FISEVIER

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

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



Microhabitat selection of free-ranging beef cattle in south-boreal forest

Mélanie Spedener^{a,*}, Morten Tofastrud^b, Olivier Devineau^a, Barbara Zimmermann^a



- ^a Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Department of Forestry and Wildlife Management, Inland Norway University of Applied Sciences, Koppang, Norway
- b Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Department of Agricultural Sciences, Inland Norway University of Applied Sciences, Hamar, Norway

ARTICLE INFO

Keywords:
Bos taurus
Grazing
Resting
Matched case-control design
GLMM

ABSTRACT

Cattle released for summer grazing in south-boreal forest are free to select among a broad range of habitats. The goal of this study was to identify the factors influencing the microhabitat selection of such free-ranging beef cattle, for grazing and resting. We equipped sixteen female adult cows with GPS collars and activity sensors in southeastern Norway during the summer grazing season in 2017. We identified grazing and resting positions based on positioning and activity data. At these positions, we recorded habitat variables following a matched case-control sampling design. We analysed the data using generalized linear mixed models. We found differences in the cattle's microhabitat selection for grazing and resting. Within a given habitat patch, cattle selected for the most grass-rich site for grazing, whereas they selected for the most grass-rich, the flattest and the most covered site for resting.

These findings complement our knowledge on habitat selection of cattle and can be used to design cattle pastures according to the animals needs and to mitigate interest conflicts between livestock husbandry and forestry in communal forested lands in Norway.

1. Introduction

Cattle husbandry is an old and important part of agriculture worldwide (Womack, 2012; Smil, 2014) and takes different forms throughout the world. In Norway, with only a low percentage of land suitable for agriculture, the utilization of non-agricultural land, such as forest and mountain areas, as summer rangeland has a long tradition (Austrheim et al., 2008; Landbruksdirektoratet, 2018). In Southeastern Norway, where this study was conducted, cattle roam freely in large areas of south-boreal forest during the summer. Since little is known about cattles' natural habitat (Van Vuure, 2002), we do not know if this diverse forest ecosystem full of obstacles, slopes and a patchy distribution of food resources comes closer to their natural habitat than the open, flat grasslands they usually are kept on. But at least, in a forest ecosystem, they have the possibility to select from a broad range of habitats. Their selection pattern may indicate some of their basic needs that may not be covered when released on open grasslands and allow us to design cattle pastures in a more appropriate way. Moreover, predicting the cattle's space use within these forested areas could help mitigate interest conflicts between livestock husbandry, forestry, nature conservation and recreation.

Animal's habitat selection depends on the species, sex, age, perception of the environment, experience, social status, physical

condition and behavioural activity as well as on the study's temporal and spatial scale (Johnson, 1980; Manly et al., 2002; Mayor et al., 2009; Morrison et al., 2006; Prima et al., 2017). Habitat selection of 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 to certain behavioural activities (Roath and Krueger, 1982; Gillen et al., 1984; Kie and Boroski, 1996; Walburger et al., 2009; Steyaert et al., 2011; Kaufmann et al., 2013, 2017). Little is known about cattle's habitat selection on a microhabitat scale, which can be directly linked to specific activities in a cow's day and provide understanding of the patterns and the underlying mecanisms of habitat selection on larger scales. According to Kilgour (2012), cattle spend 90–95 % of their time grazing or resting, with ruminating included in resting. Therefore, the goal of this study was to determine the factors influencing cattle's microhabitat selection while grazing and resting.

We expected that: (1) The cattle would select for a different ground cover composition for grazing (i.e. select for food resources) than for resting (i.e. select for comfort). (2) Given their size and weight, cattle would always select for a low incline terrain. (3) & (4) Given cattle are subject to cold stress when exposed to precipitations or to temperatures well below 0 °C (Van laer et al., 2014), and to heat stress when temperatures rise above 25 °C (Berman et al., 1985; Hahn, 1999; Ominski

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

^{*} Corresponding author.

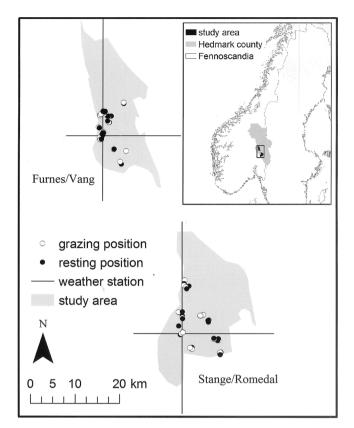


Fig. 1. Map of the areas (FVA and SRA, shaded in grey) where our study on microhabitat selection of free ranging beef cattle at grazing and resting sites in south-boreal forest was conducted in summer 2017. Grazing sites (white points), resting sites (black points) and installed weather stations (crossing of the lines). Created in ArcGIS 10.2.2 (ESRI, 2011) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

et al., 2002), we expected canopy cover and rainfall, sun exposure and temperature to influence habitat selection for both grazing and resting cattle. (5) Finally, because bears and wolfs, which are predators likely to attack cattle (Pimenta et al., 2017; Rovbase, 2018; Steyaert et al., 2011), are present in the study area (Rovbase, 2018), we expected the cattle to select for either low or high horizontal visibility habitat as a predator-avoidance behaviour.

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 two geographically distinct communal forested lands Furnes/Vang (FVA) and Stange/Romedal (SRA) (Fig. 1). The climate in the study area is continental with cold winters, warm summers and a short growing season. FVA is about 120 km² with the altitude ranging from 600 to 700 m.a.s.l. Around 40% of this area is covered by spruce (Picea abies) forest, 20% by pine (Pinus sylvestris) forest and 40% by wetland (Rekdal, 2010). SRA is about 150 km² with the altitude 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). Around 740 cows and 1 700 sheep were released in the study area for summer grazing from late June til beginning of September in 2017 (number of grazing days, mean = 99, sd = 13). Water is no limiting factor in these surroundings full of lakes, ponds, streams and wetlands and no extra water was provided to the livestock. We conducted our fieldwork between the 28th of June and the 24th of August 2017.

2.2. Weather stations

Since the closest weather stations of the Norwegian Meteorological Institute are situated at lower altitudes, collecting data irrepresentative for the weather in our study area, we installed two weather stations with-in the study area (Fig. 1). These WH-1080 weather stations (Clas Ohlson AB, Insjön, Sweden, 2010) recorded and stored air temperature (°C) and rainfall (mm/hour) at five minutes intervals. 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.

2.3. Study animals, GPS collars and activity sensors

In the study area 740 cattle (Bos taurus) from nine farms (four in FVA and five in SVA) were released in 2017. The cattle from one farm tended to move together as one herd, but, similar to the findings by Lazo (1994), they have been observed to split up and/or merge with herds from other farms. We collared 16 adult female cows (eight in FVA and eight in SRA), representing all nine farms and five different breeds, namely Charolais, Hereford, Simmental, Limousin and cross-breeds. Our study animals had been ranging freely previously and were used to wearing cow bells. They were equipped with Followit Tellus Medium Plus (Followit Lindesberg Sweden AB, 2013) GPS collars with integrated dual-axis accelerometer, recording the back-forth (x-axis) and left-right (y-axis) neck movements in pulses/sec. 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™ and located at http:://geo.followit.se/. The GPS were programmed and the data was validated as described by Tofastrud et al. (2018), using the same material on the same animals.

2.4. Sampling design

As typically done for habitat selection studies (Manly et al., 2002), and following Arthur et al. (1996), we compared used to available habitat by defining availability separately for each observation of use. At a given habitat patch, we defined five plots: A plot used at a given time by a given animal and four control plots not used at that given moment by that given animal. The control plots were $10 \, \mathrm{m}^2$ in size (i.e. $1.78 \, \mathrm{m}$ radius) and at $50 \, \mathrm{m}$ to each cardinal direction from the used plot. We considered the distance of $50 \, \mathrm{m}$ short enough to represent availability on the microhabitat scale and large enough to account for inaccuracy in the GPS positions.

A former study conducted in the same project (Tofastrud et al., 2018) allowed us to determine the cattle's activity based on positioning and activity data. Following Tofastrud et al. (2018), grazing sessions were defined as a series of positions with an activity of above 0.3 pulses/sec on both X and Y axis and distances below 100 m travelled between positions, whereas resting sessions were defined as a series of positions with an activity of 0 pulses/sec on both X and Y axis and no distance travelled over a period of several positions. The accurany of activity classification reported by Tofastrud et al. (2018) was 86.1% for resting and 74.8% for grazing.

Every morning, we chose a cow we had not encountered the previous day, with data available for the last 24 h and identified clear grazing and resting sessions in the data set. By this we made sure not to influence the observed patterns by our own presence. Once we had identified such sessions, we chose one position per session to visit in the field for data collection that day. By visiting the chosen positions no

Table 1
Variables recorded to study the microhabitat selection of free ranging beef cattle at grazing and resting sites in south-boreal forest in summer 2017 and their definitions.

Variable	Definition	
Ground cover composition	Composition of the obstacles dead material lichens and mosses herbs shrubs	ground cover according to the following categories, adding up to 100 % at each plot: rocks, trees, water surfaces, etc., preveting a cow from standing or lying on this plot, in % of the plot area bare ground, gravel, dead plant material, etc, in % of the plot area all lichen and moss species, in % of the plot area all herbaceous plant species as well as ferns, in % of the plot area woody species, including heather (<i>Erica</i> spec. and <i>Calluna</i> spec.), berries (<i>Rubus idaea</i> and <i>Vaccinium</i> spec.) and tree seedlings under 30 cm height, in % of the plot area all graminoid species, including the families Poaceae, Cyperaceae and Juncaceae, in % of the plot area
Incline Canopy cover Sun exposure Visibility	mean of the absolut area (in %) above t absence (1) or prese	te inclines (in %) in the four cardinal directions, he plot covered by the canopy. ence (0) of any cover between cow and sun (e.g. trees or hills), not taking into account cloud cover. es (in m) to the first obstacle at cattle eye level (i.e. 0.5 m for resting cattle and 1.5 m for grazing cattle) parallel to the ground in the

later than one day after the cow had been there, field conditions were similar to those the cow had the day before (especially with regard to the vegetation). We managed to visit up to three of these positions for data collection per day. We aimed for a balanced sample by using three grazing and three resting positions per cow for data collection in the field during the study period. Out in the field, we checked for signs of recent grazing (i.e. freshly grazed vegetation) or resting (i.e. flattened vegetation in the shape of a "cow bed") at the chosen location and we discarded locations without such signs. Plots inaccessible to cattle (e.g. because of a fence) were discarded from the sample. The experimental unit in the final analyses is the plot. In the end, the sample for grazing cattle included in total 178 plots and the sample for resting cattle in total 223 plots.

2.5. Recorded variables

At each plot we recorded the variables as shown and defined in Table 1. Incline and ground cover composition were recorded on the plot area, while canopy cover, sun exposure and visibility were recorded at the plot center. Incline was measured in percentage with a 1.78 m long stick and a clinometer. Ground cover composition was recorded by visual judgement. Canopy cover was recorded using the application HabitApp on a Samsung Galaxy Tab 10.1 T M (Samsung Electronics, 2016) tablet. This application turns mobile phone photos into black and white images and then calculates the percentage shade value e.g. black pixels as a percentage of total pixels. Sun exposure was recorded 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 TM tablet. We set the value 0 for night time or presence of trees and hills shading the cow and the value 1 for day time and absence of any such trees and hills. Sun exposure does not take into account cloud cover. Visibility was measured in meters with a measure tape.

2.6. Data analyses

We modelled the probability of use for each plot according to habitat characteristics using logistic regression (i.e., resource selection probability functions RSPF, as per Manly et al. (2002) separately for grazing and resting. We analysed our data in R (R Core Team, 2017), with the RStudio interface (RStudio Team, 2016), following two protocols by Zuur et al. (Zuur et al., 2010; Zuur and Ieno, 2016). We used the isometric logratio (ilr) transformation (Hron et al., 2012) to alleviate the collinearity between the categories of ground cover composition. We first analysed ground cover composition on its own to identify the important categories, which we then used in the main model. For the ilr-transformation, we used the R package compositions (van den Boogaart et al., 2014). The categories for which the 90% confidence

interval of the parameter estimate did not include the value 0 were included in the global models later on. Because there were too few occurrences of rainfall or of temperature exceeding 20 °C in our data, we excluded the variables *rainfall* and *temperature* from our analyses. We used generalized linear mixed models (GLMMs) of the binomial family. In order to account for the dependency structure in our data, for changing availability between positions and for unbalanced sampling among cows, we included habitat patch ID nested within cow ID nested within herd ID as random intercepts. 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.

$$Y \sim Bin(1; \pi)$$

$$logit(\pi) \sim \alpha + \beta_1 * grasses + \beta_2 * incline + \beta_3 * canopycove$$

$$+ \beta_4 * sunexposure + \beta_5 * visibility + \beta_6 * visibility^2 + b_{herd} + b_{cow}$$

$$+ b_{habitatratch}$$
(1)

where Y is the probability of use.

To improve the interpretability of the regression parameters, we 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 (Bates et al., 2015). Since the random effects resulted from the study design, we only selected on the fixed effects. We selected for the model with the lowest second order Akaike Information Criterion (AICc) value using the R package MuMIn (Barton, 2017) and considered models with a difference in AICc value below 2 as equivalent. Among equivalent models, we chose the simplest one following the principle of parsimony. We checked the model assumptions using the R package DHARMa (Hartig, 2017).

3. Results

3.1. Positioning success

Two out of the 18 collars failed and were discarded from this study. For the remaining 16 collars, 94.1% of the targeted positions were obtained. The dilution of precision (DOP) had a mean value of 1.1 and a standard deviation of 0.51. The number of satellites had a mean value of 7.94 and a standard deviation of 2.1.

3.2. Recorded variables

Mean and standard error of the recorded variables are shown in Table 2.

Table 2Mean and standard error of the variables recorded to analyse the microhabitat selection of free ranging beef cattle at grazing and resting sites in south-boreal forest in summer 2017.

Activity	Variable	at plots used by the cow		at control plots	
		mean	SE	mean	SE
Grazing		(n = 36)		(n = 142)	
	Percentage of grass in the ground cover (%)	44.00	4.30	28.40	2.27
	Incline (%)	5.80	0.73	7.44	0.47
	Canopy cover (%)	9.00	3.74	21.10	2.33
	Sun exposure (0 - 1)	0.44	0.08	0.34	0.04
	Visibility (m)	15.9	1.70	14.90	0.88
Resting		(n = 45)		(n = 178)	
	Percentage of grass in the ground cover (%)	35.60	4.97	21.00	1.74
	Incline (%)	4.50	0.38	6.30	0.33
	Canopy cover (%)	26.80	5.00	26.80	2.23
	Sun exposure (0 - 1)	0.33	0.07	0.24	0.03
	Visibility (m)	11.20	1.19	9.90	0.53

3.3. Preliminary ground cover composition analyses

The results of the *ground cover composition* analyses are presented in Fig. 2. For both grazing and resting, only the 90% confidence interval of the parameter estimate for 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.

3.4. Probability of use by grazing cattle

The best models are shown in Table 3. Our best model for explaining the variation in probability of use by grazing cattle, included the fixed effect *grasses*. The relative variable importance of *grasses* was 0.79. The estimated variance for all random effects was very close to 0. Model validation indicated no violations of the underlying assumptions. The model output and predictions are presented in Fig. 3. Within a given habitat patch, cattle selected for the most grass-rich site for grazing.

Table 3 The best models (\triangle AICc < 2) for predicting probability of use by free ranging beef cattle at (a) grazing and (b) grazing sites in south-boreal forest in summer 2017. All the models include an intercept and the random effects *habitat patch ID* nested within *cow ID* nested within *herd ID*.

Fixed effects included in the model	Df	AICc	Δ (AICc)	AICc weight
a) grazing				
grasses	4	178.6	0.00	0.093
grasses + canopy cover	5	178.9	0.31	0.080
grasses + incline	5	179.1	0.54	0.071
canopy cover + grasses + incline	6	179.3	0.70	0.066
canopy cover + incline	5	180.3	1.70	0.040
grasses + sun exposure	5	180.3	1.74	0.039
b) resting				
canopy cover + grasses + incline	6	215.2	0.00	0.195
canopy cover + grasses + incline + visibility	7	215.9	0.68	0.139
canopy cover + grasses + incline + sun	7	216.6	1.37	0.098
exposure				

3.5. Probability of use by resting cattle

The best models are shown in Table 3. Our best model for explaining the variation in probability of use by resting cattle, included the fixed effects *grasses*, *incline* and *canopy cover*. The relative variable importance of *grasses*, *incline* and *canopy cover* were 0.99, 0.88 and 0.80, respectively. The estimated variance for all random effects was very close to 0. Model validation indicated no violations of the underlying assumptions. The model output and predictions are presented in Fig. 4. Within a given habitat patch, cattle selected fot the most grass-rich, the flattest and the most covered site for resting.

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 the microhabitat selection of cattle. We found differences in the cattle's habitat selection for different activities: while grazing cattle were influenced by the amount of grass in the ground cover only, resting cattle were influenced by the amount of grass, incline and canopy cover. Cattle selected for both grazing and resting sites with a high amount of grass. Cattle are grazers, that have been shown to forage on herbs, shrubs and trees as well (Holechek et al., 1982; Kie and Boroski, 1996; Rutter, 2006; Mandaluniz et al., 2011; Bele et al., 2015). Our findings

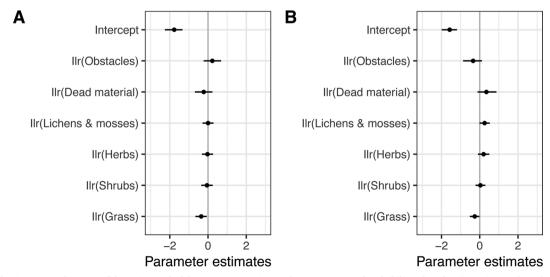


Fig. 2. Results, that is mean and 90% confidence interval of the parameter estimates from regression of probability of use by A) grazing cattle and B) resting cattle on the ilr-transformed ground cover categories in a study on microhabitat selection of free ranging beef cattle in south-boreal forest in summer 2017.

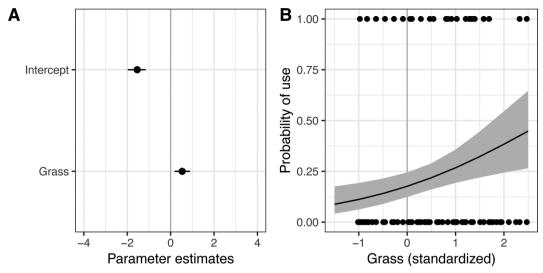


Fig. 3. Results of a study on microhabitat selection of free ranging beef cattle in south-boreal forest in summer 2017: model output and predictions for the best grazing model: A) mean and 95% confidence interval of the parameter estimates and B) predicted probability of use (line) with 95% confidence interval (ribbon) and observed presence/absence (points) by grazing cattle against the standardized variable *grass*, with the remaining variables set at their mean.

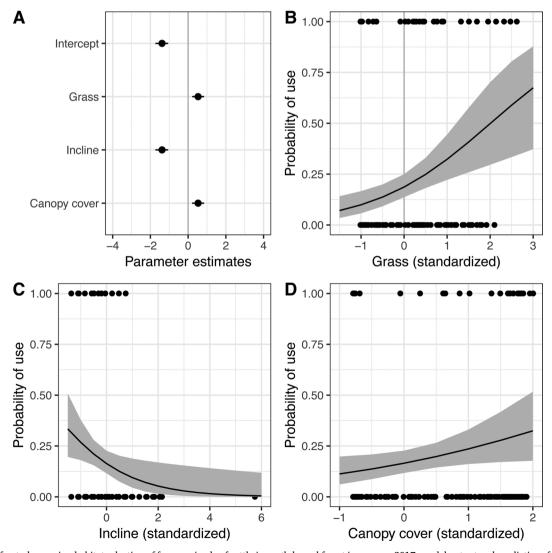


Fig. 4. Results of a study on microhabitat selection of free ranging beef cattle in south-boreal forest in summer 2017: model output and predictions for the best resting model: A) mean and 95% confidence interval of the parameter estimates. Predicted probability of use (line) with 95% confidence interval (ribbon) and observed presence/absence (points) by resting cattle against the standardized variables B) *incline*, C) *canopy cover* and D) *grass*, with the remaining variables set at their mean.

underline the importance of grass as food resource for cattle. Resting cattle might select for grass in the ground cover because of its bedding layer qualities or because they rested at the same spot that they had been grazing on before. Cattle selected for resting sites with low incline. This could be due to the fact that getting up from lying to standing position requires more ground support than moving around (Dalgaard and Gjødesen, 2010). The selection for low incline of free-ranging cattle in boreal forest, on various spatial scales and independent on their activity, has been shown in several other studies as well (Gillen et al., 1984; Walburger et al., 2009; Kaufmann et al., 2013).

Cattle selected for resting sites with high canopy cover. Even though Bjor and Graffer (1963) and Vandenheede et al. (1995) found that cattle seek shelter when it is raining, the use of canopy cover as shelter from rain can be excluded as possible explanation for our findings since it rained for very few of our observations. Our study animals could have been seeking shelter from potential rainfall, to avoid moving in case it would start raining during their rest. They could also have been seeking shelter from harassing insects, which have been shown to influence habitat selection of cattle (Bjor and Graffer, 1963) and, further up in the mountains, the habitat selection of reindeer (Rangifer tarandus) (Skarin et al., 2004; Vistnes et al., 2008).

Cattle were not affected by sun exposure when choosing grazing and resting sites. Given we only had a few observations with temperatures above 20 °C, we can not exclude some confounding effect between sun exposure and temperature. Cows have indeed been shown to spend more time in shade on days with high ambient temperature and solar radiation in other studies (Bjor and Graffer, 1963; Bennett et al., 1985; Schütz et al., 2009).

Cattle were not affected by visibility when choosing grazing and resting sites. Visibilty might not be the best measure for cattle's antipredator behaviour, as both cattle and their predators might not rely on the sense of vision alone. Moreover, being gregarious animals (Lazo, 1994), cattle's anti-predator behaviour might be dependent on herd size (Fortin et al., 2009; Kie, 1999). Kie (1999) also showed evidence for ungulates to modify their behaviour in the actual presence of predators. Our study animals might not have encountered any predator during the study period.

With our cattle herds showing some fusion-fission behaviour, as defined by Lazo (1994), we can not be sure of the herd compositions at every moment. It would be interessting to put GPS collars on all the animals released in a certain area to closely look at their fusion-fission behaviour. With more individuals, one could also account for differences between different breeds. Moreover, it would be interesting to record and include distance to roads and forage quality/quantity attributes in the analyses, factors that have been shown to influence habitat selection of cattle in other studies (Kaufmann et al., 2013; Ganskopp et Bohnert, 2009).

Usually, habitat selection studies do not take into account the activity status of the animals (but see e.g. Moe et al., 2007; Zimmermann et al., 2014). Our study is accounting for different activities, in this case grazing and resting, when analysing habitat selection of cattle. Based on direct field observations and continuous variables, it relies on fewer assumptions than studies based on maps and categorical variables.

Ensuring animal welfare is dependent on knowledge on a species' natural behaviour, which is hard to study on domesticated cattle (Kilgour, 2012). The findings of our study on temporally feral cattle, providing insight into their natural habitat selection, can be used to design pastures according to the animals' needs.

One challenge faced by the management of communal lands in Norwegian south-boreal forests are the conflicting interests between cattle husbandry and forestry: cattle tend to damage young trees of commercial interest (Norway spruce, *Picea abies*) (Hjeljord et al., 2014). Tofastrud et al. (2019) studied the habitat selection of the same cattle in the same study area on a larger scale and found that they select for summer farm meadows and clearcuts under 15 years. It is exactly on these clearcuts that cattle cause most damage. Now we know that on a

smaller scale, they are selecting for grass, low incline and horizontal cover. Fencing vulnerable young forest and offering alternative grassy, flat sites with some horizontal cover to the cattle could be on way to mitigate this conflict.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

The study was funded by grants of the County governor of Hedmark (2015/3581 and 2015/2595) and the Norwegian Agricultural Agency (15/18102-3).

Acknowledgements

The authors want to thank the cattle owners and the managers of Furnes, Vang and Stange/Romedal almeninger for their goodwill and cooperation in the implementation of this study, the students Steve Ehlen and Jack Räisänen for carrying out fieldwork and everybody contributing to the manuscript with their comments and suggestions.

References

Arthur, S.M., Manly, Bryan F.J., McDonald, L.L., Garner, G.W., 1996. Assessing habitat selection when availability changes. Ecology 77, 215–227.

Austrheim, G., Solberg, E.J., Mysterud, A., Daverdin, M., Andersen, R., 2008. Hjortedyr og husdyr på beite i norsk utmark i perioden 1949–1999 (in Norwegian). Rapport zoologisk serie 2 2008.

Barton, K., 2017. MuMIn: Multi-Model Inference.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using {lme4}. J. Stat. Softw. 67, 1–48.

Bele, B., Johansen, L., Norderhaug, A., 2015. Resource use by old and modern dairy cattle breeds on semi-natural mountain pastures, Central Norway. Acta Agriculturae Scandinavica, Section A—Animal Science 65, 73–84.

Bennett, I.L., Finch, V.A., Holmes, C.R., 1985. Time spent in shade and its relationship with physiological factors of thermoregulation in three breeds of cattle. Appl. Anim. Behav. Sci. 13, 227–236.

Berman, A., Folman, Y., Kaim, M., Mamen, M., Herz, Z., Wolfenson, D., Arieli, A., Graber, Y., 1985. Upper critical temperatures and forced ventilation effects for high-yielding dairy cows in a subtropical climate. J. Dairy Sci. 68, 1488–1495.

Bjor, K., Graffer, H., 1963.) Beiteundersøkelser På Skogsmark. The Office for Agricultural Research, Oslo.

Dalgaard, I., Gjødesen, M.U., 2010. Indretning Af Stalde Til Kvæg: Danske Anbefalinger: Tværfaglig Rapport (in Danish), (5.ed.) Århus: Dansk Landbrugsrådgivning. Videncenteret for landbrug, Århus.

Eager, C.D., 2017. Standardize: Tools for Standardizing Variables for Regression in R. ESRI, 2011. ArcGIS. Redlands, CA.

Fortin, D., Fortin, M.-E., Beyer, H.L., Duchesne, T., Courant, S., Dancose, K., 2009. Groupsize-Mediated habitat selection and group fusion-fission dynamics of Bison under predation risk. Ecology 90, 2480–2490.

Ganskopp, D.C., Bohnert, D.W., 2009. Landscape nutritional patterns and cattle distribution in rangeland pastures. Appl. Anim. Behav. Sci. 116 (2-4), 110–119.

Gillen, R.L., Krueger, W.C., Miller, R.F., 1984. Cattle distribution on mountain rangeland in northeastern Oregon. J. Range Manage. 37, 549–553.

Hahn, G.L., 1999. Dynamic responses of cattle to thermal heat loads. J. Anim. Sci. 77, 10--20.

Hartig, F., 2017. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Hjeljord, O., Histøl, T., Wam, H.K., 2014. Forest pasturing of livestock in Norway: effects on spruce regeneration. J. For. Res. 25 (4), 941–945.

Holechek, J.L., Vavra, M., Skovlin, J., Krueger, W.C., 1982. Cattle diets in the blue mountains of Oregon II. Forests. J. Range Manage. 35, 239–242.

Hron, K., Filzmoser, P., Thompson, K., 2012. Linear regression with compositional explanatory variables. J. Appl. Stat. 39, 1115–1128.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.

Kaufmann, J., Bork, E.W., Blenis, P.V., Alexander, M.J., 2013. Cattle habitat selection and associated habitat characteristics under free-range grazing within heterogeneous Montane rangelands of Alberta. Appl. Anim. Behav. Sci. 146, 1–10.

Kaufmann, J., Bork, E.W., Alexander, M.J., Blenis, P.V., 2017. Cattle utilization of coniferous cut blocks under open range grazing and associated impact on tree seedlings. Agrofor, Syst. 91, 623–635.

Kie, J.G., 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. J. Mammal. 80 (4), 1114–1129.

Kie, J.G., Boroski, B.B., 1996. Cattle distribution, habitats, and diets in the Sierra Nevada of California. J. Range Manag. 49, 482–488.

Boston, MA.

- Kilgour, R.J., 2012. In pursuit of "normal": a review of the behaviour of cattle at pasture. Appl. Anim. Behav. Sci. 138, 1–11.
- Landbruksdirektoratet, 2018. Retrieved From https://www.landbruksdirektoratet.no/filserver/pt900/1620/1620l99f.hTm (in Norwegian), on the 25.04.2018.
- Lazo, A., 1994. Social segregation and the maintenance of social stability in a feral cattle population. Anim. Behav. 48, 1133–1141.
- Mandaluniz, N., Aldezabal, A., Oregui, L.M., 2011. Diet selection of beef cattle on Atlantic grassland-heathland mosaic: are heathers more preferred than expected? Livest. Sci. 138, 49–55.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002.

 Resource Selection of Animals: Statistical Design and Analysis for Field Studies, 2nd ed. Dordrecht: Kluwer.
- Mayor, S.J., Schneider, D.C., Schaefer, J.A., Mahoney, S.P., 2009. Habitat selection at multiple scales. Ecoscience 16, 238–247.
- Moe, T.F., Kindberg, J., Jansson, I., Swenson, J.E., 2007. Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (Ursus arctos). Can. J. Zool. 85 (4), 518–525.
- Morrison, M., Marcot, Bruce G., William Mannan, R., 2006. Wildlife-Habitat Relationships: Concepts and Applications. Island Press, Washington.
- Ominski, K.H., Kennedy, A.D., Wittenberg, K.M., Moshtaghi Nia, S.A., 2002. Physiological and production responses to feeding schedule in lactating dairy cows exposed to short-term, moderate heat stress. J. Dairy Sci. 85, 730.
- Pimenta, V., Barroso, I., Boitani, L., Beja, P., 2017. Wolf predation on cattle in Portugal: assessing the effects of husbandry systems. Biol. Conserv. 207, 17–26.
- Prima, M.-C., Duchesne, T., Fortin, D., 2017. Robust inference from conditional logistic regression applied to movement and habitat selection analysis. PLoS One 12, 1–13.
- R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rekdal, Y., 2010. Vegetasjon Og Beite I Furnes, Vang Og Løten Almenninger. Rapport Fra Vegetasjonskartlegging I Kommunene Ringsaker. Hamar og Løten (in Norwegian). Norsk institutt for skog og landskap.
- Rekdal, Y., 2017. Vegetasjon Og Beite I Deler Av Romedal-og Stange Almennninger (in Norwegian). NIBIO Rapport.
- Roath, L.R., Krueger, W.C., 1982. Cattle grazing and behaviour on a forested range. J. Range Manage. 35, 332–338.
- Rovbase, 2018. Retrieved From http://rovbase.nO (in Norwegian) on the 25.04.18. RStudio Team, 2016. RStudio: Integrated Development Environment for R. RStudio. Inc.,
- Rutter, S.M., 2006. Diet preference for grass and legumes in free-ranging domestic sheep and cattle: current theory and future application. Int. Soc. Appl. Ethol. (ISAE) Special Issue 2004 (97), 17–35.

- Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. Methods Ecol. Evol. 1, 103–113.
- Schütz, K.E., Rogers, A.R., Cox, N.R., Tucker, C.B., 2009. Dairy cows prefer shade that offers greater protection against solar radiation in summer: Shade use, behaviour, and body temperature. Appl. Anim. Behav. Sci. 116, 28–34.
- Skarin, A., Danell, Ö., Bergström, R., Moen, J., 2004. Insect avoidance may override human disturbances in reindeer habitat selection. Rangifer 24, 95–103.
- Smil, V., 2014. Harvesting the Biosphere: What We Have Taken From Nature. MIT Press, Cambridge.
- Steyaert, S.M., Støen, O.-G., Elfström, M., Karlsson, J., Van Lammeren, R., Bokdam, J., Zedrosser, A., Brunberg, S., Swenson, J.E., 2011. Resource selection of sympatric freeranging dairy cattle and brown bears Ursus arctos. Wildlife Biol. 17, 389–403.
- Tofastrud, M., Hegnes, H., Devineau, O., Zimmermann, B., 2018. Activity patterns of freeranging beef cattle in Norway. Acta Agric. Scand. A 1–9. https://doi.org/10.1080/ 09064702.2018.1524928.
- Tofastrud, M., Devineau, O., Zimmermann, B., 2019. Habitat selection of free-ranging cattle in productive coniferous forests of south-eastern Norway. For. Ecol. Manage. 1–9. https://doi.org/10.1016/j.foreco.2019.01.014.
- van den Boogaart, K.G., Tolosana, R., Bren, M., 2014. Compositions: Compositional Data Analysis.
- Van laer, E., Moons, C.P.H., Sonck, B., Tuyttens, F.A.M., 2014. Importance of outdoor shelter for cattle in temperate climates. Livest. Sci. 159, 87–101.
- Van Vuure, C.T., 2002. History, morphology and ecology of the aurochs (Bos taurus primigenius). Lutra 1–16.
- Vandenheede, M., Nicks, B., Shehi, R., Canart, B., Dufrasne, I., Biston, R., Lecomte, P., 1995. Use of a shelter by grazing fattening bulls: effect of climatic factors. Anim. Sci. 60. 81–85.
- Vistnes, I.I., Nellemann, C., Jordhøy, P., Støen, O.-G., 2008. Summer distribution of wild reindeer in relation to human activity and insect stress. Polar Biol. 31, 1307.
- Walburger, K.J., Wells, M., Vavra, M., DelCurto, T., Johnson, B., Coe, P., 2009. Influence of cow age on grazing distribution in a mixed-conifer forest. Rangel. Ecol. Manag. 62, 290–296
- Womack, J., 2012. Bovine Genomics. Oxford, UK. Wiley-Blackwell.
- Zimmermann, B., Nelson, L., Wabakken, P., Sand, H., Liberg, O., 2014. Behavioral responses of wolves to roads: scale-dependent ambivalence. Behav. Ecol. 25 (6), 1353–1364.
- Zuur, A.F., Ieno, E.N., 2016. A protocol for conducting and presenting results of regression-type analyses. Methods Ecol. Evol. 7, 636–645.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14.