Inland Norway
University of
Applied Sciences

Faculty of Applied Ecology, Agricultural Sciences and Biotechnology

Morten Tofastrud

Grazing behaviour and weight performance of free-ranging cattle in the boreal forest

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Sammendrag

En økende interesse for norsk storfekjøttproduksjon basert på utenlandske kjøttferaser har ført til en økning i antall ammekyr på beite i utmarka. Mine hovedmål var å undersøke beiteadferd og vektutvikling hos disse dyrene på beiter i ekstensive beiter i den boreale skogen i Sørøst-Norge. Jeg studerte ammekyr utstyrt GPS-halsbånd med innebygd aktivitet sensor i to almenningsskoger, hvor dyretettheten var beregnet som høy og lav. Jeg fant at kyrene brukte ca. 1/3 av sitt daglige tidsbudsjett på å beite, noe som kan sammenlignes med beitetiden i andre heterogene miljøer. Kyrene tilpasset sitt daglige tidsbudsjett til daglengde og økte daglige beitetid gjennom beitesesongen. Størrelsen på hjemmeområdene ble funnet positivt korrelert med andelen vegetasjonstyper klassifisert som dårlige beiteområder i dyrets hjemmeområdet. Kyr uten diende kalv i området med lav dyretetthet brukte særlig store hjemmeområder. Kyrne viste høyeste preferanse for grasrike habitater, som hogstflater og de mer spredte setervollene både under beiting og hvile. De foretrakk unge hogstflater (yngre enn15 år gamle) og preferansen for disse var sterkest når kyrne beitet sammenlignet med under hvile og forflytning. Videre fant jeg at habitat seleksjon varierte mellom studieområdene. Kyr i området med høy dyretetthet brukte størst andel lavproduktive habitater og områder lokalisert i større avstand fra veger. Generelt fant jeg høyere tilvekst hos ammekyr uten diende kalv enn hos kyr med diende kalv. Jeg fant tilvekst hos ammekyr positivt korrelert med lengden på beiteperioden og negativt korrelert med individuelle avvik fra gjennomsnittsvekt for rasen ved beiteslipp. Jeg kunne ikke finne noen sammenheng mellom tilvekst hos ammekyr og de ytre miljøfaktorer som størrelse på hjemmeområde og andelen av hjemmeområdet dekket av de foretrukne beite habitater, setervoller og hogstflater yngre enn 15 år. Kyr og kalver som beitet i området med lav dyretetthet hadde høyere tilvekst enn de i området med høg dyretetthet. Vårfødte oksekalver oppnådde høyst tilvekst etterfulgt av vårfødte og høstfødte kvigekalver. I området med lav dyretetthet hadde ammekyr og kalver av de tidlig slaktemodne rasene høyere tilvekst enn de seint voksende rasene. I denne avhandlingen har jeg vist at det er fullt mulig å utnytte den borealskogen i Sørøst-Norge som beiter for kjøttfe av internasjonale raser Jeg antar at dette i hovedsak er et resultat av den beiteressursen som utgjøres av store hogstflater dannet gjennom moderne skogbruksdrift. Det er imidlertid verdt å påpeke at tilpasning av dyretettheten til den estimerte fôrproduksjonen for beiteområdet er av stor betydning for dyras tilvekst og velferd i beiteperioden.

Abstract

Increasing interest in Norwegian beef production based on non-native beef cattle breeds has led to an increase in the number of suckler cows turned-out in unimproved lands. My main goals were to investigate grazing behaviour and weight performance of these animals on extensive pastures in the boreal forest of south-eastern Norway. I studied suckler cows fitted with GPS collars with built-in activity sensors in two communal forests, one with a high and the other with a low stocking density. I found that the cows spent about 1/3 of their daily time budget on grazing, which is comparable to time spent grazing in other heterogeneous environments. The cows adapted their daily time budget to the hours of daylight and increased the daily time spent on grazing throughout the season. I found a positive relationship between the home range size of suckler cows and the proportion of the home range covered by poor forage quality. Dry cows in the low stocking density area used particularly large home areas. I found that both grazing and resting cows showed highest preference for grass-rich habitats, i.e. the widespread patches of abandoned summer farm meadows and clearcuts created by timber harvesting. Cows preferred also young forest stands less than 15 years old, and the preference was strongest while grazing, compared to resting and walking. Furthermore, habitat selection varied with study area. Cattle in the area of high stocking density selected more frequently low productivity habitats and areas further from roads. Overall, dry cows gained more weight than lactating cows. I found weight gain in suckler cows to be positively correlated with length of the grazing period and negatively with the individual deviation from breed-specific weight at turnout. I could not find any relationship between weight gain in suckler cows and the extrinsic factors home range size and the proportion of the home range covered by the preferred grazing habitats, i.e. summer farm meadows and clearcuts younger than 15 years. Cows and calves in the low stocking density area gained more weight than those in the high stocking density area. Spring-born bull calves gained most weight followed by spring-born and autumn-born heifers. In the low stocking density area, cows and calves of early-maturing breeds had higher weight gain than those of late maturing breeds. In this thesis, I have shown beef cattle of international breeds fully suitable for grazing in the boreal forest in south-east Norway. I assume that this is mainly a result of the pasture resources of the large clear-cut areas, created by modern forestry operations. It is worth pointing out that appropriate stocking densities for the estimated production of forage are of particular importance for both weight performance and the behaviour of grazing cattle.

Preface

My PhD position and research was financed by Inland Norway University of Applied Sciences. In addition, the project received founding from Fylkesmannen i Innlandet and Landbruksdirektoratet. The project started as an exchange of ideas between former Dean Harry P. Andreassen and me. Harry supported my ideas and participated actively in the early stages of the project, but unfortunately, Harry passed away before my work was finished, and I will therefore dedicate this thesis to him.

The project has allowed me to work on a theme that has always interested me, and I have enjoyed the whole period with all its challenges and all the people involved, this work had not been possible without their support. First, I will express my gratitude to the person of greatest importance for my work, Professor Barbara Zimmermann who has been an excellent supervisor through all phases of this work. Always patient and enthusiastic, with a positive attitude that made me look forward to supervisory meetings, even though they always ended up with more work for me. My grateful appreciations also goes to Olivier Devineau for introducing me to the world of data science and helping with me cleaning up messy data, performing statistical analysis and co-authorship. I am also very thankful to co-supervisor Anna Hessle for constructive contributions to early stage planning of the project and co-authorship.

I would like to give a special thanks to the farmers who participated in this research project by weighing cattle and attaching GPS collars to animals who were not always in a cooperative mood. These studies would not been possible without your help. I want to thank Vegard Urset and Joar Brukvangen at Fylkesmannen i Innlandet and, Stein Enger and Hege Ottinsen at Hedmarken Landbrukskontor for your support with realising this project. I will also thank the managers and staff at Stange and Romedal almenninger and, Furnes and Vang Almenninger for their support and contribution to this project.

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Ridabu, 28th August 2019

Morten Tofastrud

Table of contents

List of publications

This thesis is based on the following original publications and manuscripts:

1) Tofastrud, M., Hegnes, H., Devineau, O. & Zimmermann, B. (2018) Activity patterns of free-ranging beef cattle in Norway, *Acta Agriculturae Scandinavica, Section A — Animal Science 68,* 39-47.
2) Tofastrud, M., Devineau, O. & Zimmermann, B. (2019) Habitat selection of free-ranging cattle in productive coniferous forests of south-eastern Norway, *Forest Ecology and Management 437*, 1-9.
3) Spedener, M., Tofastrud, M., Devineau, O. & Zimmermann, B. (2019) Microhabitat selection of free-ranging beef cattle in south-boreal forest, *Applied Animal Behaviour Science 213*, 33-39.
4) Tofastrud, M., Hessle, A., Rekdal, Y. & Zimmermann, B. Weight gain of free-ranging beef cattle grazing in the boreal forest, (Manuscript submitted to: *Livestock Science*)

1. Introduction

1.1. The applied context of the thesis

The expected growth of the human population will cause a rising demand for food, which is expected to be limited by the Earth's land resources, and cannot be met by maximizing agricultural productivity alone (Godfray *et al.* 2010). Today, 33% of the Earth’s cultivated land is used for livestock production, and the proportion is expected to increase in the future (Schader *et al.* 2015a). An increased demand for livestock products is expected to contribute to human-induced reduction of biodiversity, due to loss and fragmentation of habitats for wild animal and plant species (Green *et al.* 2005). Three main strategies are suggested for increasing the sustainability of livestock production; increasing livestock productivity, reducing the demand for animal products, and changing livestock feed rations to reduce their content of food that could be consumed by people (Schader *et al.* 2015a). The latter implies a better utilization of natural resources by focusing on a grassland-based ruminant production and reduced amounts of livestock feedstuffs grown on arable land.

1.1.1 Norwegian livestock production on unimproved lands

In Norway, only 3% of the land area is cultivated (Ministry of Agriculture and Food 2018), but food production on unimproved land has a long tradition. Unimproved land (“utmark”) consists of forests, bogs, mountains, lakes and coastal areas, in short all areas that are not built-up or cultivated for agricultural production (Sevatdal 2006). Total annual feed intake of livestock grazing on unimproved land in Norway corresponds to the grass harvested from 100 000 ha of cultivated land (Ministry of Agriculture and Food 2011), and only half of the available grazing resources of unimproved areas in Norway are utilized (Schärer 2016).

Traditionally, the silvopastoral systems in northern Scandinavia consisted of extensive livestock grazing in boreal forests (Bruteig, Austrheim & Norderhaug 2003) and over the last 2000 years, livestock dominated the guild of large herbivores in large parts of Norway (Austrheim *et al.* 2008). The forests were often communal and provided multiple ecosystem services besides livestock production, e.g. fire wood, construction materials, game meat, mushrooms and berries (Bele & Norderhaug 2013). Livestock grazing and other human activities had a large impact on the structure and composition of the forests (Ericsson, Östlund & Axelsson 2000). The diversity and density of trees varied with grazing pressure, logging intensity and local ecological conditions. This system of communal use is still practised in

Norway, but today, the Scandinavian forests are managed more intensively and the major focus is on timber production (Östlund, Zackrisson & Axelsson 1997; Aasetre & Bele 2009).

Throughout the latter half of the 1900s, there has been a dramatic decline in livestock grazing unimproved lands, mainly as a result of a decline in the use of these lands for cattle (*Bos taurus*) grazing (Austrheim *et al.* 2008). During this period, development of modern breeding programmes and rational management operations led to an increase of the individual milk yield in dairy cows and resulted in a decline in the dairy cow population (Tine Rådgivning 2019). Because beef production was based on surplus animals of the dairy production line, this resulted in a net deficit in Norwegian beef production. The government took steps to stimulate beef production, which resulted in a steady increase of the population of specialized beef cattle in the recent years (Ministry of Agriculture and Food 2011) (Figure 1). Norwegian cattle herds are generally small, but the average herd size of beef cattle has increased rapidly from 6.7 cows in 1999 to 15.4 in 2014 (Norwegian Agriculture Agency 2016). The focus on national beef production has led to a growing interest in utilizing grazing resources of unimproved land. In 2016, a total of 252 666 cattle grazed on unimproved land for at least eight weeks (Norwegian Agriculture Agency 2017).

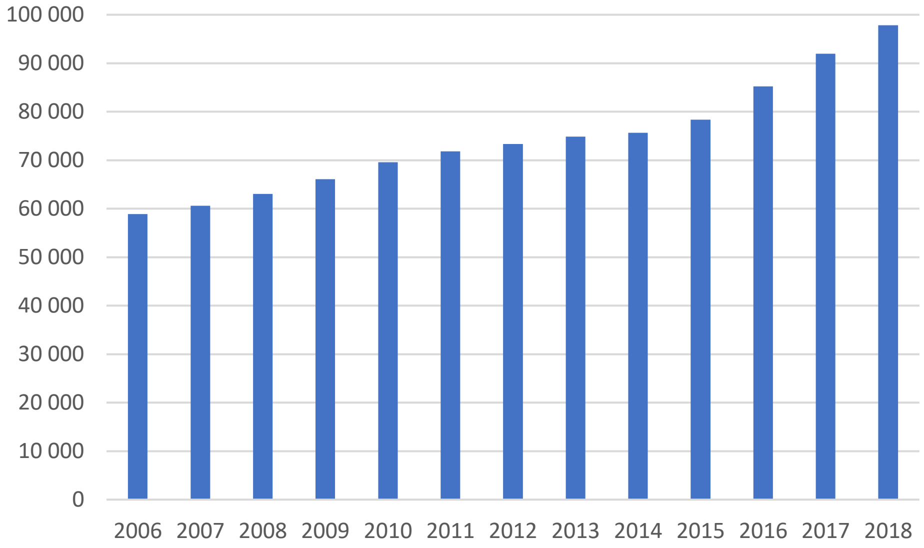

Figure 1: *Increase of the suckler cow population in Norway during the past decade as a result of governmental stimulation of national beef production (Animalia AS 2019).*

Specialised beef cattle are kept as herds of suckler cows of either Continental or British beef breeds. In Norway the most common beef cattle breeds are Charolais (Continental) and Hereford (British), accounting for 21% and 14% of all suckler cows, respectively (Animalia

AS 2019). Beef cattle breeds can also be classified as early- or late-maturing breeds, based on their weight gain capacity. Characteristic late-maturing breeds are Charolais, Simmental and Limousin (all Continental), while Hereford and Aberdeen Angus (British) represent the early maturing breeds. In general, there is a growing interest among the beef farmers in Norway to use bulls of late-maturing breeds for crossbreeding (Animalia AS 2019).

Although these breeds have been present in Norway for decades, there is little knowledge about the grazing behaviour and performance of suckler cows and their suckling calves in extensive grazing regimes. We need an understanding of the foraging ecology of these large herbivores, in particular their foraging behaviour, area use, habitat selection and weight performance, to manage unimproved lands in a way that maintain ecological, social and economic interests, and to optimize animal production, health and welfare. In my thesis, I specifically studied these topics for free-ranging cattle turned-out to the boreal forest.

1.1.2. Boreal forest as grazing resource for cattle in Norway

Forests cover 37.4% of the total land area in Norway (Statistics Norway 2018). Traditionally, these unimproved areas were the most important areas for summer grazing livestock in south-eastern Norway, followed by the alpine region when summer farms were available (Bele & Norderhaug 2013). The public interest in utilization of unimproved lands for both economical and recreational purposes is increasing and the management of these areas requires information as a basis for decision-making (Larsson & Rekdal 2000). Since 1987, the Norwegian Institute of Bioeconomy Research (NIBIO) has been working on mapping vegetation types on unimproved lands as a systematic tool for assessing the quality of unimproved pasture areas (Dahlström, Hessle & Kumm 2018). Vegetation maps are built by interpretation of aerial photos and inspection of the areas and are based on 45 vegetation types and 9 other area types (Rekdal 2017). Vegetation types are defined as characteristic groups of plant species with equal biotic and abiotic requirements (Rekdal & Angelhoff 2016). This system is built on the assumption that species composition, plant production and nutrient content in foraging plants within vegetation types show similarity from locality to locality in geographically limited areas (Hofsten, Rekdal & Strand 2014). Vegetation types are categorised into foraging classes by their approximate grazing value as a tool to manage grazing livestock (Rekdal 2010; 2017). These resource maps do however not account for the successional stage of different forest stands, despite of this being a crucial factor for plant production and grazing value in the boreal forest (Rekdal 2010; 2017). The shading effect of the standing forest favours the shade-tolerant bilberry while open clearcuts supply light and heat to the field layer and favour grass species. In a Norwegian study, Bjor and Graffer (1963) found that the clearcuts of the boreal forests lost importance as foraging areas for livestock 12–15 years after timber harvesting. Clearcut areas dominated by wavy hair grass (*Avenella flexuosa*) have a production potential of up to 2000 kg dry matter per hectare (Larsson & Rekdal 2000). Therefore, the proportion of clearcuts is considered as highly important for the production of forage inside pasture areas of the boreal forest.

The boreal forests of Norway are commonly subject to intensive commercial forestry managed by clearcutting followed by scarification, restocking and thinning (Aasetre & Bele 2009). In order to improve timber production, young spruce seedlings are planted on the clearcuts within 2-3 years after harvesting. Cattle can impact on forest regeneration areas by trampling and bedding on the seedlings and cause damages to roots and bark of older trees, which may increase reforestation costs and reduce the value of timber (Adams 1975; Mayer *et al.* 2006; Hjeljord, Histøl & Wam 2014). Nonetheless, grazing livestock have also been considered as a positive factor for modern forestry because of their fertilizing and weeding effect, which can lead to reduced competition for nutrients, water and light for the young spruce trees (Adams 1975; Östlund, Zackrisson & Axelsson 1997). However, adapting stocking rates and timing of grazing period to available plant resources is a prerequisite for sustainably managing forestry and grazing cattle (Kaufmann *et al.* 2013b; Galleguillos, Keeley & Ventura 2018).

Clearcutting together with age- and sex-specific harvest regulations (Lavsund, Nygrén & Solberg 2003) are believed to contribute to the high productivity of the Scandinavian moose (*Alces alces*) population. As a browser, moose feed mainly on deciduous tree species, young pines, shrubs and bilberry, and they are not considered as competitors of grazing livestock (Dorn 1970; Wam & Hjeljord 2010). However, moose may avoid areas of livestock grazing due to interference competition or grazing-induced changes in the amount and composition of forage (Herfindal *et al.* 2017).

1.2. Foraging ecology of free-ranging cattle: theory and knowledge base

1.2.1. Foraging behaviour of herbivores

Although herbivores generally live in a green world of vegetation, the quality and quantity of potential forage plants vary with time and space (Owen-Smith 2002). Forage plants are usually patchily distributed and herbivores must make their decisions about “where to feed” (Senft *et al.* 1987; Bailey *et al.* 1996) and “how to distribute daily feeding bouts” (Gregorini

2012; Kilgour 2012). In addition, foraging activity and habitat use of herbivores are constrained by social interactions (Pratt *et al.* 1986; Scott, Provenza & Banner 1995), predation risks (Underwood 1983; Beier & McCullough 1990) and topography (Homburger *et al.* 2014; Bailey, Stephenson & Pittarello 2015).

According to the optimal foraging theory animals seek for maximizing the intake of energy in a minimum of time (Stephens & Krebs 1986). However, application of the optimal foraging theory to describe foraging behaviour of herbivores has been problematic, as especially the ruminants do not always optimize their energy intake (Distel *et al.* 1995) but perform their foraging strategies based on a trade-off between forage quality and quantity (Fryxell 1991; Wallis de Vries & Daleboudt 1994; Raynor *et al.* 2017). In addition, foraging decisions are based on environmental conditions (topography, distance to water, predators and human disturbance) (Senft *et al.* 1987; Weterings *et al.* 2018) and individual factors (spatial memory, social interactions) (Lazo 1995; Bailey *et al.* 1996; Roguet, Dumont & Prache 1998). Therefore, optimal foraging theory can be used to predict diet selection of ruminants, but does not necessarily imply that their foraging is optimal in an evolutionary sense (Parker & Smith 1990), especially for livestock species bred for maximising production and enhancing animal handling, such as cattle.

The digestive physiology and body size is of major importance for foraging time, digestive capacity and nutritional requirements of herbivores (Demment & Van Soest 1985; Belovsky & Slade 1986; Clauss *et al.* 2013). Large herbivore species are commonly less selective feeders compared to the smaller species as daily requirements depend on the non-linear relationship between the basal metabolic rate BMR and the body mass M ($BMR \sim M^{0.75}$). This so-called “Jarman–Bell Principle” (Geist 1974) indicates a decrease in nutritional demands per unit of body weight along a continuum of small- to large-bodied individuals. In addition, the microbiological digestion of plant material in large herbivores has been described as more effective than that of small herbivores due to the greater volume of the gastrointestinal tract (Demment & Van Soest 1985). The observed higher intake of low-quality diets in large herbivores may be seen as a strategy to cover the overall higher total energy demand by spending less time to search for high quality food resources compared to smaller herbivores who require more energy relative to their body weight (Müller *et al.* 2013). The selectivity for high-quality resources observed in small herbivores can therefore be explained on the basis of ecological opportunities rather than physiology related to body mass (Clauss *et al.* 2013).

Foraging activity is normally defined as the sum of behaviours associated with the intake of forage including transfers to new feeding localizations (Owen-Smith, Fryxell & Merrill 2010). The proportion of feeding, measured as intake of plants during foraging time, varies between different herbivores and the feed intake of grazers and browsers constitutes 80-90% and 65-80% of foraging time, respectively (Owen-Smith 2002). Mainly due to difference in the distribution of forage between vertically oriented trees and shrubs compared to the horizontally directed grass patches (Owen-Smith, Fryxell & Merrill 2010). Generally, foraging activities follow a diurnal rhythm characterised by peaks in activity around sunrise and sunset interspersed with resting periods during the day (Howery *et al.* 1996; Kilgour 2012).

Herbivores adapts foraging activity to the quantity and quality of forage (Di Marco & Aello 2001; Henkin, Ungar & Dolev 2012; Manning *et al.* 2017a). In ruminants, the forage intake increases with digestibility (Huhtanen *et al.* 2006), and daily forage intake is normally limited by the filling capacity of the gastrointestinal tract rather than time available for feeding (Beekman & Prins 1989; Farnsworth & Illius 1998). The digestibility of organic and dry matter in foraging plants increases during the day as a result of the photosynthetic activity (Orr *et al.* 1997; Gregorini *et al.* 2009). Therefore, the foraging activity of herbivores is commonly peaking during the afternoon/evening until dusk in order to maximize daily energy intake and provide a steady release of nutrients during night hours while resting and ruminating (Gregorini 2012).

Environmental conditions such as human disturbance and heat periods have caused a shift of the feeding activity to night hours in red deer (*Cervus elaphus*) (Kamler, Jędrzejewski & Jędrzejewska 2007) and cattle (Schoenbaum *et al.* 2017), respectively. Disturbance by predators has caused cattle to gather in higher stocking densities (Laporte *et al.* 2010) and can cause shifts in habitat use of herbivores which may lead to an overuse of certain habitats and increased use of poor quality habitats (Howery & DeLiberto 2004; Fortin *et al.* 2005; Weterings *et al.* 2018). In addition, presence of predators may reduce foraging activity of herbivores by causing increased vigilance (Welp *et al.* 2004; Steyaert *et al.* 2011) and daily movements (Clark & Johnson 2009).

1.2.2. Hierarchical foraging

Herbivores perform foraging activities over a hierarchy of spatial and associated temporal scales (Senft *et al.* 1987). Foraging behaviours are performed as bites at the smallest spatial scale, leaving the herbivore to decide how much of a given plant it should remove (Laca *et al.* 1992). Within a foraging patch, herbivores select for different plant species and plant parts. A foraging patch is defined as a spatial unit that differs from the surrounding units by generating changes in the herbivore's intake rate caused by e.g. changes in time spent on walking and searching while performing foraging activity (Searle, Thompson Hobbs & Shipley 2005). The feeding patches themselves are distributed inside daily, seasonal or annual home ranges (Senft *et al.* 1987; Bailey *et al.* 1996), areas where animals live and perform their normal activities (Powell & Mitchell 2012). At an even larger spatial scale, herbivores select specific areas to establish or maintain their home range, which defines the availability of forage for each individual.

In heterogeneous vegetation, foraging patches are spatially and temporally dispersed and the individual needs to move between feeding locations (Owen-Smith, Fryxell & Merrill 2010). Spatial memory in herbivores has proved crucial for an effective use of favoured foraging patches (Bailey *et al.* 1996; Van Moorter *et al.* 2009). The nutritional quality of the foraging plants decreases as they mature due to an increased content of fibre. In grasses, most of the digestible material is concentrated in the leaves and the fibre fraction is mainly found in the stems where it is required for maintaining plant structure (McDonald *et al.* 2011). Grazing results in consumption of the most digestible plant parts that in turn could be depleted. However, plants adapted to herbivory often have an opportunity for regrowth after grazing, and by selection of earlier grazed patches, herbivores can maintain their nutrient intake through the summer season (Dumont, D'Hour & Petit 1995; Wallis De Vries 1996). Although earlier grazed patches have less above-ground standing crop, they constitute a highly available feed resource in poor-quality pastures (Owen-Smith, Fryxell & Merrill 2010). Seidel and Boyce (2015) found that elk (*Cervus canadensis*) returned to their favoured foraging patches on average 15 days after foraging during the growing season. Howery *et al.* (1996) found that cattle showed high affiliation to previous used home ranges and that the selection of foraging patches inside home ranges are transferred from mother to calves. In sheep (*Ovis aries*), ewes are the main social model for their offspring and important for foraging learning (Thorhallsdottir, Provenza & Balph 1987). Lazo (1994) reported that semi-wild cattle in Spain, living with minimal management, maintained already established territories or home ranges, even under periods when resources were limited.

This memory-based foraging enables herbivores to continue foraging in already used areas. By utilizing regrowth in foraging plants, they can maintain a higher intake of digestible plant material rather than feeding on less digestible parts of matured plants (Seidel & Boyce 2015; Merkle, Potts & Fortin 2017). Models of spatial and temporal memory of herbivores have been used to explain variation in individual home range size (Van Moorter *et al.* 2009; Seidel & Boyce 2016).

1.2.3. Home range size

The variation in home range size among and within species has been claimed to be a linear function of the metabolic body mass ($M^{0.75}$) of terrestrial mammals (McNab 1963; Gompper & Gittleman 1991). This has limited validity in ungulates because differences in habitat use and species characteristics affect the relationship between body mass and home range size (Ofstad *et al.* 2016). The distribution of habitat patches is considered as a major factor determining home range size of wild ungulates, as high cover of unproductive habitat types are commonly resulting in larger home ranges, and higher proportions of preferred habitat types are found in smaller home ranges (Borger *et al.* 2006; Saïd *et al.* 2009; Bjørneraas *et al.* 2012). Factors such as social organization, population density and reproductive status have also proven influential for the home range size of herbivores (Saïd *et al.* 2005; van Beest *et al.* 2011; Vander Wal, Laforge & McLoughlin 2014). Increased population density may reduce individual home range size (Ofstad *et al.* 2016), while individual attributes such as sex and age barely contributed to the observed variation in individual home range size of roe deer (*Capreolus capreolus*) (Lovari, Serrao & Mori 2017).

1.2.4. Factors that affect habitat selection

Generally, ***abiotic factors*** such as distance to water and topography are considered to be of greatest importance for herbivore distribution inside home ranges (Senft *et al.* 1987; Pinchak *et al.* 1991; Bailey *et al.* 1996; Henkin, Ungar & Dolev 2012). Several studies have determined distance to water as a crucial factor for distribution of grazing cattle (Roath & Krueger 1982a; Pinchak *et al.* 1991; Putfarken *et al.* 2008; Ganskopp & Bohnert 2009). Cattle have also shown an ability of alternating more frequently among foraging sites in more even versus rugged terrain (Henkin, Ungar & Dolev 2012) and in more homogeneous versus heterogeneous vegetation (Bailey, Stephenson & Pittarello 2015). Wild herbivores such as elk, red deer and pronghorns (*Antilocapra Americana*) (Licoppe & De Crombrugghe 2003; Seidel & Boyce 2015; Christie, Jensen & Boyce 2017) prefer areas further from roads. On the other hand, roads may be attractive for cattle as they enable easy traveling routes through rough and forested terrain (Roath & Krueger 1982a; Sæther *et al.* 2006). Shy cattle grazing in

Canadian forests avoided human disturbance by using roads only for travelling (Kaufmann *et al.* 2013b).

The most important biotic factor of habitat selection is the ***vegetation*** itself. Inside the home range, accessibility of highly productive patches and the proportion of nutritive foraging plants are important factors of the distribution of herbivores (Lazo 1995; Kie & Boroski 1996; Wallis De Vries 1996; van Beest *et al.* 2011). The different herbivores prefer different types of vegetation and subsequently avoid others (Hall 1988; Gordon 1989). Grazers are more commonly found in open areas while browsers commonly use closed habitat types (Ofstad *et al.* 2016). Cattle are typical grazers that select vegetation communities with high biomass production consisting of mainly grass and forbs (Holechek *et al.* 1982; Pratt *et al.* 1986; Gordon 1989; Kaufmann *et al.* 2013a). In a heterogonous landscape, cattle must interact with resources over multiple scales due to a spatio-temporally changing distribution of high quality forage (Senft *et al.* 1987; Bailey *et al.* 1996). They use patches of grass in the vegetative phase for maximization of their energy intake, but selectivity is constrained by availability and the costs of searching for the preferred forage resources (Laca *et al.* 1992; Wallis de Vries & Daleboudt 1994). Cattle favour plants with higher than average content of crude protein and digestibility of organic matter (Ganskopp & Bohnert 2009; Selemani *et al.* 2013). Further, calves and small and medium-sized cows are more selective grazers than older cows and large bulls (Lazo & Soriguer 1993; Cazcarra & Petit 1995b).

The ***stocking density*** can largely influence habitat use: Livestock in areas of low stocking densities are able to select for the highest productive sites and they perform repeated grazing on specific patches due to nutrient-rich vegetative regrowth, while other patches within the home range may be avoided (Dumont, D'Hour & Petit 1995). High stocking densities may lead to an overuse of high quality patches and increased use of low quality patches (Mobæk *et al.* 2009; Owen-Smith, Fryxell & Merrill 2010; van Beest *et al.* 2014; Schoenbaum *et al.* 2017). This grazing behaviour is consistent with the ideal-free distribution (IFD) theory that predicts a more even use of habitats in areas with high stocking density compared to low density areas (Fretwell & Lucas 1969b). As an example, cattle grazing wetlands in the Netherlands were less selective in their choice of forage species at high stocking densities truly because of a poorly adapted digestive physiology for grazing patches of low sward heights (Cornelissen & Vulink 2015). In a simulated study performed in Netherlands, cattle moved more frequently and walked longer distances between foraging patches when the density of animals increased (Wallis De Vries 1996).

Habitat demands vary with the ***behavioural state*** of the animals. Sheep in an alpine area preferred vegetation types with high quality forage for grazing, and used habitats of lower productivity while resting (Mobæk *et al.* 2009). European bison (*Bison bonasus*) preferred habitats with high tree density while resting (Schneider, Kowalczyk & Köhler 2013). In recent decades, behavioural studies of cattle have been facilitated by the use of GPS-monitoring in combination with activity sensors that measure body movements in multiple dimensions and therefore allow a classification into different behavioural states(Ganskopp 2001; Ungar *et al.* 2005; Augustine & Derner 2013; Roberts, Cain & Cox 2016; Manning *et al.* 2017b). With frequent battery change of such equipment, movement and activity can be monitored continuously and at short time intervals (Ungar *et al.* 2005). Astoundingly, I found only one study on cattle habitat selection where the behaviour of cattle was classified with activity sensors instead of direct observations. In this study from the Swiss Alps, grazing activity of GPS-tracked cattle was positively related to forage quality and negatively to terrain slope (Homburger *et al.* 2014). In a Swedish study, Hessle, Rutter and Wallin (2008) recorded jaw moments in combination with GPS positions and found that heifers of both native and international beef cattle breeds preferred grazing in dry and mesic habitats and avoided wet areas.

Habitat selection may also be a result of ***seasonality***, which has a major influence on quality and quantity of forage (Parsons *et al.* 2003). Free-ranging sheep in alpine environments of Norway decreased their preference of high quality patches towards the late summer season in areas of both high and low stocking densities (Mobæk *et al.* 2009; Jørgensen, Steinheim & Holand 2018). Cattle grazing in forests of Germany (Putfarken *et al.* 2008) and Israel (Schoenbaum *et al.* 2017) selected for different types of vegetation in different seasons in order to utilize patches of good nutritional quality and to provide shelter from the sun in warm periods. In Norway, cattle decreased their use of summer farm meadows and increased use of clearcuts through the grazing season (Bjor & Graffer 1963).

The habitat use and distribution of large herbivores is affected by ***social conditions*** caused by species-specific traits, individual characteristics and social learning (Howery *et al.* 1998; Bailey *et al.* 2015; Goodman *et al.* 2016). Social affiliation between individuals is not found in cattle (Boyland *et al.* 2016) and sheep (Lawrence & Wood-Gush 1988), but they are gregarious animals that commonly establish fusion-fission subgroups within a larger herd within the same home range area (Kimura & Ihobe 1985; Hall 1986; Lazo 1994; Howery *et al.* 1996). Cattle in small herds show greater associations and form subsequently less subgroups compared to cattle within larger herds (Harris *et al.* 2007). The home ranges of herds are commonly described as very stable from year to year (Howery *et al.* 1996), and the current composition of individuals within sub-groups is influenced by environmental factors such as topography, vegetation structure, patchiness and herd size (Howery *et al.* 1998; Stephenson & Bailey 2017). Therefore, several studies have raised concerns regarding the independence of observations from GPS tracked herd animals within the same areas as these animals are likely to be influenced by social interactions regarding locations and activities (Minta 1992; Weber, Burcham & Marcum 2001; Swain *et al.* 2011; Stephenson & Bailey 2017).

1.2.5. Range management and weight performance

Sustainable utilization of unimproved land for livestock grazing involves a grazing management that optimizes livestock performance while taking into account biodiversity and other ecosystem services (Rosa García *et al.* 2013; Austrheim *et al.* 2016). This can be achieved by adjusting herd size and stocking densities, selecting appropriate livestock species and breeds, and composing an optimal sex and age structure suitable for a given pasture type (Rook *et al.* 2004; Fraser *et al.* 2009a).

Stocking density: Sustainable use of pastures for grazing livestock requires good information in terms of stocking densities and the effects of density on habitat use and animal performance (Pakeman & Nolan 2009). Stocking rate is described as the most important factor of grazing management, as even slight changes in plant quality can influence the cattle's ability to select and consume a highly nutritious diet which in turn affects weight performance (Murray & Illius 2000; Olson 2005). Further, maintaining high densities of herbivores in low productive areas for several years can favour the growth of less palatable low-quality plants and vegetation types (Simard *et al.* 2008; Skonhoft, Austrheim & Mysterud 2010).

Livestock species: Differences in dental and digestive anatomy of livestock species affects their dietary choice as well as plant communities and livestock production (Rook *et al.* 2004). For example, woody vegetation in heathland areas in the northwest of Spain has been more widespread in areas grazed by sheep than in areas with goats (*Capra aegagrus hircus*) (Jáuregui *et al.* 2009). Cattle are not particularly selective while foraging and they avoid grazing close to the ground (Pykälä 2005). Therefore, cattle will perform poorly when foraging on vegetation of low nutritional value or lower sward heights, compared to the smaller and more selective sheep, and compared to horses (*Equus ferus caballus*) that are anatomically better adapted to grazing on low sward heights (Rosa García *et al.* 2013; Cornelissen & Vulink 2015).

Breed: Several studies found has that livestock performance is affected by an interaction between genotype and grazing environment (Wright *et al.* 1994; Molinuevo 1997; Fraser *et al.* 2009a). Late maturing beef cattle breeds are bred for intensive meat production and hence adapted to energy-dense feed rations. Late maturing breeds of both sheep and cattle have a higher intake potential than smaller early maturing breeds while grazing improved pastures with good availability of preferred foraging plants (Osoro *et al.* 1999). On the other hand, animals with smaller body size are more efficient on nutrient-poor pastures where the availability of preferred species is low (Ferrell & Jenkins 1985; Osoro *et al.* 1999). As a result, these breeds are considered less efficient in utilizing energy of low quality forage than early maturing livestock breeds (Webster 1989). However, Fraser *et al.* (2009a) found that the composition of foraging plants had a greater influence on weight performance of beef cattle on low-productive, unimproved lands, compared to breed.

Animal management: High indoor feeding intensity during winter affects weight gain of cattle negatively during the recovery period after turnout to pasture (Nams & Martin 2007; Hessle, Dahlström & Wallin 2011). The nutritional intake of suckling offspring is mainly provided by milk and their weight gain depends largely on the milk yield potential of their mother (Wright *et al.* 1994; Casasús *et al.* 2002a). This may explain why studies has reported similar weight gain of spring-born suckler calves, independent of if they were grazing unimproved lands or cultivated pastures (Niemelä *et al.* 2008; Steinshamn *et al.* 2010).

Season: Weather conditions during the summer season affects growth and maturing of plants and is a source of yearly variation in weight performance of both wild and domesticated herbivores (Sæther 1985; Casasús *et al.* 2002a; Steinshamn *et al.* 2010).

2. Aims of the thesis

The broad aim of this thesis was to evaluate factors affecting behaviour and live weight performance of beef cattle grazing in the boreal forest of south-eastern Norway. The aim responds to the global growing interest in livestock production on unimproved land, known as semi-natural grasslands, rangelands or rough grazing (Hessle, Rutter & Wallin 2008; Niemelä *et al.* 2008; Fraser *et al.* 2009a). In Norway, the Ministry of Agriculture and Food has emphasized the need for knowledge about animal welfare, grazing behaviour and the synergy between grazing and other social considerations on unimproved land (Ministry of Agriculture and Food 2011; Steine *et al.* 2012). To meet these various considerations, a greater understanding is required of how cattle utilize unimproved lands and what factors affect cattle area use across heterogeneous landscapes (Kaufmann *et al.* 2013b; Larson-Praplan *et al.* 2015). It is also particularly important to estimate the production potential of different cattle groups (e.g. breeds, reproductive status and age) on different types of unimproved lands (Bailey *et al.* 2001; Fraser *et al.* 2009a).

Free-ranging suckler cows and their calves are turned out into the forest in early summer with minimal human intervention during the grazing season. The forests are often in rugged terrain with variable topography and the cattle meet an environment that is completely different from the high-productivity grasslands close to the farm. The food patches consist mostly of widespread summer farm meadows and clearcuts in the productive forest, distributed irregularly within a mosaic of even-aged forest stands (Figure 2). Within the food patches themselves, forage plants may be patchily distributed, and forestry waste, tree stumps and stones can hinder access for cattle. I was therefore interested to study the grazing behaviour, habitat selection and performance of non-native beef cattle in these heterogeneous environments. For this, I had access to two communal forests, one with low cattle stocking density and the other with high density. **Paper 1** aimed to explore the time budget of free-ranging cattle in these areas, by determining the proportion of time spent grazing, resting and walking. **Paper 2** aimed to describe the habitat selection of cattle on heterogeneous forest pastures as a function of stocking density and behavioural state, i.e. while grazing, resting and walking. **Paper 3** aimed to explore the microhabitat selection of free-ranging beef cattle while performing grazing and resting activities. **Paper 4** aimed to measure live weight gain in cows and calves during the summer grazing period, and to relate individual performance to age, breed, reproductive status, animal density and habitat use by the cattle. Finally, as **part of the**

synopsis, I calculated individual home ranges to explore how home range size relates to cattle breed, reproductive status, animal density and availability of specific vegetation types.

Figure 2: *Suckler cows grazing meadows of an abandoned summer farm in Stange - Romedal Almenning (SRA, left) and of a young forest stand in Furnes - Vang Almenning (FVA, right) (Photographers: Hilde Hegnes 2015 (left) and Lisa Dickel 2016 (right)).*

3. Materials and methods

3.1. Study area

I studied free-ranging beef cattle grazing in parts of the communal lands of Stange - Romedal Almenning (SRA) (2015–2017) and Furnes - Vang Almenning (FVA) (2016 and 2017), both in Hedmark County in south-eastern Norway (60˚ N, 11˚ E). The study areas of SRA and FVA were 150 and 100 km^2, respectively, with elevation ranges from 300 – 600 and 600 - 700 meters above sea level (m.a.s.l.), respectively (Figure 3). The bedrock was dominated by acidic and nutrient-poor rocks such as gneiss and granites in SRA and southern FVA, and dark sandstone in northern FVA (The Geological Survey of Norway (NGU) 2018).

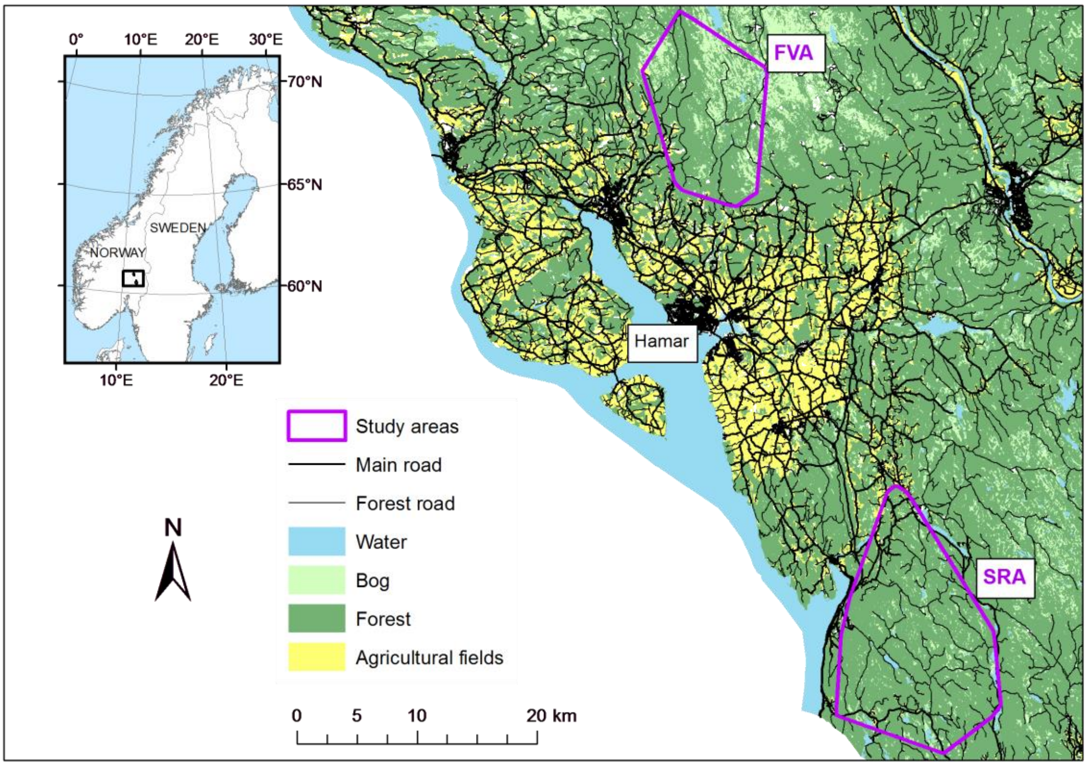

Figure 3: *Location of the study areas in Furnes/Vang almenninger (FVA) in 2016 and 2017 and Stange/Romedal almenninger (SRA) from 2015 to 2017 in south-eastern Norway*

Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) are the dominant conifers of the boreal forests in northwestern Europe. The understory vegetation of the forest floor is dominated by ericaceous species as bilberry (*Vaccinium myrtillus*) and lingonberry (*Vaccinium vitis-idaea*), feather mosses (*Hylocomium splendens, Pleurozium schreberi, Ptilium crista-castrensis*) and lichens (*Cladonia spp*., *Cladonia stellaris*) (Boonstra *et al.* 2016). In early successional stages after clearcutting, the wavy hair grass can cover up to 80%

of the ground and is the most dominant species of the understory vegetation and thereby considered as most important foraging plant for grazing livestock (Figure 4) (Larsson & Rekdal 2000; Dahlström, Hessle & Kumm 2018). Tufted hair grass (*Deschampsia cespitosa)* and sedges (*Carex sp.)* are species that commonly grow in wet areas (Todnem & Lunnan 2017), and avoided by cattle when other foraging plants are available (Hessle, Rutter & Wallin 2008).

Figure 4: *Suckler cow with calf resting inside a prethinning forest stand (left) and grazing a clearcut (right) in SRA with an understory vegetation dominated by bilberry (Vaccinium myrtillus) heather and wavy hair grass (Avenella flexuosa), respectively*. *(Photographer: Morten Tofastrud 2015)*

In SRA, parts of the area were rugged and difficult for grazing cattle to access, with bogs covering 2 % of the area. FVA was more accessible but bogs covered about 14 % of the area (Table 1). Both study areas were dominated by the bilberry-spruce forest vegetation type, which covered 58 % and 44 % of the area in SRA and FVA, respectively (Rekdal 2010; 2017).

Table 1*: Areal distribution (%) of vegetation types of the boreal forests in Stange - Romedal Almenning (SRA) and Furnes - Vang Almenning (FVA) study areas in south-eastern Norway (Rekdal 2010; 2017).*

Vegetation types	SRA	FVA
Lichen and heather pine forest	13.2	21.6
Bilberry pine forest	17.2	0.0
Bilberry spruce forest	58.0	44.4
Meadow spruce forest	1.8	4.0
Bogs and non-productive areas	2.0	14.5
Summer farm meadows	0.7	0.8
Bog and swamp forests	7.1	14.7

The coniferous forests in both study areas are managed using commercial forestry methods, resulting in a patchwork of even-aged stands. These stands are grouped into five cutting classes by age and development as: (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). The studies of Bjor and Graffer (1963) showed that grazing cattle prefer forest stands younger than 15 years, and the grazing value of cutting class 2 is considered to decrease over time (Larsson & Rekdal 2000). Therefore, I regrouped cutting class 1 with class 2-stands younger than 15 years into a new class 2.1 and cutting class 2-stands older than 15 years as 2.2. Cutting classes 4 and 5 were combined into new class 4.5 because these cutting classes have similar grazing value (Larsson & Rekdal 2000) (Table 2).

Table 2. *Distribution (%) of forest stands in regrouped cutting classes (New-Class) based on random points (reflecting availability) equal to the number of cow positions within each cow's home range 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 (Allma - Allskog Mjøsen Skog og AT Plan 2017).*

New-Class	Definition	SRA	FVA
2.1	Young forest stands ≤ 15 years	15.7	14.3
2.2	Young forest stands > 15 years	14.4	15.5
3	Early production stands in thinning stage	31.6	42.1
4.5	Mature and old-growth forest stands	38.3	28.1

3.2. Study animals and GPS collars

I recruited animals from five and four commercial farms in SRA and FVA, respectively. Cattle belonging to the same farm were considered as one herd. The number of adult cows determined herd size, and all herds included both lactating and dry cows. Herd size ranged from minimum seven to maximum 54 adult cows, with only slight changes from year to year.

The farmers reported information about the herd, including individual genotype, reproductive status and birth-period of calves. I grouped all individual animals into categories referred to as "main breed", based on the breed representing the highest proportion of the animal's genotype or the maternal breed in the case of 50/50 crosses. Furthermore, cattle were grouped as early and late maturing breeds depending on the "main breeds", with Hereford as early- and Charolais, Limousin and Simmental as late-maturing breeds. In SRA, the most common breeds were Hereford and Charolais. In FVA, most of the cows were of the late-maturing breeds, Charolais, Limousin and Simmental.

Calves were born in two calving periods (autumn and spring) and both heifer and bull calves were turned out to forest pastures, but national legislation prohibits the use of communal pastures for bulls older than six months. I grouped calves based on birth-period and sex as spring-born bulls, spring-born heifers and autumn-born heifers. Number of calves per group varied with breed group and study area (Table 3).

The farmers weighed the cattle at turnout and housing date (Table 3). All animals were kept indoors until turnout day but some had access to outdoor yards.

Table 3*: Average weight (± SD) at turnout (AWT) of early and late maturing breeds of suckler cows and spring-born (SB) and autumn-born (AB) suckling calves grazing in boreal forests of SRA and FVA in south-eastern Norway.*

Cattle	Study area	N (cows)	AWT, kg (± SD)	N (SB calves)	AWT SB calves, kg (± SD)	N (AB calves)	AWT AB calves, kg (± SD)
Early maturing	SRA	107	597 (±94.2)	60	129 (±41.6)	20	320 (±20.0)
Late maturing	SRA	45	659 (±121.2)	113	162 (±40.9)	22	268 (±38.4)
Early maturing	FVA	6	693 (±64.8)	7	200 (±22.2)	-	-
Late maturing	FVA	178	711 (±94.4)	30	172 (±55.1)	18	299 (±52.8)

At turnout day, farmers equipped cows with either a GPS collar or a cowbell. I 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 the remote data link. The GPS collars recorded positions and activity at 5-minute intervals in 2015 and 2017. In 2016, I programmed all Basic collars and seven GSM collars in SRA to take positions at 10-minute intervals during the night resting period, to save battery power and increase the length of the monitoring period in areas with poor satellite and GSM coverage. The number of GPS collars in use varied among years because of technical failures or collars that fell off during the grazing season (Table 4). GPS collars were distributed between the herds proportionally to the number of cows per herd, with at least two collars per herd (one with and one without a GSM link). In 2015, all Basic collars ran out of power after a few weeks due to incorrect programming by the manufacturing company. Data from these collars were excluded from further analysis. The GPS collars had a built-in two-axis accelerometer for measuring activity based on neck movements. During each positioning attempt, the collars measured activity as the number of electric pulses in horizontal direction, for left-right and forward-backward neck movements.

Table 4*: Distribution of the success and failure of GPS collars between SRA and FVA in the study years 2015- 2017 and the total successfully acquired GPS positions as counts and as a percentage of all positioning attempts (GPS success) across collar types.*

GPS collars

		Tellus Medium plus GSM		Tellus Medium plus Basic		Successfully acquired GPS positions	
Year	Study area	Success	Failure	Success	Failure	Count	GPS success
2015	SRA	18	0	0	13	453122	98.9
2016	SRA	9	0	5	2	242948	99.7
	FVA	9	0	5	1	293652	98.2
2017	SRA	8	1	6	0	371235	99.2
	FVA	8	1	6	1	333603	91.5[2]
	Total	52	2[1]	22	17[1]	1694560	97.8

[1] Data from collars with failures were not included in subsequent analyses.

[2] Low success rate due to unexpected deviations from programmed time intervals of "basic" collars during the period.

In the behavioural study (Paper 1), I used data from 18 GPS collars with a GSM link attached to cows turned out in SRA in 2015. These cows were six purebred Charolais (all lactating cows), five purebred of Hereford (three lactating and two dry cows) and seven crosses classified as Herefords (three lactating and four dry cows). The data were validated with observational data to build a model to classify cattle activities. I used the model to classify the activity of 52 suckler cows of different breeds and reproductive status with GPS-GSM collars during two and three grazing summers in SRA and FVA, respectively (Table 4). In the studies of home range size and habitat selection (synopsis, Paper 2), I used GPS data from 74 suckler cows, including the 52 cows used for paper 1 and 22 cows with Basic collars (Table 4). In the microhabitat study (Paper 3), I used activity and position data from 16 adult cows with GPS-GSM collars (eight in each study area) in the summer season 2017. The cows were representing all nine farms and distributed on early and late maturing breeds by five and 11 animals, respectively.

In the study on live weight performance (Paper 4), I used the weight at turnout and housing of 336 suckler cows and 270 suckling calves as a basis for measures of weight gain during the grazing season (Table 3). The cattle represented 40% and 30% of the cattle population turned out in SRA (in 2015-2017) and FVA (in 2016 and 2017), respectively. The reproductive status of the weighed suckler cows was 55 and 134 dry, and 97 and 50 lactating in SRA and FVA, respectively. Main breeds of both suckler cows and calves were unevenly distributed between the study areas, with cows of early maturing breeds dominating in SRA and late maturing breeds dominating in FVA. Fifty-three of the weighed cows were equipped with GPS collars and I used data from these collars to investigate the effects of environmental factors on weight gain in suckler cows.

3.3. Grazing regime

The periods of extensive grazing lasted between 80 and 120 days. In SRA, the grazing season typically occurred from the end of May to the middle of September, while the cattle in FVA were turned out in early June and housed in early September. This difference in grazing period between study areas was mainly due to the higher elevation of FVA and therefore shorter vegetation period. In addition, the grazing period varied between herds, mainly due to differences in calving time and farm management.

Forage production in heterogeneous patches of boreal forest pastures is highly variable, caused by varying access to water and nutrients within the vegetation types. In addition, the establishment of trees after timber harvesting can differ between the patches. In this study, cattle were roaming in large areas with highly heterogeneous habitats, making on-place forage production assessments too time-consuming and costly. Therefore, I used a large-scale approach for estimation of grazing capacities based on the foraging classification of different vegetation types by Rekdal (2010); (2017) (Table 5).

Table 5: *Percentage distribution of three foraging classes; less good, good and very good, and the estimated grazing capacity for beef cattle in SRA and FVA (Rekdal 2010; 2017). Vegetation types represented in the study areas are grouped by their grazing value based on the production and nutrient content of the characteristic plant species.*

Foraging classes	Estimated grazing capacity (beef cows ha^{-1})	SRA	FVA	Vegetation types
Less Good	0.05–0.08	21 %	29 %	Lichen and heather pine forest
Good	0.08–0.12	76 %	67 %	Bilberry pine forest Bilberry spruce forest Bogs and wet areas[1]
Very Good	0.12–0.17	2 %	4 %	Meadow spruce forest

[1] Different types of bogs and swamp forests may be considered to have either less good or good pasture value. The dominant types in both study areas were classified as areas of good grazing value.

Sheep, native cattle breeds and dairy heifers were also grazing in the study areas. Based on methods used by Rekdal (2010); (2017) all livestock were transformed to cow units and included in estimates of stocking density with the ratio of 6.5 sheep equal to 1 beef cattle unit. Cattle of native breeds and dairy heifers were considered as 0.75 beef cow units. The possible impact of wild herbivores on forage production was not measured. The utilization of grazing capacity was estimated as the relationship between the proportion of good and very good foraging areas and number of cattle turned out and thereby estimated to 38% and 148% in SRA and FVA, respectively. Consequently, the stocking densities were defined as low (0.04 cows ha^{-1}) in SRA and high (0.16 cows ha^{-1}) in FVA. In general, the grazing capacity of the boreal forest is considered as extremely low compared with cultivated pastures (Larsson & Rekdal 2000).

3.4. Resource maps

To analyse habitat selection (Paper 2) and the effects of habitat on home range size (Synopsis) and live weight performance (Paper 4), I created the following layers in ArcGIS 10.6 (Esri 2017):

Vegetation layer: I created polygon layers based on the information from the vegetation maps (Rekdal 2010; 2017). These layers included unprocessed information about all vegetation types inside areas of coniferous forest and summer farm meadows (Table 1). In order to restrict the number of small-scale or less used vegetation types, I merged bogs and non-productive areas into one group called “open areas”, and all swamp forests and deciduous forests into “other forests”.

Forestry layer: I created polygon layers of the regrouped cutting class (New-Class) based on information from the forestry plan services (Allma - Allskog Mjøsen Skog og AT Plan 2017), with permission from the managers of the respective communal area (Table 2).

Topography and road layers: I created polygon layers as topographical raster layers describing elevation, slope and aspect at 25m resolution, based on the official digital elevation model of the Norwegian Mapping Authorities (Kartverket 2017). I classified aspect into the four cardinal directions, north, east, south, and west, in addition to flat ground when slope = 0°. I created a raster layer of Euclidean distances to roads by using the Spatial Analyst tool in ArcGIS.

3.5. Classification of cattle behaviour

For papers 1, 2 and 3, I needed the behavioural state of the cows at each GPS-location. For this, I validated the activity data collected by the collars by performing observational studies of the 18 cows equipped with GPS-GSM collars during hours of daylight in different habitats in SRA in 2015. Observations were performed in 5-minute intervals simultaneously with the collars’ positioning and activity measurements, for observation periods lasting for up to one hour. I recorded all behaviours observed within the first 90 seconds of each positioning attempt, to cover the maximum acquisition time for GPS-positions (time-to-fix TTF). A total of 114 observation periods resulted in 1105 monitored positioning attempts. I followed Ungar *et al.* (2005) and divided all recorded behaviours into the following activity groups; “Low” (all resting behaviours, i.e. lying and standing with/without ruminating), “Grazing” (standing or moving with head towards the ground), and “High” (other active behaviours carried out with neck in horizontal position, mostly walking), hereafter called resting, grazing and walking, respectively. The most dominant activity group within the TTF was the response variable in classification trees including the focal animals’ neck movement and distance travelled between 5 minute positions. I developed the algorithm with the *evtree* package (Grubinger, Zeileis & Pfeiffer 2014) in R ver. 3.5.1 (R Core Team 2018). The model accuracy of the resulting classification tree was evaluated by using 75% of the observation data as a training set and the remaining 25% as a validation set. Based on the classification model, I classified more than 1.2 million 5-minutes positions obtained during three grazing seasons into the three activity groups to predict the time budget of 52 cows.

3.6. Analysis of the activity budget of suckler cows (Paper 1)

The activity of suckler cows was investigated by building logistic mixed effects models (GLMMs) in the *lme4* package (Bates *et al.* 2015) in R ver. 3.5.1. I built six candidate GLMMs with grazing (1) or non-grazing (0) as binomial response and the following fixed variables: hour of the day, week number, the interaction of hour and week, year, study area, main breed and reproductive status. I standardized continuous variables from 0 to 1 in order to compare the strength of selection among these covariates and achieve better model performance. The experimental design was unbalanced between individuals and study years and the data lacked independence within individuals. Therefore, I included a random effect with individual (animal-id) nested in year in each model. I selected the final model as the one with the fewest informative variables within ΔAIC < 2 (Burnham & Anderson 1998).

3.7. Analysis of home range size

The home range size of suckler cows equipped with GPS collars was estimated as 100% Minimum Convex Polygons (MCP) in ArcGIS 10.6 (Esri 2017) and investigated by fitting linear mixed models with maximum likelihood (ML) procedure in the R-package *nlme* (Pinheiro et al. 2018). For each GPS-collared cow and seasonal home range, I created the same number of random (available) positions as cow (used) positions. Log-transformed home range size was fitted as response variable in all models. I used the proportion of available positions inside each home range located in standing forest (New Class 3 and 4.5) and in bogs, swamp forests and pine forests, as measures of standing forest (stand_for) and Less Good foraging areas (poor_veg), respectively. These were included as explanatory variables in the models together with the individuals' average distance to roads (dist_roads), herd size (herd_size), main breed (breed_group) and the interaction between reproductive status and study area. All continuous variables were standardized. I used herd as a random effect to control for the possible lack of independence between individuals of the same herds and an unbalanced experimental design between herds. I built five candidate models and selected the best model using the criteria ΔAIC < 2.

3.8. Resource selection modelling at the patch scale (Paper 2)

I performed patch-scale habitat selection modelling of suckler cows by following Johnson's third-order selection (Johnson (1980), which relates the use to the availability of different habitats within an individual's home range. I followed the design III approach in resource selection modelling (Manly *et al.* 2002), and built GLMMs in the *lme4* package in R with use (1) versus availability (0) as binomial response. Availability was defined with random points, see chapter 3.7. I first modelled selection of vegetation type (Table 1) separately for each study area (vegetation models). I then subsetted the data and retained all positions in forest to model selection for cutting class (New-Class, Table 2), again separately for each study area (forest models). As covariates in the vegetation and forest models, I included distance to road, slope, elevation and aspect. Finally, I repeated the forest models separately for positions categorized into grazing, resting and walking (chapter 3.5). I standardized all continuous variables in the GLMMs and used Bayesian information criteria (BIC) to find the best among competing models (Burnham & Anderson 1998).

3.9. Resource selection modelling at the site scale (Paper 3)

The microhabitat selection study included in total 36 and 45 sites used by 16 GPS-collared cows for grazing and resting, respectively. Each site consisted of the cow's position (used plot) and four control plots at 50 m from the central plot in each cardinal direction (available plots, not used at the time of positioning by the monitored cow). Features of the ground cover composition (obstacles, dead material, lichens and mosses, herbs, shrubs and grasses), slope, canopy cover, sun exposure and visibility in the four cardinal directions were recorded for all used and control plots in the field.

I applied resource selection probability functions (Manly *et al.* 2002) with binomial GLMMs in the R package *lme4*. The binomial response variable was used plot (1) versus available plot (0). The first set of models included only the compositional group of ground cover, alleviated for their collinearity with the isometric logratio transformation (Hron, Filzmoser & Thompson 2012) in the R package compositions (van den Boogaart & Tolosana-Delgado 2008). The ground cover classes whose 90% confidence intervals of the estimates did not include 0, were included in the next set of models, together with slope, canopy cover, sun exposure, and the squared effect of visibility. All continuous variables were centred and standardized by using the *standardize* package in R (Eager 2017). The nested variables site ID, cow ID and herd ID were included as random effects to correct for autocorrelation. The data was modelled separately for grazing and resting sites. Model selection and estimation of the relative variable importance was based on AICc in the R package MuMIn (Barton 2017). Among models within ΔAICc < 2, the most parsimonious model was selected.

3.10. Modelling weight gain in cows and calves (Paper 4)

I investigated live weight gain in 1) all suckler cows, 2) suckler cows fitted with GPS collars and 3) suckling calves by building linear mixed models in the R-package *nlme*. For the models of all suckler cows, the fixed covariates were reproductive status (dry or lactating), breed group, the interaction between breed group and study area, the deviation of the turnout weight from the breed-specific average weight (to describe if the cow was lighter or heavier than expected at turnout) and number of grazing days. For GPS-cows, I included home range size, number of grazing days, herd size and the proportion of cow positions in meadows and forest stands younger than 15 years (New_class 2.1, Table 2). For suckling calves, I included the combination of sex and birth period (spring-born bulls – spring-born heifers – autumn-born heifers), number of grazing days and the interaction between breed group and study area. I standardized all continuous variables and included year as a random factor in all three models as the experimental design was unbalanced between the study years and areas. In addition, this random effect corrected for annual differences in weight gain due to forage quality and quantity deviations caused by yearly variations in summer temperature and precipitation (Sæther 1985; Steinheim *et al.* 2004; Steinshamn *et al.* 2010). I selected the best-ranked models as those with ΔAIC < 2, and used the conditional model averaging approach by applying the *dredge* function in the *MuMin* package in R for interpretation of the best-ranked models (Grueber *et al.* 2011).

4. Results

4.1. Activity budget and time spent grazing (Paper 1)

I developed a model for classification of cattle activities with a total accuracy of 79.4%. The model categorized resting (86.1%) with the highest accuracy followed by grazing (74.8%) and walking (52.6%). Overall, cattle spent 15.1 ± 0.5, 8.1 ± 0.5 and 0.8 ± 0.2 hours per day (mean ± SD) on resting, grazing and walking, respectively. I found an increase in the daily time spent grazing throughout the season, from 31.6 % in the beginning of June to 34.2% in September.

I found that lactating cows spent more time grazing (8.2 ± 0.5 hours day^{-1}) than dry cows (7.7 ± 0.5 hours day^{-1}). Dry cows spent more time resting (15.4 ± 0.5 hours day^{-1}) than lactating cows (14.9 ± 0.5 hours day-1). Cows in the low stocking density area spent on average 3.7% more time grazing compared with cows at the high stocking density.

The cows were mostly active in hours of daylight and rested more in hours of darkness. Most of the cows were inactive for 4 – 6 hours of the night and then grazing activity increased gradually around dawn and continued until midday. The length of the midday resting period varied through the season with 60 - 70% of cows resting between 11.00 and 18.00 in the early season while the midday resting period lasted for only 3 hours in the late season. The afternoon grazing period lasted until dusk. In early season, the probability of grazing was higher in the evening than in the morning. However, when the days became shorter later in the season, grazing intensity increased during daylight hours.

4.2. Home range size

The average home range size of cows in the low and high stocking density areas was 3 979 ± 344 and 2 554 ± 246 ha (± SE), respectively. Both the smallest and largest home ranges were used by dry cows; in 2017 a dry Charolais cow in FVA ranged over 705 ha, and in 2015 a dry Hereford cow in SRA ranged over 8 989 ha (Figure 5).

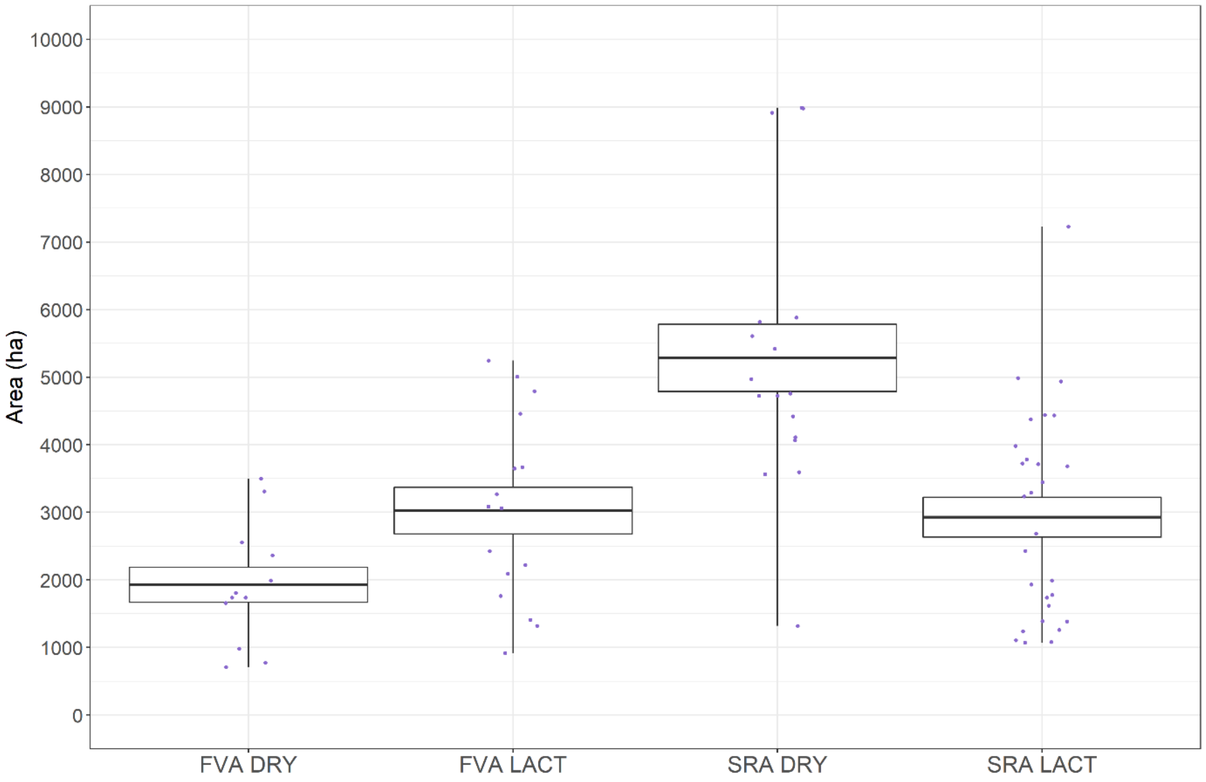

Figure 5: *Boxplots showing average home range sizes (ha) (horizontal middle line inside boxes), standard errors (upper and lower lines of the boxes) and the range of observations (purple dots and vertical lines) used by beef suckler calves in boreal forests of south-eastern Norway in 2015 -2017. The cows are divided into study areas of low (SRA) and high stocking density (FVA) and reproductive status, dry (DRY) and lactating (LACT).*

The best linear mixed model explaining home range size of suckler cows included the covariates proportion of poor vegetation inside the cow’s home range, study area and the interaction between reproductive status and study area (Table 6). I found a positive relationship between home range size of suckler cows and the proportion of poor quality vegetation types inside the home range (Figure 6). However, I found the largest home ranges in the low stocking density area, where the proportion of poor vegetation types is lower (19 ± 3 % (SE)) than in the high stocking density area (45 ± 9 %). Herd size, breeding group, proportion of mature and old forest inside the home range area and the cow’s average distance to roads during grazing season were not related to home range size.

Table 6: *Fixed effects, degrees of freedom (d.f.), Akaike's information criterion (AICc) values, and ΔAICc of 6 linear models used to study variation in home range size of free-ranging beef suckler cows grazing in low (SRA) and high (FVA) stocking density areas in boreal forests of south-eastern Norway in 2015 – 2017.*

Model	Fixed effects	d.f.	AICc	ΔAICc
Mod5HR	poor_veg + repro*study area	7	60.64	0.00
Mod4HR	poor_veg + dist_roads + repro*study area	8	63.06	2.42
Mod3HR	poor_veg + dist_roads + stand_for + repro*study area	9	64.74	4.10
Mod2HR	poor_veg + dist_roads + stand_for + herd_size + repro*study area	10	67.08	6.45
Mod1HR	poor_veg + dist_roads + stand_for + herd_size + breed_group + repro*study area	11	69.82	9.18

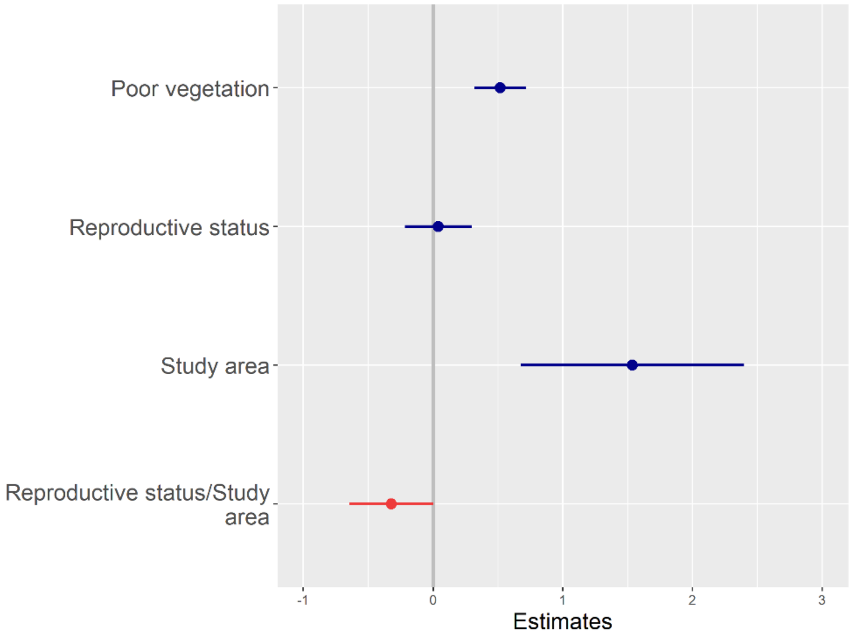

Figure 6: *Parameter estimates from home-range size models of free ranging cows during summer in boreal forest of south-eastern Norway. The estimates of reproductive status and study area refer to lactating cows and low stocking density areas (SRA), respectively.*

4.3. Habitat selection at the patch scale (Paper 2)

The use of vegetation types by cattle was not proportional to their availability. Overall, the cows spent about three quarters of their time in areas of productive coniferous forests. They preferred spruce forests and avoided pine forests. The most preferred vegetation type were the widespread summer farm meadows that covered about 1% of the area but hosted about 10% of the cow positions. I found higher probability of use of low productive habitats (deciduous/swamp and lichen pine forests) in the area of high compared to the one with low stocking density. Open bogs were strongly avoided in the area of high stocking density where the distribution of available and used positions was 15% and 1%, respectively.

In productive forests, the most preferred stands were clearcuts and young forests less than 15 years. In the high stocking density area FVA, the cows also preferred pre-thinning stands more than 15 years. In the low stocking density area SRA, cows used New-Class 2.2 slightly more and, New-Class 3 and 4.5 less than expected from availability. In the productive spruce forest, amounted New-Class 3 and 4.5 greatest proportion of the area, these were used less than expected from availability (Figure 7).

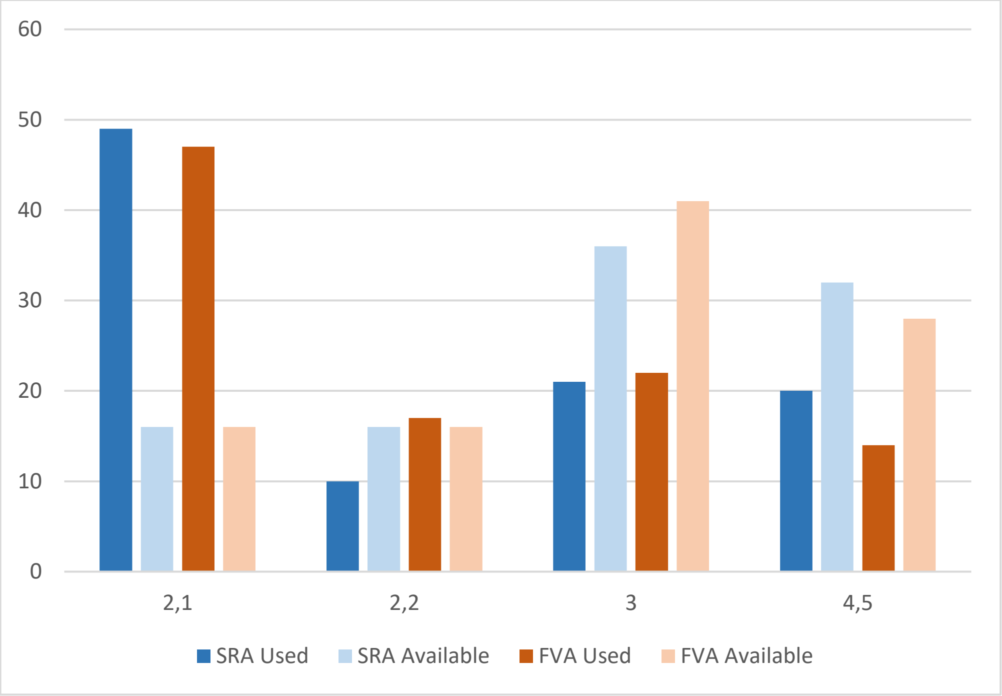

Figure 7: *Distribution (%) of available and used positions in regrouped cutting classes (New-Class) in the productive spruce forest (Bilberry and Meadow spruce forest)) for the study areas with low (SRA) and high (FVA) stocking density in south-eastern Norway. For definition of cutting classes, see Table 2.*

Cows selected most strongly for forest stands younger than 15 years during all activities, but the selection for young forest stands was 1.6 and 2.5 times stronger while grazing than while resting or walking, respectively. 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.

4.4. Habitat selection at the site scale (Paper 3)

A preliminary analysis of ground cover composition showed only grass cover of importance for the use of grazing and resting sites, while obstacles, dead materials, lichen and mosses, herbs, and shrubs were not included in the final GLMM models. The average percentage of grass cover on the ground of plots used by the cows was 44.0% and 35.6% for grazing and resting plots, respectively.

The best-ranked GLMMs for explaining the use of a site for grazing and resting showed increased probability of use with increasing percentage of grass cover. This variable was the only variable of importance for microhabitat selection of cows while grazing and the relative importance of the variable was 0.79. The probability of use for cows while resting increased with grass and canopy cover and decreased with slope. The relative importance of these variables was highest for grass cover (0.99) followed by slope (0.88) and canopy cover (0.80).

4.5. Weight performance in cows and calves (Paper 4)

During the grazing season, dry and lactating suckler cows in the low stocking density area gained on average 31 ± 5.1 kg (± SE) (n = 55) and 6 ± 4.2 kg (n = 97), respectively. In the high stocking density area, dry and lactating cows lost on average 18 ± 4.6 kg (n = 134) and 38 ± 4.6 kg (n = 50), respectively (Figure 8). Model averaging of the best-ranked linear mixed models showed increased weight gain for dry versus lactating cows, cows with a long grazing season and cows with lower turnout weight than the average of their respective breed. Early maturing breeds in SRA (low stocking density) had highest weight gain, and weight gain was lower in FVA (high stocking density), with a less pronounced difference between breed groups.

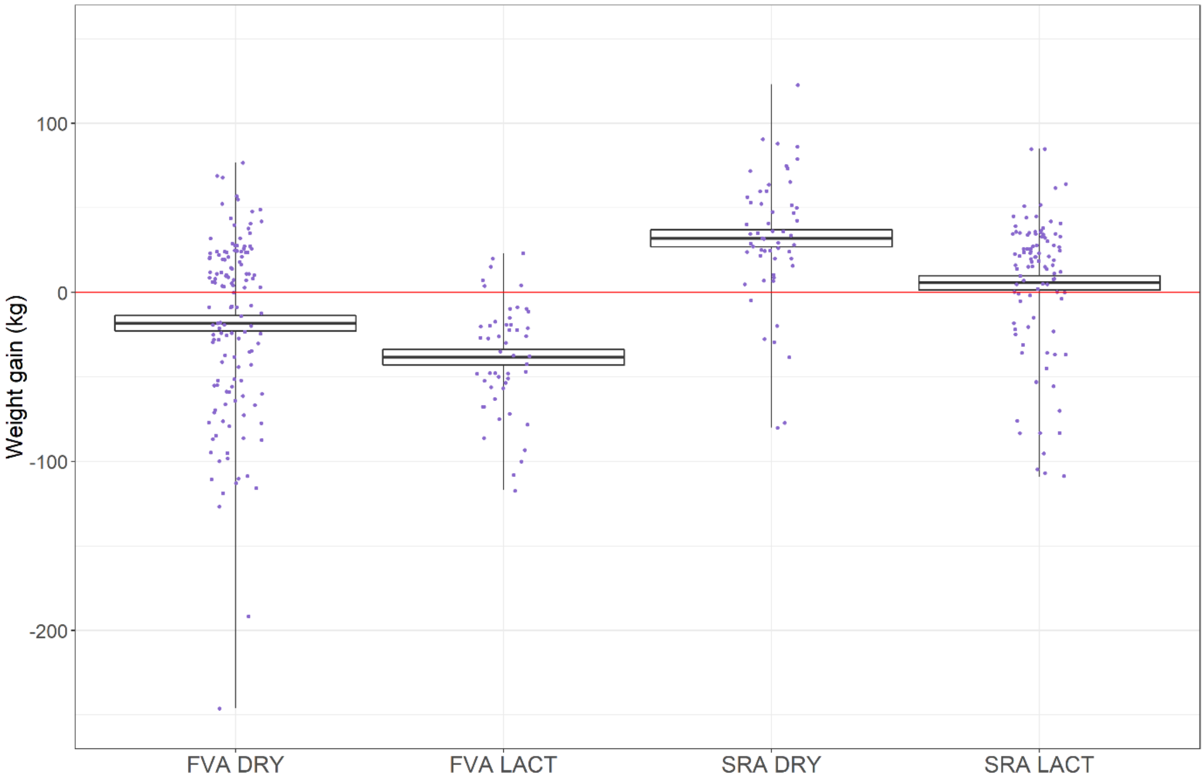

Figure 8: *Boxplots showing average weight gain (kg) (horizontal middle line inside boxes), standard errors (upper and lower lines of the boxes) and the distribution of observations (purple dots and vertical lines) in beef suckler cows in boreal forests of south-eastern Norway in 2015 -2017. The cows are divided into study areas of low (SRA) and high stocking density (FVA) and reproductive status, dry (DRY) and lactating (LACT).*

The best-ranked models explaining weight gain of 53 cows equipped with GPS collars showed also a positive relationship between the weight gain in suckler cows and the number of grazing days. Weight gain had only a weak negative relationship with home range size and use of summer farm meadows. Time spent in clearcuts younger than 15 years and herd size were not included in the best models explaining weight gain in suckler cows equipped with GPS collars.

Spring-born bull calves showed the highest weight gain during the summer grazing period, followed by spring-born heifers over autumn-born heifers (Figure 9). The latter showed notably lower weight gain in the high stocking density area. Overall, calves of the same birth periods and sex in the low stocking density area gained more weight compared to those in the high stocking density area. Early maturing breeds tended to gain more weight than late maturing breeds. The number of grazing days was less important for weight gain in suckling calves compared with cows.

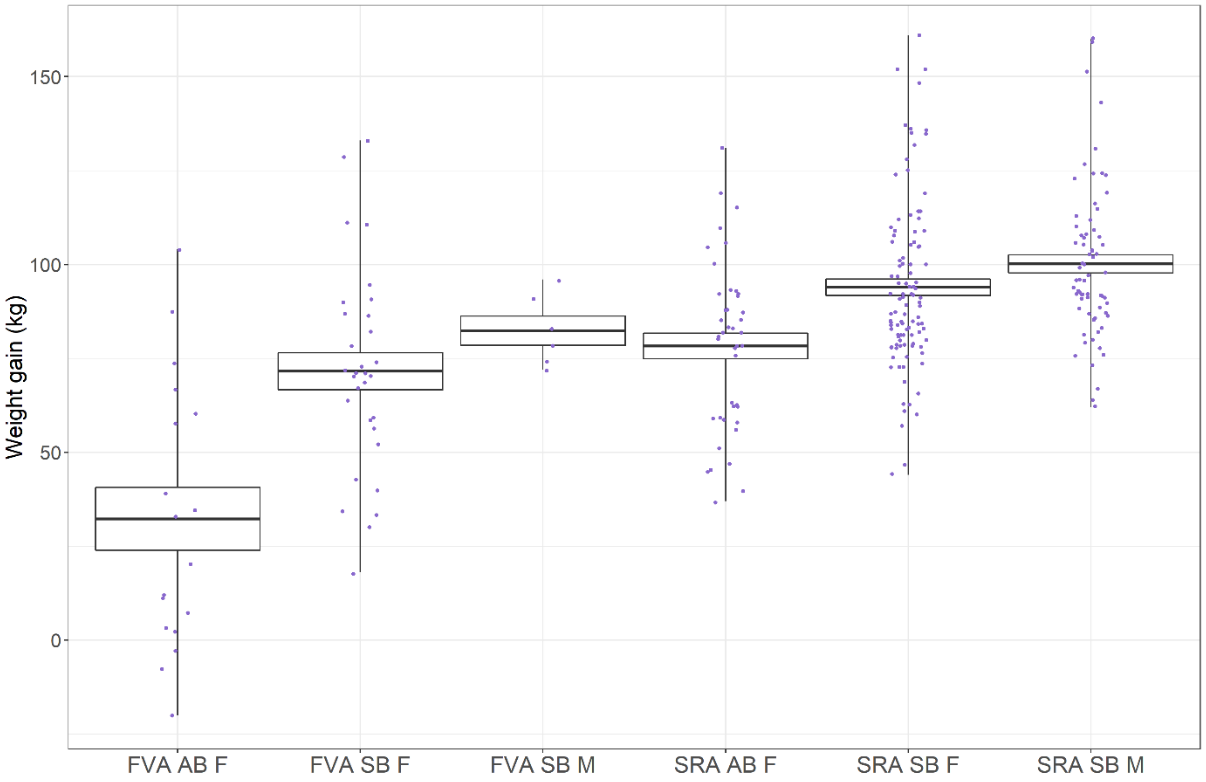

Figure 9: *Boxplots showing average weight gain (kg) (horizontal middle line inside boxes), standard error (upper and lower lines of the boxes) and the distribution of observations (purple dots and vertical lines) in beef suckler calves in boreal forests of south-eastern Norway in 2015 -2017. The calves are divided into study areas of low (SRA) and high stocking density (FVA), autumn- (AB) and spring-born (SB), and female (F) and male (M).*

5. Discussion

My objective was to identify factors that affect grazing behaviour, habitat selection and weight performance of beef cattle grazing in the boreal forests of south-eastern Norway. I was particularly interested in the effects of vegetation and forest classes, stocking densities, breeds and reproductive status on cattle activity, home range size, habitat selection and live weight gain of the cattle (Figure 10). In addition, I investigated temporal effects on activity of GPS collared cows and weight gain in suckler cows and suckling calves. In the following, I will discuss these effects more in detail.

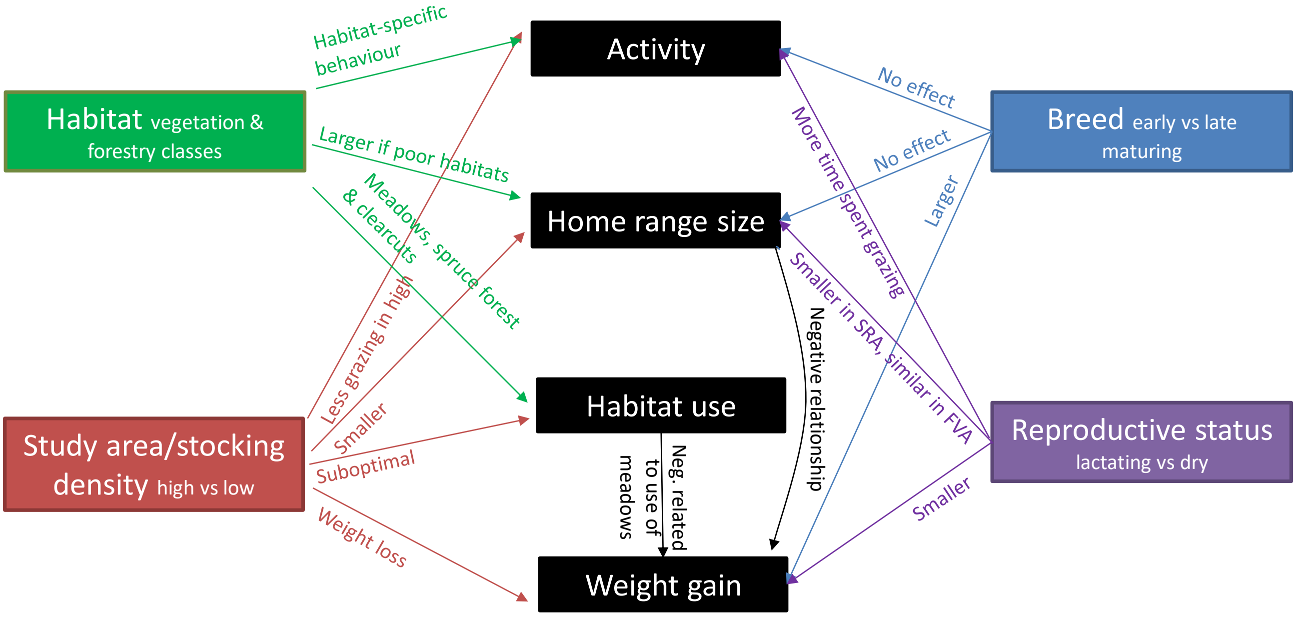

Figure 10: *Summary of main results showing how extrinsic and intrinsic factors affect cattle activity, habitat size, habitat use and weight gain on free-range cattle grazing in the boreal forest during the summer period.*

5.1. Multiple effects of habitat

The habitat characteristics were important determinants of cattle activity, home range size, area use and indirectly also weight gain (Fig. 10). In accordance with previous studies of dairy cattle (Bjor & Graffer 1963) and sheep (Warren & Mysterud 1991) in the Norwegian boreal forest, I found that suckler cows selected grass-dominated areas, i.e. summer farm meadows and clearcuts, mainly in spruce forests. Grass-dominated bogs have been classified as good pastures for cattle grazing unimproved lands of Norway (Bjor & Graffer 1963; Rekdal 2010; 2017). However, the cows in my study used bogs far less than expected from availability.

This is in agreement with Hessle, Rutter and Wallin (2008) and Hessle *et al.* (2014) who assumed that cattle prefer plant species of dry areas over wetland species with low digestibility. The suckler cows in my study were much heavier than the native dairy breeds studied by Bjor and Graffer (1963). To move in wetlands is probably more energy-demanding and risky for heavy breeds because they are sinking deeper than smaller breeds. This may also explain why the cows in my study mostly avoided the wetlands.

Sheep are grazing open forest areas in early season but they gradually move into the denser forest as the season progresses (Warren & Mysterud 1991). In dense forests, most of the wavy hair grass is sterile and energy and crude protein content are maintained longer throughout the summer and fall (Rekdal 2017). My studies did not include spatiotemporal analyses of habitat selection, but cows are less selective feeders than sheep and more likely to select open grass-rich areas rather than grazing widespread patches of grass inside the standing forest (Grant *et al.* 1985; Fraser *et al.* 2009b).

In both study areas, cows selected for lower elevations which may be due to higher productivity, higher temperatures and lush valley bottoms at lower elevations (Rekdal 2010; 2017). Generally, I found terrain slope of low importance for cattle habitat selection, in contradiction to previous studies where, cattle avoided steep slopes (Homburger *et al.* 2015; Bailey *et al.* 2018). However, the slopes in my study areas rarely exceeded 20%, a threshold value found for cattle grazing on hills and mountain sides in Oregon (Ganskopp & Vavra 1987). As reported by Senft, Rittenhouse and Woodmansee (1985) the cows preferred terrain facing south, especially while resting, and mostly avoided north- and east-facing terrain.

Despite of these general patterns of habitat selection, I found considerable differences in habitat use depending on the behavioural state of the cows. Their preference for clearcuts was strongest while grazing and less pronounced while resting, similar to sheep in mountain areas that preferred high-productive areas during grazing and areas of lower productivity while resting (Mobæk *et al.* 2009). While traveling, the cows preferred forest roads. At the microhabitat level, the cows preferred grass-rich sites while grazing and grass-rich, flat sites while resting, similar to a study of dairy cattle at high elevations in the Alps (Homburger *et al.* 2014). They also preferred sites with canopy cover for resting. European bison selected resting sites inside coniferous forest in order to seek cover from blood-sucking insects and other disturbances (Schneider, Kowalczyk & Köhler 2013). In Norway, Bjor and Graffer (1963) observed that cows in the boreal forest seeked cover inside the dense forest during periods of heavy rain and while disturbed by swarms of flies. Generally, summer temperatures were below 20 °C during these study years and the cows likely spent less time seeking shelter from sun exposure and heat compared with cattle in warmer regions of the world (Bennett, Finch & Holmes 1985; Widowski 2001; Schoenbaum *et al.* 2017).

Average home range size of the suckler cows in my boreal, forested study area was comparable to that of cows grazing in mixed-conifer forests in California (Kie & Boroski 1996), but two to ten times larger than that of cows grazing in grass- and shrub-dominated landscapes of Spain (Lazo 1994) and Idaho (Howery *et al.* 1996). Further, the home ranges were smaller than summer home ranges of European bison (Krasińska, Krasiński & Bunevich 2000) and elk (Seidel & Boyce 2016) in forested habitats of Poland/Belarus and Alberta, respectively. In general, the relatively large home range areas of cattle in this study can be seen as a result of nutrient-poor environments. Even within my study, home ranges of cows in areas with a high proportion of low-quality habitat were larger than those of cows in areas dominated by high-quality habitat. This finding corresponds with previous studies that identified forage quantity and quality as primary factors affecting home range size of herbivores (McLoughlin & Ferguson 2000; van Beest *et al.* 2011; Naidoo *et al.* 2012; Walter *et al.* 2018).

Cows that frequently used summer farm meadows had a slightly lower weight gain than those that did not use summer farms so often. Cattle from several herds were often gathering on the small, dispersed summer farms meadows, so these were heavily grazed throughout the season. Thus, the sward heights of these areas constantly kept low which is believed to influence the feed intake and weight performance of cattle negatively. Potentially, these meadows have attracted cows that otherwise had low access to other high-quality habitat types. I could not differentiate between the weight performance and time spent on resting and grazing on the preferred habitat types as this data was only available for cows with GSM-collars (Paper 1).

5.2. Effects of study area or stocking density

I found that cows in the high stocking density area FVA spent less time grazing, had smaller home ranges, used more frequently suboptimal vegetation types and gained less or even lost weight during the grazing period, compared to cows in the low stocking density area SRA (Fig. 10). It is tempting to explain these differences with density-dependence. However, the two study areas SRA and FVA differed not only in regard to stocking densities, but also in elevation, composition of vegetation types and topography. The difference in elevation can affect the development of foraging plants, especially in early and late season, as temperature is generally reduced by 0.6 °C per 100 altitudinal meters (Gommes 2002), which corresponds to a difference of 1 – 2 °C for the two study areas. The large proportion of wetlands in the high stocking density area FVA makes large parts of this area inaccessible and can thus affect cattle movement and grazing behaviour by forming barriers between preferred habitats. On the other hand, higher prevalence of steep slopes and rough terrain in the low stocking density area SRA can reduce the accessibility to parts of the area.

The stocking densities in my study areas were either far below (33% in SRA) or far above (140% in FVA) the estimated grazing capacity (Rekdal 2010; 2017). To disentangle the effects of stocking density from other study area-specific characteristics, measurements of sward height or biomass availability would have been useful, but were not prioritized in my thesis due to time constraints. However, a study of plant fragments in faecal samples collected during the grazing season 2016 was performed using microhistological analysis (Putman 1984). Samples of the low stocking density area contained larger proportions of wavy hair grass than those of the high stocking density (34.4% ± 13.9% in SRA versus 18.2% ± 8.5% in FVA (mean ± SD)) (Aletengqimuke & Tofastrud 2018, Unpublished). The proportion of wavy hair grass increased by 30.1% in samples from early to late season in the low stocking density area while the proportion remained unchanged in the high density area. Wavy hair grass differs from other foraging plant species by sustaining a high energy value throughout the summer (Lunnan & Todnem 2011). In accordance with previous studies (Roath & Krueger 1982b; Mandaluniz, Aldezabal & Oregui 2011), the cattle were more selective in the beginning of the grazing season, whereas areas with less preferred species were grazed to a higher extent later in the grazing period. Cows in the low stocking density area had the opportunity to increase their intake of wavy hair grass in late season while the cows in the high stocking density area grazed more of the less preferred species growing on nutrient poor soils of wet areas (Sæther *et al.* 2006; Hessle, Rutter & Wallin 2008).

Herbivores adjust their time spent on foraging in order to meet their nutritional demands (Manning *et al.* 2017a). High stocking densities lead to declining amounts of the preferred forage as a result of reduced sward heights (Bailey *et al.* 1996; Cornelissen & Vulink 2015) which often leads to an increase in daily grazing time (Allison 1985; Hejcmanová *et al.* 2009; Schoenbaum *et al.* 2017). My results did not support this, as cows in the high density area spent less time grazing than those in the low stocking density area. However, Hepworth *et al.* (1991) found that cattle grazing under heavy stocking rates reduced grazing time and movement in order to save energy in patches of shorter sward heights. In an Australian study performed in paddocks over 15 days, Manning *et al.* (2017a) reported an increase in daily grazing activity from 31% to 69% as a result of declining pasture biomass. Grazing activity of cattle is found to increase in areas of palatable forage (Bailey *et al.* 1996) and decrease in areas of poor forage quality (Homburger *et al.* 2015). Therefore, I speculate that the lower grazing activity in the high stocking density area was a result of reduced availability of preferred forage plants and that the palatability of the remaining plants did not stimulate for increased grazing activity.

Average home-range size was smaller in the area with high compared to low stocking density. The inverse relationship between home range size and population density is commonly observed in other mammal species (Massei *et al.* 1997; Klemen 2012; Efford *et al.* 2016). For herbivores grazing at high densities, it is likely that the energy cost of increasing home ranges in the search for new foraging areas will be higher than the energy gained and the animals may respond by preferring less favoured habitats inside an already established home range (McLoughlin & Ferguson 2000; Crimmins *et al.* 2015; Schoepf *et al.* 2015). In accordance with Roath and Krueger (1982b) and Howery *et al.* (1996), I found home ranges of the herds overlapping from year to year (Tofastrud, unpublished). However, home range size was not affected by herd size, which also correspond to the farmers' claim that the area use of their herds has remained stable over the years, although the size of their herds has increased. Since the cows often are recruited from the herd, this behaviour may be the result of social learning from mother to female offspring from generation to generation (Howery *et al.* 1998; Broad, Curley & Keverne 2006).

Cattle are generalists who adjust their intake through a trade-off between quantity and quality of foraging plants (Stephens & Krebs 1986). In accordance with previous habitat selection studies of cattle (Hart *et al.* 1991; Sawalhah *et al.* 2016; Schoenbaum *et al.* 2017), sheep (Mobæk *et al.* 2009) and horses (van Beest *et al.* 2014), and in support of the Ideal free distribution model (IFD) (Fretwell & Lucas 1969b), cows in the high density area had a more even use of vegetation types and forest stands than those in the low density area. The reduced selectivity in the high stocking density area may be due to the reduced availability of foraging plants in preferred grazing habitats. Generally, cows prefer gravel roads in order to save energy while traveling in habitats with rough terrain and dense vegetation (Williams 1954; Workman & Hooper 1968; Kaufmann *et al.* 2017). I found that cows in the low stocking density area preferred the gravel roads, while cows in the high density area stayed further from roads. This finding is in support of the IFD, but may also be explained by differences in terrain ruggedness: While cows may have preferred to travel on gravel roads in the rough terrain of SRA, they did not have the same needs when travelling in the more flat terrain of FVA.

Despite the nutritional-poor environments of the boreal forest, the beef cattle of international breeds performed remarkably well when stocking density did not exceed the grazing capacity of the area. In the high stocking density area, both dry and lactating cows of early and late maturing breeds lost weight in both study years. Previous studies have generally reported negative density-dependent effects on weight performance (Hart & Ashby 1998; McCollum *et al.* 1999; Sims & Gillen 1999) due to reduced forage availability (Bailey *et al.* 1996; Brosh *et al.* 2006) and low sward heights (Cornelissen & Vulink 2015).

Overall, average weight gain was higher in calves of the low stocking density area compared to those of the same sex and birth period in the high stocking density area. I assume that milk constitutes a larger proportion of the nutrient intake in spring-born calves, which is especially advantageous when grazing extensive pastures (Rutledge *et al.* 1971). The weight performance of autumn-born calves in the high stocking density area was remarkably poor which was likely caused by the limited ability for compensation of their mother's decreasing milk production with intake of forage in this area due to lower sward heights and reduced availability of high quality forage (Wright & Russel 1987).

5.3. Breed matters for weight performance

In my study, there was no difference between breeds in the daily time that the cows spent on grazing. This finding is in support of results from several previous studies (Funston *et al.* 1991; Sæther, Bøe & Vangen 2006; Hessle, Rutter & Wallin 2008; Braghieri *et al.* 2011; Hessle *et al.* 2014). Further, breed had no effect on home range size. To my knowledge, there is a lack of studies on breed-specific variation in home range size of free-ranging cattle. A Norwegian study showed that free-ranging sheep of the light-weight native breed used larger areas than those of the heavier crossbred type (Jørgensen, Steinheim & Holand 2016).

I used the deviation from the average breed-specific weight at turnout as a proxy for body condition to study the effect of body size on weight gain in the grazing period. I found a slightly negative effect between weight gain and deviation from breed-specific weight at turnout, which may be caused by both genetic variation and the winter feeding regime. Hessle, Dahlström and Wallin (2011) found that steers on higher intensity winter-feeding lost more weight and had a markedly longer recovery period on pasture than steers on a lower intensity indoor feed regime. In a study performed during summer 2018 close to the study area of my thesis (Toten Almenning, 30 km straight line distance west of SRA), live weight gain of adult dry suckler cows during the summer grazing period was negatively related to their body condition score at turn-out (Kjeserud & Tofastrud 2019, Unpublished). This result is in agreement with previous studies that showed that the feeding level of the previous winter affects grazing time (Cazcarra & Petit 1995a) and weight gain in cattle (Wright, Russel & Hunter 1989).

Cows of early maturing breeds gained more weight than those of late maturing breeds in the low stocking density area. The lack of such a relation in the high stocking density area was probably due the small sample size of early maturing breeds in this study area. Energy required for maintenance functions represents up to 75 % of total energy requirements in cattle and variation in energy requirements for maintenance appears to be greater between breeds than that for growth (Ferrell & Jenkins 1985). Previous studies have described early-maturing breeds as more effective than late-maturing breeds when forage is less available or of poor nutritional value (Ferrell & Jenkins 1985; Webster 1989; Molinuevo 1997; Fraser *et al.* 2009a). In their study performed in the 1950s, Bjor and Graffer (1963) stated that pastures in the boreal forest were suitable for cattle of lower production and hence nutritional demand.

5.4. Lactation sets constraints

In accordance with Le Neindre (1989) and Casasús *et al.* (2002a), I found grazing time to be positively associated with lactation, most probably as a direct result of a higher energy demand in lactating cows (Montaño-Bermudez & Nielsen 1990).

Similar to previous studies of Howery *et al.* (1996) and Kie and Boroski (1996), I found large individual variation in home range size. This variation was partly explained by the interaction of the reproductive status of the cows and the study area. Interestingly, dry cows used the smallest home ranges in the high density area and the largest home ranges in the low density area, while lactating cows had about equal home range sizes in the two study areas. Hypothetically, cows without calves are expected to move more freely and therefore use larger areas than those with calves, particularly in areas of low stocking densities where interference competition is low and the distance to other cows for social interaction large. On the other hand, lactating cows could be expected to use larger areas than dry cows due to higher energetic requirements, particularly in areas with low forage availability. Comparable studies of wild herbivores found both larger (roe deer, Saïd *et al.* 2005), smaller (moose, van

Beest *et al.* 2011) and similar (moose, Cederlund & Sand 1994) home range size of lactating females, compared to non-reproducing females.

I found lower weight gain in lactating than in dry cows, truly because of the higher energy demand during lactation. In the literature, there are examples of both weight gain and loss for free-ranging cattle on unimproved land. This variation has not only be explained by the cows' milk production potential (Montaño-Bermudez & Nielsen 1990), but also by an interaction between genotype and grazing habitats (Wright *et al.* 1994).

5.5. Temporal effects on grazing activity and weight performance

Activity patterns reflect evolutionary adaptations of ungulate species to their habitat (Owen-Smith & Goodall 2014). Initially, I expected the cows in my forested study area to spend more time grazing than cows on open homogenous grasslands, because heterogeneous habitat can lead to increased time spent on foraging activities (Belovsky & Slade 1986). I also expected the cows to expand their grazing time into night hours during the bright summer nights of Norway. Kilgour (2012) summarized studies from all over the world on cattle behaviour on pastures. He used studies from pastures of various quality and found that cows spent on average between 6.8 and 13.0 hours per day (h/d) on grazing. Average grazing time for the cows in my study was 8.1 h/d, well within the time interval reported by Kilgour *et al.* (2012). However, the cows in my study spent less time on grazing compared with cows in unimproved lands of the mountains in Montana (11.9 h/d, Funston *et al.* 1991) and scrub-oak woodland of Israel (9.7 h/d, Schoenbaum *et al.* 2017). Therefore, I assume that the cows in my study had the ability to increase their time spent on grazing if necessary.

In accordance with several studies of grazing livestock (Warren & Mysterud 1991; Howery *et al.* 1996; Orr *et al.* 1997; Gregorini 2012), I found a strong diurnal pattern in grazing activity. The cows were grazing in three main bouts during daylight and grazing activity peaked around dusk and dawn. I found an intensification of the grazing bouts during daytime in late season (August and September), and assume that decreasing hours of daylight are the main driver for this pattern. Cattle generally perform resting behaviours during night, and previous studies report 5 – 40% of total grazing activity performed during this period (Gregorini 2012; Kilgour 2012). The large variation in grazing time during night in these studies may be a result of adaption to the local environment e.g. high daytime temperature and vegetation composition. In my study, cattle grazed in an especially patchy and challenging environment with tree trunks and residues from timber harvesting, which makes locomotion during the dark hours of late summer particularly difficult.

An increasing content of fibre in forage plants during August and September is leading to a lower digestibility and energy concentration (Hessle, Rutter & Wallin 2008). I hypothesized cattle to increase their time spent on grazing throughout the season in order to meet their energy demands and observed an overall increase in average grazing time of 2.6% during the study, which was lower than expected compared to the results reported in previous studies (Scarnecchia, Nastis & Malechek 1985; Funston *et al.* 1991; Manning *et al.* 2017a). It is worth noting that the cattle in these studies were grazing at high stocking densities in areas of more homogenous vegetation. In my study areas, date of housing is constrained by the onset of moose hunting in end of September. I assume that in particular cows in the low stocking density area would have been able to find forage in the forest for at least 2-3 more weeks until leave fall.

Weight gain in suckler cows was slightly positively related to the length of the summer grazing period. Cattle commonly lose weight for a period after turnout to pastures and will need a recovery period before gaining weight (Nams & Martin 2007; Hessle, Dahlström & Wallin 2011). This may explain why cattle that were turned out for only a short period, had on average a lower weight gain or even lost weight, compared to those with a longer grazing period. In addition, cows turned out late will miss the early stage of plant development, with new shoots rich in energy.

6. Conclusions

The overall aim of this thesis was to investigate activity budgets, habitat selection and live weight performance of beef cattle grazing in boreal forests of Norway, and I found significant differences for cows grazing in a high stocking density area compared to those in a low stocking density area. The areas do not only differ with regard to livestock stocking density, but also other biotic and abiotic factors. It is therefore difficult to disentangle density effects from other factors. However, most of my results are in support of previous studies that reported similar effects of stocking densities on grazing behaviour, habitat selection and weight performances in cattle.

In this study, I found the daily time budget of the cows comparable to that of cows grazing in environments with high and low nutritional concentrations. Therefore, I consider that the cows in my study had good opportunities to perform a "normal" time budget during the grazing season. Although forested habitats differ strongly from the highly productive, open grasslands commonly used as pastures for cattle, trees are offering shelter from weather and insects. Trees on pastures can reduce fear responses in cattle (Broom, Galindo & Murgueitio 2013), and shy animals have been shown to prefer dense forest stands rather than open clearcuts (Kaufmann *et al.* 2013b).

In this thesis, I found cattle of the international beef breeds, weighing about 200-300 kg more than the previously studied dairy breeds (Bjor & Graffer 1963), as fully suitable for grazing in the boreal forest in south-eastern Norway as long as the number of grazing animals does not exceed the area's feed production capacity. This capacity is dependent on the availability of young clearcuts (less than 15 years) which provide high biomass production of grass and other herbages. Therefore, cattle grazing can be highly compatible with modern forestry operations, given a sustainable management adapted to economic, ecological and social aspects of the boreal forest. Further research should focus on potential positive and negative impacts of cattle grazing in boreal forests, such as weeding and increased nutrient cycling, damages to young trees due to trampling, and interactions with the currently returning large carnivore populations.

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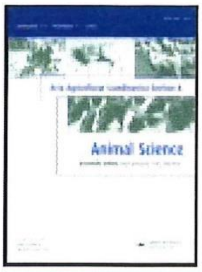

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Activity patterns of free-ranging beef cattle in Norway

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ABSTRACT
The aims of this study were to: 1) build a model to classify cattle activities based on locomotion and neck movement data and 2) study the daily time budget of non-native beef cattle in the boreal forest of southeastern Norway. We used GPS collars programmed to take positions and activity measures every five minutes on 18 cows during the grazing seasons 2015–17, together with behavioural observations in the field. The model classified the collar data into Grazing, Low (resting behaviours) and High (other active behaviours) activity with an accuracy of 79.4%. The cows spent 8.1 ± 0.5 (mean ± SD) hours per day grazing, corresponding to 34% ± 0.5% of their daily time budget. Daily grazing time increased during summer and was longer for lactating than dry cows and at low compared to high stocking density.

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Introduction

The time budget of grazing ruminants is flexible and influenced by day length, climate and other environmental factors (Dulphy et al., 1980; Gregorini et al., 2006). The time budget is also a result of behavioural adjustments of food intake and digestion related to the nutritional value of forage plants (Gregorini, 2012). Therefore, studies of the time-budget are considered as beneficial to examine the natural behaviour of free ranging cattle (Kilgour, 2012) with the purpose of finding genotypes (Sæther et al., 2006; Hessle et al., 2008; Braghieri et al., 2011) and animal groups (e.g. age and reproductive status) suitable for various sward structures (Rook et al., 2004).

In Norway, only 3–4% of the land area is cultivated, and grazing livestock in rangelands has therefore been of great importance for agricultural production during the past 2000 years (Austrheim et al., 2008). Traditionally, small-sized native breeds of dairy cattle have utilized the forest for pasture, but today they have been replaced by non-native beef cattle breeds selected for intensive feeding systems (Norwegian Agriculture Agency, 2017). How these breeds cope with and adapt to the extensive conditions of the boreal forest, characterized by rugged terrain and marginal grass areas, is poorly studied (but see Sæther et al., 2006 and Hessle et al., 2008 for studies on cattle grazing in Scandinavian semi-natural grasslands). Scandinavian forests are intensively managed by clear-cutting. The resulting openings produce temporary patches of ground-layer biomass available to wild and domestic herbivores (Bjor & Graffer, 1963; Edenius et al., 2002). Due to the high latitude (60° N in our study area), growing season on the clear-cuts is short, resulting in early flowering and withering of the forage plants. There is also a strong seasonality in day length, with 19 h of daylight (sunrise to sunset) in June to 13 h in mid-September.

Observational studies of cattle behaviour are challenging in forested habitats due to poor visibility caused by rugged terrain and high tree density, often combined with shyness of the free-ranging cattle (Kaufmann et al., 2013). In recent decades, GPS with built-in accelerometers brought new opportunities for continuous measurement and insights in foraging ecology and activity of both wild (Moen et al., 1996; Gottardi et al., 2010) and domestic herbivores ((Ungar et al., 2005; Dutta et al., 2015).

A review of studies on cattle activity (Kilgour, 2012) reports a large variation among studies in the time allocated to different behaviours. The number and timing of grazing bouts varied between two or three bouts in the morning, midday and evening, depending on temperature and day length (Low et al., 1981; Schoenbaum et al., 2017). In addition, various studies report an increase (Scarnecchia et al., 1985; Hessle et al., 2008) or decrease (Henkin et al., 2012) of grazing activity as a

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result of a seasonal decrease in the quality and quantity of the forage.

The objectives of the present study were to:
(1) Develop of a model for the classification of free-ranging cattle activity based on activity sensors and (2) describe the activity of non-native beef cattle in the Norwegian boreal forest.

Materials and methods

Study areas and animals

The study took place on two common lands, Stange-Romedal Almenning (SRA, 150 km^2) and Furnes-Vang Almenning (FVA, 100 km^2) in Hedmark County, Norway (60° N, 11° E) (Figure 1). The elevation ranged 300–600 m a.s.l. in SRA and 600–700 m a.s.l. in FVA. For the three study years 2015–2017, average summer (June-September) air temperature was 13.2°, 14.6° and 13.2° C, and precipitation was 75 mm, 48 mm and 88 mm in 2015, 2016 and 2017, respectively (Norwegian Meteorological Institute, 2018). The summer nights in these latitudes are bright from late May to August when nights turn dark. Livestock were turned out by the end of May in SRA and early June in FVA, and housed throughout September.

Both study areas are managed by commercial forestry, resulting in a patchwork of even-aged stands. The dominating vegetation type was bilberry-spruce forest (*Vaccinio-Piceetea*), with the ground layer dominated by bilberry heather (*Vaccinium myrtillus*) on regrown forest stands and wavy hair grass (*Avenella flexuosa*) on clear-cuts, covering 60–80% of the ground (Rekdal, 2017). Rekdal (2010) and Rekdal (2017) assessed the grazing value of the mapped vegetation in the study areas based on species composition, production and nutrient content of the plants in the respective vegetation types. The grazing value of the vegetation was combined with knowledge of the grazing habits of cattle and

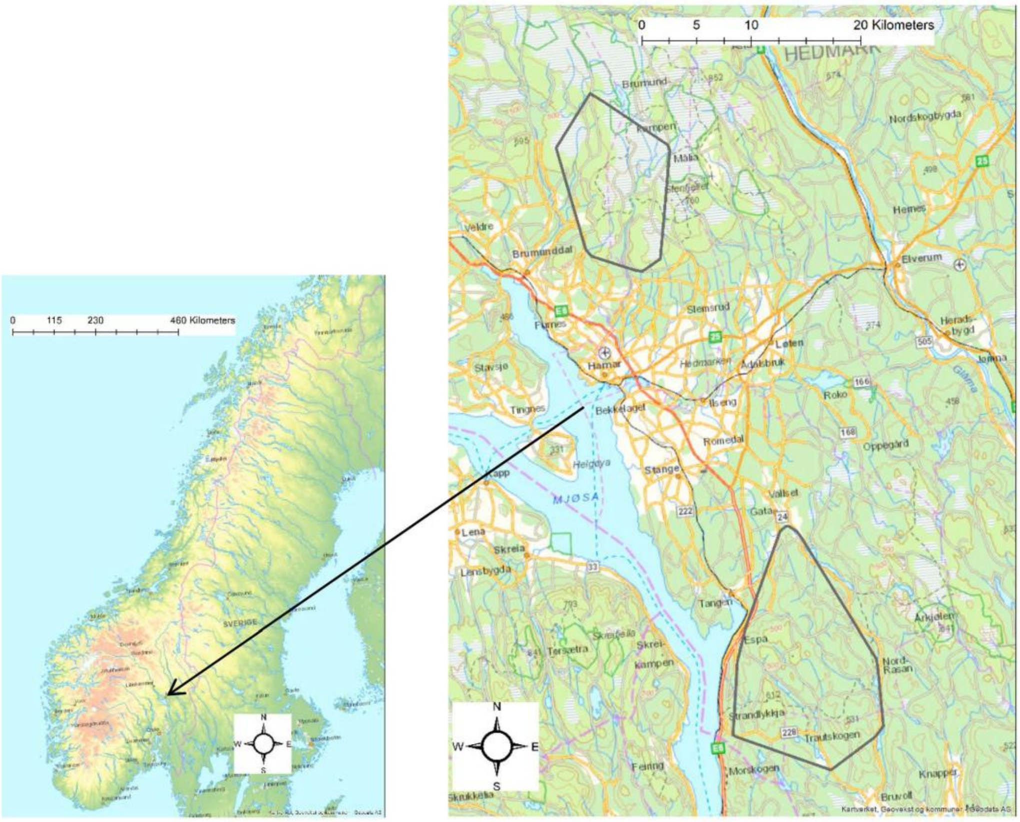

Figure 1. Location of the study areas in Furnes/Vang FVA (north) and Stange/Romedal SRA (south) in south- eastern Norway.

formed a basis for a rough division into three foraging classes to estimate the grazing capacity of the study areas: 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}) (Rekdal, 2010, 2017). 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). We defined SRA (0.04 cows ha^{-1}) as low and FVA (0.16 cows ha^{-1}) as high stocking density areas based on the utilization of the grazing capacity, which was estimated to 38% and 148%, respectively.

Each summer, we monitored 18 individual cows, resulting in 52 cow-summers (Table 1) (Supplementary Material 1). Fortyfive cows were monitored for just one summer season, eight for two and one for three seasons. In 2015, all 18 monitored animals were released in SRA. In summers 2016 and 2017, cows were equally distributed between SRA and FVA. They were beef cattle breeds of Hereford and crossbreeds of Hereford, 51.2% of all animals and Charolais, Limousine, Simmental and crossbreeds mainly of Charolais and Hereford, 48.8%. We grouped the study animals according to their reproductive status into lactating cows with suckling calves and dry cows. The ratio of lactating to dry cows varied with 12/6, 11/7, and 14/4 for the seasons of 2015, 2016 and 2017, respectively (Table 1).

We fitted the study animals with GPS-collars equipped with two-axis accelerometer (Tellus GPS medium plus, Followit Sweden AB, Lindesberg, Sweden), programmed to acquire a position every five minutes. The maximum time for the GPS collar to fix position (TTF) was set to 90 sec during which the accelerometer sensor recorded the back-forth (x-axis) and left right (y-axis) neck movements (Followit Lindesberg AB, 2013). The activity sensors were programmed for maximum sensitivity. The GPS collars included a GSM download option and positioning data was available in real-time through an internet based positioning portal, Followit Geo™ (http://wildlife.followit.se/).

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 GPS collars successfully acquired all programmed positions and only 2.6% of these had a DOP (dilution of position higher than 2. The DOP is used in satellite telemetry to describe the precision of a given position as a function of the distance and angle between satellites and receiver. Average deviation from the position mean was 9.9 m ± 9.4 (SD) for positions with DOP < 2 and 12.7 m ± 7.9 for DOP > 2. To use DOP as a method to eliminate location errors is not recommended as it does not detect all major errors and removes valuable data (Bjørneraas et al., 2010, Ironside et al., 2017). We therefore decided to use all positioning data in the analyses, irrespective of DOP.

We loaded all data from the GPS collars into R version 3.4.2 (R Core Team, 2018) and screened them for positional errors by adjusting the script developed by Bjørneraas et al. (2010). The adjusted script removed positions > 20 km from previous and next position, and positions > 2 km from an average moving window of 21 positions, including the 10 preceding and 10 following positions. Furthermore, we removed all positions that generated a spike in the movement trajectory, with outgoing and incoming speed exceeding 1500 m/h and the turning angle being between 166° and 194°. After eliminating errors and accounting for missing data due to poor satellite coverage, the GPS success (percentage successful locations) of the 52 cow-summers was 99.8% of a total of 1 231 957 positioning attempts.

Table 1. Distribution of cows equipped with GPS collars by breed and reproductive status in the study areas Stange and Romedal almenninger (SRA) and Furnes and Vang almenninger (FVA) in southeast Norway during the three summers 2015–2017. The triplets separated by slashes represent total number of cows / number of lactating cows / number of dry cows.

Year	2015	2016		2017		Total
Study area	RSA	RSA	FVA	RSA	FVA	
Breeds:						
Charolais	6 / 6 / 0	2 / 1 / 1	4 / 2/ 2	6 / 5 / 1	2 / 1 / 1	20 / 15 / 5
Hereford	5 / 3 / 2	2 / 1 / 1	3 / 3 / 0	1 / 1 / 0	3 /3/ 0	14 / 11/ 3
Cross (Hereford)	7 / 3 / 4	5 / 3 / 2	0 / 0 / 0	2 / 2 / 0	0 / 0 / 0	14 / 8 / 6
Limousin	0 / 0 / 0	0 / 0 / 0	1 / 0 / 1	0 / 0 / 0	1 / 0 / 1	2 / 0 / 2
Simmental	0 / 0 / 0	0 / 0 / 0	1 / 1 / 0	0 / 0 / 0	1 / 1 / 0	2 / 2 / 0
Reproductive status:						
Lactating cows	12	5	6	8	5	36
Dry cows	6	4	3	1	2	16
Total						52

Classification of cattle behaviour

To validate the activity data, we performed observational studies by focal animal sampling (Altmann, 1974) of 18 cows equipped with GPS collars in SRA during the grazing season 2015. Poor GSM-cover in parts of SRA sometimes hindered the immediate access to a given cow in the field and resulted in a slightly biased number of observations per cow. We observed the focus animals at distances of 1–50 m for up to one hour. We recorded all the behaviour for a period of 90 sec (i.e. maximum TTF), every five minutes (i.e. corresponding to GPS locations). We recorded each change in behaviour by tapping on screen fields on an IPad with pre-defined activity, using the application 'WhatISee' (https://itunes.apple.com/store/). The output of each recorded 90 sec interval was a text file containing the exact date and time of each change in behaviour.

Recorded behaviours were 'Low' (Lying with/without ruminating, standing with/without ruminating), 'Grazing' (standing or moving with head towards the ground), and 'High' (moving with head up and other active behaviours other than moving and grazing). The categorization based on neck position of the focal animal followed the classification by Ungar et al. (2005).

We standardized the activity data along the X- and Y-axis by dividing these values by TTF. The standardized activity indices Xt and Yt, the Euclidean distance travelled between five minute positions and the temperature (measured by the GPS unit and affected by ambient and body temperature (http://wildlife.followit.se) were available for an algorithm to explain the most dominant behaviour during TTF, i.e. the behaviour that lasted longest during the TTF interval. We applied the *evtree* package (Grubinger et al., 2014) in R for building a classification tree. We used 75% of the observation data as a training set to build the tree, and the remaining 25% as a validation set to evaluate the resulting model accuracy of the tree.

Modelling grazing activity

We used the resulting model from the above classification to predict the behavioural state for each 5 min position of all 52 cow-summers (Table 1). To model grazing behaviour as a function of time, reproductive status, breed and study area, we fitted logistic mixed effect models (GLMM) by applying the 'glmer' function of the lme4 package (Bates et al., 2015) in R. We performed model selection by building six candidate binomial GLMMs with the following fixed covariates: hour of the day (categorical with 24 levels), week number (continuous), the interaction of hour and week, year (three-level categorical), breed (two-level categorical) and reproductive status (two-level categorical). We used Pearson correlation and plots of factorial variables to check for collinearity between numerical and categorical predictors, respectively. To control for autocorrelation and uneven sample sizes among individuals and years, we included individual nested within year as random factor. Since cattle were released and housed at different times, we truncated the activity data to weeks 23–39 to accommodate for small sample sizes in the beginning of the grazing season (weeks 20–22).

We used AIC model selection and selected the final model among models with ΔAIC < 2 by the lowest proportion of informative variables, i.e. variables whose 95% confidence interval of the coefficient did not include zero. We validated the fitted model by creating plots of standardized or Pearson residuals against the fitted values.

Results

Classification algorithm for activity

Of the 18 GPS-collared cows on SRA in 2015, each cow was observed on average five times (range 1–11), resulting in 114 observation periods. The periods lasted on average 48.5 min (range 25–60 min), resulting in a total of 1105 monitored positioning attempts and activity measurements. The most dominant behaviour during observation was Low (50.5%), followed by Grazing (34.8%) and High (14.7%) (Table 2). Low was characterized by low values of neck movement and distance moved during the preceding 5 min interval. During High, the cows doubled their movement between successive GPS positions compared to Grazing (Table 2). Collar temperature was similar for the three activities (mean 21.3° C ± 4.0) and not used for building the classification tree.

Total classification accuracy of the two-three split model (Figure 2) was found to be 79.4%. The categories Low, Grazing and High of the validation set were classified with an accuracy of 86.1%, 74.8% and 52.6%, respectively (Table 3).

Activities of free ranging cattle

We used the resulting classification model on the remaining 1 229 493 five-minutes positions after error-screening to predict cow behaviour for all study animals of the three grazing seasons resulting in 52

Table 2. Descriptors (mean ± SD) of activities of $n = 18$ GPS-collared, free ranging cows in southeastern Norway during 1105 observations. Activity was grouped into Grazing (all movements with head towards the ground), High (all movements with head up from the ground including walking) and Low (resting and ruminating while lying and standing). Xt and Yt = number of electric pulses s-1 measured by the activity sensors along the X-axis (back –forth neck movements) and Y-axis (left –right neck movements). Dist_previous = distance in meters between previous and current 5 min position. Temperature = average collar temperature, influenced by environmental and body temperature.

Activity	N observations	Xt (pulses s^{-1})	Yt (pulses s^{-1})	Dist_prev (m)	Temperature
Low	558	0.13 ± 0.11	0.15 ± 0.11	16.86 ± 25.69	21.9 ± 3.7
High	162	0.33 ± 0.11	0.32 ± 0.10	75.95 ± 83.64	20.8 ± 4.1
Grazing	385	0.38 ± 0.08	0.36 ± 0.08	33.10 ± 41.22	20.4 ± 4.4

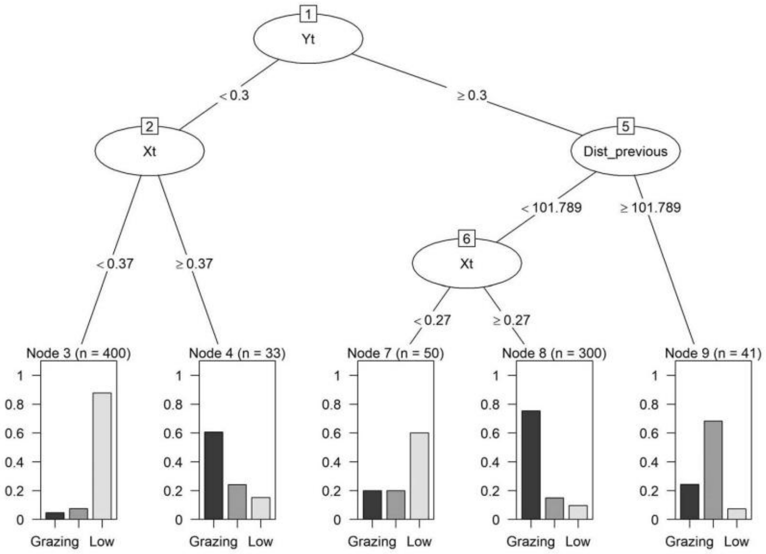

Figure 2. Classification tree used for predicting the activity of GPS-collared, free-ranging cattle in southeastern Norway. Behaviour was grouped into Grazing (all movements with head towards the ground), High (all movements with head up from the ground including walking) and Low activity (resting and ruminating while lying and standing). Xt and Yt = number of electric pulses s-1 measured by the activity sensors along the X-axis (back –forth movements) and Y-axis (left –right movements). Dist_previous = distance in meters between previous and current 5 min position.

cow-summers (Supplementary material 1). A global time budget for the two study areas and all three grazing seasons showed that the cows spent 15.1 ± 0.5, 8.1 ± 0.5 and 0.8 ± 0.2 h per day (mean ± SD), or 63 ± 0.5%, 34 ± 0.5% and 3 ± 0.2% of the time on Low, Grazing and High, respectively.

The probability that a cow was grazing rather than on high or low activity was best explained by a model that included the interaction between time of day and week number, the study area and the reproductive status of the cow. Breed did not contribute to the best-ranked model (Table 4). The model predicted that cows increased their daily time spent grazing throughout the season, from 31.6% in beginning of June to 34.2% in September. We also found a strong diel pattern with the probability of grazing being highest around dusk and dawn (Figure 3) (Supplementary Material 2). We found grazing bouts around dawn to be more diffused coupled with sunrise and distributed over a longer

Table 3. Frequency of observed and predicted dominant activities of free-ranging cattle in southeastern Norway. Predictions are based on a classification tree (Figure 2) using data from two-axis accelerometers and 5 min GPS positions. The matrix indicates correct classification rates (in bold numbers) of the training and validation sets and the distribution of the observed activities.

	Observed activity (%)	Predicted activity (%)			Number of observations
		Grazing	High	Low	
Training set	Grazing	**73.9**	15.9	10.2	333
	High	24.4	**68.3**	7.3	41
	Low	6.4	8.9	**84.7**	450
Total classification accuracy 79.5%					824
Validation set	Grazing	**74.8**	18.0	7.2	111
	High	36.8	**52.6**	10.5	19
	Low	6.6	7.3	**86.1**	151
Total classification accuracy 79.4%					281

Table 4. Top ranked models (ΔAIC < 5) explaining the probability for grazing activity of free-ranging cattle in southeastern Norway. The table shows the top ranked candidate models, the number of parameters in the model (K), difference in the Akaike's information criterion (ΔAIC), AIC weights (AICc Wt) and negative likelihood (LL). Cow ID was included as a random intercept for all models.

Grazing activity models		K	Delta_AICc	AICc Wt	LL
Mod.1	hour:week + reproductive status + study area	51	0.00	0.49	−640944.6
Mod.2	hour:week + reproductive status + study year	52	1.43	0.24	−640944.3
Mod.3	hour:week + reproductive status + breed	51	2.80	0.12	−640946.0
Mod.4	hour:week + breed + study area	51	3.46	0.09	−640946.3
Mod.5	hour:week + study area + year	52	4.07	0.06	−640945.7

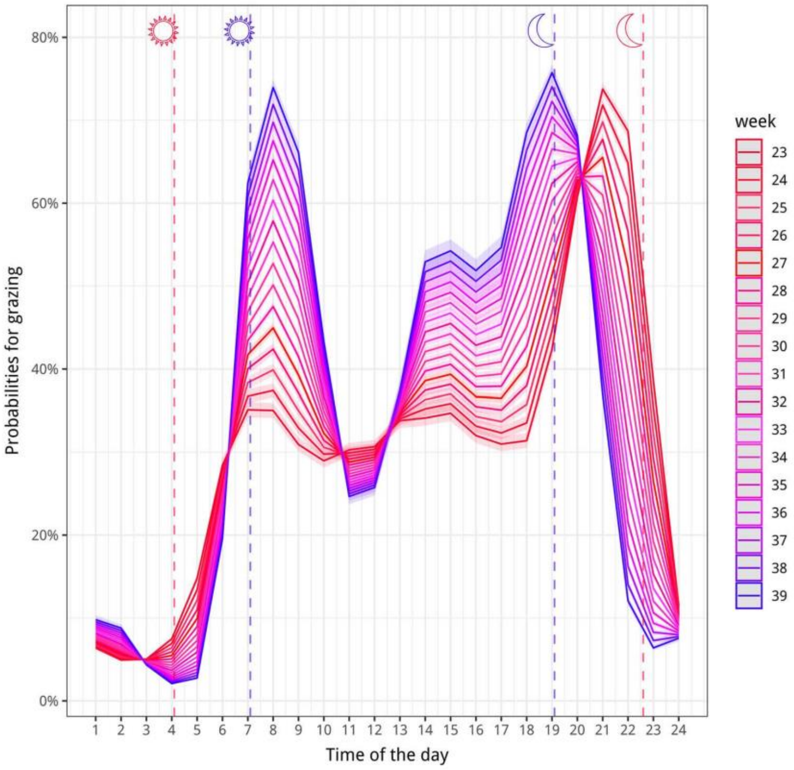

Figure 3. Grazing activity of free-ranging cattle in southeastern Norway as a response to time of day and week number, predicted by the best ranked generalized mixed model (GLMM). The colour scale from warm (red) to cold (blue) indicates the increasing week number throughout the grazing season. The sun and moon symbols in red and blue indicate sunrise and sunset in weeks 23 and 39, respectively.

period, especially early in the season. Grazing bouts during dusk were more intense and concentrated in time for the whole season. Later in the season, we found grazing bout intensity and length similar on both ends of daylight.

Lactating cows spent on average half an hour more time grazing (8.2 ± 0.5 h day^{-1}) than did dry cows (7.7 ± 0.5 h day^{-1}). Correspondingly, dry cows spent on average half an hour more on low activity (15.4 ± 0.5 h day^{-1}) than did lactating cows (14.9 ± 0.5 h day^{-1}). Cows spent on average 3.7% more time grazing in the area of low stocking density, compared to the cows of the high stocking area.

Discussion

We were successful at predicting the activity of free-ranging cows in the boreal forest of Norway by converting data of cow locomotion during five minutes intervals and activity measured with a dual axis accelerometer fixed to a neck collar. The overall misclassification rate of 20.6% using a two-three split classification model was higher than the results from previous studies. Ungar et al. (2005) used data from four two-axis Lotek GPS collars on several cows for building a classification tree of 5 min position data and ended up with a misclassification of 12%. Another study on grazing cattle using the same GPS technology and a binary classification tree that split into four categories had a misclassification rate of 16% (Augustine & Derner, 2013). The relatively high misclassification in our study is mostly due to incorrect classification of Grazing and High (Table 3). High encompasses mostly locomotion, but to some minor extent also active behaviour while stationary, e.g. social behaviour. Grazing on the other hand is not always stationary, but can also include slow locomotion. A more fine-scale classification of behaviour might have been useful to achieve lower misclassification. Generally, data from neck movements alone may not be sufficient to describe behaviour, especially in heterogeneous terrain with varying sward structure. Ungar et al. (2011) combined GPS collars with pedometers on the cow's leg and found a remarkable decrease of misclassification rate, provided use of a highly splitting classification tree. We consider pedometers as not applicable due to dense understory vegetation and no possibility of changing batteries during the grazing period.

The overall grazing time of 8.1 h per day found in our study corresponds with studies of grazing cattle from extensive grazing areas in other parts of the world. Kilgour (2012) reviewed 22 articles and found variations in the time spent grazing from 6.8 to 13.0 h per day for cattle that have access to grazing over the whole 24 h period. The large variation in grazing time among studies is due to methodological issues, such as length of observations and number of focal animals, but also to seasonal changes in quality and quantity of available forage (Funston et al., 1991; Hejcmanová et al., 2009; Schoenbaum et al., 2017). In particular, the ambient temperature in the various study areas may be essential for variations in grazing activity. Hahn (1999) states 25° C as a threshold temperature, which above causes a stress heat resulting in a decrease of the feed intake of cattle. In all three years of our study, temperature exceeded this threshold 19 times (Norwegian Meteorological Institute, 2018). As described by Bjor & Graffer (1963), we observed that the cows extended their resting periods on warm days. In a study performed in Israel, Schoenbaum et al. (2017) found that total grazing time and grazing activity decreased around mid-day in periods of high summer temperature.

The time budget shows that grazing activity is carried out in hours of daylight (Figure 3). We found the highest grazing activity during dusk, followed by dawn. Several studies reports evening as the main grazing period, constituting over 45% of the diel grazing time (Orr et al., 1997; Gregorini et al., 2006; Schoenbaum et al., 2017). Grazing during dusk will fill the rumen and is thereby of great importance for a steady release of nutrients through the night hours (Gregorini, 2012). In addition, the dry matter content and the digestibility of the forage increases through the hours of daylight and stimulate to a higher intake of forage (Orr et al., 1997; Delagarde et al., 2000; Gregorini et al., 2009).

During night hours (22–03), the cows in our study mostly rested and had only 7% of their activity allocated to grazing, or 5% of all grazing activity (Figure 3). Cattle generally perform resting behaviours during night, and previous studies report 5–40% of total grazing activity performed during this period (Johnstone-Wallace & Kennedy, 1944; Smith, 1959; Kilgour, 2012). We found an intensification of the grazing bouts during daytime in late season (August and September, Figure 3), and assume that daylight conditions are the main driver for this pattern. The cows grazed in a patchy environment with tree trunks and residues from timber harvesting, making locomotion during the dark hours of late summer especially challenging for these big animals. A longer resting period in late summer leads to the lowest diel ruminal fill in the morning hours (Gregorini, 2012), which might explain the increased grazing intensity and synchronization in the mornings of late summer.

As predicted and in accordance with previous studies, we observed increased grazing activity throughout the summer, most likely related to a decrease in forage quality. In a Swedish study, Hessle et al. (2008) found remarkable lower energy and higher fibre content in the herbage mass of the autumn compared with early spring and assumed that these conditions affected grazing activity.

Grazing was positively associated with lactation. Le Neindre (1989) observed a similar influence of the reproductive status on grazing activity for cows in France. Lactating cows have a higher energy demand than dry cows (Montaño-Bermudez et al., 1990), and increased grazing activity is most probably a direct result of this. However, differences in grazing activities may be difficult to detect in mixed herds of dry and lactating cows as a result of social affiliation. Cattle are known to increase (Broom & Fraser, 2007) and synchronize (Arnold & Dudzinski, 1978) their grazing time while kept in herds, and grazing animals may motivate the less energy demanding dry cows to adapt the behaviour of the more energy demanding lactating cows.

Although, the pastures were of the same low quality in both study areas, we found the cows in the low stocking density area (SRA) to spend more time grazing than the cows of the high density area (FVA). The effect of cattle stocking density has been studied under various conditions with conflicting results. Generally, higher grazing densities lead to a decrease in available forage as a result of lower sward heights and reduced forage quality (Bailey et al., 1996; Cornelissen & Vulink, 2015) and ruminants have shown to compensate for this reduction in forage availability by increasing their total grazing time to some extent (Allison, 1985). This positive relationship between grazing activity and stocking density can vary with season (Schoenbaum et al., 2017). Other studies performed under controlled grazing systems have shown that cattle spend more time grazing at moderate than high stocking rates as spending more time on grazing may be an ineffective use of energy in patches of shorter sward heights (Hepworth et al., 1991; Cornelissen & Vulink, 2015). The stocking densities in our two study areas were either far below (SRA) or far above (FVA) the estimated grazing capacity

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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

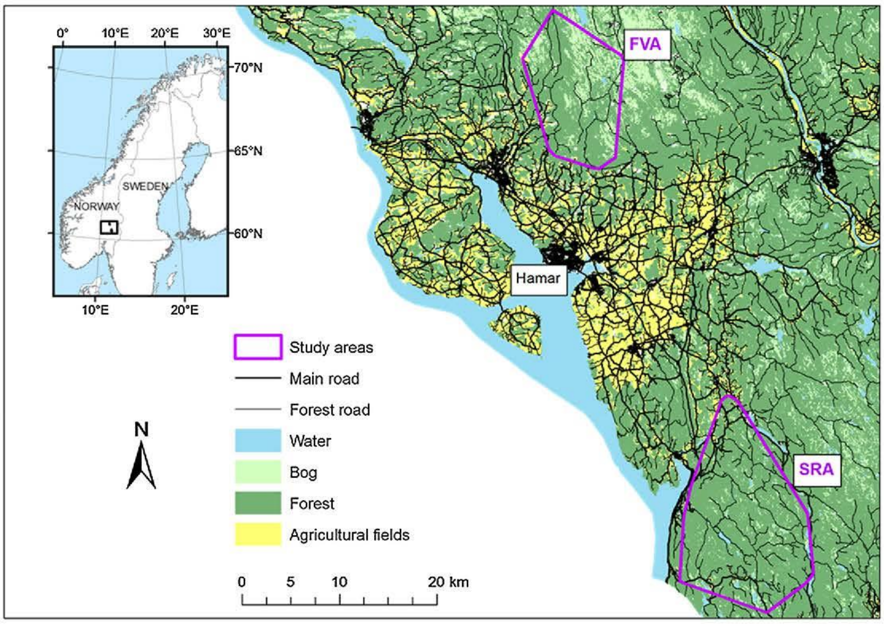

Fig. 1. Location of the study areas in Furnes/Vang almenninger (FVA) in 2016 and 2017 and Stange/Romedal almenninger (SRA) from 2015 to 2017 in south-eastern Norway.

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

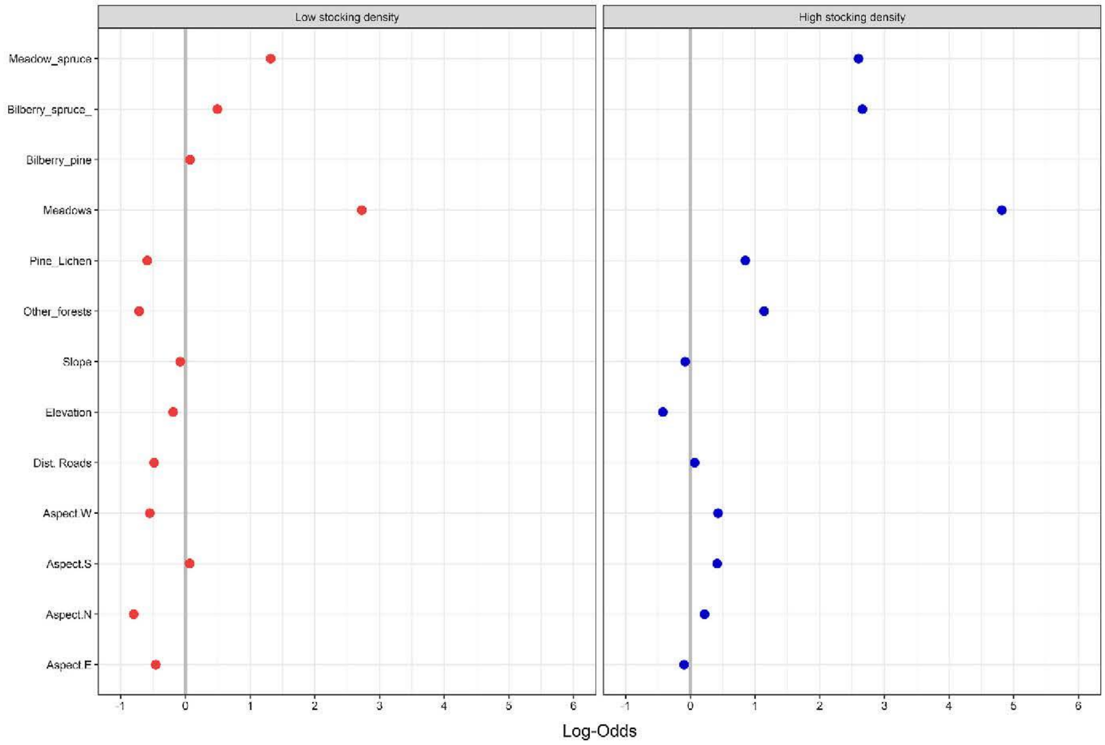

Fig. 2. Parameter estimates (log-odds) from vegetation models of free ranging cows during summer in boreal forest of southeastern Norway, at low (SRA) and high (FVA) stocking density. The log-odds of the vegetation types and aspects refer to bogs/non-productive and flat areas, respectively. The log-odds 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.

(Table 5).

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

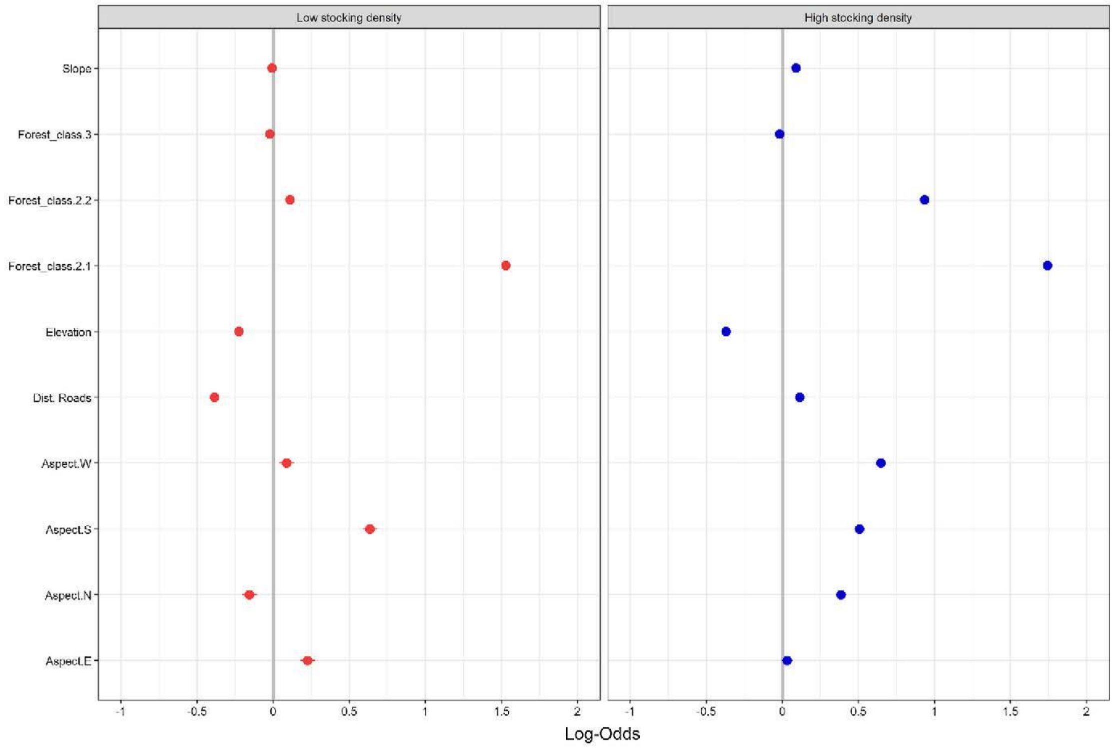

Fig. 3. Parameter estimates (log-odds) from forest models of free ranging cows in productive forests stands, at low (SRA) and high (FVA) stocking density. The log-odds of the forest classes and aspects refer to forest class 4.5 (mature and old growth forest) and flat areas, respectively. The log-odds 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.

trails for timber harvesters. The cows in our study used these trails as important travel routes between clearcuts. We assume that this is the 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

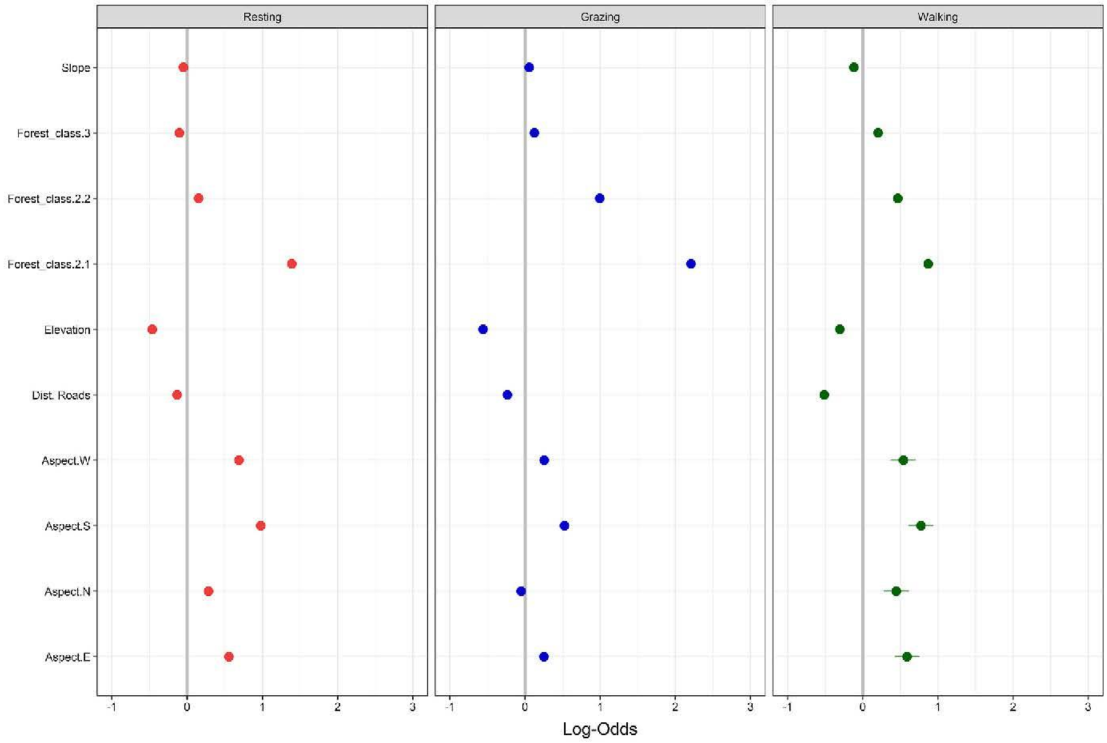

Fig. 4. Parameter estimates (log-odds) from activity models of cows in productive forests stands, during Resting, Grazing and Walking. The log-odds of the forest classes and aspects refer to forest class 4.5 (mature and old-growth forest) and flat areas, respectively. The log-odds of the continuous scaled 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.

improved grazing opportunities for cattle. While the summer farm meadows were originally established for livestock grazing in the previous 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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Microhabitat selection of free-ranging beef cattle in south-boreal forest

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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

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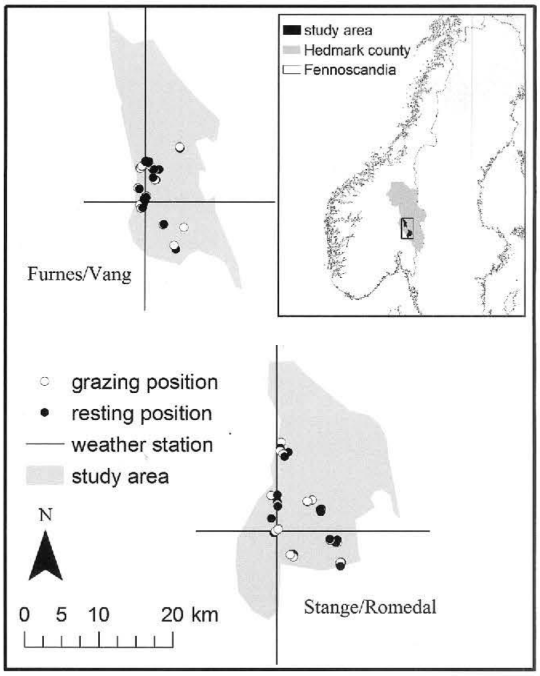

Fig. 1. Map of the areas (FVA and SRA, shaded in grey) where our study on microhabitat selection of free ranging beef cattle at grazing and resting sites in south-boreal forest was conducted in summer 2017. Grazing sites (white points), resting sites (black points) and installed weather stations (crossing 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 km^2 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 km^2 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 were10 m^2 in size (i.e. 1.78 m radius) and at 50 m to each cardinal direction from the used plot. 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.

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 ground cover according to the following categories, adding up to 100 % at each plot:	
	obstacles	rocks, trees, water surfaces, etc., preveting a cow from standing or lying on this plot, in % of the plot area
	dead material	bare ground, gravel, dead plant material, etc, in % of the plot area
	lichens and mosses	all lichen and moss species, in % of the plot area
	herbs	all herbaceous plant species as well as ferns, in % of the plot area
	shrubs	woody species, including heather (*Erica* spec. and *Calluna* spec.), berries (*Rubus idaea* and *Vaccinium* spec.) and tree seedlings under 30 cm height, in % of the plot area
	grasses	all graminoid species, including the families Poaceae, Cyperaceae and Juncaceae, in % of the plot area
Incline	mean of the absolute inclines (in %) in the four cardinal directions,	
Canopy cover	area (in %) above the plot covered by the canopy.	
Sun exposure	absence (1) or presence (0) of any cover between cow and sun (e.g. trees or hills), not taking into account cloud cover.	
Visibility	mean of the distances (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 four cardinal directions.	

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 T M 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.

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

$$\begin{aligned} logit(\pi) &\sim \alpha + \beta_1 * grasses + \beta_2 * incline + \beta_3 * canopycove \\ &+ \beta_4 * sunexposure + \beta_5 * visibility + \beta_6 * visibility^2 + b_{herd} + b_{cow} \\ &+ b_{habitatpatch} \end{aligned} \tag{1}$$

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 2
Mean 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 (ΔAICc < 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 exposure	7	216.6	1.37	0.098

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

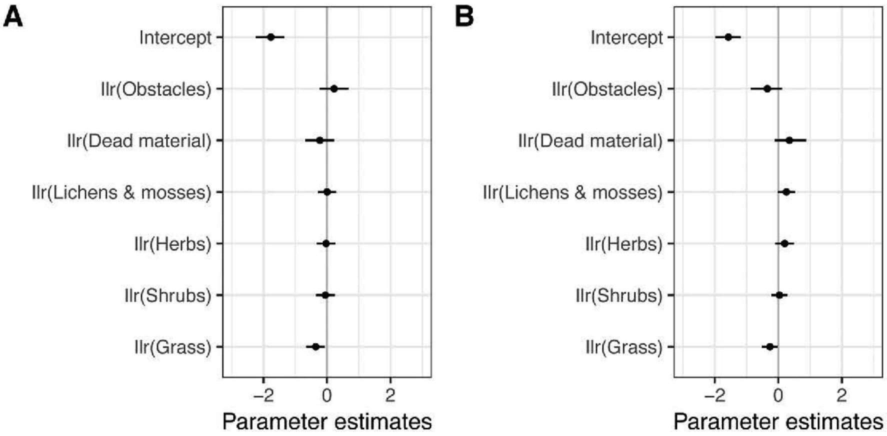

Fig. 2. Results, that is mean and 90% confidence interval of the parameter estimates from regression of probability of use by A) grazing cattle and B) resting cattle on the ilr-transformed ground cover categories in a study on microhabitat selecion of free ranging beef cattle in south-boreal forest in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

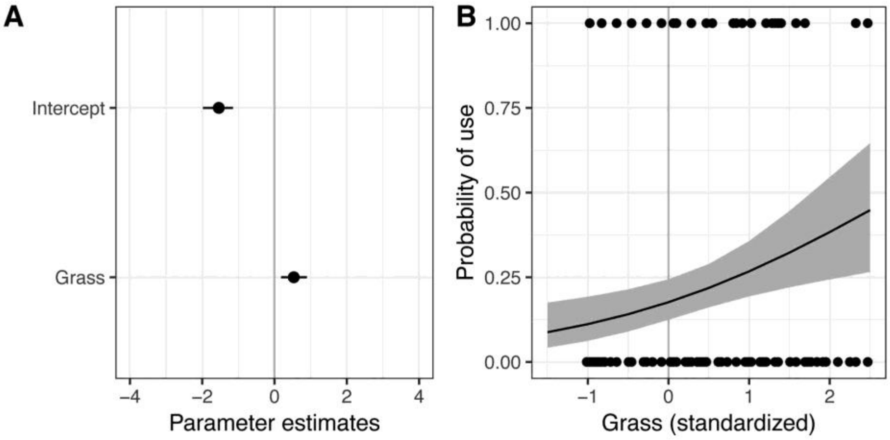

Fig. 3. Results of a study on microhabitat selection of free ranging beef cattle in south-boreal forest in summer 2017: model output and predictions for the best grazing model: A) mean and 95% confidence interval of the parameter estimates and B) predicted probability of use (line) with 95% confidence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

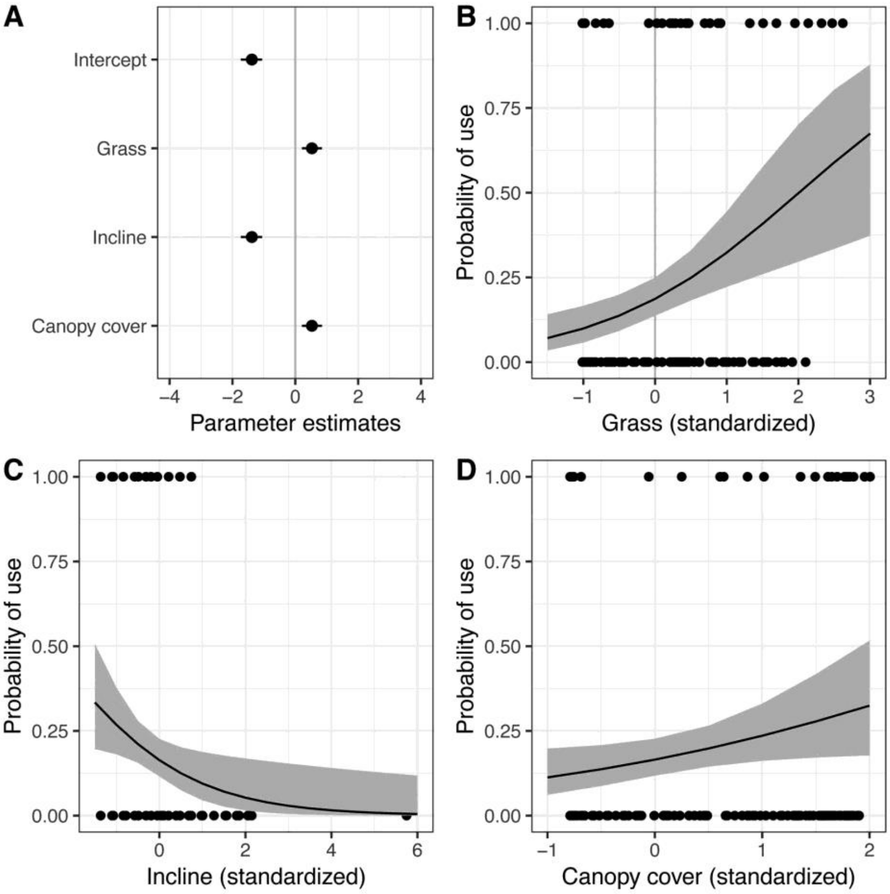

Fig. 4. Results of a study on microhabitat selection of free ranging beef cattle in south-boreal forest in summer 2017: model output and predictions for the best resting model: A) mean and 95% confidence interval of the parameter estimates. Predicted probability of use (line) with 95% confidence interval (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 anti-predator 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.

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4

Weight gain of free-ranging beef cattle grazing in the boreal forest of south-eastern Norway

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Abstract

Young forest stands and clearcuts in the boreal forest created by modern forestry practices along with meadows of abandoned summer farms may contribute as feeding areas for beef cattle. The patchy distribution and varying quality and diversity of forage on such unimproved lands may affect cattle productivity. We monitored weight gain of 336 beef cows and 270 calves free-ranging during three summer grazing seasons in boreal forests of south-eastern

Norway, in areas of high (0.16 cows ha^{-1}) and low (0.04 cows ha^{-1}) stocking density. We used linear mixed effect models for assessing intrinsic correlates of weight gain in cows and calves in the two areas. Habitat use and home range size of a subsample of 53 cows were monitored by using GPS collars programmed to take locations at 5-minute intervals during the grazing season. We then tested for these additional extrinsic correlates of weight gain for the subsampled cows using a linear mixed model.

Average weight gain of beef cows grazing in the low stocking density area was positive among cows of early maturing breeds (represented by Hereford cows) which gained 24 ± 2.8 kg (± SE), while cows of late maturing breeds (mainly represented by Charolais cows) had an average weight loss of 9 ± 8.4 kg. In the high stocking density area, average weight gain was negative for beef cows of both early (Herefords) and late maturing breeds (mainly represented by Charolais but also Limousin and Simmental cows). Within both breed groups, there was a negative relationship between breed-specific average weight of cows at turnout and weight gain during the grazing period, while a prolonged grazing period was slightly positively related to weight gain. We could not find any relationship between weight gain and the extrinsic factors home range size and proportion of grazing habitat for the 53 cows fitted with GPS collars.

We found higher weight gain in calves of the low compared to the high stocking density area. There was no breed effect on weight gain in calves. Across study areas, spring-born suckler calves gained more weight than autumn-born calves (92 ± 1.7 kg vs. 65 ± 4.4 kg). Furthermore, we found higher weight gain of spring-born bull-calves rather than spring-born heifers (100 ± 2.4 kg vs. 94 ± 2.2 kg).

Overall, the results indicate that it is possible to achieve acceptable weight gains in cattle grazing in coniferous forest by finding breeds suitable for these extensive areas and stocking at moderate densities.

Highlights:

- Beef cows of early-maturing breeds gained more weight than late-maturing breeds on summer pastures in the boreal forest
- Beef cows and calves grazing in low stocking density area gained more weight than those in high stocking density area
- Weight gain in beef cows was negatively related to the deviation from the average breed-specific weight
- Suckling spring-born calves had higher weight gain than suckling autumn-born calves

Keywords: Growth, extensive grazing, boreal forest, beef cows, suckling calves

1. Introduction

Human population growth is causing an increase in demand for food that is not expected to be met by maximizing agricultural productivity on arable land alone (Godfray *et al.* 2010). Sustainable food production should be increased by utilizing natural environments at individual sites and managing resources in a way that benefits biodiversity, ecosystems services, agricultural production and other multiple purposes (Broom, Galindo & Murgueitio 2013). Cattle grazing in forests are utilizing resources that otherwise could not be used as food and are a valuable contribution to global meat and milk production while decreasing the pressure on arable land (Schader *et al.* 2015b). The boreal forests, the second largest biome on the Earth, are mainly managed for the production of timber (Gauthier *et al.* 2015), but also provide multiple ecosystem services as well as grazing for domestic livestock (Bele & Norderhaug 2013; Kaufmann *et al.* 2013b; Gauthier *et al.* 2015). However, forestry and livestock farming are not totally compatible. On the one hand, cattle grazing has been associated with damage to young trees by trampling and bedding in areas of regeneration (Hjeljord, Histøl & Wam 2014; Kaufmann *et al.* 2017) and on the other, cattle productivity may be impacted by the forest's heterogeneous environment with a patchy distribution of herbage and quickly declining quality and quantity of forage plants through the grazing season (Garmo 1986). To assess the sustainability of such grazing regimes in this semi-natural environment, it is important to measure the productivity of cattle in relation to breed and stocking density.

In Norway, forests and alpine areas are abundant whereas only 3-4% of the land area is cultivated. Therefore, livestock grazing in forests and alpine areas (referred to here as "unimproved land") during the summer has been of great importance for agricultural production in Norway over the past 2000 years (Austrheim *et al.* 2008). However, during the last part of the 20th century, intensification of dairy production caused a decline in the number of cattle turned out onto Norwegian unimproved land. Today, a growing interest in suckler-based beef production has led to a resurgence in the number of beef cattle grazing on unimproved land during summer (Norwegian Agriculture Agency 2017). The cattle are a mix of early and late maturing beef breeds. The continental breeds Charolais, Limousin and Simmental are all late-maturing beef breeds bred for intensive meat production and hence adapted to high feed intensities with a demand for energy-dense feed rations (Webster 1989). British beef breeds are Hereford and Aberdeen Angus, which are early-maturing breeds adapted to more extensive production methods based on lower feed intensities and less energy-dense rations (Webster 1989). In Norway, Charolais and Hereford are the most common breeds and compromise 21% and 14 % of the beef cow population, respectively (Animalia AS 2018).

In general, the weight performance of beef cows and their suckling calves depends on the interactions between intrinsic factors, e.g. cattle breeds (Niemelä *et al.* 2008), time of calving (Casasús *et al.* 2002b), body size (Demment & Van Soest 1985) productivity (lactation) (Ferrell & Jenkins 1985; Montaño-Bermudez & Nielsen 1990) and extrinsic factors e.g. pasture nutritional quality (Fraser *et al.* 2009a) and availability of the foraging plants (Lowman *et al.* 1996). The availability of preferred feeding plants and sward heights is dependent on stocking density, and high densities have shown to affect body condition and weight gain of cattle negatively (Wright & Russel 1987; Senft 1989; Cornelissen & Vulink 2015). In addition, the feeding regime during the preceding winter can affect the growth recovery period after turn-out to pasture (Hessle, Dahlström & Wallin 2011). Some studies have reported that weight gain of young weaned cattle on Nordic unimproved land is similar to that on cultivated pastures (Bjor & Graffer 1963; Niemelä *et al.* 2008; Hansen, Bøe & Okkenhaug 2009; Steinshamn *et al.* 2010). However, the feeding regime of suckling calves differs from that of older cattle as their main nutritional intake is provided by milk, and hence the weight gain of these calves depends mainly on the cows' ability to uphold milk production (Wright & Russel 1987; Casasús *et al.* 2002b).

Since the 1950s, forestry in Scandinavia has intensified, becoming dominated by rotational management and clearcutting which creates patches of uniformly-aged forest stands (Aasetre & Bele 2009). Primarily, the meadows of abandoned summer farms, young forest stands (< 15 years since clearcutting) and clearcuts offer sufficient densities of herbage for foraging cattle (Tofastrud, Devineau & Zimmermann 2019), as these areas are suitable for light-demanding grass species and herbaceous plants (Strand 1997). Consequently, at a landscape scale, the herbage has a patchy distribution very unlike open grassland pastures. The clearcuts may be in rugged terrain and are often full of obstacles, e.g. stones, tree stumps and logging waste. Such conditions and the need for cattle to move between grazing patches affect energy expenditure and consequently most likely the performance of the animals. The young forest stands are also considered of great importance for as feeding resource of the Scandinavian moose (*Alces alces*) population (Edenius *et al.* 2002). However, interspecific interactions (Herfindal *et al.* 2017) and dietary overlap between moose and livestock are considered as low (Dorn 1970). Despite the widespread practice of grazing cattle in boreal forests around the northern hemisphere, relevant studies of the performance of improved beef cattle breeds in the extensive conditions of the boreal forest are scarce. The last major research on cattle grazing in boreal forests was performed in the 1950s and focused on cows and heifers of dairy breeds (Bjor & Graffer 1963).

To fill this knowledge gap, we studied the performance of cows and calves of different beef cattle breeds in free-ranging herds in the boreal forests of south-eastern Norway during summer. We were interested in intrinsic factors, such as breed, age and reproductive status, as well as extrinsic factors, such as stocking density, length of the grazing season, habitat use and home range size. Based on the compiled studies above, we expected higher weight gain in beef cows of early-maturing breeds, dry cows and cows with lower initial breed-specific body weights due to the winter-feeding intensity. Finally, we expected higher live weight gain in spring-born calves based on the importance of milk as a source of energy, in calves of the early-maturing breeds and in bull calves based on their greater ability for energy utilization into weight gain (Turton 1969; Fraser *et al.* 2009a).

We expected weight gain in beef cows to be negatively related to the overall stocking density and, at a smaller scale, to the herd size due to intra-herd competition for herbage. Based on studies from other types of uncultivated land, we expected to find some interactions between breed and pasture type (Wright *et al.* 1994; Fraser *et al.* 2009a). Cattle of early-maturing breeds are more efficient at utilizing energy of poorer quality herbage and therefore probably best suited to grazing these areas (Webster 1989). Herbivores are foraging in hierarchies of spatial and temporal scales in daily, seasonal or annual home ranges (Senft *et al.* 1987; Bailey *et al.* 1996). Home range sizes of large herbivores vary with habitat and resource distribution (Lazo 1995; Kie & Boroski 1996; van Beest *et al.* 2011), stocking density (Vander Wal, Laforge & McLoughlin 2014) and reproductive status (Saïd *et al.* 2005; van Beest *et al.* 2011). Knowledge about the home range size of cattle is important for managing grazing resources and conservation of ecosystems (Ofstad *et al.* 2016). Little is known about the relationship between weight gain in domestic cattle and home range size but we assumed home range size to be negatively related to the amount and quality of the available herbage. We therefore expected that cows with large home ranges would have less weight gain then cows with small home ranges.

2. Material and methods

2.1 Study sites

This study was carried out in two forested areas in south-eastern Norway (60˚ N, 11˚ E) (WGS-1984) in Stange - Romedal Almenning (SRA, 150 km^2) and Furnes - Vang Almenning (FVA, 100 km^2) in the summers of 2015 (SRA only) to 2017. The elevation ranged 300 - 600 and 600 - 700 m above sea level (a.s.l.) in SRA and FVA, respectively. The average ambient air temperature for the study period June-September in the three study years was 13.2 ˚, 14.6 ˚ and 13.2˚ C, and precipitation was 75, 48 and 88 mm in 2015, 2016 and 2017, respectively. The summer of 2016 was warmer and drier, while 2015 and 2017 were slightly colder than normal (Norwegian Meteorological Institute 2018). The bedrock of SRA and southern FVA is dominated by nutrient-poor acidic rocks such as gneiss and granites, while northern FVA consists of dark sandstone (The Geological Survey of Norway (NGU) 2018).

Typical boreal tree species in Norway include the Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Bilberry spruce forest was the dominant vegetation type, covering

58.0% and 44.4% of the area in SRA and FVA, respectively (Rekdal 2010; Rekdal 2017). The vegetation types of each study area were mapped by the Norwegian Institute of Bioeconomy Research (NIBIO) in 2010 and 2017 for FVA and SRA, respectively (Rekdal 2010; Rekdal 2017). The grazing value of the dominant vegetation types was then estimated by species composition, plant production and the nutrient content of the most important ground layer species of each vegetation type. Consequently, the vegetation types were roughly classified into three foraging classes with differing grazing capacity: 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}) (Rekdal, Garmo & Steinheim 2000). The assessments concluded that both study areas had a grazing capacity for about 0.11 cows ha^{-1}. However, the stocking densities during our study were 0.04 (SRA) and 0.16 cows ha^{-1} (FVA). The utilization of the grazing capacity was therefore estimated to be 38% and 148% in SRA and FVA, respectively (Rekdal 2010; Rekdal 2017).

The proportion of young forest stands and clearcuts (0 -15 years after clearcutting) in the study areas was 16% and 14% in SRA and FVA, respectively (Tofastrud, Devineau & Zimmermann 2019). The study areas were interspersed by bogs and small summer farm meadows. The meadows made up less than 1 % of the area in both SRA and FVA (Rekdal 2010; Rekdal 2017). In general, the grazing value of the coniferous forest was extremely low compared with cultivated pastures (Larsson & Rekdal 2000). The herbage production of spruce forest on nutritious and moderately nutritious soils have previously been estimated as 2000 kg dry matter (DM) ha^{-1} and 670 kg DM ha^{-1}, respectively (Hansen, Bøe & Okkenhaug 2009). However, measurement of herbage yield in these areas is associated with high uncertainty, caused mainly by their patchy distribution and varying re-growth of the forage plants, dependent on the density of grazing herbivores.

2.2 Study animals and intrinsic factors

We recruited cattle from five and four local commercial farms in SRA in FVA, respectively. Cattle from the same farm were considered as one herd. The number of animals varied greatly among the herds, from seven up to 98 beef cows of various age and reproductive status. Farmers weighed their cattle at turnout and at re-housing and weight gain was calculated (Tables 1 & 2). The weighed animals made up about 40% and 30% of all cattle turned out to SRA and FVA, respectively. During the three study years, 336 cows (Table 1) and 270 calves (Table 2) were monitored. Eighty-one and eleven cows were studied repeatedly for two and three summers, respectively, whereas 136 cows were studied for one summer only. The studied cattle were purebred Hereford, Charolais, Limousin, Simmental and crossbreds of these breeds (34.4% of calves and 23.5% of cows). Hereford and Charolais were the dominant breeds in SRA and FVA, respectively. Simmental and Limousin were only present in FVA, with the exception of one Simmental cow in SRA. Thirteen calves of Aberdeen Angus were grazing in SRA. Calves were born either in spring or in autumn. Typical of calves in this part of Norway, spring-born calves were born in February – March and autumn-born calves in October – November. All autumn-born calves were suckling heifer calves, as national legislation prohibits turning out bulls older than six months on pastures of communal lands (Ministry of Agriculture and Food, 1970). We divided all animals into categories referred to as ‘main breed’, based on the breed representing the highest proportion of the animal’s genotype or, the maternal breed in the case of 50/50 crosses. Furthermore, the breeds were grouped as early and late maturing breeds.

The cattle were continuously grazing and the grazing period varied between herds from 80 to 120 days, from late May to early September. The average number of grazing days (±SE) varied between the two study areas, with 122 (1.37) and 96 days (0.87) in SRA and FVA, respectively.

For cows, we used the individual deviation from the average weight at turnout of animals of the same breed to take into account variation in both body size and weight caused by the winter-feeding period. The average weight (± SE) of the at turnout was 602 ± 8.9 kg and 702 ± 6.8 kg for early and late maturing breeds, respectively.

Table 1: *Number of studied beef cows grazing in boreal forests of south-eastern Norway, grouped by study year (2015-2017) and study area (Stange - Romedal Almenning (SRA) and Furnes - Vang Almenning (FVA)). The total number of cows and number of cows fitted with GPS collars are shown, as well as the breakdown by breed group and reproductive status.*

Study area	SRA			FVA		
Year	2015	2016	2017	2016	2017	Total
Total number of weighed cows	42	58	52	75	109	336
Collared cows	9	12	7	11	14	53
Early maturing breeds[1]:	39	39	29	2	4	113
Late maturing breeds[2]:	3	19	23	73	105	223
Reproductive status:						
Lactating cows	24	35	38	30	20	147
Dry cows	18	23	14	45	89	189

[1] Hereford; [2] Charolais, Limousin and Simmental

Table 2: *Number of suckling calves studied in boreal forests of south-eastern Norway by study year (2015-2017), study area (Stange - Romedal Almenning (SRA) and Furnes - Vang Almenning (FVA)), breed group and period of birth.*

Study area	SRA			FVA		
Year	2015	2016	2017	2016	2017	Total
Number of calves	60	65	90	30	25	270
Breed group:						
Early-maturing breeds[1]	24	24	32	1	6	87
Late-maturing breeds[2]	36	41	58	29	19	183
Period of birth:						
Spring-born calves	54	59	60	15	22	210
Autumn-born calves	6	6	30	15	3	60

[1] Hereford and Aberdeen Angus; [2] Charolais, Limousin and Simmental

2.3 Data collection for extrinsic factors

We monitored habitat use of 53 weighed adult beef cows with GPS-collars (Tellus Medium plus and Tellus Basic, Followit International AB, Lindesberg, Sweden) (Tofastrud, Devineau & Zimmermann 2019). Among those, 37.7 % were dry cows and 62.3 % lactating. The number of GPS collared cows varied between years and study areas due to technical failures or collars that fell off during the grazing season (Table 1). We programmed the GPS collars to record positions at 5-minutes intervals, with the exception of night hours in 2016, when collars were scheduled for 10-minutes intervals to save battery power. We defined the individual home ranges by creating 100% minimum convex polygons (MCP) which included all positions per animal and year. We defined herd size as the total number of cattle turned out from a given farm.

We used ArcGIS 10.6 (Esri 2017) to find the proportion of GPS positions per cow in different vegetation types (Rekdal 2010; Rekdal 2017) and forest stands within the home range of each individual. The age of forest stands related to the year of last timber harvesting and was provided by the regional forestry plan service (Allma - Allskog Mjøsen Skog og AT Plan 2017). We quantified the proportion of cow positions located on summer farm meadows and young forest stands < 15 years of age.

2.4 Statistical analysis

We tested the impact of different variables on weight gain during the summer grazing period in all cows, cows with GPS collars and calves by fitting linear mixed models with maximum likelihood (ML) procedure in the *nlme* package (Pinheiro *et al.* 2018) in R version 3.5.1 (R Core Team 2018). Since the experimental design was unbalanced between the study years and areas (Table 1 and 2), we included year (2015 – 2016 - 2017) as a random factor in the models of all three animal groups. We tested the effect of the following fixed covariates on weight gain in all cows: deviation from the average breed-specific weight (continuous), reproductive status (dry - lactating), breed (early- and late-maturing), and number of grazing days (continuous). We investigated the effect of breed groups in low and high stocking density areas by testing the interaction between breed group and study area.

We investigated the individual variation in weight gain of beef cows fitted with GPS collars by using the following fixed covariates: home range size (continuous), grazing days (continuous), size of the herd (continuous), and the proportion of cow positions in meadows (continuous) and forested stands younger than 15 years (continuous). 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.

The individual variation in weight gain of the calves was investigated by the following fixed covariates: sex and birth period (spring-born bulls – spring-born heifers – autumn-born heifers), number of grazing days and the interaction between breed groups (early - late-maturing breeds) and study area (SRA – FVA).

We used Akaike's information system criteria (AIC) to select the most plausible models with the optimal structure of fixed effects (Burnham & Anderson 1998). We generated a full model set by using the dredge function in the *MuMin* package in R for the interpretation of all models with ΔAIC < 2, thereafter; we used the conditional model averaging approach to construct model-averaged estimates of the parameters (Grueber *et al.* 2011). We used 95% confidence intervals to identify uninformative parameters (CIs which included zero) and evaluate the relative importance of potential predictor variables (Tables 4, 6 & 8) (Arnold 2010). We checked the fixed predictors for collinearity using a Pearson correlation coefficient $r_s < 0.6$ and plots of factorial variables.

3. Results

On average, beef cows of early maturing breeds in the low stocking density area (SRA) were the only group of cattle that gained weight during the grazing season (24 ± 2.8 kg (SE), n = 107) (Figure 1). Beef cows of early maturing breeds in FVA and of late maturing breeds in SRA and FVA were housed with an average weight loss of -58 kg ± 16.6 (n = 6), - 6 ± 8.5 (n = 45), and - 22 ± 3.7 kg (n = 178), respectively. We found average weight gain of dry cows of early and late maturing breeds as 29 ±4.6 and -13 ± 4.6 kg, respectively. On average, lactating cows of both early and late maturing breeds lost weight during the grazing season, respectively, -14 ± 4.4 (n = 69) and -30 ± 4.3 (n = 78) kg.

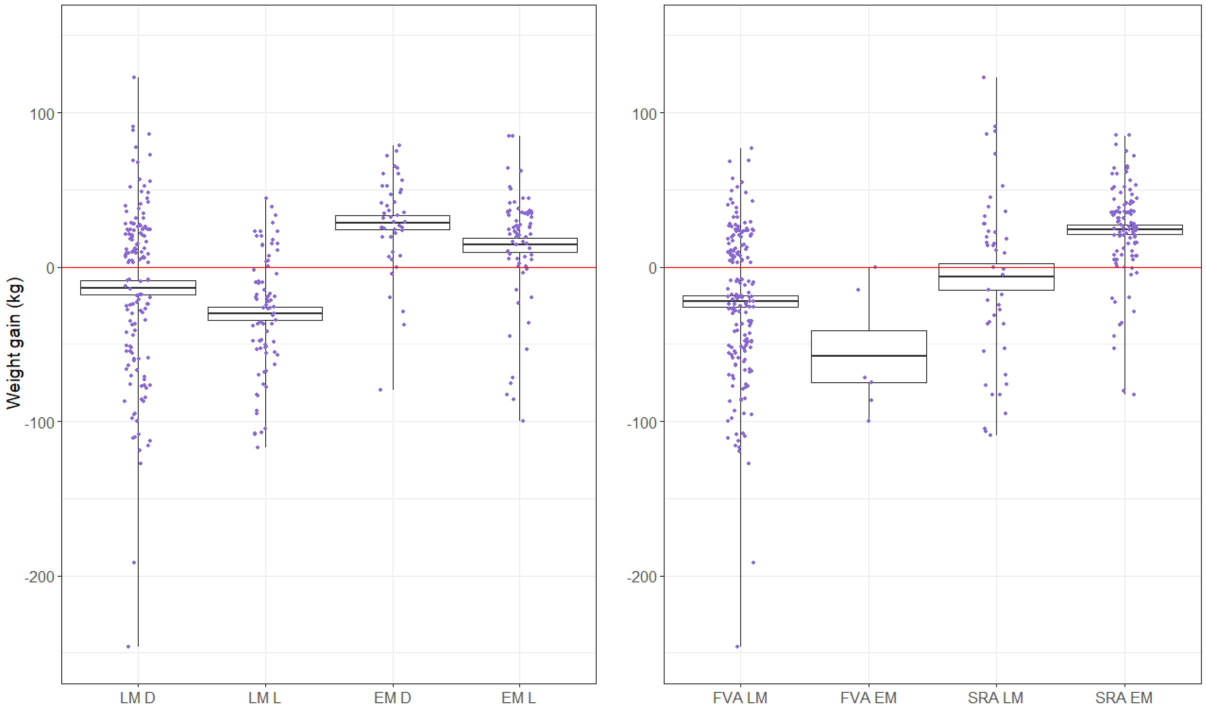

Figure 1: *Boxplots showing average weight gain (horizontal middle line inside boxes), standard error (upper and lower lines of the boxes) and the distribution of observations (purple dots and vertical lines), in beef cows grazing in boreal forests in south-eastern Norway in 2015 -2017. The cows were divided into late (LM) and early maturing (EM) breeds and dry (D) and lactating (L) cows (left), and in areas of low (SRA) and high stocking density (FVA) (right).*

The best-ranked models explaining weight gain in all studied beef cows included the coefficients individual deviation from mean breed-specific turnout weight, number of grazing days, reproductive status and the interaction between breed groups and study areas (Tables 3 & 4). Weight gain of cows was positively correlated to number of grazing days and negatively correlated to deviation from breed-specific average turnout weight (Table 4). In general, weight gain was lower for lactating than dry cows. The interaction between breed group and study area indicated that early maturing breeds in SRA (low stocking density) had highest weight gain, and that weight gain was lower in FVA (high stocking density), with a less pronounced difference between breed groups (Figure 1, Table 4). The confidence interval of interaction term overlapped 0 marginally, while the single terms did so strongly, indicating a weak relationship only between weight gain and breed/study area.

Table 3: *Coefficients, Akaike information criterion (AIC) values: degrees of freedom (d.f.), Log-Likelihood, AICc, ∆AIC and AIC weights, of best-fitting (∆AIC < 2) linear mixed models for investigation of weight gain of beef cows in in boreal forests of Stange and Romedal almenninger (SRA) and Furnes and Vang almenninger (FVA) in south-eastern Norway in 2015 – 2017.*

Model	Intercept	Grazing days	Dev. Turnout weight/breed	Reproductive status	Breed	Study area	Breed * Study area	d.f.	Loglik	AICc	ΔAIC	Weight
1	+	+	+	+	+	+	+	9	-1698.49	3415.54	0.00	0.54
2	+	+	+	+	+	+		8	-1700.28	3416.99	1.45	0.26
3	+	+	+		+	+	+	8	-1700.54	3417.52	1.98	0.20

Table 4: *Model-averaged coefficients, 95% confidence intervals (CI), standard errors and relative importance of the variables included in three models with ∆ AIC (Akaike information criterion) < 2 of independent variables explaining the variation in individual weight gain of beef cows grazing at low and high stocking density in boreal forests of Stange and Romedal almenninger (SRA) and Furnes and Vang almenninger (FVA) in south-eastern Norway in 2015 - 2017. References are for late maturing breeds, dry cows for reproductive status, and FVA for study area.*

Model coefficients	Estimate	CI (2.5% – 97.5%)	S.E	Relative importance
Intercept	-106.46	(-142.37, -70.54)	18.26	
Grazing days	0.93	(0.58, 1.27)	0.18	1.00
Dev. turnout weight of the breed	-0.18	(-0.22, -0.13)	0.02	1.00
Reproductive status (Lactating)	-10.55	(-20.35, -0.75)	4.98	0.84
Breed (Early maturing)	-7.80	(-45.67, 30.07)	19.28	1.00
Study area (SRA)	7.96	(-6.86, 22.78)	7.54	1.00
Breed (Early maturing) * Study area (SRA)	35.00	(-0.20, 70.19)	17.89	0.74

The best-ranked models used to explain weight gain in the subsample of 53 cows equipped with GPS included the covariates grazing days, home range size and the use of summer farm meadows (Table 6). As in the models above, we found weight gain to increase with the length of the grazing period. Average weight gain was negatively related to home range size and the proportion of time spent on summer farm meadows, but these relationships were weak (95% CI including 0). The average (SE) home range size of GPS collared cows was 39.7 ± 3.7 km^2 and 23.7 ± 2.4 km^2 in SRA and FVA, respectively. The average (SE) proportion of time spent on summer farm meadows was 13 ± 0.01% and 9.4 ± 0.01% for cows in SRA and FVA, respectively. Size of the herd (number of cattle turned out per farm) and the use of forested stands younger than 15 years were not retained in the three best-ranked models.

Table 5*: Coefficients (standardized values), Akaike information criterion (AIC) values: degrees of freedom (d.f.), Log-Likelihood, AICc, ΔAIC and AIC weights, of best-fitting (ΔAIC < 2) linear mixed models for investigation of weight gain of beef cows fitted with GPS collars in boreal forests of Stange and Romedal almenninger (SRA) and Furnes and Vang almenninger (FVA) in south-eastern Norway in 2015 – 2017.*

Model	Intercept	Grazing days	Loc. meadows	Home range size	d.f.	Loglik	AICc	ΔAIC	Weight
1	+	+			4	-278.40	565.62	0.00	0.55
2	+	+	+		5	-277.99	567.25	1.62	0.24
3	+	+		+	5	-278.12	567.52	1.89	0.21

Table 6: *Model-averaged coefficients, 95% confident intervals (CI), standard errors and relative importance of the variables included in three models with* Δ *AIC (Akaike information criterion) < 2 on the effects affecting weight gain variation in beef cows grazing boreal forests in south-eastern Norway in 2015 -2017 in areas of low stocking density in Stange and Romedal almenninger (SRA) and high stocking density in Furnes and Vang almenninger (FVA).*

Model coefficients	Estimates	CI (2.5% – 97.5%)	S.E	Relative importance
Intercept	-21.96	(-39.47, -4.45)	8.73	
Grazing days	35.97	(21.03, 50.92)	7.46	0.55
Home range size	-1.80	(-21.01, 6.15)	4.60	0.24
Summer farm meadows	-1.13	(-20.18, 9.53)	4.04	0.21

The two best-ranked models (AIC < 2) used to explain variation in weight gain in suckling calves contained the combination of sex and birth period and study area as the strongest predictors (Tables 7 and 8). Across all three study years, average weight gain of spring-born calves was 96 ± 1.6 kg (SE) in the low stocking density area (SRA) and 73 ± 4.2 kg in high stocking density (FVA) (Figure 3). The average (SE) weight gain of autumn-born heifer calves was lower and varied more across study areas, with 78 ± 3.4 and 32 ± 8.4 kg in SRA and FVA, respectively. The number of grazing days showed less importance for weight gain in suckling calves (confidence interval is slightly overlapping zero). The average (SE) number of grazing days in SRA and FVA were 108 ± 1.0 and 90 ± 1.5 days, respectively.

Spring-born bull calves showed the highest weight gain (99 ± 2.3 kg) during the summer grazing period followed by spring-born heifers (88 ± 2.2 kg) over autumn-born heifers (64 ± 4.4 kg). Calves of the early maturing breeds (102 ± 2.1 kg) tended to gain more weight than those of late maturing breeds (78 ± 2.6 kg) (confidence interval is slightly overlapping zero). The interaction between breed group and study area was included in the averaged models but not found significant to explain weight gain in suckling calves as the confidence interval was overlapping zero and the relative variable importance was very low (Table 8).

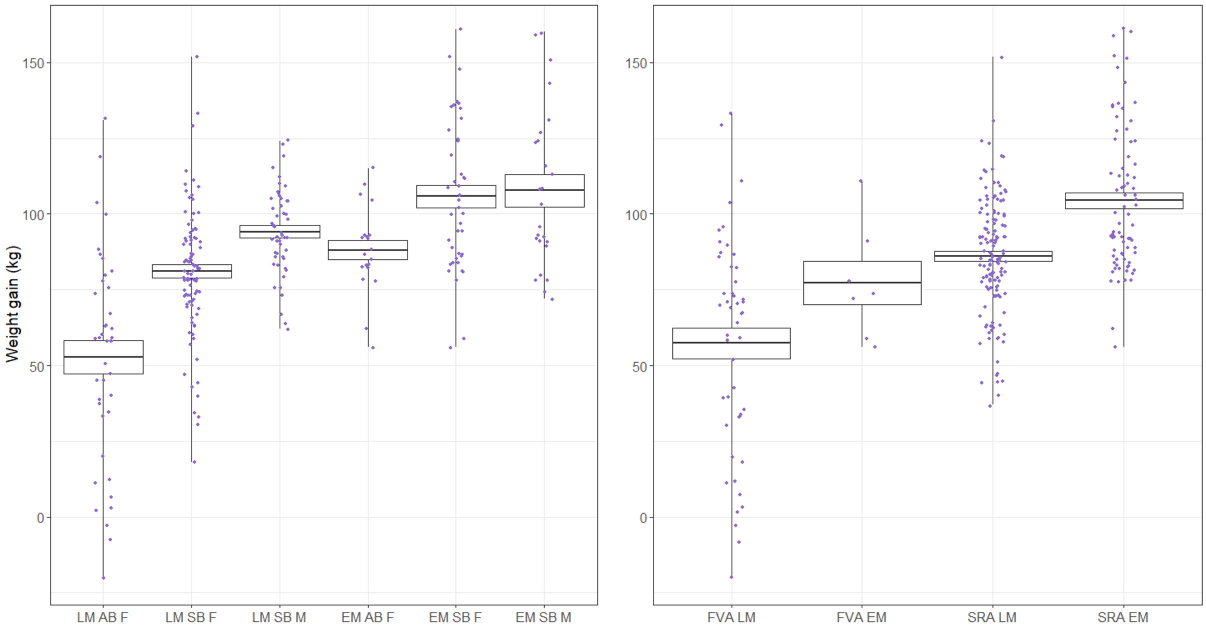

Figure 2: *Boxplots showing average weight gain (horizontal middle line inside boxes), standard error (upper and lower lines of the boxes) and the distribution of observations (purple dots and vertical lines), in beef suckler calves grazing in boreal forests in south-eastern Norway in 2015 -2017. The calves were divided into late (LM) and early maturing breeds (EM) and autumn-born (AB) and spring-born (SB) calves and, female (F) and male (M) calves (left), and in an area of low (SRA) and high stocking density (FVA) (right).*

Table 7: *Coefficients (standardized values), Akaike information criterion (AIC) values: degrees of freedom (d.f.), Log-Likelihood, AICc, ΔAIC and AIC weights of best-fitting (ΔAIC < 2) linear mixed models for investigation of weight gain of suckling calves in boreal forests of Stange and Romedal almenninger (SRA) and Furnes and Vang almenninger (FVA) in south-eastern Norway in 2015 – 2017.*

Model	Intercept	Grazing days	Sex/birth period	Breed	Study area	Breed * Study area	d.f.	Loglik	AICc	ΔAIC	Weight
1	+	+	+	+	+		8	-1211.70	2439.96	0.00	0.62
2	+	+	+	+	+	+	9	-1211.14	2440.97	1.01	0.38

Table 8: *Average effects of parameters, 95% confident intervals (CI), standard errors and relative importance of the variables included in two models with* Δ *AIC (Akaike information criterion) < 2 on the effects affecting weight gain variation in suckling calves in boreal forests of Stange and Romedal almenninger (SRA) in south-eastern Norway in 2015 -2017. References are autumn-born heifers for sex and birth period, late-maturing breeds for breed, and FVA for study area.*

Model coefficients	Estimates	CI (2.5% – 97.5%)	S.E	Relative importance
Intercept	17.40	(-6.91, 41.71)	12.34	
Grazing days	0.25	(-0.01, 0.49)	0.12	1.00
Sex and birth period				1.00
Spring-born heifers	25.87	(18.74, 33.00)	3.62	
Spring-born bulls	32.56	(24.33, 40.78)	4.18	
Breed (Early-maturing)	12.87	(-1.75, 27.47)	7.43	1.00
Study area (SRA)	19.17	(11.13, 27.20)	4.08	1.00
Breed (Early maturing) * Study area (SRA)	10.20	(-8.95, 29.35)	4.08	0.38

4. Discussion

In this study, we compared weight gain in beef cows and their calves on forest pastures across two study areas with differing stocking densities, breeds, reproductive status of cows, age of calves, and years. Generally, cows grazing in the low stocking density area (SRA) gained more weight than those of the high stocking density area (FVA; Figure 1), where a majority of both dry and lactating cows lost weight in both study years. As predicted from the Ideal free distribution theory (Fretwell & Lucas 1969a), we have previously found an increased use of sub-optimal habitats by the cows in FVA (Tofastrud, Devineau & Zimmermann 2019), eventually combined with uptake of less nutritious herbage. We assume that the high stocking density influenced the sward heights and availability of preferred feeding plants in the area and thus further influenced weight gain in cows negatively (Cornelissen & Vulink 2015). However, no such measurements on herbage availability were done in this study. Although cattle have the opportunity to increase the time spent grazing to compensate for the smaller bites that shorter swards provide, they may still be unable to fulfil their nutritional requirements (Chacon, Stobbs & Dale 1978). Hence, sward height and stocking density can have a strong effect on feed intake and performance of both grazing beef cows and their suckling calves (Wright & Russel 1987; Wright *et al.* 1994). Since breed composition and number of grazing days differed between the two study areas, direct comparisons of weight gain between the two study areas are however limited and need to be interpreted with caution.

Previous studies of beef cows kept on unimproved land have shown factors such as size of cows, milk yield potential and variation in maintenance requirements to be important for weight gain (Wright *et al.* 1994; Casasús *et al.* 2002b). In general, large herbivores are better adapted to low quality forage than smaller ones due to the relationship between the body size and the digestive tract, which in turn enables extended microbial activity and thus more energy obtained from the plant material (Demment & Van Soest 1985). On the other hand, early maturing beef breeds, mainly represented by Hereford in this study, were originally bred for lower-quality nutritional environments than those of late maturing breeds, resulting in differences in maintenance and growth requirements (Webster 1989). The Norwegian

Hereford breeding goal of today is emphasizing a more extensive production rather than those of late maturing breeds (TYR 2016). As a result, cattle of early-maturing breeds are more efficient in utilizing energy in low quality forage, whereas late-maturing breeds are more efficient when fed rations with a high energy density (Webster 1989). Hence, early-maturing breeds, often with a smaller body size, are believed to be better suited to nutrient-poor pastures (Osoro *et al.* 1999), whereas animals with a genetic potential for high productivity may be less suitable for grazing such nutrient-poor environments (Ferrell & Jenkins 1985). In accordance, Fraser *et al.* (2009a) found higher weight gain of steers of an early-maturing native beef cattle breed over Charolais/Limousin crosses on semi-natural grassland, whereas the crosses gained more weight on improved pastures. Contrary, Hessle, Rutter and Wallin (2008) could not find any significant effect of breed when comparing weight gain in heifers of a native breed and Charolais. Also, Hansen, Bøe and Okkenhaug (2009) reported no difference in daily weight gain of heifers of different breeds grazing in boreal forests of Norway. The number of animals was low in both studies. Overall, we assume that the early maturing breeds are better adapted to meet their nutritional needs for maintenance and growth on unimproved pastures than those of late maturing breeds. In accordance with the results of previous studies (Braghieri *et al.* 2011; McCabe *et al.* 2018), we could not find any differences in time spent on grazing between GPS-collared cows of early and late maturing breeds (Tofastrud *et al.* 2018).

Lactating cows had a higher average weight loss than dry cows of the same breed group. Previous studies have shown lactating cows to both lose (Montaño-Bermudez & Nielsen 1990) and gain weight (Wright *et al.* 1994; Casasús *et al.* 2002b) on unimproved land. These contrasting results are most likely due to variations in cattle breeds and pasture quality. A comparison of the time budget of GPS-collared lactating and dry cows showed that lactating cows spent on average 30 minutes more per day grazing (Tofastrud et al. 2018) and therefore truly compensated for the higher energy demands of raising a calf. Including information about the sex and birth date of their calf would had been useful, but this data is unfortunately not available, as these factors affect the amount of milk produced by the cow (Espasandin *et al.* 2016).

When cattle are turned out to pasture, their feed type changes dramatically, associated with changes in diet digestibility and intake and accompanied by losses in intestinal fill, which constitutes a considerable part of live weight (Spörndly, Olsson & Burstedt 2000; Hessle, Nadeau & Johnsson 2007). The feeding regime before the grazing period affects weight loss during the recovery period, measured as live weight. Weight loss of up to 30-40 kg has been reported during the first weeks on pasture and, in general, a reduction in weight is greater for cattle having had higher levels of indoor feeding (Hinks *et al.* 1999; Hessle, Dahlström & Wallin 2011). In our study, the winter-feeding regimen was not recorded but instead we used individual deviation from the mean breed-specific weight to measure individual weight variation at turnout date. In our study, cows that were heavier than the average at turnout gained less weight than those being below average. This is in accordance with previous studies where weight gain in cattle grazing on unimproved areas was found to be negatively correlated with body weight at turnout date (Bjor & Graffer 1963; Hessle, Dahlström & Wallin 2011). We therefore argue that farmers should maintain a moderate feeding regime during the winter in order to enable an effective grazing summer. In addition to differences in winter-feeding intensity, deviation from the mean breed-specific weight might be caused by both individual variation in body size or feed intake capacity of the individual cow caused by genetic variations (Herd, Oddy & Richardson 2004).

Several studies (Casasús *et al.* 2002b; Hansen, Bøe & Okkenhaug 2009; Steinshamn *et al.* 2010) report year as a source of variation in weight gain for cattle. Studies have shown a relationship between weather conditions in the grazing season and the feeding value of forage plants (e.g.; (Sæther 1985; Steinheim *et al.* 2004)). Low summer temperatures appear to have a positive effect on quantity and quality of the herbage and subsequently the weights of northern ungulates. During our three-year study period, the summer of 2016 was remarkably warmer and drier than the summers of 2015 and 2017. In this study, we used the effect of year as a random effect to correct for unbalanced numbers of study years between the two areas, but also to correct for annual differences in temperature and precipitation (Table 1 & 2). The effect of year may also be due to the fact that the individual animals were not exactly the same between years and there were differences in winter feeding regime between the years.

The number of grazing days varied both between individual cows and between farms, and in general the length of the grazing period was positively correlated with weight gain in cows (Tables 4 & 6). As the time for re-housing cattle in September is strictly regulated due to the start of hunting season, variations were mainly caused by a delayed turnout date. Some cows gave birth in late spring, which delayed their turnout, as the farmers wanted to check the next gestation before turnout to the forest. Pasture herbage grows very rapidly in early spring with a subsequent decline in growth rate in the late season (Nams and Martin (2007). At the end of the grazing period, night frost may occur in September, which causes stagnation in plant growth and reduces the cow's rumen and intestinal fill. As in our study, Nams and Martin (2007) found lower weight gain of Canadian beef cattle turned out to pastures later in the season and explained this as a loss of grazing time in the period of maximum growth potential. As stated above, cattle lose weight during their first weeks on pasture and need a recovery period for adapting to the new regime before reaching a net gain in weight (Nams & Martin 2007). Cows with a short grazing period will therefore lose weight over a greater proportion of their grazing period and, hence, have fewer days available for positive weight gain before housing.

Home range size in our study were much larger than reported in previous studies of free-ranging cattle on unimproved lands (Lazo 1995; Howery *et al.* 1996; Kie & Boroski 1996). As in the studies of Roath and Krueger (1982a), home range size of individuals and herds were stable from year to year (Tofastrud, unpublished data). A possible explanation may be that the size of the home range depends on the availability of resources (van Beest *et al.* 2011) and the phenology of foraging plants (Lazo 1995; Ofstad *et al.* 2016), but may also result from social learning in young calves from following their mother (Howery *et al.* 1998) and spatial memory of foraging sites (Launchbaugh & Howery 2005). Bjor and Graffer (1963) observed intense use of summer farm meadows early in the season, followed by a decreasing use through the summer. In contrast, we observed cattle gathering in large herds on the meadows of abandoned summer farms throughout the season. This may be explained by antipredator behaviour related to disturbances by human activity or the presence of large carnivores which were frequently observed in these areas. We found no effect of the use of forest stands younger than 15 years or herd size on weight gain in beef cows. We assume that several factors might have influenced this result; there was a relatively low number of collared cows in this study, the variation in weight gain was relatively high and there was low prevalence of preferred foraging habitats in the coniferous forest.

Weight gains of suckling calves in the present study (Figure 2) was similar to results from Niemelä *et al.* (2008) and Steinshamn *et al.* (2010) who found daily weight gain of suckling calves grazing coastal meadows and mountains pastures at 1000 and 900 gram, respectively. Weight gain of young calves has been shown to be dependent on the milk yield of the cow (Wright *et al.* 1994), where 60% of the variance of the gain in suckling calves can be attributed directly to the effect of the cow's milk yield (Rutledge *et al.* 1971). Overall, our spring-born calves gained more weight than autumn-born calves (Table 7), which were all heifers. A possible explanation is that the autumn-born suckling calves needed a higher proportion of nutrient intake from the herbage as their mothers were at the end of their lactation period and their milk production was low (McDonald *et al.* 2011). Previous studies have shown that high feed intake from pasture may be demanding for young cattle even on cultivated pastures (Wright & Russel 1987; Spörndly, Olsson & Burstedt 2000; Blanco *et al.* 2014). Wright and Russel (1987) showed that suckling beef calves compensated for reduced access to milk by increasing their grass intake, thus this compensation is again dependent on the availability of nutritious herbage. On average, the weight gain in autumn-born calves was notably lower in the high compare to the low stocking density area. We assume that the high stocking density may have led to reduced sward heights in these nutrient poor pastures and consequently increased the risk of not meeting the feeding requirements for growth in young calves.

As a result of early maturing breeds' superior ability to utilize the feed resources in the area of low stocking density (SRA), the weight gain of calves of early-maturing breeds was higher than those of the late-maturing breeds (Table 7). Obviously, this capability surpassed the fact that Hereford cows, which represent all early maturing cows in this study, are known as a breed with low milk production potential (Montaño-Bermudez, Nielsen & Deutscher 1990).

As expected, bull calves grew more than heifers due to their higher feed efficiency caused by growth of muscle mass rather than fat (Turton 1969) (Table 7). The growth potential of bull calves is effectively realized as long as the mother's milk production meets their needs, which seemed to be the case especially for the Hereford cows. However, some farmers claimed weight gain of bull calves was not satisfactory and kept them at the farm on higher feed intensities.

5. Conclusion

We found forest habitats in Northern Scandinavia to be valuable grazing resources for free-ranging beef cattle, with acceptable weight gain of spring-born calves in accordance with previous studies. Weight gain in beef cows varied widely among individuals and breeds, but the relatively small weight reduction found in adult cows of this study is likely to be quickly recovered after housing. Weight gain differed between the study sites, and our results indicate a potential negative relationship between weight gain and stocking density. To reach economic and ecological sustainability, stakeholders should cooperate to find the optimal stocking density based on the grazing value of the area.

We found higher weight gain in both calves and cows of early compared to late maturing beef breeds. Although the interest of using late-maturing beef breeds, suitable for intensive production, is growing among Norwegian farmers, our results show that cattle production based on early-maturing beef breeds is likely to be more suitable for unimproved land and in particular, in systems with spring calving.

6. Management implications

All in all, our results show that farm operation management, including calving period, winter-feeding regime and cattle breed, are crucial factors for an efficient utilization of unimproved land and should be considered in the context of grazing low-quality pastures in the boreal forest. Our study is based on a limited number of animals, but indicates opportunities for identifying various factors related to operational management and relevant genotypes of cattle related to effective grazing.

Because the length of the study period is positively related to cattle growth and defined by the turn-out date rather than the date of housing (onset of moose hunting season), we suggest early turn-out to optimize access to energy-rich plant shoots in the spring. Turn out and housing involves a lot of work for the farmers, an extended grazing will be an advantage period and also lead to less use of the farm's winter fodder.

This study shows that autumn-born calves have limited opportunities to realize their growth potential. This is also known by the farmers who rely on the potential for compensatory growth and turnout such heifer calves for practising important social learning, for the day they will graze the forest as adult cows.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Inland Norway
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Non-native beef cattle breeds has been increasingly popular in Norway and stimulation of national beef production has led to an increase in the number of suckler cows turned-out in unimproved lands. The main goals of this study were to investigate grazing behaviour and weight performance of these animals on extensive pastures in the boreal forest of south-eastern Norway.

In three grazing summers, suckler cows were fitted GPS collars with built-in activity sensors in two communal forests, one with a high and the other with a low stocking density. The cows spent about 1/3 of their daily time budget on grazing and they adapted their daily time budget to the hours of daylight.

Suckler cows in the low density area had the largest home ranges and there was a positive relationship between the home range size of and the proportion of the home range covered by poor forage quality. The cows selected for grass-rich habitats, i.e. the widespread patches of abandoned summer farm meadows and less than 15 years old clearcuts. Cattle in the area of high stocking density selected more frequently low productivity habitats and areas further from roads.

Overall, non-lactating cows gained more weight than lactating cows. Cows and calves in the low stocking density area gained more weight than those in the high stocking density area. In the low stocking density area, cows and calves of early-maturing breeds had higher weight gain than those of late maturing breeds.

Beef cattle of international breeds was found fully suitable for grazing in the boreal forest in south-east Norway. Mainly because of the pasture resources on the large clear-cut areas, created by modern forestry operations. The potential forage production based on the actual vegetation types and forest classes should be used as a basis for estimating proper stocking densities since this is of importance for both weight performance and grazing behaviour of cattle in the boreal forest.