculty in the given context. We might be wrong assuming that the anti-predator behaviour of individual cows consists of watching out or hiding away from predators. Being big and large animals, they might follow rather fight than flight strategies and being gregarious animals (Lazo 1994), their anti-predator behaviour might be based on the group's rather than on the individual's situation. In bisons (*Bison bison*), anti-predator behaviour has been shown to be dependent on group size (Fortin et al. 2009). We might be wrong assuming that cattle do show anti-predator behaviour. Reasons for this could be the absence of need or ability to express such a behaviour. The need might be enhanced by a low predation risk of the present predator species on cattle, by habitat segregation between the species (Steyaert et al. 2011) or by a low density of predators. The ability might be enhanced as a result of domestication, which cattle has been under for 10.000 years (Womack 2012).

In a future study, the factors concealment, insect harassment and groups size should be included. Concealment could be measured following the methods by Camp et al. (2013) or Ordiz et al. (2009). Insect harassment is hard to measure, since it is dependent on cattle presence and impossible to assess remotely, without disturbing the cattle and modifying their behaviour and habitat selection. Group size is hard to measure for similar reasons. In our study area, the cattle of the different farms have been observed to split up into groups changing in size throughout the grazing period, which is in agreement with the findings by Lazo (1994) on cattle groups' fusion-fission behaviour. Information on group size could be obtained remotely with all the cows released in the study area wearing GPS collars. Other factors shown to influence micro habitat selection by cattle in coniferous forest are distance to roads and water, biomass availability and crude protein concentration (Kaufmann et al. 2013).

Habitat selection has been shown to vary among individuals, breeds and according to group size (Bennett, Finch & Holmes 1985; Fortin et al. 2009; Walburger et al. 2009; Pruitt et al. 2011; Bele, Johansen & Norderhaug 2015). This variation could be accounted for by including individual, breed and group size as random coefficient on the explanatory variables of interest (Gillies et al. 2006; Aarts et al. 2008; McLoughlin et al. 2010). To investigate the cattle's functional response to different resources, position ID could be included as random intercept and coefficient on the explanatory variables of interest (Gillies et al. 2006). Since the sample size of our data is too small to fit such complex models, more data should be collected.

We defined availability separately for each observation, creating four control plots at a distance of 50 m form the actual position. A more appropriate approach would have been to define availability not according to the actual, but the previous position and chose the distance to the control plots according to the distance potentially travelled by the animal during the time step between previous and actual position, that is 5 minutes in this study.

This study is unique by accounting for different behaviours when analysing habitat selection by cattle in boreal forest. Based on direct field observations and continuous variables, it relies on fewer assumptions than studies based on maps and categorical variables. Conducted on the microhabitat scale, this study provides an insight into the relations between cattle and the different resources and conditions present in their immediate environment.

The results of this study are of interest for both science and management. In science, our findings complement the understanding of cattle's habitat selection by supplementing the findings on cattle's habitat selection on other spatio-temporal scales (Mayor et al. 2009; Wiens 1989). Our findings can also help to understand the patterns in cattle’s habitat selection observed in other ecosystems. In the management of common used forested lands, our findings can help to avoid or mitigate potential interest conflicts between livestock husbandry, forestry, nature conservation and recreation by predicting cattle's space use. In the management of cattle at pastures, our findings can help to increase animal welfare by designing the pastures according to the animals' needs.

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Appendix S1

***Table S1**: Models for probability of use by grazing cattle. Table with the 10 models with the lowest AICc values. The models with a Δ(AICc) < 2 are in black, the others in grey. All the models include the random effects* position ID *and* cow ID.

Fixed effects included in the model	Df	AICc	Δ (AICc)	AICc weight
Intercept + *grasses*	4	178.6	0.00	0.093
Intercept + *grasses* + *canopy cover*	5	178.9	0.31	0.080
Intercept + *grasses* + *incline*	5	179.1	0.54	0.071
Intercept + *canopy cover* + *grasses* + *incline*	6	179.3	0.70	0.066
Intercept + *canopy cover* + *incline*	5	180.3	1.70	0.040
Intercept + *grasses* + *sun exposure*	5	180.3	1.74	0.039
Intercept + *grasses* + *incline* + *sun exposure*	6	180.7	2.10	0.033
Intercept + *grasses* + *visibility*	5	180.7	2.11	0.033
Intercept + *canopy cover*	4	180.9	2.30	0.030
Intercept + *canopy cover* + *grasses* + *visibility*	5	180.7	2.11	0.029

***Table S2:** Models for probability of use by resting cattle. Table with the 10 models with the lowest AICc values. The models with a Δ(AICc) < 2 are in black, the others in grey. All the models include the random effects* position ID *and* cow ID.

Fixed effects included in the model	Df	AICc	Δ(AICc)	AICc weight
Intercept + *canopy cover* + *grasses* + *incline*	6	215.2	0.00	0.195
Intercept + *canopy cover* + *grasses* + *incline* + *visibility*	7	215.9	0.68	0.139
Intercept + *canopy cover* + *grasses* + *incline* + *sun exposure*	7	216.6	1.37	0.098
Intercept + *canopy cover* + *grasses* + *incline* + *sun exposure* + *visibility*	8	217.5	2.27	0.063
Intercept + *grasses* + *incline* + *visibility*	6	217.5	2.30	0.062
Intercept + *canopy cover* + *grasses* + *incline* + *visibility* + *visibility*^{2}	8	218.0	2.81	0.048
Intercept + *grasses* + *incline* + *visibility*	6	219.1	3.88	0.028
Intercept + *canopy cover* + *grasses* + *visibility*	6	219.4	4.16	0.024
Intercept + *canopy cover* + *grasses*	5	219.5	4.21	0.024
Intercept + *grasses* + *incline* + *sun exposure*	6	219.6	4.40	0.022