Norwegian University of Life Sciences
Faculty of Biosciences

Philosophiae Doctor (PhD)
Thesis 2018:24

Sheep breeds in contrasting environments - pasture utilization at different spatiotemporal scales

Saueraser i forskjellige miljø - utnyttelse av utmarksbeite på ulike skalaer i tid og rom

Nicolai Hermann Jørgensen

Sheep breeds in contrasting environments - pasture utilization at different spatiotemporal scales

Saueraser i forskjellige miljø - utnyttelse av utmarksbeite på ulike skalaer i tid og rom

Philosophiae Doctor (PhD) Thesis

Nicolai Hermann Jørgensen

Norwegian University of Life Sciences
Faculty of Biosciences
Department of Animal and Aquacultural Sciences

Ås 2018

Thesis number 2018:24
ISSN 1894-6402
ISBN 978-82-575-1503-4

SHEEP BREEDS IN CONTRASTING ENVIRONMENTS - PASTURE UTILIZATION AT DIFFERENT SPATIOTEMPORAL SCALES

Philosophiae Doctor (PhD) Thesis

Nicolai Hermann Jørgensen

Norwegian University of Life Sciences
Faculty of Biosciences
Department of Animal and Aquacultural Sciences

Ås 2018

Thesis number: 2018:24
ISSN: 1894-6402
ISBN: 978-82-575-1503-4

CONTENTS

PAPER I

PAPER II

PAPER III

ACKNOWLEDGMENTS

This study, a part of the research project “Sau i Drift”, aimed to investigate potential effects of genotype and environment and the genotype*environment (G*E) interactions in sheep summer grazing behavior. The project was funded by Norwegian Research Council, the Regional Småfefondet and NMBU.

First, I would like to express my gratitude to my main supervisor Professor Øystein Holand for giving me this opportunity to be a part of the project, for your patience and guidance. I am also grateful to my co-supervisor Dr. Geir Steinheim for his support and guidance. I also thank my co-supervisor Dr. Håvard Tveite for GIS-matters.

Second, thanks to sheep farmers in Spekedalen and Bratthøa, Rune Granås at NLR Nord-Østerdal, Jørgen Todnem, Michael Angeloff and Yngve Rekdal, NIBIO. Also thanks to Kami Safi, Bart Kranstauber, Andy Lyon, Bret Collier, the Animove community, Maryam Teimouri and Juliette Viel. Thanks to all my colleagues for an inclusive working environment.

Finally, but not the least, I am sincerely grateful to Nanna and our two children for your understanding and support during these years.

Ås, February 2018

Nicolai Hermann Jørgensen

ABSTRACT

In Norway, approximately 2 million sheep are released onto outer fields for summer grazing. Indeed, during the summer months sheep are the most common large herbivores in most Norwegian mountain areas. The sheep, of which 80% are the heavy, docile Norwegian White sheep (NWS) and 13% short tailed, light-footed, agile and more gregarious Spælsau (SP), are released onto a range of summer grazing environments; from coastal to mountainous inland areas. However, little is known about phenotypic plasticity in ranging behavior of sheep, how different sheep breeds interact with different rangeland habitats and how they are able to adjust their foraging behavior at different spatiotemporal scales. Indeed, these complex behavioral processes are hierarchical, as large herbivores operate on several spatial and temporal scales to maximize nutritional acquisition and hence fitness. This is imperative for understanding the grazing dynamic of sheep and for a sustainable grazing management adapted to the available natural and ever-changing resources.

In this study, 51 ewes of the two aforementioned breeds were fitted with GPS collars in two contrasting environments, during the summer grazing seasons 2013 and 2014. The two study areas were vegetation mapped and classified regarding their quality for sheep grazing (Spekedalen; poor, and Bratthøa; rich pasture). The collars logged position every hour and were equipped with sensors that recorded activity during time-to-fix (TTF). I defined several

temporal scales from the whole grazing season to bounding individual time steps. I defined three spatial scales; 95, 50 and 20% utilization distribution areas (UDs). The spatial scales for all but the time-step temporal scales were extracted from the dynamic Brownian Bridge Movement Model (dBBMM). The time-step time-indexed UDs were based on Dynamic Brownian Motion variation extracted from every two consecutive timestamped relocations. I calculated the proportion of three sheep grazing quality classes: "Less Good", "Good" and "Very Good", within each UD and at all spatial scales.

Using general mixed models I was thus able to infer area use across spatiotemporal scales, when both active and inactive, (papers I and II), habitat use across spatiotemporal scales and habitat selection, when active, (paper III) for both breeds in both environments, using a resource selection function (RSF) approach.

I found that both breeds had non-significant larger seasonal UD area in poor Spekedalen as compared to rich Bratthøa. At finer temporal scales, 95% UD differences were found between the two study areas. However, these differences could be confounded by the higher density of salt blocks in Bratthøa, at least at large scale. SP had larger UD area than NWS at all but the finest temporal scale. The effect of breed and environment on sheep area use was stronger at the 50% UD as compared to the 95% UD scales, at all temporal scales. Although the two breeds may differ in their area use, I was not able to detect differences in habitat use and selection, in neither

time nor space. However, effects of vegetation class and study area on habitat use and selection were found. My findings highlight the increased importance of the scarce “Very Good” patches with finer scales, in poor Spekedalen. Indeed, this high-quality class is probably more important for nutrient extraction and acquisition than the use indicates. The lack of environment by breed interactions in area and habitat use suggests that the two breeds respond equally to range quality, at all spatiotemporal scales. I appreciate that, in my study, the large individual variation may have overshadowed the effects of the intrinsic and extrinsic determinants.

I conclude that scale has to be considered when comparing pasture utilization across spatial and temporal scales in contrasting environments and between sheep genotypes. My findings are thus important for management of grazing resources in multipurpose land use planning.

SAMMENDRAG

I Norge slippes det omlag 2 millioner sau på utmarksbeite hver sommer og er det vanligste store beitedyret i de fleste norske fjellområder. Av den norske sauepopulasjonen tilhører ca. 80% den relativt nye, tunge rasen norsk kvit sau mens ca. 13% er spælsau, en noe lettere, korthalesau av nordisk type som går mer samlet i flokk enn norsk kvit sau. Sauene går på utmarksbeite under svært ulike miljøforhold: fra kyst til høgfjell og fra sør til nord. Likevel vet vi lite om hvordan miljøforholdene påvirker sauens beiteatferd, og hvordan ulike raser opptrer i ulike habitater. Vi vet også lite om beiteatferden på ulike skalaer i tid og rom. De komplekse beslutningene knyttet til beiting er hierarkiske, og dette må det tas hensyn til i studier av hvordan sau effektivt utnytter ressursgrunnlaget. Forståelse av beiteatferd på ulike skalanivå er avgjørende for å etablere kunnskap om hvordan sau utnytter beiteområder, og dermed for å kunne utvikle bærekraftig forvaltningsstrategier som er tilpasset beiteområder langs en multi-dimensjonal miljøgradient.

I studiet ble 51 søyer, av de to rasene nevnt over, utstyrt med GPS-klaver; dyra ble somrene 2013 og 2014 sluppet i to ulike beiteområder med svært forskjellig beitekvalitet. De to beiteområder ble vegetasjonskartlagt og klassifisert med hensyn til deres kvalitet som sauebeite (Spekedalen, fattig beite, og Bratthøa, rikt beite). Klavene registrerte posisjon og aktivitet hver time. Jeg definerte flere tidsskalaer: fra hele beitesesongen og ned til hver time, videre

tre romlige skalaer; 95, 50 og 20% utilization distribution (UD). De romlige skalaene, bortsett fra time-skalaen, ble estimert ved hjelp av en dynamisk Brownian Bridge Movement Model (dBBMM). Timeskala-UD'ene ble basert på dBBMM-variasjon hentet fra posisjoner ved to og to fortløpende tidspunkter. Vi beregnet andelen av tre beitekvalitetsklasser: "Mindre Godt", "Godt" og "Svært Godt", innen hver UD, for hver romlige skala.

Jeg var dermed i stand til, ved hjelp av generalisert lineær blanda modell, å estimere arealbruk ved ulike skalaer i tid og rom, uavhengig av aktivitet (artikkel I og II), og habitatbruk ved forskjellige skalaer i tid og rom og habitatvalg når sauene var aktive (artikkel III). Jeg brukte en ressursvalgfunksjonstilnærming (RSF) for estimering av habitatbruk.

Jeg fant at begge sauerasene hadde større sesongbaserte 95% UD-områder i fattige Spekedalen sammenlignet med i rike Bratthøa, men denne forskjellen var ikke signifikant. På finere tidsskala ble det imidlertid funnet 95% UD forskjeller mellom de to studieområdene, Den høyere tettheten av saltstein i Bratthøa kan ha bidratt til dette, særlig på stor skala. Raseforskjeller ble funnet på alle temporære skala, med større arealbruk for spælsau enn norsk kvit sau, bortsett fra på den fineste temporale skalaen. Effekten av rase og miljø på arealbruken var sterkere ved 50% UD romlig skala sammenlignet med 95% UD, for alle tidsskalaer. Selv om de to rasene kan ha noe ulik arealbruk, fant jeg ingen forskjeller i bruk og valg av habitat av ulik beitekvalitet, hverken i tid eller rom. Jeg fant klare effekter av vegetasjonsklasse og studieområde på habitatbruk og -valg. Funnene mine viser at områdene med "Svært Godt" beite øker i betydning for sauen på finere skalaer, især i det fattige Spekedalen. Faktisk kan denne vegetasjonsklassen, med sin høye beitekvalitet og -kvantitet, være enda viktigere for sauens næringstilgang enn andel tid brukt tyder på. Mangelen på samspillseffekt på areal- og habitatbruk mellom miljø og rase antyder at de to saueraser responderer relativt likt på ulike beiteområdes kvalitet, ved ulike skalaer i tid og rom. Den store individuelle variasjon kan imidlertid ha overskygget disse effektene.

Jeg konkluderer at skala må tas hensyn til når man sammenligner beiteutnyttelse mellom beiteområder av forskjellige kvalitet og mellom ulike saueraser. Mine funn er derfor viktige for forvaltning av beiteressurser.

LIST OF ORIGINAL PAPERS

I. Jørgensen, N.H., Steinheim, G., Holand, Ø., 2016. Area use of two sheep breeds in contrasting summer alpine grazing environments in southern Norway. Acta Agriculturae Scandinavica, Section A - Animal Science. 1-7. https://doi.org/10.1080/09064702.2016.1215513

II. Jørgensen, N.H., Steinheim, G., Holand, Ø., 2018. Does scale matter? Variation in area use across spatiotemporal scales of two sheep breeds in two contrasting alpine environments. Rangeland Ecology & Management. https://doi.org/10.1016/j.rama.2017.11.001

III. Jørgensen, N.H., Steinheim, G., Holand, Ø., 2018. Scale matters - habitat use and selection by two sheep breeds in two contrasting alpine environments. Small Ruminant Research. Manuscript. Submitted

1. INTRODUCTION

In Norway, approximately 2 million sheep are released onto outer fields for summer grazing. The density varies greatly due to geographical distribution of farms, variable natural grazing conditions and management regimes (Mysterud et al., 2001). Indeed, during the summer months sheep are the most common large herbivores in most Norwegian mountain areas.

The two most common sheep breeds are the heavy Norwegian White Sheep (NWS) which originates from old Nordic breeds with substantial crossing with English lowland breeds, and the lighter Spælsau (SP) which is a traditional Nordic landrace less influenced by foreign breeds (Drabløs, 1997). NWS is generally considered to be more docile, with reduced alertness and weak gregariousness, forming smaller, more stationary family groups distributed throughout the grazing areas (Drabløs, 1997). The SP, in contrast, has retained more of the survival traits, such as gregariousness, agility and alertness (Drabløs, 1997; Hansen et al., 2001). Also, their grazing behavior differ; the NWS breed being a typical grazer while the SP is more of a mixed grazer/browser type (Steinheim et al., 2005, 2003). The SP may thus be regarded as well adapted to marginal rangeland conditions (Drabløs, 1997). Nielsen et al. (2013) found that SP showed less between year variations in lamb autumn weights than NWS. Indeed, this breed might be more plastic in a highly stochastic climatic environment.

Due to the severe winter condition, the Norwegian sheep industry is rather intensive as compared to in e.g. UK and New Zealand. Ewes are released with young offspring in spring to utilize the growth of infield pastures after a long indoor feeding period before let out onto outfield summer pastures (Fig. 1). The industry's unique advantage is the available 'free' rangeland pasture resources that facilitate in general high body growth, high quality meat products and good animal welfare. In autumn some 25 000 tons of prime meat is delivered to the food industry (www.animalia.no, 2016).

Figure 1. Traditional Norwegian sheep production system. In the spring, after lambing, sheep are kept near the farms for infield grazing prior to the outfield summer grazing. In the autumn, after slaughtering the sheep are kept near the farms for infield grazing prior to winter indoor feeding.

The potential harvestable feed units (1 feed unit is equivalent to 6.9 MJ net energy for lactation (Ekern, 1991)) from the rangeland during the summer months by domestic ruminants is estimated to approximately 900 million units, of which 600 million are practically usable for grazing (Yngve Rekdal, 2001). Today only half of the 600 million feed units are harvested yearly from the rangelands, indicating that there is a large potential for future increase in utilization of rangelands through livestock grazing (Rekdal, pers. comm., 2012). This is in line with Meld.St.11 (2016-2017) where the Government's focus is on better utilization of Norwegian fodder resources not least from rangeland areas.

Norway is a 2500 km long country with a 25000 km rugged coastline indented by fjords. There is considerable variation in elevation, topology and vegetation coverage (open plains, forest, and arctic tundra) and the climate varies considerably along these gradients. Thus, considerable variations in resources availability and quality ranges from coastal to mountainous grazing areas are seen.

In recent years, a decisive challenge for utilization of the outfields by ruminants has surfaced. Their enteric methane emission contributes substantial to the anthropogenic global climate change (Olivier et al., 1999). However, there are many "X's" related to the warming effects of GHG emission of grazing animals (Buddle et al., 2011). Pastures may act as carbon sinks (Schuman et al., 1999). de Wit et al. (2014) argue that keeping up the albedo effect by keeping the landscape open and hence the forest and shrub expansion in check by grazing animals may actually outweigh the positive feedback through forest carbon sequestration. Indeed, climate feedbacks from land cover change are complex (Bonan, 2008) and yet poorly quantified (de Wit et al., 2014). Non-fertilized pastures may in fact mean neutral or even positive climatic feedback effects (Allard et al., 2007; Soussana et al., 2007, Soussana et al., 2010).

The sheep industry is a cornerstone of the economy in many rural areas of Norway. In addition, they provide ecological services; creating an open and outdoor activity friendly grazing-induced transitional zone between “nature and culture”, rich in biodiversity and pleasing to the human’s eye (Ten Brink et al., 2016). This is regarded crucial for the growing rural based tourist industry (Bryn, Dramstad, and Fjellstad, 2010). However, Norwegian sheep farmers are faced with an increased competition from other area-extensive businesses (Ross et al., 2016). Fewer and larger flocks being a trend in Norwegian sheep farming, also challenge the traditional grazing regime and grazing rights (see e.g. Strand (2016)). Therefore, it is imperative to understand sheep range use including breed differences in area and habitat use and selection and their plastic response to different environmental conditions. Such analyses must be undertaken in a multi-scale framework (Mayor et al., 2009), and could be a stepping-stone in the ongoing development of dynamic multi-purpose natural resource management plans.

I therefore set out to investigate how the two dominating Norwegian sheep breeds, NWS and SP, adjust their area use and foraging behavior in time and space in two contrasting environments, namely the poor Spekedalen and the rich Bratthøa (Rekdal, 2007, 2009), situated in Hedmark County.

2. FORAGING THEORY FRAMEWORK

2.1. Scale – fundamental for understanding ecological processes

The environment changes in time and space and will have implications for how individuals, populations and species of large herbivores distribute themselves. This results, through movement, in variation in space use across time; which have fitness consequences (Gaillard et al., 2010; Owen-Smith, Fryxell, and Merrill, 2010). Movement processes in connection with foraging behavior take place at different spatiotemporal scale, from selection of food items in seconds to seasonal home range selection. As a consequence, area use and selection across scales will occur hierarchically from the species geographical range (first order), an individual' home range (second order), habitats and patches within the home range (third order) to selection of specific food items within patches (fourth order) (Johnson, 1980; Senft et al., 1987). The hierarchical trans-scale ordering does not occur in discreet steps, but will be in a continuum, from the coarsest to the finest scale. Senft et al. (1987) advocated that the relative importance of plant-herbivore interactions decline toward larger spatial scales, as abiotic factors increase in importance. At the home range scale much of the work has been influenced by the ideal free distribution (IFD) theory (see e.g. McLoughlin et al. (2007), whereas at the finer (fourth order) scale (Johnson, 1980) many studies have applied optimal foraging approach (see e.g. Belovsky and Schmitz, 1994).

Figure 2 depicts an animal's area use and at which spatiotemporal scales it is operating.

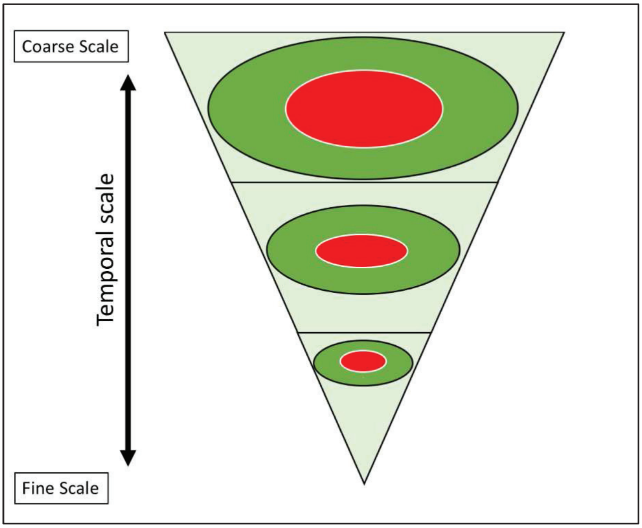


Figure 2. Conceptual overview of the expected effects of spatiotemporal scales on area use. The decreasing size of the ovals at each temporal scale depicts the expected effect of spatial scale (e.g. 95%, green, and 20% UD, red) on space use.

2.2. Ideal free distribution

Large herbivores are able to alter their foraging behavior and area use in response to spatial and temporal resource distributions (Fretwell and Lucas, 1970; Seagle and Mcnaughton, 1992; Senft et al., 1987; WallisDeVries, 1996). The ideal free distribution theory (Fretwell and Lucas, 1970) predicts that herbivores should distribute themselves relative to the profitability of the resources available. Given equal animal density, large herbivores in a poor environment will utilize a large area compared to those in an area with more recourses (Owen-Smith et al., 2010).

2.2.1. Area use and the effect of spatiotemporal scales

Animal by environment interactions creates space use patterns (Morales et al., 2010). This can be used to characterize how an animal uses its surroundings (Tufto, Andersen, and Linnell, 1996). Animals often restrict themselves to their home range, and are likely to increase their foraging efficiency and hence fitness as familiarity with that area increases (Van Moorter et al., 2009). As animals operate on different functional scales, causes for variation in home range size may thus differ within as well as between species. Differences between species are generally driven by body mass (Carbone et al., 2005), whereas intraspecific variation may be caused by a number of intrinsic factors such as age (Saïd et al., 2005, 2009), sex (Main and Coblentz, 1996), body mass (Floris M. van Beest et al., 2011) and reproductive status (Tufto et al., 1996). Social organization (Wronski et al., 2006), activity patterns (Owen-

Smith et al., 2010) and extrinsic factors such as population density (Dussault et al., 2005; Saïd et al. 2005, 2009) and climate (Börger et al., 2006) may also cause variation.

An animal's space use can be characterized by its utilization distribution (UD) which can be calculated using statistical methods like Brownian bridge movement models (Horne et al., 2007) or variations thereof, i.e. dynamic Brownian bridge movement model (Bart Kranstauber et al., 2012). The 95% and 50% area used represent the most commonly used spatial estimators (see e.g. van Beest et al. (2011)). The 95% UD is an animal's estimated "home range", whereas the 20% UD "core area" represents an animal' most intensively used foraging and or resting areas. However, the two spatial scales need not conform to a certain percentage of the estimated UD, per se, and may depend on the species' or breed's behavior. Individual animals may thus have the same UD sizes, but with different ratios of intensively used foraging patches because resources are distributed differently within the areas (Van der Wal and Rodgers, 2012). Indeed, intensively used areas may be more important within heterogeneous habitats with greater forage availability or quality than in areas with fewer or homogeneously distributed resources (McLoughlin and Ferguson, 2000). Further, an animal's use of space within a short time-span should intuitively be smaller than the area used during a longer period within a specific environment (WallisDeVries et al., 1999; Fortin et al., 2003).

Landscape characteristics, including range quality (Bjørneraas et al., 2012) and heterogeneity (Bartlam-Brooks et al., 2013), topography (Mysterud et al., 2001), and elevation (Killeen et al., 2014) can influence how individuals in spatially structured populations interact with the environment. However, studies that address spatiotemporal processes affecting area use are scarce (Bjørneraas et al., 2012), but see Van Beest et al. (2011). Since spatial and temporal scales may co-vary (Wiens, 1989), it is imperative to include both when analyzing ecological processes and to select the most informative scales of analysis (Dayton and Tegner, 1984; Mayor et al. 2009).

2.3. Optimal foraging theory

According to the optimal foraging theory (Charnov, 1976; Rosenzweig, 1981), an animal, should use patches of food until the harvest rate falls below the rates of the averages of all patches. The forager will accordingly spend a high proportion of foraging in high versus low quality patches. Thus, habitat use and selection should reflect availability and quality of food, but be constrained by trade-offs accompanied with foraging e.g. anti-predator behaviors (vigilance) and weather conditions (A. Illius and Fitzgibbon, 1994; Olson et al., 2015). However, the habitat use alone may not be a sufficient to elucidate why a forager spend time in a patch of a specific vegetation type before moving on to the next. In general, daily intake is considered a function of time spent grazing (Newman et al., 1995). Nevertheless, time spent foraging does not necessarily reflect a vegetation type' importance for nutrient extraction and acquisition. In a (time) constraint setting, the opportunity for selection diminish when food quality and availability is low (Van Beest et al., 2010). Animals in a poor homogeneous environment may thus spend more of their time foraging in vegetation of low quality and less time in vegetation of high quality, although the energy extraction and acquisition from the these two, are closer to each other than simple time-budget interpretations might indicate.

2.3.1. Habitat use and selection and functional scale

A fine spatiotemporal scales habitat use and selection is not only a function of forage quality and quantity; it has to be traded off with other fitness related factors, e.g. shelter related to thermoregulation and predator avoidance (Mount, 1979; Lima and Dill, 1990; Mysterud and Ims, 1998). Further, on which scales, and how, large herbivores are able to respond to environmental variation is species specific (Fahrig, 1992). This includes livestock breeds selected to cope with specific environmental conditions (see review by Carson et al. (2009)).

At fine scales, (optimal) foraging theory (Charnov, 1976; Rosenzweig, 1981) has been used to predict large herbivores foraging behavior (e.g. Bazely (1988); Illius et al. (1992); Langvatn and Hanley (1993)). The forager will spend a high proportion of foraging time in high versus low quality patches. The utilization will depend on patch distribution and size within the animal's known environment; as movement between patches and exploratory behavior to keep track of the environmental variation are costly time and energy wise (Russell et al., 2003; Fagan et al., 2013) and cognitively challenging (Dall et al., 2005). Indeed, searching and foraging are normally intermingled activities at fine scales (Stefano Focardi and Marcellini, 1995), and may not be readily separated as discreet activities.

These general predictions based on foraging theory are hard to test in an ever changing environment (but see Ward and Saltz (1994); Focardi et al. (1996); Fryxell et al. (2008); Bjørneraas et al (2011)). Detailed information of relationships between habitat characteristics and animal area use at finer scales has up to recently been scarce because of shortcomings in acquisition of such data (Cagnacci et al., 2010) and lack of computational power and adequate software to handle such analyses (Byrne et al., 2014). However, methods of GPS tracking of livestock and wildlife and collection of geographical information have improved both in spatial accuracy and in possibilities of frequent sampling. This has opened up new avenues for analyses of fine scale spatial and temporal information of movement data linked to habitat characteristics (e.g. Byrne et al. (2014); Iversen et al. (2014)).

Selection is the process where an individual use a set of available resources non-randomly (Morris, 2003). Indeed, the evolutionary pressure for a selective foraging strategy at different scales has been advocated (e.g. White (1983)). Often the (seasonal) home range is regarded as known and hence available to choose from in foraging patch choices, this is called second-order selection (Johnson, 1980). As pointed out by Johnson (1980) this estimation of selection depend on the investigator's notion of what component are available to the animals", based on inter- and intraspecific factors that are expected to affect home range size (reviewed by Ofstad et al. (2016)). Although site fidelity is seen in most large herbivores (F. M. van Beest et al., 2013; Wittmer et al., 2006), they are often found to track the temporal variation in forage quality and quantity within their range (e.g. Mysterud et al. (2007); Rivrud et al. (2016)). This suggests that they sample the environment on a relatively fine temporal scale before choosing patches. Habitat availability depends on the individual's current position (Arthur et al., 1996; Hjermann, 2000; Rhodes et al., 2005). Manly et al. (2002) argued that use and availability should be measured at the same temporal scale when inferring selection. New models introduced by Byrne et al. (2014) open up for same temporal scale habitat use and selection analyses, with emphasis on time-indexed consecutive relocations. The choice of scale for defining use and availability is therefore crucial (Aebischer et al., 1993; Börger et al., 2008) and may have implications for understanding the dynamic use and functional selection (Arthur et al., 1996; Mysterud and Ims, 1998), which not necessarily is congruent across scales.

Environments are heterogeneous on many temporal as well spatial scales (Wiens, 1989; González-Megías et al., 2007). Therefore, on what spatiotemporal scales habitat measurements are performed, do matter and has to be related to the species or breeds studied, i.e. the scales on which they are able to respond to this heterogeneity. On finer scales, patches often unfold into continuous resource gradients (Alexander et al., 2000). To be able to handle them spatially we delineate and organize them into structural vegetation units (i.e. types or classes, depending on scale) shaped by abiotic conditions (i.e. topography, aspect, soil, drainage and climate) and influenced by ecological processes (Alexander et al., 2000; Bryn et al., 2010).

This static classification based on plant physiognomy may further be translated into herbivore species as well as ecotype/breed-specific patch quality based on body mass, foraging strategies and behavior (Krausman, 1999). Until recently, the fine scale temporal dimension of environmental heterogeneity has been difficult to map. But, progress in satellite remote sensing and monitoring capabilities have improved greatly in terms of spatial resolution in recent years (Watmough et al., 2017), thus making it possible to add temporal information of phenological changes to static vegetation mapping. Indeed, the temporal dimension in patch quality is strong and may result in temporal variation in use and preference of vegetation classes. Hence animals may respond by following the green wave upwards in their home ranges (Rivrud et al., 2016). However, ruminants may face a trade off in their use and selection of high quality patches; i.e. forage quality versus forage abundance (Van Soest, 1994).

Patch use and functional selection are the result of complex interactions between an individual and its environment. In a poor and homogenous environment Witt et al. (2012) reportet that large herbivores to do “the best out of a bad job” by utilizing the dominating patches of low quality. However, what is apparent at one scale - e.g. doing the best of a bad job at a seasonal scale - can mask utilization of less dominating non-mapped patches of high quality at a finer spatial scale (Senft et al., 1987). Contrary, in heterogeneous rich environments, ruminants are able to, but might not need to, realize their selection potential. This could be manifested in a high use of the high-quality patches, at the expense of the lower quality patches, albeit with a weak or neutral preference of the high-quality patches.

As described above responses to environmental effects are mostly species-specific. In the case of grazing livestock, the genetic dimension of breed will also come into play. Body size, anatomy and behavior will often vary substantially between breeds, and may result in differences in behaviors, including foraging behavior and diet selection (Fisher et al., 2011). Depending on the genetic distance between breeds adapted to different environments, the effect of breed should potentially approach that of species when interacting with environmental variation. Breed by environment (G*E) interactions related to habitat use and selection may thus be scale dependent.

3. PRINCIPAL OBJECTIVE AND SUB GOALS

The main objective was to investigate how the two dominating Norwegian sheep breeds adjust their summer grazing area use and habitat use and selection in time and space in relation to the resource quality in two contrasting environments.

The sub-goals were to study:

a. if sheep on low quality pasture (Spekedalen) utilize a larger summer area compared to sheep on good quality pasture (Bratthøa) (paper I).

b. if SP utilizes larger summer areas compared to NWS (paper I).

c. how spatiotemporal scales affects sheep area use in Spekedalen compared to in Bratthøa (paper II).

d. how spatiotemporal scales affects breed area use in Spekedalen compared to in Bratthøa (paper II).

e. if there is a genotype by environment interaction effect on area use across spatiotemporal scales (paper I & II).

f. how large-scale environment affect the sheep's use and selection of vegetation classes across spatiotemporal scales (paper III).

g. if breeds differ in use and selection of vegetation classes across spatiotemporal scales (paper III).

h. if there is a genotype by environment interaction effect on habitat use and selection (paper III) across spatiotemporal scales.

4. MATERIALS AND METHODS

4.1. Study area

Bratthøa commons in the northern part of Tolga municipality and Spekedalen commons in northern part of the Rendalen municipality, both in Hedmark county, Norway, are two typical alpine inland sheep summer grazing areas approximately 60 km apart. Both areas' vegetation communities were mapped by NIBIO (Rekdal, 2007, 2009). Although geographically close, they differ significantly in terms of distribution and abundance of vegetation types suitable for sheep grazing.

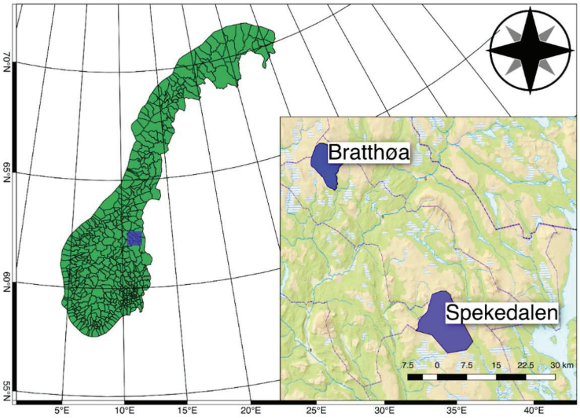


Figure 3. Study areas: Bratthøa commons in the northern part of Tolga municipality and Spekedalen commons (a part of Sølendalen commons) in northern part of the Rendalen municipality, both in Hedmark county, Norway (Source: Statens Kartverk, 2015).

Spekedalen study area (Fig. 3) (hereafter called Spekedalen), a part of Sølendalen grazing commons, is situated in the northern part of Rendalen municipality, Hedmark county, in south-eastern Norway (11°21’ E, 62°4016’ N), covering 97 km^2 spanning from 688 to 1604 meters above sea level (m.a.s.l.). The mean annual temperature is 1.1°C with a January low of -8.2°C and a July high of 11.3°C, and mean annual precipitation is close to 550 mm (Rekdal, 2007). Weather conditions are of a typical inland climate (i.e. cold relatively winters with little precipitation and relatively dry and warm summers) with high annual and between year variations (http://www.met.no).

The bedrock is uniform and dominated by sparagmite, an arkosic sandstone, interspersed with base rich layers. Mobæk and Pedersen (1977) characterized the vegetation below the tree line as dominated by lichen and heath rich pine forest (41%), whereas above the tree-line dwarf shrub heath dominated on ridges and dry higher ground (32%). Low shrubs dominated the lee-sides, intermixed with lichens. Rekdal (2007) estimated that the carrying capacity of the Spekedalen area is between 850 and 1050 sheep, i.e. 50 sheep per km^2 of area suitable for grazing (here defined as “Good” and “Very Good” vegetation classes for sheep grazing).

Bratthøa commons (hereafter called Bratthøa) (Fig. 3) in Vingelen is situated in the northern part of Tolga municipality, covering approximately 62 km^2 spanning from 790 to 1229 m.a.s.l. The climate is similar to that of Spekedalen (Rekdal, 2009). The bedrock in is dominated by phyllite with areas of fine-grained moraine material. In combination with sufficient water supply, this bedrock type results in rich vegetation. It was estimated that the carrying capacity in Bratthøa is between 2700 and 3300 sheep, i.e. 80 sheep per km^2 of suitable (“Good” and “Very Good” classes) grazing area (Rekdal, 2009).

The total density of sheep in the Spekedalen study area was approximately 3 sheep per km^2 in both 2013 and 2014, whilst in Bratthøa density was 38 and 40 sheep per km^2 in 2013 and 2014 respectively (Angeloff, pers. comm.). The sheep density in Spekedalen commons in 2013 and 2014 was 12 and 14 sheep per km^2 of “Good” and “Very good” grazing habitat respectively, whereas the number of sheep released in Bratthøa commons in 2013 and 2014 was 63 (2013) and 67 (2014) sheep per km^2 of “Good” and “Very good” grazing area respectively. Indeed, the densities in both commons, both in 2013 and 2014, were below the estimated carrying capacities (Rekdal, 2007, 2009).

4.1.1. Vegetation quality classes and heterogeneity

We classified the 24 vegetation types into three main vegetation classes, “Less good”, “Good” and “Very good” according to Rekdal (2007, 2009) (Table 1).

Table 1. The percentage (%) a given vegetation type covers in Spekedalen and Bratthøa study areas, respectively (Rekdal, 2009). Vegetation classes (Class); "Less Good" (LG). "Good" (G) and "Very Good" (VG) based on 24 vegetation types. Bold font type indicates the dominating vegetation class of a given vegetation type if classified in more than one vegetation class.

Vegetation type		**Spekedalen**		**Bratthøa**	
		%	Class	%	Class
1a	Moss snow-bed	0.12	LG	0.55	LG
1b	Sedge and grass snow-bed	0.48	**G**/LG	3.78	**G**/LG
1c	Stone polygon	2.11	LG	0.29	LG
2b	Dry grass heath	11.30	**LG**/G	2.30	LG
2c	Lichen heath	32.53	LG	20.39	LG
2d	Mountain avens heath	-	-	0.14	LG
2e	Dwarf schrub heath	22.68	**G**/LG	29.26	**G**/LG
2f	Alpine heather heath	3.32	LG	-	-
3a	Low herb meadow	0.03	VG	4.49	VG
3b	Tall forb meadow	0.62	VG	5.20	VG
4a	Lichen- and heather birch forest	9.63	LG	-	-
4b	Bilberry birch forest	4.68	**G**/VG	11.99	G
4c	Meadow birch forest	0.55	VG	2.45	VG
6a	Lichen- and heather pine forest	3.04	LG	-	-
8b	Bog forest	-	-	0.01	LG
8c	Poor swamp forest	0.02	LG	0.05	LG
8d	Rich swamp forest	0.06	G	0.56	G
9a	Bog	3.51	LG	0.64	LG
9b	Deer-gras fen	0.00	LG	-	-
9c	Fen	5.18	LG	17.48	**LG**/G
9d	Mud-bottom fens and bogs	0.02	LG	0.06	LG
9e	Sedge marsh	0.06	LG	0.08	LG
11a	Fully cultivated land	0.01	VG	0.02	VG
11b	Cultivated pastures	0.04	VG	0.26	VG

Figure 4 shows the distribution and proportion of the vegetation classes in the two study areas and Table 1 summarizes the proportion of the vegetation types in the two study areas. The two study areas differed in vegetation class patch sizes and numbers. In Bratthøa the patches were in general more numerous and larger for the “Very Good” and “Good” as compared to Spekedalen, which in turn had more and larger “Less Good” patches (Fig. 4). Shannon Diversity Index (H’) (Morris et al., 2014) underlines the spatial heterogeneity differences between the two study areas, with Bratthøa being more heterogeneous than Spekedalen (Fig. 4), The difference in pasture quality is reflected in the mean lamb autumn live weights (1993 to 2013) of 47 kg in rich Bratthøa as compared to 40 kg in poor Spekedalen (Fig. 4) (Steinheim et al., unpublished data).

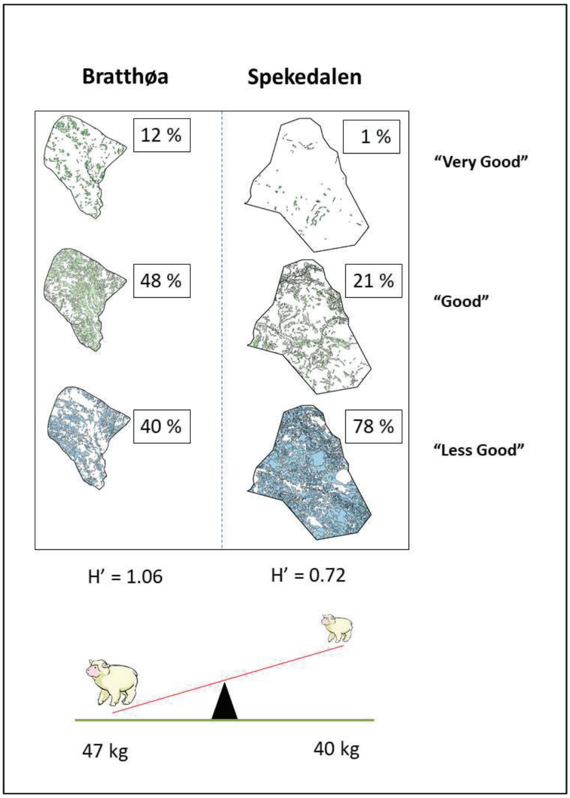


Figure 4. Spatial distribution of patches of vegetation classes for sheep grazing in Bratthøa and Spekedalen (Rekdal, 2007, 2009). Shannon Diversity Index (H') denotes the vegetation heterogeneity of the two study areas, based on the number of patches of the three vegetation classes in relation to the total number of patches. The mean autumn lamb live weights (Steinheim et al. unpublished data) are given in the bottom of the figure.

4.2. Study animals

The NWS, a relatively new composite breed, is prolific and with heavy lambs and adults (adult ewes often > 90 kg (Drabløs, 1997)), and is by far the most used breed in Norway. The SP is a short-tailed breed with many of the old Nordic breeds' characteristics; it is smaller (60 – 70kg (Drabløs, 1997; Trodahl, 1989)) than the NWS but with similar litter size. The SP is agile and more gregarious than the NWS. NWS have a higher digestive capacity, relative to body size, as compared to SP (Steinheim et al., 2003) and spend less of their foraging time browsing on trees, bushes and heather (Steinheim et al., 2005). According to NGS (http://www.ngs.no) the NWS and the SP constitute approximately 80% and 13%, respectively, of the Norwegian sheep population registered in the Norwegian sheep recording system (for description of database: Eikje et al. (2008)).

The free-range summer outfield grazing started on 23rd of June and lasted to 2nd of September in both 2013 and 2014. Fifty-one lactating ewes, with GPS collars, of SP and NWS of known age and with two lambs at foot, were released into the two study areas (Table 2). The study animals were recruited from six sheep farms that had used the study areas for summer grazing several years previous to the study.

Table 2. Number of GPS collared NWS and SP released in Bratthøa and Spekedalen in 2013 and 2014.

	Breed	**2013**	**2014**
Spekedalen	**NWS**	**7**	**6**
	SP	**7**	**3**
Bratthøa	**NWS**	**9**	**6**
	SP	**7**	**6**

4.3. Data collection

4.3.1. GPS collars

Ewes were fitted with Followit Tellus GPS-collars that registered positions every 60 min. Some positions were removed from the dataset due to inaccuracy: I set a DOP (dilution of precision) criteria for data inclusion to ≤ 2.0, which is considered “good quality data” (Parkinson et al., 1996). GPS-fixes from days around the release and capture were removed, as were unsuccessful GPS-fixes (time-out after 90 sec acquisition time). One collar failed during 2013 and six failed during 2013; all data from these seven animals were excluded. The estimated error rate of the GPS collars is +/- 20m.

Usable GPS-positions accounted to 73.7 % in 2013 (60701 of 82396) and 95.4 % in 2014 (70965 of 74400). The data was divided into year (2013 or 2014), area (Spekedalen or Bratthøa) and breed (SP or NWS) for further analyses. In 2013, several of the study animals in Spekedalen were collected prior to general sheep gathering in September, and kept temporarily on semi-natural pastures; to secure comparative data the summer grazing season was reduced to 60 days for both 2013 and 2014 (23th June – 23th August) in both study areas.

4.3.2. Activity classes

The GPS collars recorded collar movements in the horizontal (x) and vertical (y) plane in the time the GPS used to get a fix from at least 3 satellites (Time-to-fix: TTF). For each location, activity was calculated as $ACTSUM = \left(\frac{Act\_x}{TTF} + \frac{Act\_y}{TTF}\right)$ based on collar movements, where act_y and act_x is number of times the activity sensor is triggered during the TTF. Based on calibration tests (Jørgensen unpublished results) animals were defined as inactive at the location if ACTSUM < 0.26 and active if ACTSUM was ≥ 0.26 (Fig. 5). All locations, regardless of activity level, were included in the area use analyses (papers I and II), whereas only locations where animals were active were included in the habitat use and selection analyses (paper III).

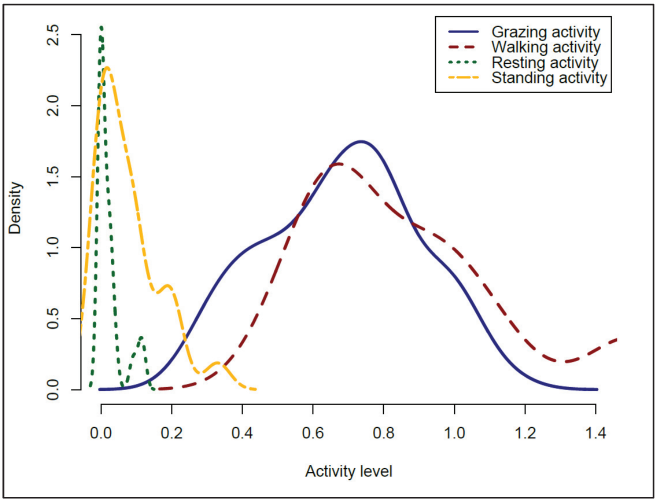


Figure 5. Activity levels from calibration tests for four behavioral types: Grazing, Walking, Resting and Standing (Jørgensen et al. unpublished).

4.4. Area utilization modelling

4.4.1. Dynamic Brownian Bridge Movement Model

The dynamic Brownian bridge movement model method (dBBMM) was used to calculate the utilization distribution (UD) area, following the guidelines in the Move package, incorporating the temporal characteristics of the movement paths (Kranstauber et al., 2012; Kranstauber and Smolla; 2015). A window size of 24 locations (1 days), a margin of 3 locations, location error of 20 meters, raster size of 20x20 meters, extension of 0.25 and a 60-min time step were used when calculating the dBBMM for each animal (papers I and II).

Prior to the calculation of the UD for temporal variation comparisons, the grazing season was divided into intervals of 5, 10, 15, 20, 30 and 60 days. For the spatiotemporal variation analyses a total of 28,576 UDs were calculated by year, area, breed, UD sizes, interval and period. Each UD was a summation the number of raster cells for each spatial scale (50% and 95%) and temporal scale (Interval: 5, 10, 15, 20, 25, 30 and 60 days) (Kranstauber et al., 2012, 2011).

The 5 days minimum for the temporal scales was based on a mean variogram function from the ctmm R package (Fleming and Calabrese, 2016). The mean population variogram levelled out at approximately 5 days, which can thus be considered as the lower temporal limit of where the data are not auto-correlated.

4.5. Habitat use and selection

Following Byrne et al. (2014) I used the moveud R package (Collier, 2016) to estimate the 20, 50 and 95% UD for each time-step between time-stamped relocation for each sheep. Each time-step was indexed by the time of the first location in each pair of locations. I extracted the compound 20, 50 and 95% contours of the dBBMM UDs for the two coarsest temporal scales (seasonal and 5 days' intervals), for each animal. The dBBMM UD and time-step compound contours were intersected with digital vegetation maps covering both study areas (QGIS Development Team, 2016), and vegetation type coverage within the individual contour were extracted and transformed into vegetation classes (Table 1).

Prior to calculations, I excluded time-steps where animals had been inactive. Time-steps with extreme movement variances (DBMvar > 10000), indicating unrealistic large time-step UD size (> ≈ 5 km^2 95% UD), were also omitted; these accounted for some 5% of the time-steps. I aggregated hourly time-steps to a mean time-step per day.

For each individual sheep, I calculated the mean proportional use of each vegetation class on the seasonal, 5 days' intervals and hourly temporal scales at the three spatial scales (20, 50 and 95% UDs).

Habitat selection was calculated using the Manly-Chesson standardized Habitat Selection Index (Manly et al., 1972; Chesson, 1978), which quantifies the relative proportional use of each vegetation classes relative to its proportional availability. I define the proportional use of each vegetation class within 95% spatial scale, on all temporal scales, as the vegetation class type available for a sheep, and the mean proportional use of each vegetation class within 20% spatial scale as used.

Only cases where all vegetation classes were at the 95% level were included in the analyses of habitat selection. The index formula is as follows:

$$\alpha_i = \frac{{}^{r_i}/_{p_i}}{\sum_{i=1}^{m} {}^{r_i}/_{p_i}}$$

where $\mathrm{r_i}$ is the proportional use of vegetation class i, p_i is the proportional available vegetation class i, and m in the number of vegetation classes. I thus obtained standardized selection ratios by scaling selection ratios between 0 and 1 for each vegetation class. A ratio of 0 would indicate total avoidance, a ratio of 1 total preference and a ratio of 1/3 (1/m, here m = 3) would indicate neutral selection.

4.6. Statistical analyses

To analyze effects on UD (papers I and II) and effect of vegetation class on vegetation use and selection (paper III), I used a general linear mixed models (employing the SAS University Edition 3.4 Inc. 2015) with restricted maximum likelihood estimates and asymptotic standard errors. The Satterthwaite option was used to achieve correct degrees of freedom. I used a 5% significant level in paper I and III, and a 10% level in paper II.

5. BRIEF SUMMARY OF PAPERS I-III

5.1. Paper I

Area use of two sheep breeds in contrasting summer alpine grazing environments in southern Norway

The objective of this study was to test if sheep on low-quality pasture (Spekedalen) utilize a larger area compared to sheep on good quality pasture (Bratthøa, called Vingelen in paper I) during a grazing season, and if Spælsau (SP) utilizes larger areas compared to Norwegian White Sheep (NWS) on summer alpine grazing environments in southern Norway. I also set out to investigate whether differences between the breeds in area use vary between different pasture qualities, that is, if there was a genotype by environment interaction effect on area use.

Main results:

- Type 3 F tests of fixed effects showed no significance in the main effects with differences between areas ($P = 0.28$) and between breeds ($P = 0.22$).
- In Spekedalen, the estimated UD was non-significantly larger than in Bratthøa (2.32 km^2, $P = 0.51$).
- NWS used a non-significant smaller estimated UD area compared to SP (-3.31 km^2, $P = 0.31$).
- No area* breed interaction effect ($P = 0.89$) was found.

Conclusion:

I found no support for the predictions that sheep on low-quality summer pasture utilize larger area compared to sheep on good-quality pasture, although the two breeds do use an estimated larger area in Spekedalen compared to Bratthøa. Albeit not significant, SP showed a tendency to utilize an estimated larger mean area as compared to NWS. No breed*pasture interactions was found. I appreciate that there is a large individual variation in our study.

5.2. Paper II

Does scale matter? Variation in area use across spatiotemporal scales of two sheep breeds in two contrasting alpine environments

The objective of this study was to explore how temporal scales affects sheep area use on 50% UD and 95% UD spatial scales in poor Spekedalen compared to in rich Bratthøa, and how temporal scales affects breed area use on 50% UD and 95% UD spatial scales in the two study areas. I also set out to investigate, if there is a genotype by environment interaction effect on area use across spatiotemporal scales.

Main results:

- UD areas on both spatial scales showed an increase with coarser temporal scales, with considerable variation within each spatial scale.
- In general, sheep used larger areas in Spekedalen compared to Bratthøa, at all temporal and both spatial scales.
- Type 3 F-tests of fixed effects for the 50% UD showed significant differences between the study areas for all temporal scales, while differences for the 95% UD were found for all, but the 60 days' temporal scale.
- In general SP used larger areas compared to NWS, on all temporal and at both spatial scales.

- Significant breed differences was found for all for the 50% and 95% UD, except at the 5 days intervals temporal scale.
- The area by breed interaction term was not significant on any spatial or temporal scale.

Conclusion:

When comparing area use between contrasting environments and breeds, scales may matter. I notice that the effect of breed and environment on sheep area use is stronger at the 50% UDs as compared to the 95% UDs. This is in line with general scale theory. I found it counterintuitive, that the heavier NWS having higher metabolic requirements, had smaller 95% UDs compared to SP, but explained it by differences in flocking behavior and forage preferences between breeds. To understand the ecological processes of sheep area use and on which spatiotemporal scales they are working is imperative. Therefore, such analyses should be undertaken in a multi-scale framework.

5.3. Paper III

Scale matters - Habitat use and selection by two sheep breeds in two contrasting alpine environments

My objective was to investigate sheep summer foraging habitat use and selection, and to explore potential breed differences in different environments at different spatiotemporal scales. I set out to infer foraging habitat selection using a resource selection function approach.

Main results:

- Habitat use was affected by vegetation class and was environment specific, at all temporal and spatial scales
- No breed specific effects were found.
- In Spekedalen, at all temporal scales, the use of “Less Good” vegetation decreased and “Very Good” increased with finer spatial scales, while the use of “Good” was fairly constant.
- In Bratthøa, at all temporal scales, the use of “Good” dominated at the coarsest spatial scale, whereas the use of “Very Good” increased and almost equalled the use of “Less Good”, at the two finest spatial scales.
- Habitat selection was affected by vegetation class at all temporal scales, but only by environment at the two finest temporal scales.

- In Spekedalen, both breeds selected for “Very Good”, with increasing intensity with finer temporal scales, while “Good” and “Less Good” were in general selected against.
- In Bratthøa, the selection for “Very Good” decreased towards neutral and the selection against “Less Good” approached neutral with finer temporal scales, while “Good” was selected weakly against at the two finest scales.

Conclusion:

Vegetation class within study area, study area, and spatial level affected habitat use at all temporal scales. In poor Spekedalen at the 95% spatial scale and at all temporal scales, both breeds seem to make the best of a bad job. However, breeds are able to find and use the sparsely distributed “Very Good” patches at finer spatial scales, resulting in a clear selection for “Very Good” at the expense of selection for “Less Good” and “Good”, in spite of the two latter being used the most. Indeed, sheep showed a clear plastic foraging response to Spekedalen’s spatial distribution of vegetation classes: few and small “Very Good” patches in a matrix dominated by “Less Good”. These high quality patches is probably more important for nutrient acquisition than indicated by their use. In Bratthøa both breeds respond to the more numerous, larger and more spread out patches of “Good” and “Very Good”, typical for a rich and diverse resource base. The ewes do not have to travel far to find good forage. Thus, even if breeds in Bratthøa do not select for "Good" and "Very Good" as strongly at the two finest temporal scales, as in Spekedalen, the two vegetation classes are used the most, and are a stable part of their diet.

6. GENERAL DISCUSSION

This study was conducted to elucidate how spatiotemporal scales affect pasture utilization of sheep of two breeds in two contrasting environments. Previous studies have showed how spatial and temporal scales may affect the space use of e.g. moose (van Beest et al., 2011) and roe deer (Mancinelli et al., 2015). To my knowledge, no studies have analyzed if sheep breeds respond differently to their environment across spatiotemporal scales.

6.1. Scale dependent area use

Animal by environment interaction creates space use patterns at different spatiotemporal scales (Morales et al., 2010). The last decades an array of new methods and techniques for estimation of UD at different spatiotemporal scales have been developed (Clapp and Beck, 2015; Tomkiewicz et al., 2010). The hourly sampling combined with the dBBMM enabled me to estimate UD and to assess patterns of area use of sheep of the two breeds in the two contrasting environments at two spatial and across multiple temporal scales during the summer grazing season.

Home range is a well-established concept in ecology. It is the key area where an animal performs most of its activities, e.g. foraging, resting and reproducing (Powell and Mitchell, 2012). An estimate of an animal's area 95% UD is often assumed to represent its realized "home range" (Kie et al., 2010). On this coarsest temporal and spatial scale (seasonal 95% UD) I found weak support for the predictions that sheep in poor Spekedalen utilize larger area as compared to sheep in rich Bratthøa. The number of sheep released in Bratthøa is closer to the areas' grazing capacity as compared to Spekedalen (Rekdal, 2007, 2009) and could counter such an effect. The lack of 95% UD differences between the two environments could therefore indicate that at the seasonal scale the density effect first sets in, when the resources are starting to be depleted late in the season in Bratthøa. Indeed, sheep used larger areas at the 95% UD scale in the poor Spekedalen environment, as compared to the rich Bratthøa, across all finer temporal scales. At the finer 50% UD scale sheep utilized larger areas in the poor as compared to the rich environment, at all temporal scales. These findings are in line with the general ideal free distribution theory (Fretwell and Lucas, 1970) which predict that herbivores' UD sizes are larger in poor as compared to rich foraging quality environments (e.g. Tufto et al. (1996) ;Saïd and Servanty (2005); van Beest et al. (2011)). The stronger effects found at the finer spatial scale (50% UD) as compare to the 95% UD comply with Senft et al. (1987) argument that the relative importance of plant-herbivore interactions decline toward larger spatial scales. Actually, the 50% UD was about 1/10 of the 95% UD across temporal scale (Fig. 2 in paper II). At both spatial scales, the UD increased with temporal scales and seemed to approach an asymptotic level at the 60 days temporal scale. Hence, the 60 days temporal scale seems a reliable proxy of their seasonal "home range" (95% UD) and "core area" (50% UD), estimated to 1.6 and 1.0 km^2 in Spekedalen and 13.9 and 10.2 km^2 in Bratthøa, respectively, but with big individual variation. This implies a high degree of overlap in area use. These are to my knowledge the first recorded estimates of sheep area use in Norwegian alpine environments.

SP had larger 50% and 95% UD than NWS at all temporal scales, but the finest (Fig. 3 in paper II). In paper I the estimated 95% UD at the seasonal temporal scale showed no breed specific difference, although a trend of SP having a larger UD was reported. This divergence is due to slightly different modelling approaches between the two papers. Year was included in the model in paper II, as it is well known that home ranges are handed down from mother to female offspring from generation to generation (Broad et al., 2006). I appreciate that the large individual variation may have overshadowed the breed effects at the finest scale. The SP normally forms larger groups compared to NWS, and is more selective in diet choice than the “bulk feeder” NWS (Steinheim et al., 2005). I thus expect SP to be more exposed to within-breed competition, and that it may deplete the forage resources quicker, at least at coarser temporal scales, both of which should lead to use of larger areas. This could conceivably be counteracted by the NWS being around 20% heavier than SP (Drabløs, 1997) and thus may be required to use larger grazing areas in order to meet higher energy demands. Unfortunately, I did not have autumn weights for all of the ewes and thus used ewe age as a proxy of body mass (Näsholm and Danell, 1990) in preliminary models. I did not find any effects of age on area use; hence, I excluded age in the final models. Body size differences between the two breeds seem therefore not to play an important role compared to flocking behavior in terms of effect on area use. This is in line with what Van Beest et al. (2011) stated, that only interspecific and sex intraspecific studies could report that body size is a major factor determining home range size. Individual variation is in itself important when area use of animals is to be described and understood. I was able to eliminate one of the intrinsic factor that could cause variation, namely the reproductive status effect, as all ewes had the same lactation cost of having two lambs at heel. Indeed, it is more costly to raise offspring, compared to an e.g. 10 kg body weight increase (SP versus NWS) would have. Thus, differences in numbers of offspring would have larger effects on UD size, than body size differences.

Nielsen et al. (2013) pointed out that SP is less sensitive to climate variations in general. I therefore expected SP to be more plastic in their UD response to the two very different environments, as compared to NWS. However, no environment by breed interactions were found at any spatiotemporal scales. This result is not necessarily valid in all environments, as I have no information regarding the response curves in between these two extreme environments. Additional information regarding environments between these two extreme environments would be required to determine the actual shape of the response curves.

6.2. Scale dependent habitat use and selection

Linking UDs with vegetation maps, I found, as expected an effect of environment and abundance of vegetation classes on habitat use at all temporal and spatial scales. The use of “Very Good” was considerably higher in Bratthøa as compared to Spekedalen, whereas “Less Good” was used to a much higher degree in Spekedalen as compared to Bratthøa. Indeed, variation in foraging pattern is often reflected in variation in vital rates (Mobaek et al., 2012), as here seen in the higher live lamb autumn weights in Bratthøa as compared to Spekedalen. It is noteworthy that spatial level within each temporal scale affected habitat use. This suggests that the resources are not evenly distributed within the two study areas and that the sheep habitat use is not random at any spatial scales. This is in accordance with what e.g. Gross et al. (1995) found, that movement rules based on random walks are clearly inappropriate for many herbivores. Habitat selection, in the two study areas, seemed to be affected by the available vegetation class’s at all three temporal scales, whereas an effect of study area was noted at the two finest temporal scales. While the vegetation class specific selection in Bratthøa approached neutral selection, the selection in Spekedalen was getting stronger with finer temporal scales. Breed did not affect habitat use at any temporal nor spatial scales and breed at any temporal scale did not affect habitat selection. Nor did breed by environment effect habitat use or habitat selection at any spatiotemporal scales.

At the seasonal temporal scale, in rich Bratthøa, both breeds selected strongly for the "Very Good" and strongly against the "Less Good" (Fig. 4 in paper III). Indeed, they were clearly able to express their plastic foraging response by utilizing the "Very Good" patches. This was amplified with finer spatial scales. The use of "Good" at all spatial scales accounted for ≈50% indicating that forage from this vegetation class makes up the staple part of the summer diet in Bratthøa. At the hourly temporal scale, however, the approximately neutral selection for all vegetation classes could be explained by the available patches of "Good" and "Very Good" being numerous, large and evenly distributed (Fig. 4) and hence easily reachable. The ewes do not have to travel that far to find good forage patches and can utilize these for a longer period before moving on to the next patch (see e.g. Searle et al. (2005)). This is supported by my unpublished results showing that sheep travelled shorter mean daily distances in Bratthøa as compared to Spekedalen (≈ 5.5 km vs ≈ 6.6 km). It is possible that in Bratthøa the relative high availability at 95% UD scale of "Very Good" and high use at 20% UD means that the ewes are able to easily meet their energy requirements, at this fine scale, without showing a strong selection for high quality patches.

In poor Spekedalen, at the seasonal temporal scale, both breeds used the vegetation classes according to the overall availability (2% vs 1%, 25% vs 21% and 73% vs 78% respectively for "Very Good", "Good" and "Less Good"), at the 95% spatial scale. However, the dominating use of “Less Good” declined and the use of “Good” and “Very Good” increased, with finer spatial scales (Fig. 3 in paper III). Thus, what appears to be making the best of a bad job by the sheep at the coarsest spatial scale can mask the use at finer spatial scales in accordance with Kotliar et al. (1990) predictions. This resulted in clear selection for the less abundant “Very Good” patches, and clear selection against the abundant “Less Good” patches.

These findings are, to some degree, in accordance with the general theory regarding scale dependent habitat selection (Johnson, 1980) and plant-herbivore interactions (Senft et al., 1987). In poor Spekedalen, the habitat selection for the scarce “Very Good” patches is indeed getting stronger with finer temporal scale, whereas the strongest habitat selection for “Very Good” in rich Bratthøa is noticed at the coarsest temporal scale, with a decline towards neutral with finer temporal scales. Although the abundance of the vegetation classes is driving the habitat use, the animals are able to find and utilize “Very Good” patches at the finest spatial scale, especially in Spekedalen. The strong selection for “Very Good” at the landscape and seasonal scale, in Bratthøa, may be attributed to a more heterogeneous and smaller patch size distribution (Fig. 2 in paper III).

Interestingly, the overall proportion of “Very Good” in Bratthøa amounts to 12% (Fig. 2), whereas the estimated proportional use of this vegetation class at seasonal 95% UD spatial scale is about 24% (Fig. 3 in paper III), i.e. showing a clear selection for “Very Good” at the landscape scale in Bratthøa. The same pattern is seen in Spekedalen although the use amounted to 2% versus 1% availability (Fig. 2). Thus, in spite of the seasonal selection for the “Very Good” is similar between the two study areas (Fig. 4 in paper III), the underlying use of that class in each study area are very different (Fig. 3 in paper III). This explain why I did not find significant between area differences in habitat selection at the seasonal temporal scale (Table 2 in paper III). It seems that availability of the vegetation classes is driving the habitat use especially in Spekedalen, at these highest spatiotemporal scales, although the selection for “Very Good” also at the landscape scale in Spekedalen would be positive. The strong selection for “Very Good” at the landscape and seasonal scale, in Bratthøa, may be attributed to a more heterogeneous and smaller patch size distribution (Fig. 2 in paper III).

In Spekedalen at the two finest temporal scales, the vegetation class use patterns resembled what I observed at the coarsest temporal scales, with an increasingly higher proportional use of “Very Good”. It appears that ewes in Spekedalen are more actively seeking out the “Very Good” quality class, at the hourly temporal scale, as compare to in Bratthøa. Still, the animals are using the more abundant “Good” and “Less Good” as their staple food resources.

In general, daily forage intake is considered a function of time spent grazing (Newman et al. 1995). Nevertheless, time spent foraging does not necessarily reflect a vegetation class’ importance for nutrient extraction and acquisition. Indeed, forage intake rate and quality is normally higher in vegetation type productivity, biomass quality (Van Soest, 1994). I therefore suggest that although the sheep in Spekedalen spend more than half of their time foraging in the “Less Good” vegetation class and their use of “Very Good” does not exceed 20% even at the finest scales; the energy extraction and acquisition from the two classes are close to each other.

Indeed, “Very Good” patches may act as magnets for the animals, especially in Spekedalen at fine scales, although these patches are smaller and more spread out as compared to in Bratthøa (Fig. 4), making them more costly, both time and energy wise, to exploit. Actually, some of the allocated time in Spekedalen may be connected to transportation legs between “Very Good” (and “Good”) patches in this “Less Good” dominated matrix. However, “Less Good” is dominated by dry lichens ridges and fens (Table 2) and is well suitable for cost efficient movements. Consequently, the time used in “Less Good” is most likely higher than the actual time foraging in this vegetation class, especially in Spekedalen.

White (1983) assumed the same energy costs for animals foraging selectively or not. I argue that energy expenditure for transportation between, as well as searching for patches, and thus the energy requirement, will be higher in Spekedalen as compared to Bratthøa. Thus the higher lamb live autumn weights, in Bratthøa as compared to Spekedalen (47kg versus 40kg, Steinheim et al. unpublished), can partly be explained by the cost of being selective.

Small “Very Good” patches in connection with run-offs and depressions within the “Less Good” and “Good” vegetation classes are of importance for sheep in Spekedalen (Rekdal pers. comm.). However, the current resolution of the vegetation map (scale 1:10000) is not sufficient to depict these features (Rekdal, 2007). This will lead to an underestimation of the use of high quality small patches and points to the obvious fact that the resource resolution will influence the interpretation of the results (Mayor et al., 2009). I could have analyzed habitat use and selection for all the 24 vegetation types. However, these small patches accounts for less than half a percentage of the total area (Rekdal, pers. Comm.), some of them have a minor appearance and not all are found in both study areas. I have therefore chosen Rekdal’s three vegetation classes classification, as this is the only empirically based functional grazing classification system available.

6.3. Confounding extrinsic factors: density, salt blocks and predators

Sheep pasture utilization did vary between the two contrasting environments. I have attributed these differences to the pronounced contrast in pasture quality between Spekedalen and Bratthøa. However, confounded effects with other extrinsic factors have to be considered. Density, predator pressure as well as the use of salt blocks do vary between the two areas (Granås, pers. comm.) and such factors have been reported to influence foraging behaviour and habitat use in other systems (see e.g. Laundré et al., 2001; Ayotte et al., 2008; Mobæk et al., 2009).

Competition for food is regarded as the main driver for density dependent effects (Stewart et al., 2005). However, little information is available how density may affect habitat use and selection of sheep (but see Mobaek et al. (2009)). Sheep seem to tolerate rather high densities before density effects are seen, compared to many other medium bodied sized ruminants, e.g. reindeer (Colman et al., 2009), in line with the bite quality hypothesis (Murray and Illius, 2000).The total density in Bratthøa is about 13 times higher than in Spekedalen, ≈39 sheep per km^2 and ≈3 sheep per km^2 respectively. Rekdal (2007, 2009) estimated the grazing capacity to be four times higher in Bratthøa than in Spekedalen, i.e. ≈48 and ≈12 sheep per km^2 respectively, both above the total density seen, especially in Spekedalen. I therefore conclude that density effects play a minor role and will in any case be rather similar in the two areas.

Mineral resources are known to attract herbivores (McNaughton, 1988) and may influence their spatial distribution (Ayotte et al., 2008). Indeed, salt blocks are extensively used in range management in ecosystems with poor availability of essential nutrients (Van Soest, 1994). Also in Norway, salt blocks are supplied in great quantities and regarded an important management tool for the sheep farmers. In Bratthøa 11 salt blocks were distributed, whereas in Spekedalen only three were put out (Granås, pers. comm.). This means that the average walking distance for visiting a salt block is longer in Spekedalen as compared to Bratthøa. Further, a ewe, on average, visited a salt block every 15 days during the grazing season in Bratthøa, as compared to every 6 days in Spekedalen, indicating a lower forage content of some essential minerals in poor Spekedalen. Indeed, both the lower salt block density and the higher visiting rate in Spekedalen could contribute to the longer daily walking distance and larger UD in Spekedalen as compared to Bratthøa. I argue that pasture quality differences probably influence UD most pronounced at the 50% spatial scale as compared to the 95%. It remains to be seen, however, how salt blocks may influence spatiotemporal dependent area use and habitat use and selection in contrasting environments.

Laundré et al. (2010) propose that the spatial and temporal use of a landscape is fear driven. Indeed, the predation risk may influence how preys are utilizing their resources. The estimated losses of sheep to predators in Spekedalen in 2013 and 2014 amounted to approximately 10 percentage each year (Granås, pers. comm.), whereas in Bratthøa these losses were neglectable. Obviously, the predator pressure was highest in Spekedalen, but none of the GPS marked ewes were lost to predators during the two years of study. Further, based on the activity and movement patterns of the GPS ewes in Spekedalen, I have no indication that they were exposed to predators during the summer season. I therefore conclude that predators did not heavily influence the study animals' space and habitat use in Spekedalen and Bratthøa.

MAIN CONCLUSIONS

I found only weak support for the predictions that sheep in low quality environment (Spekedalen) utilize larger seasonal area compared to sheep on good quality habitat (Bratthøa). I accounted the weak support to a large individual variation that may have overshadowed the effects of intrinsic breed differences and extrinsic pasture quality differences. However, I found that sheep used larger areas at the 95% UD scale, at all but the 60-day temporal scale, in Spekedalen compared to Bratthøa. This is in line with general ideal free distribution theory that predict that herbivores' home range sizes are larger in poor than in rich foraging quality environments, and that it was, as expected, amplified at the 50% UD. SP utilize larger area than NWS at all but the 5-day intervals' temporal scale for both the 50% UDs and 95% spatial. This is counterintuitive, but flocking behavior differences may be the main reason. I conclude that when comparing area use between contrasting environments and breeds, scale may matter. I notice that the effect of breed and environment on sheep area use is stronger at the 50% UD as compared to the 95% UD scale. I also notice that breed by environment did not affect habitat use or habitat selection at any spatiotemporal scales.

Vegetation class within study area, study area, and spatial level affected habitat use at all temporal scales. In poor Spekedalen at the 95% spatial scale and at the two coarsest temporal scales, both breeds seem to make the best of a bad job. However, both breeds are able to find and use the sparsely distributed “Very Good” patches at finer spatial scales, resulting in a clear selection (and clearest at finest temporal scale) for “Very Good” at the expense of selection for “Less Good” and “Good”, in spite of the two latter being clearly used the most. Indeed, the sheep showed a strong plastic foraging response to spatial distribution of vegetation classes in Spekedalen: few and small “Very Good” patches in a matrix dominated by “Less Good”. In Bratthøa both breeds respond to the more numerous, larger and more spread out patches of “Good” and “Very Good”, typical for a rich and diverse resource base, by using and selecting them at the highest temporal scale. Thus, even if breeds in Bratthøa do not select for (and probably don’t need to select for) “Good” and “Very Good” as strongly at the two finest temporal scales, as in Spekedalen, the two vegetation classes are used the most, and seem to be a stable part of their diet. However, “Very Good” may be more important for the sheep, in terms of net energy acquisition, than reflected in their actual use.

Clearly, the abundance of vegetation classes suitable for sheep grazing are driving the habitat class use across spatiotemporal scales in Spekedalen. However, whereas the selection for vegetation classes approaches neutral selection across spatial scales in Bratthøa, a clear diversification in favor of selection for “Very Good” in Spekedalen is observed.

MANAGEMENT IMPLICATIONS

Increased competition with other area-extensive businesses challenges the sheep industry in the north Atlantic region (Ross et al., 2016). My results are important for area use administrators and planners at different management levels, as well as for farmers and commons that need to highlight rangeland area demands. The estimated area use across temporal scales approached an asymptotic maximum at the coarsest temporal scale and could thus be used as a good estimate of how much space a sheep would use during a grazing season. Hence, when determining total need for grazing area one have to consider the 95% UD at the seasonal scale, as a minimum. One has to keep in mind, however, that there is large individual variation within breeds.

When establishing management plans breed and environment differences should be taken into account. However, the foraging quality and the heterogeneity within grazing rangelands (e.g. rich Bratthøa and poor Spekedalen) seems to affect sheep's area use and habitat use and selection more than breed differences. My results therefore suggest that breeds may not necessarily play an important role in the range management assessment plans when establishing the density and type of breed to be released onto outer fields. At least not in the Norwegian Alpine rangelands.

Overall, when analyzing and discussing sheep area use, habitat use and selection is it imperative to determine the spatiotemporal scale context do avoid mismatch between research result and management implementations. These findings are important for management of limited grazing resources, with fewer and larger flocks being a trend in Norwegian sheep farming. Thus, information of distribution of vegetation classes within grazing rangelands along with information regarding area use and habitat use and selection, must be taken into account when establishing management plans.

The results cannot necessarily be transferred directly to new pastures, but is an important contribution to illuminate the sheep industry's interests in land management issues, which are becoming increasingly important in the years ahead.

REFERENCES

Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional Analysis of Habitat Use From Animal Radio-Tracking Data. Ecology 74, 1313–1325. https://doi.org/10.2307/1940062

Alexander, R.W., Millington, A.C., Royal Geographical Society (with The Institute of British Geographers). Biogeography Research Group., 2000. Vegetation mapping : from patch to planet. Wiley.

Allard, V., Soussana, J.F., Falcimagne, R., Berbigier, P., Bonnefond, J.M., Ceschia, E., D’hour, P., Hénault, C., Laville, P., Martin, C., Pinarès-Patino, C., 2007. The role of grazing management for the net biome productivity and greenhouse gas budget (CO2, N2O and CH4) of semi-natural grassland. Agric. Ecosyst. Environ. 121, 47–58. https://doi.org/10.1016/j.agee.2006.12.004

Arthur, S.M., Manly, B.F.J., McDonald, L.L., Garner, G.W., 1996. Assessing Habitat Selection when Availability Changes. Ecology 77, 215–227. https://doi.org/10.2307/2265671

Ayotte, J.B., Parker, K.L., Gillingham, M.P., 2008. Use of Natural Licks by Four Species of Ungulates in Northern British Columbia. J. Mammal. 89, 1041–1050. https://doi.org/10.1644/07-MAMM-A-345.1

Bartlam-Brooks, H.L.A., Bonyongo, M.C., Harris, S., 2013. How landscape scale changes affect ecological processes in conservation areas: External factors influence land use by zebra (Equus burchelli) in the Okavango Delta. Ecol. Evol. 3, 2795–2805. https://doi.org/10.1002/ece3.676

Bazely, D.R., 1988. Foraging behaviour of sheep (Ovis aries L.) grazing on swards of perennial ryegrass (Lolium perenne L.). Dr Leonard Pol. thesis Digit.

Belovsky, G.E., Schmitz, O.J., 1994. Plant Defenses and Optimal Foraging by Mammalian Herbivores. J. Mammal. 75, 816–832. https://doi.org/10.2307/1382464

Bjørneraas, K., Herfindal, I., Solberg, E.J., Sæther, B.-E.E., van Moorter, B., Rolandsen, C.M., 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. Oecologia 168, 231–243. https://doi.org/10.1007/s00442-011-2072-3

Bjørneraas, K., Solberg, E.J., Herfindal, I., Moorter, B. Van, Rolandsen, C.M., Tremblay, J.-P., Skarpe, C., Sæther, B.-E., Eriksen, R., Astrup, R., 2011. Moose Alces alces habitat use at multiple temporal scales in a human-altered landscape. Wildlife Biol. 17, 44–54. https://doi.org/10.2981/10-073

Bonan, G.B., 2008. Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. Science (80-.). 320.

Broad, K.D., Curley, J.P., Keverne, E.B., 2006. Mother-infant bonding and the evolution of mammalian social relationships. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 361, 2199–214. https://doi.org/10.1098/rstb.2006.1940

Bryn, A., Dramstad, W., Fjellstad, W., 2010. Viten fra Skog og landskap – 1/10 Mapping and Monitoring of nordic Vegetation and LandScapeS conference proceedings.

Buddle, B.M., Denis, M., Attwood, G.T., Altermann, E., Janssen, P.H., Ronimus, R.S., Pinares-Patiño, C.S., Muetzel, S., Neil Wedlock, D., 2011. Strategies to reduce methane emissions from farmed ruminants grazing on pasture. Vet. J. 188, 11–17. https://doi.org/10.1016/j.tvjl.2010.02.019

Byrne, M.E., Clint McCoy, J., Hinton, J.W., Chamberlain, M.J., Collier, B.A., 2014. Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. J. Anim. Ecol. 83, 1234–1243. https://doi.org/10.1111/1365-2656.12205

Börger, L., Dalziel, B.D., Fryxell, J.M., 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecol. Lett. 11, 637–650. https://doi.org/10.1111/j.1461-0248.2008.01182.x

Börger, L., Franconi, N., Ferretti, F., Meschi, F., De Michele, G., Gantz, A., Coulson, T., 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. Am. Nat. 168, 471–485. https://doi.org/10.1086/507883

Cagnacci, F., Boitani, L., Powell, R.A., Boyce, M.S., 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 365, 2157–62. https://doi.org/10.1098/rstb.2010.0107

Carbone, C., Cowlishaw, G., Isaac, N.J.B., Rowcliffe, J.M., 2005. How far do animals go? Determinants of day range in mammals. Am. Nat. 165, 290–297. https://doi.org/10.1086/426790

Carson, A., Elliott, M., Groom, J., Winter, A., Bowles, D., 2009. Geographical isolation of native sheep breeds in the UK—Evidence of endemism as a risk factor to genetic resources. Livest. Sci. 123, 288–299. https://doi.org/10.1016/j.livsci.2008.11.026

Charnov, E.L., 1976. Optimal Foraging: Attack Strategy of a Mantid. Am. Nat. 110, 141. https://doi.org/10.1086/283054

Chesson, J., 1978. Mesuring preference in selective predation. Ecology 59, 211–215. https://doi.org/10.2307/1936364

Clapp, J.G., Beck, J.L., 2015. Evaluating distributional shifts in home range estimates. Ecol. Evol. 5, 3869–3878. https://doi.org/10.1002/ece3.1655

Collier, B., 2016. moveud: moveud: Dynamic brownian bridge movement model individual time-step utilization distributions (R 3.2.5 Build).

Colman, J.E., Mysterud, A., Jørgensen, N.H., Moe, S.R., 2009. Active land use improves reindeer pastures: Evidence from a patch choice experiment. J. Zool. 279, 358–363. https://doi.org/10.1111/j.1469-7998.2009.00626.x

Dall, S., Giraldeau, L., Olsson, O., McNamara, J., Stephens, D., 2005. Information and its use by animals in evolutionary ecology. Trends Ecol. Evol. 20, 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Dayton, P.K., Tegner, M.J., 1984. The importance of scale in community ecology: A kelp forest example with terrestrial analogs, in: A New Ecology, Novel Approaches to Interactive Systems. pp. 457–481.

de Wit, H.A., Bryn, A., Hofgaard, A., Karstensen, J., Kvalevåg, M.M., Peters, G.P., 2014. Climate warming feedback from mountain birch forest expansion: reduced albedo dominates carbon uptake. Glob. Chang. Biol. 20, 2344–2355. https://doi.org/10.1111/gcb.12483

Drabløs, D., 1997. Soga om smalen: jubileumsskrift Norsk sau-og geitalslag 1947±1997 (The tale of the sheep: festschrift for the Norwegian sheep and goat breeders' association 1947 -1997). Norwegian Sheep and Goat Breeders., Oslo.

Dussault, C., Quellet, J.P., Courtois, R., Huot, J., Breton, L., Jolicoeur, H., 2005. Linking moose habitat selection to limiting factors. Ecography (Cop.). 28, 619–628. https://doi.org/10.1111/j.2005.0906-7590.04263.x

Eikje, L.S., Ådnøy, T., Klemetsdal, G., 2008. The Norwegian sheep breeding scheme: description, genetic and phenotypic change. animal 2, 167–176. https://doi.org/10.1017/S1751731107001176

Ekern, A., 1991. A new system of energy evaluation of food for ruminants. Nor. Landbruksforskning 5, 273–277.

Fagan, W.F., Lewis, M.A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U.E., Tang, W., Papastamatiou, Y.P., Forester, J., Mueller, T., 2013. Spatial memory and animal movement. Ecol. Lett. 16, 1316–1329. https://doi.org/10.1111/ele.12165

Fahrig, L., 1992. Relative importance of spatial and temporal scales in a patchy environment. Theor. Popul. Biol. 41, 300–314. https://doi.org/10.1016/0040-5809(92)90031-N

Fisher, J.T., Anholt, B., Volpe, J.P., 2011. Body mass explains characteristic scales of habitat selection in terrestrial mammals. Ecol. Evol. 1, 517–528. https://doi.org/10.1002/ece3.45

Fleming, C.H., Calabrese, J.M., 2016. ctmm: Continuous-Time Movement Modeling.

Focardi, S., Marcellini, P., 1995. A mathematical framework for optimal foraging of herbivores. J. Math. Biol. 33, 365–387. https://doi.org/10.1007/BF00176378

Focardi, S., Marcellini, P., Montanaro, P., 1996. Do Ungulates Exhibit a Food Density Threshold? A Field Study of Optimal Foraging and Movement Patterns. J. Anim. Ecol. 65, 606. https://doi.org/10.2307/5740

Fortin, D., Fryxell, J.M., O'Brodovich, L., Frandsen, D., 2003. Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. Oecologia 134, 219–27. https://doi.org/10.1007/s00442-002-1112-4

Fryxell, J.M., Hazell, M., Borger, L., Dalziel, B.D., Haydon, D.T., Morales, J.M., McIntosh, T., Rosatte, R.C., Börger, L., Dalziel, B.D., Haydon, D.T., Morales, J.M., McIntosh, T., Rosatte, R.C., 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proc Natl Acad Sci U S A 105, 19114–9. https://doi.org/10.1073/pnas.0801737105

Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., Van Moorter, B., 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 365, 2255–2265. https://doi.org/10.1098/rstb.2010.0085

González-Megías, A., María Gómez, J., Sánchez-Piñero, F., 2007. Diversity-habitat heterogeneity relationship at different spatial and temporal scales. Ecography (Cop.). 30, 31–41. https://doi.org/10.1111/j.2006.0906-7590.04867.x

Gross, J.E., Zank, C., Hobbs, N.T., Spalinger, D.E., 1995. Movement rules for herbivores in spatially heterogeneous environments: responses to small scale pattern. Landsc. Ecol. 10, 209–217. https://doi.org/10.1007/BF00129255

Hansen, I., Christiansen, F., Hansen, H.S., Braastad, B., Bakken, M., 2001. Variation in behavioural responses of ewes towards predator-related stimuli. Appl. Anim. Behav. Sci. 70, 227–237. https://doi.org/10.1016/S0168-1591(00)00155-6

Hjermann, D.Ø., 2000. Analyzing habitat selection in animals without well-defined home ranges. Ecology 81, 1462–1468. https://doi.org/10.1890/0012-9658(2000)081[1462:AHSIAW]2.0.CO;2

Horne, J.S., Garton, E.O., Krone, S.M., Lewis, J.S., 2007. Analyzing animal movements using Brownian bridges. Ecology 88, 2354–2363. https://doi.org/10.1890/06-0957.1

Illius, A., Fitzgibbon, C., 1994. Costs of vigilance in foraging ungulates. Anim. Behav. https://doi.org/10.1006/anbe.1994.1067

Illius, A.W., Clark, D.A., Hodgson, J., 1992. Discrimination and Patch Choice by Sheep Grazing Grass-Clover Swards. J. Anim. Ecol. 61, 183. https://doi.org/10.2307/5521

Iversen, M., Fauchald, P., Langeland, K., Ims, R.A., Yoccoz, N.G., Bråthen, K.A., 2014. Phenology and Cover of Plant Growth Forms Predict Herbivore Habitat Selection in a High Latitude Ecosystem. PLoS One 9, e100780. https://doi.org/10.1371/journal.pone.0100780

Johnson, D.H., 1980. The Comparison of Usage and Availabilty Measurements for Evaluating resource Preference. Ecology 61, 65–71. https://doi.org/10.2307/1937156

Killeen, J., Thurfjell, H., Ciuti, S., Paton, D., Musiani, M., Boyce, M.S., 2014. Habitat selection during ungulate dispersal and exploratory movement at broad and fine scale with implications for conservation management. Mov. Ecol. 2, 15. https://doi.org/10.1186/s40462-014-0015-4

Kotliar, N.B., Wiens, J.A., Wiens Kotliar, J.A., Wiens, N.B., Kotliar, N.B., Wiens, J.A., 1990. Multiple Scales of Patchiness and Patch Structure: A Hierarchical Framework for the Study of Heterogeneity Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Source: Oikos OIKOS 59, 253–260.

Kranstauber, B., Cameron, A., Weinzerl, R., Fountain, T., Tilak, S., Wikelski, M., Kays, R., 2011. The Movebank data model for animal tracking. Environ. Model. Softw. 26, 834–835. https://doi.org/10.1016/j.envsoft.2010.12.005

Kranstauber, B., Kays, R., LaPoint, S.D., Wikelski, M., Safi, K.,

2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. J. Anim. Ecol. 81, 738–746. https://doi.org/10.1111/j.1365-2656.2012.01955.x

Krausman, P., 1999. Some basic principles of habitat use. Grazing Behav. Livest. Wildl.

Langvatn, R., Hanley, T.A., 1993. Feeding-patch choice by red deer in relation to foraging efficiency - An experiment. Oecologia 95, 164–170. https://doi.org/10.1007/BF00323486

Laundré, J.W., Hernández, L., Ripple, W.J., 2010. The Landscape of Fear: Ecological Implications of Being Afraid. Open Ecol. J. 3, 1–7.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640. https://doi.org/10.1139/z90-092

Main, M.B., Coblentz, B.E., 1996. Sexual segregation in Rocky Mountain mule deer. J. Wildl. Manage. 60, 497–507. https://doi.org/10.2307/3802067

Mancinelli, S., Peters, W., Boitani, L., Hebblewhite, M., Cagnacci, F., 2015. Roe deer summer habitat selection at multiple spatio-temporal scales in an alpine environment. Hystrix 26. https://doi.org/10.4404/hystrix-26.2-11223

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource selection by animals: statistical design and analysis for field studies. Technology 221. https://doi.org/10.1007/0-306-48151-0

Manly, B.F.J., Miller, P., Cook, L.M., 1972. Analysis of a Selective Predation Experiment. Am. Nat. 106, 719–736. https://doi.org/10.1086/282808

Mayor, S.J., Schneider, D.C., Schaefer, J.A., Mahoney, S.P., 2009. Habitat selection at multiple scales. Écoscience 16, 238–247. https://doi.org/10.2980/16-2-3238

McLoughlin, P.D., Ferguson, S.H., 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. Ecoscience.Sainte-Foy 7, 123–130. https://doi.org/10.2307/42902482

McLoughlin, P.D., Gaillard, J.-M., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P., Delorme, D., Moorter, B. Van, Saïd, S., Klein, F., 2007. Lifetime reproductive success and composition of the home range in a large herbivore. Ecology 88, 3192–3201. https://doi.org/10.1890/06-1974.1

McNaughton, S.J., 1988. Mineral nutrition and spatial concentrations of African ungulates. Nature 334, 343–345. https://doi.org/10.1038/334343a0

Mobaek, R., Mysterud, A., Egil Loe, L., Holand, Ø., Austrheim, G., 2009. Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach. Oikos

118, 209–218. https://doi.org/10.1111/j.1600-0706.2008.16935.x

Mobaek, R., Mysterud, A., Loe, L.E., Holand, Ø., Austrheim, G., 2012. Experimental evidence of density dependent activity pattern of a large herbivore in an alpine ecosystem. Oikos 121, 1364–1369. https://doi.org/10.1111/j.1600-0706.2012.20286.x

Mobæk, A., Pedersen, S.P., 1977. Sølendalen – en registrering og bruk vurdering. Hovedoppg. ved Norges landbrukshøgskole.

Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R.A., Merrill, E.H., Haydon, D.T., 2010. Building the bridge between animal movement and population dynamics. Philos. Trans. R. Soc. B Biol. Sci. 365, 2289–2301. https://doi.org/10.1098/rstb.2010.0082

Morris, D.W., 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136, 1–13. https://doi.org/10.1007/s00442-003-1241-4

Morris, E.K., Caruso, T., ßois Buscot, F., Fischer, M., Hancock, C., Maier, T.S., Meiners, T., M€ Uller, C., Obermaier, E., Prati, D., Socher, S.A., Sonnemann, I., W€ Aschke, N., Wubet, T., Wurst, S., Rillig, M.C., Morris, C.E.K., 2014. Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. Ecol. Evol. 4, 3514–3524. https://doi.org/10.1002/ece3.1155

Mount, L.E., 1979. Adaptation to thermal environment. Man and his productive animals. Adapt. to Therm. Environ. Man his Product. Anim.

Murray, M.G., Illius, A.W., 2000. Vegetation modification and resource competition in grazing ungulates. Oikos 89, 501–508. https://doi.org/10.1034/j.1600-0706.2000.890309.x

Mysterud, A., Ims, R.A., 1998. Functional responses in habitat use: Availability influences relative use in trade-off situations. Ecology 79, 1435–1441. https://doi.org/10.1890/0012-9658(1998)079[1435:FRIHUA]2.0.CO;2

Mysterud, A., Iversen, C., Austrheim, G., 2007. Effects of density, season and weather on use of an altitudinal gradient by sheep. Appl. Anim. Behav. Sci. 108, 104–113. https://doi.org/10.1016/j.applanim.2006.10.017

Mysterud, A., Langvatn, R., Yoccoz, N.G., Stenseth, N.C., 2001. Plant phenology , migration and geographical variation in body weight of a large herbivore : the effect of a variable topography. J. Anim. Ecol. 70, 915–923. https://doi.org/10.1046/j.0021-8790.2001.00559.x

Nielsen, A., Steinheim, G., Mysterud, A., 2013. Do different sheep breeds show equal responses to climate fluctuations? Basic Appl. Ecol. 14, 137–145. https://doi.org/10.1016/j.baae.2012.12.005

Näsholm, A., Danell, Ö., 1990. Growth and Mature Weight of Swedish Finewool Landrace Ewes. Acta Agric. Scand. 40, 83–

92. https://doi.org/10.1080/00015129009438550

Ofstad, E.G., Herfindal, I., Solberg, E.J., Sæther, B.-E., 2016. Home ranges, habitat and body mass: simple correlates of home range size in ungulates. Proc. R. Soc. B Biol. Sci. 283, 20161234. https://doi.org/10.1098/rspb.2016.1234

Olivier, J.G.J., Bouwman, A.F., Berdowski, J.J.M., Veldt, C., Bloos, J.P.J., Visschedijk, A.J.H., van der Maas, C.W.M., Zandveld, P.Y.J., 1999. Sectoral emission inventories of greenhouse gases for 1990 on a per country basis as well as on 1°×1°. Environ. Sci. Policy 2, 241–263. https://doi.org/10.1016/S1462-9011(99)00027-1

Olson, R.S., Haley, P.B., Dyer, F.C., Adami, C., 2015. Exploring the evolution of a trade-off between vigilance and foraging in group-living organisms. R. Soc. Open Sci. 2, 150135. https://doi.org/10.1098/rsos.150135

Owen-Smith, N., Fryxell, J.M., Merrill, E.H., 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 365, 2267–78. https://doi.org/10.1098/rstb.2010.0095

Parkinson, B.W., Spilker, J.J., Axelrad, P., Enge, P., American Institute of Aeronautics and Astronautics., 1996. The global positioning system : theory and applications. Volume I. American Institute of Aeronautics and Astronautics.

QGIS Development Team, 2016. QGIS Geographic Information

System.

Rekdal, Y., 2009. Vegetasjon og utmarksbeite i Vingelen. Skog og Landsk. 13, 1–82. https://doi.org/http://www.skogoglandskap.no/filearchive/oppdragsrapport_13_09_vegetasjon_og_utmarksbeite_i_vingelen.pdf

Rekdal, Y., 2007. Vegetasjon og beite i Rendalen østfjell. Skog og Landsk. 11, 1–68. https://doi.org/http://www.skogoglandskap.no/filearchive/oppdrag11_07.pdf

Rekdal, Y., 2001. Husdyrbeite i fjellet. Vegetasjonstypar og beiteverdi.

Rhodes, J.R., McAlpine, C.A., Lunney, D., Possingham, H.P., 2005. A spatially explicit habitat selection model incorporating home range behavior. Ecology 86, 1199–1205. https://doi.org/10.1890/04-0912

Rivrud, I.M., Heurich, M., Krupczynski, P., M??ller, J., Mysterud, A., 2016. Green wave tracking by large herbivores: An experimental approach. Ecology 97, 3547–3553. https://doi.org/10.1002/ecy.1596

Rosenzweig, M.L., 1981. A Theory of Habitat Selection. Ecology 62, 327. https://doi.org/10.2307/1936707

Ross, L.C., Austrheim, G., Asheim, L.-J., Bjarnason, G., Feilberg, J., Fosaa, A.M., Hester, A.J., Holand, Ø., Jónsdóttir, I.S., Mortensen, L.E., Mysterud, A., Olsen, E., Skonhoft, A., Speed, J.D.M., Steinheim, G., Thompson, D.B.A., Thórhallsdóttir, A.G., 2016. Sheep grazing in the North Atlantic region: A long-term perspective on environmental sustainability. Ambio 551–566. https://doi.org/10.1007/s13280-016-0771-z

Russell, R.E., Swihart, R.K., Feng, Z., 2003. Population consequences of movement decisions in a patchy landscape. Oikos 103, 142–152. https://doi.org/10.1034/j.1600-0706.2003.12418.x

Saïd, S., Gaillard, J.-M., Duncan, P., Guillon, N., Guillon, N., Servanty, S., Pellerin, M., Lefeuvre, K., Martin, C., Van Laere, G., 2005. Ecological correlates of home-range size in spring–summer for female roe deer (Capreolus capreolus) in a deciduous woodland. J. Zool. 267, 301–308. https://doi.org/10.1017/S0952836905007454

Saïd, S., Gaillard, J.-M., Widmer, O., Débias, F., Bourgoin, G., Delorme, D., Roux, C., 2009. What shapes intra-specific variation in home range size? A case study of female roe deer. Oikos 118, 1299–1306. https://doi.org/10.1111/j.1600-0706.2009.17346.x

Saïd, S., Servanty, S., 2005. The influence of landscape structure on female roe deer home-range size. Landsc. Ecol. 20, 1003–1012. https://doi.org/10.1007/s10980-005-7518-8

Schuman, G.E., Reeder, J.D., Manley, J.T., Hart, R.H., Manley, W.A., 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecol. Appl. 9, 65–71. https://doi.org/10.1890/1051-0761(1999)009[0065:IOGMOT]2.0.CO;2

Searle, K.R., Thompson Hobbs, N., Shipley, L.A., 2005. Should I stay or should I go? Patch departure decisions by herbivores at multiple scales. Oikos 111, 417–424. https://doi.org/10.1111/j.0030-1299.2005.13918.x

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., Swift, D.M., 1987. Large Herbivore Foraging and Ecological Hierarchies. Bioscience 37, 789–799. https://doi.org/10.2307/1310545

Soussana, J.F., Allard, V., Pilegaard, K., Ambus, P., Amman, C., Campbell, C., Ceschia, E., Clifton-Brown, J., Czobel, S., Domingues, R., Flechard, C., Fuhrer, J., Hensen, A., Horvath, L., Jones, M., Kasper, G., Martin, C., Nagy, Z., Neftel, A., Raschi, A., Baronti, S., Rees, R.M., Skiba, U., Stefani, P., Manca, G., Sutton, M., Tuba, Z., Valentini, R., 2007. Full accounting of the greenhouse gas (CO2, N2O, CH4) budget of nine European grassland sites. Agric. Ecosyst. Environ. 121, 121–134. https://doi.org/10.1016/j.agee.2006.12.022

Steinheim, G., Nordheim, L.A., Weladji, R.B., Gordon, I.J., Adnoy, T., Holand, O., 2005. Differences in choice of diet between sheep breeds grazing mountain pastures in Norway. Acta Agric.

Scand. Sect. A Anim. Sci. 55, 16–20. https://doi.org/10.1080/09064700510009261

Steinheim, G., Nordheim, L., Weladji, R., Holand, Ø., Ådnøy, T., 2003. Digestive Tract Anatomy of Norwegian Sheep: Difference Between Breeds. Acta Agric. Scand. Sect. A - Anim. Sci. 53, 155–158. https://doi.org/10.1080/09064700310012999

Stewart, K.M., Bowyer, R.T., Dick, B.L., Johnson, B.K., Kie, J.G., 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143, 85–93. https://doi.org/10.1007/s00442-004-1785-y

Strand, G.-H., 2016. Rovviltbestandenes betydning for landbruk og matproduksjon basert på norske ressurser. Aas.

Ten Brink, P., Mutafoglu, K., Schweitzer, J.-P., Kettunen, M., Twigger-Ross, C., Baker, J., Kuipers, Y., Emonts, M., Tyrväinen, L., Hujala, T., Ojala, A., Mootoosamy, S., Paquel, K., Illes, A., Woollard, J., Taylor, K., Kotulak, M., Howe, M., Rogissart, L., Dekker, S., 2016. The Health and Social Benefits of Nature and Biodiversity Protection.

Tomkiewicz, S.M., Fuller, M.R., Kie, J.G., Bates, K.K., 2010. Global positioning system and associated technologies in animal behaviour and ecological research. Philos. Trans. R. Soc. B Biol. Sci. 365, 2163–2176.

https://doi.org/10.1098/rstb.2010.0090

Trodahl, S., 1989. Sauen som husdyr. Landbruksforlaget, Oslo.

Tufto, J., Andersen, R., Linnell, J., 1996. Habitat use and ecological correlates of home range size in a small cervid: The roe deer. J. Anim. Ecol. 65, 715–724. https://doi.org/10.2307/5670

van Beest, F.M., Rivrud, I.M., Loe, L.E., Milner, J.M., Mysterud, A., 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? J. Anim. Ecol. 80, 771–785. https://doi.org/10.1111/j.1365-2656.2011.01829.x

van Beest, F.M., Vander Wal, E., Stronen, A. V., Paquet, P.C., Brook, R.K., 2013. Temporal variation in site fidelity: scale-dependent effects of forage abundance and predation risk in a non-migratory large herbivore. Oecologia 173, 409–420. https://doi.org/10.1007/s00442-013-2647-2

Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M.S., Gaillard, J.M.-. M., Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M.S., Gaillard, J.M.-. M., 2009. Memory keeps you at home: A mechanistic model for home range emergence. Oikos 118, 641–652. https://doi.org/10.1111/j.1600-0706.2008.17003.x

Van Soest, P.J., 1994. Nutritional ecology of the ruminant. Comstock Pub.

Vander Wal, E., Rodgers, A.R., 2012. An individual-based quantitative approach for delineating core areas of animal space use. Ecol. Modell. 224, 48–53. https://doi.org/10.1016/j.ecolmodel.2011.10.006

WallisDeVries, M.F., Laca, E.A., Demment, M.W., 1999. The importance of scale of patchiness for selectivity in grazing herbivores. Oecologia 121, 355–363. https://doi.org/10.1007/s004420050939

Ward, D., Saltz, D., 1994. Forging at Different Spatial Scales: Dorcas Gazelles Foraging for Lilies in the Negev Desert. Ecology 75, 48–58. https://doi.org/10.2307/1939381

Watmough, G.R., Palm, C.A., Sullivan, C., 2017. An operational framework for object-based land use classification of heterogeneous rural landscapes. Int. J. Appl. Earth Obs. Geoinf. 54, 134–144. https://doi.org/10.1016/j.jag.2016.09.012

White, R.G., 1983. Foraging Patterns and Their Multiplier Effects on Productivity of Northern Ungulates. Oikos 40, 377. https://doi.org/10.2307/3544310

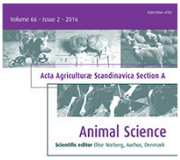
Wiens, J.A., 1989. Spatial scaling in ecology. Funct. Ecol. 3, 385–397. https://doi.org/10.2307/2389612

Witt, J.C., Webster, C.R., Froese, R.E., Drummer, T.D., Vucetich, J.A., 2012. Scale-dependent drivers of ungulate patch use along a temporal and spatial gradient of snow depth. Can. J. Zool. 90, 972–983. https://doi.org/10.1139/z2012-065

Wittmer, H.U., McLellan, B.N., Hovey, F.W., 2006. Factors influencing variation in site fidelity of woodland caribou (Rangifer tarandus caribou) in southeastern British Columbia. Can. J. Zool. 84, 537–545. https://doi.org/10.1139/z06-026

Wronski, T., Apio, A., Plath, M., 2006. Activity patterns of bushbuck (Tragelaphus scriptus) in Queen Elizabeth National Park. Behav. Processes 73, 333–341. https://doi.org/10.1016/j.beproc.2006.08.003

Paper I



Acta Agriculturae Scandinavica, Section A — Animal Science

ISSN: 0906-4702 (Print) 1651-1972 (Online) Journal homepage: http://www.tandfonline.com/loi/saga20

Area use of two sheep breeds in contrasting summer alpine grazing environments in southern Norway

N. H. Jørgensen, G. Steinheim & Ø. Holand

To cite this article: N. H. Jørgensen, G. Steinheim & Ø. Holand (2016) Area use of two sheep breeds in contrasting summer alpine grazing environments in southern Norway, Acta Agriculturae Scandinavica, Section A — Animal Science, 66:2, 99-105, DOI: 10.1080/09064702.2016.1215513

To link to this article: http://dx.doi.org/10.1080/09064702.2016.1215513

ACTA AGRICULTURAE SCANDINAVICA, SECTION A — ANIMAL SCIENCE, 2016
VOL. 66, NO. 2, 99–105
http://dx.doi.org/10.1080/09064702.2016.1215513

Taylor & Francis
Taylor & Francis Group

ORIGINAL ARTICLE

Area use of two sheep breeds in contrasting summer alpine grazing environments in southern Norway

N. H. Jørgensen, G. Steinheim and Ø. Holand

Department of Animal and Aquacultural Sciences, Norwegian University of Life Sciences, Aas, Norway

ABSTRACT
In Norway, approximately 2 million sheep are released for summer grazing onto highly heterogeneous outer-fields. The crossbred Norwegian White Sheep (NWS) is dominating, whereas the lighter short-tailed gregarious Spælsau (SP) is the second most abundant of the total Norwegian sheep population. We fitted 51 ewes with GPS collars in two contrasting alpine environment, Spekedalen (poor pasture) and Brathøa sauhavnelag (rich pasture), during the summer grazing seasons 2013 and 2014. We modelled breed differences in summer area use and found no significant effect of breed or pasture quality. No breed * pasture interaction was found. Information of pasture quality and breed characteristics is vital to understand the resource–animal interplay and may prove important for sheep management.

ARTICLE HISTORY
Received 12 May 2016
Revised 27 June 2016
Accepted 8 July 2016

KEYWORDS
Dynamic Brownian bridge movement model; habitat use; pasture quality; utilisation distribution

Introduction

Livestock grazing has a long history in Norwegian alpine habitat (Austrheim et al., 2011). In Norway, approximately 2 million sheep are released onto outer fields for summer grazing in densities varying between 10 and 80 sheep per km^2 (Mysterud et al., 2001). Indeed, during the summer months sheep are the most common large herbivores in most Norwegian mountain areas. The sheep, of which 80% are Norwegian White sheep (NWS) and 13% short-tailed Spælsau (http://www.ngs.no), are released onto a wide range of summer grazing environments; from coastal to mountainous inland areas; and these areas differ greatly in terms of local climate, topography and pasture quality for sheep. Little is known about phenotypic plasticity in ranging behaviour of sheep. Increased knowledge may help managers in optimising lamb production, and may help managers concerned with maintaining characteristics of the cultural landscapes today threatened by woody plant encroachment. The ongoing trend towards a warmer climate, less livestock rangeland grazing (Hemsing & Bryn, 2011), and fewer but larger sheep flocks (Aaby et al., 2014) means large-scale changes are underway in sheep mountain area use in Norway. To be able to predict consequences, we need to know more about how different types of sheep interact with different grazing rangeland habitats. This may also have relevance in a context of legal grazing rights.

Herbivores are able to alter their foraging behaviour and area use in response to spatial and temporal resource distributions (Fretwell & Lucas, 1970; Senft et al., 1987; Seagle & Mcnaughton, 1992; WallisDeVries, 1996). The ideal free distribution theory (Fretwell & Lucas, 1970) predicts that herbivores should distribute themselves relative to the profitability of habitat patches: given equal animal density and a homogeneous distribution of the resources, herbivores in a poor environment will utilise a large area compared to those in an area with more recourses (Owen-Smith et al., 2010). Several other factors will influence the habitat use of our sheep: lambs seem to learn from their dams how and where to forage (Provenza, 1995); also, experiences during the adult life, and ageing in itself, will influence the area use of small ruminants (Ortega-Reyes & Provenza, 1993).

Home range is a well-established concept in ecology. It is the key area where an animal lives and performs its activities, for example, foraging, resting and reproducing (Powell & Mitchell, 2012). An estimate of an animal's area use is often assumed to represent its realised home range (Kie et al., 2010). In the last decades an array of new methods and techniques for estimation of home range have evolved (Tomkiewicz et al., 2010; Clapp & Beck, 2015). However, the estimate alone is seldom enough to describe and understand an animal's spatio-temporal distribution in its home range. Intraspecific variation in home range size among large herbivores may be affected by intrinsic and extrinsic factors across spatiotemporal scales (van Beest et al., 2011): age (Said et al., 2005, 2009), body mass (Said et al., 2005, 2009),

CONTACT N. H. Jørgensen ✉ nicolai.jorgensen@nmbu.no

reproductive status (Tufto et al., 1996), forage biomass (Dussault et al., 2005) and quality (Said et al., 2005, 2009) as well as animal density (Wal et al., 2013) and climatic factors such as temperature, precipitation and daylight (Borger et al., 2006) may affect area use.

Through selection, we have created different breeds of our livestock species; breeds may be viewed as attempts to tailor phenotypes for specific habitats and production systems. An example of this is the hill and lowland sheep breeds system in the UK, with smaller, hardy animals on the hills, and larger animals producing larger offspring on the lower pastures. Sheep breeds may vary in terms of for example, body size, number of offspring, growth rate, daily energy requirements, gregariousness (Dwyer et al. 1998; Dwyer & Lawrence, 1999; Dwyer & Lawrence, 2005) and alertness (Ryder, 1964; Ryder, 1984; Hansen et al. 2001). Interactions between breed and environment might be expected when breeds are released into pastures of contrasting quality.

The two most common sheep breeds in Norway are the heavy NWS which originates from old Nordic breeds with substantial crossing with English lowland breeds, and the lighter Spælsheep (SP) which is a traditional Nordic landrace less influenced by foreign breeds. The SP may thus be more adapted to Nordic rangeland conditions (Drabløs, 1997). NWS is generally considered to be more docile, with reduced alertness and weak gregariousness, forming smaller, more stationary family groups distributed throughout the grazing areas (Drabløs, 1997). The SP, in contrast, has retained more of the survival traits, such as gregariousness, agility and alertness (Drabløs, 1997; Hansen et al., 2001). The NWS breed is a typical grazer (sensu (Hofmann, 1989), spending 80–90% of foraging time on grasses, while the SP is more of a grazer/browser type, with up to 50% of foraging spent on woody plant species (Steinheim et al., 2004; Steinheim et al., 2005; Steinheim et al., 2008). The lighter, more gregarious SP is thus more selective in its foraging, allowing it, given not too high a stocking rate, to obtain a high-quality diet even if the general pasture conditions are poor. This would result in SP being pickier and thus in need of larger areas. In this study, we aim to compare these two breeds in terms of habitat use on contrasting pastures.

We predict that:

(a) Sheep on low-quality pasture (Spekedalen) utilise a larger area compared to sheep on good quality pasture (Vingelen).
(b) SP utilises larger areas compared to NWS.

We also investigate whether differences between the breeds in area use vary between different pasture qualities, that is, if there was a genotype by environment interaction effect on habitat use.

Materials and methods

Study area

The Spekedalen study area (Figure 1), a part of Sølendalen beitelag, is situated in the northern part of Rendalen municipality, Hedmark county, in south-eastern Norway (11°21′ E, 62°4016′ N), covering 97 km^2 spanning from 688 to 1604 metres above sea level (m.a.s.l.). The mean annual temperature is 1.1°C with a January low of −8.2°C and a July high of 11.3°C, and mean annual precipitation being close to 550 mm (Rekdal, 2007). Weather conditions are of a typical inland climate with high annual and between year variations (met.no).

The bedrock is uniform and dominated by Sparagmite, an arkosic sandstone, interspersed with base-rich layers. Rekdal (2007) characterised the vegetation below the tree-line as dominated by lichen and heath-rich pine forest (41%), whereas above the tree-line dwarf shrub heath dominated on ridges and dry higher ground (32%). Low shrubs dominated the lee-sides, intermixed with lichens. Only 26% of the total survey area was classified suitable for grazing, that is, good and very good vegetation types suitable for sheep grazing, of which 1.6% were characterised as very good vegetation types. Rekdal (2007) estimated that the carrying capacity of the Spekedalen area is between 850 and 1050 sheep, that is, 50 sheep per km^2 of the area suitable for grazing. The sheep density in Sølendalen beitelag, encompassing the study area in Spekedalen in 2013 and 2014, was 12 and 14 sheep per km^2 on good and very good grazing habitat respectively (Angeloff, pers. Comm.), and is thus well below the estimated carrying capacity.

The Brathøa sauhavnelag (hereafter called Brathøa) study area (Figure 1) in Vingelen is situated northwest in Tolga municipality, covering approximately 62 km^2 spanning from 790 to 1229 m.a.s.l. The Bratthøa climate is similar to Spekedalen (Rekdal, 2009), but the bedrock is dominated by phyllite with areas of fine-grained moraine material. In combination with sufficient water supply, this bedrock type results in richer vegetation (Rekdal, 2009). Fifty per cent of the surveyed area was classified as suitable for grazing, of which 13% was characterised as having very good pastures (Rekdal, 2009). It was estimated that the carrying capacity of Brathøa sauhavnelag is between 2700 and 3300 sheep, that is, 80 sheep per km^2 of suitable grazing area (Rekdal, 2009) and with numbers of sheep released

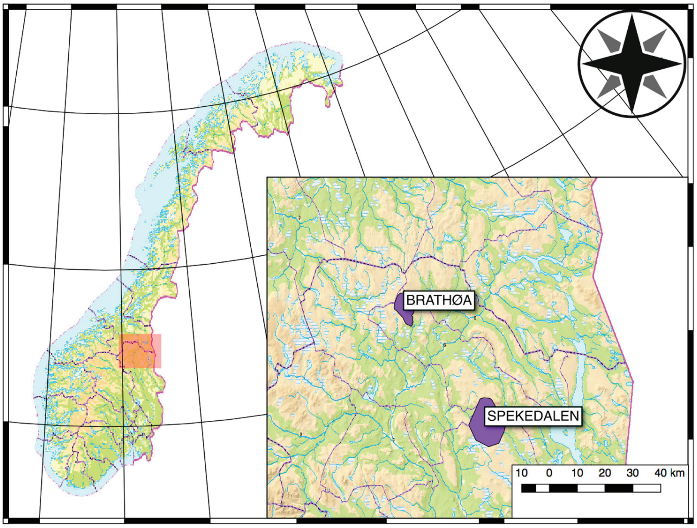


Figure 1. Nord-Østerdalen comprising of Brathøa sauhavnelag in the Tolga municipality and Spekedalen in the Rendalen municipality in the Hedmark county, Norway (Layout: print composer QGIS 2.12.1. Source: http://www.kartverket.no).

in Brathøa sauhavnelag in 2013 and 2014 of 63 and 67 sheep per km^2 on good to very good grazing area, respectively (Angeloff, pers. comm.), this is as for Spekedalen well below the estimated carrying capacity.

Table 1 summarises the distribution of pasture classes for sheep in the two study areas.

The total density of sheep in the Spekedalen study area was approximately 3 sheep per km^2 in both 2013 and 2014, whilst in Brathøa density was 38 and 40 sheep per km^2 in 2013 and 2014, respectively (Angeloff, pers. comm.).

Study animals

The summer outfield grazing started on 23rd of June and lasted to 2nd of September in both 2013 and 2014. Fifty-one lactating ewes of SP and NWS of known age and with two lambs at foot were released into the two study areas, 23 and 28 ewes in Spekedalen and Brathøa, respectively (Table 2). The study animals were recruited from six sheep farms that had used the study areas for summer grazing several years previous to the study. These ewes and lambs were individually ear-tagged by the farmers; the ewes were also tagged with an easy-to-read numbered collar attached to the GPS collar.

Table 1. Summary of pasture quality in Brathøa sauhavnelag and Spekedalen (Rekdal 2007; Rekdal 2009).

	Spekedalen	Vingelen
Less good	71%	4%
Good	27%	60%
Very good	2%	39%

Data collection

GPS collars

For the summer grazing seasons 2013–2014, ewes were fitted with Followit Tellus Wildlife Tracking GPS collars which registered their position every 60 min. For the GPS-tracking data, a proportion of the data points were removed from the dataset due to a high DOP (dilution of precision). We set the highest DOP to 2.0 which is considered "Good" (Parkinson & Spilker, 1996; Langley, 1999). GPS-fixes the first 14 days after the release and 19 days prior to capture and unsuccessful GPS-fixes (time-out after 90 s acquisition time) were also removed. Six collars failed during 2014 and one failed

Table 2. Number of GPS collared NWS and SP released by Brathøs sauhavnelag in Vingelen and Spekedalen in 2013 and 2014.

	Race	23 June 2013–22 August 2013	23 June 2014–22 August 2014
Spekedalen	NWS	7	6
	SP	7	3
Vingelen	NWS	9	6
	SP	7	6

Table 3. Type 3 *F* tests of fixed effects on utilisation distribution area.

Effect	Num DF	Den DF	*F* Value	Pr > *F*
Area	1	47	1.21	0.2771
Breed	1	47	1.52	0.2241
Area * breed	1	47	0.02	0.8904

during 2013; the incomplete data from these seven animals were not included.

The total usable GPS-positions accounted to 73.7% in 2013 (60,701 of 82,396) and 95.4% in 2014 (70,965 of 74,400). The information was uploaded to the movebank.org website and mapped according to the movebank.org guidelines (see also (Kranstauber et al., 2011). Following the upload and mapping, the data were downloaded and subsequently divided into year (2013 and 2014), area (Spekedalen and Vingelen) and breed (SP and NWS) for further analyses. In 2013, several of the study animals in Spekedalen were gathered, prior to general sheep gathering in September, and kept temporarily on semi-natural pastures. Thus, the summer grazing season was reduced to 60 days for both 2013 and 2014 (23th June–23th August) for across year comparisons.

Area use modelling

Dynamic Brownian bridge movement model

The dynamic Brownian bridge movement model method (DBBMM) was used to calculate the utilisation distribution (UD) area, following the guidelines in the Move package, incorporating the temporal characteristics of the movement paths (Kranstauber et al., 2012; Kranstauber & Smolla, 2016). A window size of 24 locations (2 days), a margin of 3 locations, location error of 20 metres, raster size of 20, extension of 0.25 and a 60 min time step were used when calculating the DBBMM for each animal.

Statistical analyses

Since all ewes had two lambs at foot, the number of lambs was not included in the analyses. Preliminary analyses showed that ewe age classes (3 age classes; 1-year-old, 2–3 years old and ≥4 years old) did not have a significant effect on area use ($F = 0.72$; $P = .55$), the same was the case for the effect of year ($F = 0.02$; $P = .89$), and the effects were thus excluded from analyses.

We used a generalised linear mixed model [employing the mixed procedure with asymptotic standard errors and Wald *Z*-test for the covariance parameter estimates (SAS University Edition 3.4 Inc. 2015)], with the UD area in km^2 as the dependent variable, and area (Spekedalen, Vingelen) and breed (NWS, SP) as independent variables

$$\mathrm{UD} = \mathrm{area} + \mathrm{breed} + \mathrm{area}{*}\mathrm{breed} + \mathrm{error}. \qquad (1)$$

Results

Type 3 *F* tests of fixed effects showed no significant trends in the main effects with differences between areas ($P = .28$) and between breeds ($P = .22$), and no interaction effect ($P = .89$) (Table 3). In Spekedalen, the estimated UD was non-significantly larger than in Vingelen (2.32 km^2, $P = .51$; Table 4), also illustrated in the boxplot in Figure 2, and NWS used a non-significant smaller estimated UD area compared to SP (−3.31 km^2, $P = .31$; Table 4), Figure 3 also illustrates this.

Discussion

We eliminated the potential effect of reproductive status by using only lactating ewes all with two lambs at foot. Ewes' age, which is closely connected to their body mass (Drabløs, 1997), did not affect UD. Further, no between years (2013 vs 2014) variation in UD was found, although the summer season 2013 was dry and warm compared to 2014's cold and wet condition (met.no). Sheep density was low and moderate in Spekedalen and Vingelen, respectively, and the within area density was almost identical between years.

Following decisions by the farmers, sheep densities are well below carrying capacity in both study areas; this imply relatively low interspecific competition for

Table 4. Solutions of the model terms explaining the area use.

Effect	Area	Breed	Estimate	Std Err	DF	*t* Value	Pr > |*t*|
Intercept			11.7170	2.2833	47	5.13	<.0001
Area	SPEK		2.3213	3.5372	47	0.66	0.5149
Area	VING		0				
Breed		NWS	−3.3102	3.2290	47	−1.03	0.3105
Breed		SP	0				
Area * breed	SPEK	NWS	0.6694	4.8311	47	0.14	0.8904
Area * breed	SPEK	SP	0				
Area * breed	VING	NWS	0				
Area * breed	VING	SP	0				

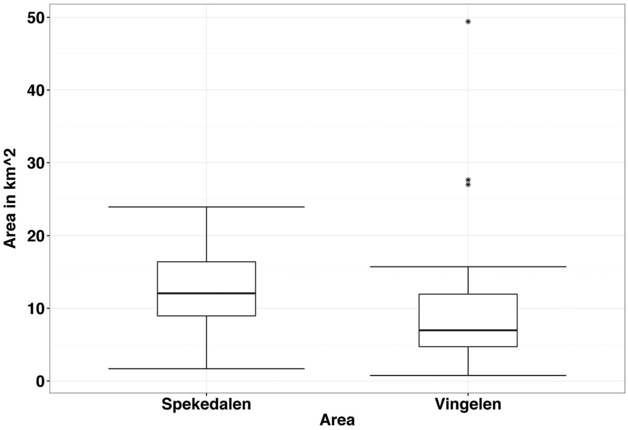


Figure 2. Boxplot of UD area in Spekedalen and Brathøa, 2013 and 2014. Area is in square kilometres. The asterisks denote outliers.

forage resources and density should thus have small implications for the calculated UD area use, given that the use is mainly determined by foraging dynamics. Indeed, we were able to rule out many intrinsic as well as extrinsic factors potentially influencing UD and this enables us to test the effect of breed and grazing quality differences on UD.

We found no support for the prediction that sheep on low-quality pasture utilise larger area compared to sheep on good-quality pasture, although the two breeds do use an estimated 2.3 km^2 larger area in Spekedalen compared to Brathøa. The mean area use for the Spekedalen study area was 12.55 km^2 (2013: 2.36–23.91 km^2, 2014: 1.69–17.05 km^2) compared to 10.06 km^2 (2013: 1.11–26.63 km^2, 2014: 0.75–49.42 km^2) for Brathøa. Individual variation in UD was large, especially in Brathøa (Figure 2) and given the UD means and variances it would take some 140–150 animals in each area for us to be able to reject the H_0 hypothesis that sheep on low-quality pasture utilise the same area compared to sheep on good-quality pasture. In our case, the low sheep densities compared to the carrying capacities may explain why area use did not differ between pasture qualities: without appreciable foraging competition, the difference

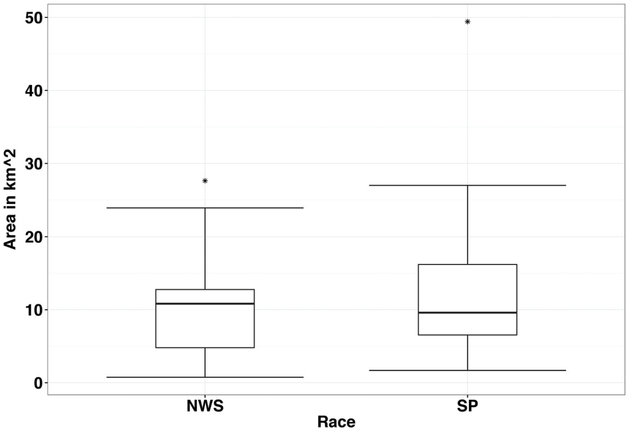


Figure 3. Boxplot of UD area for NWS and SP, 2013 and 2014. Area is in square kilometres. The asterisks denote outliers.

in quality between areas did not have substantial effects on area use.

Our UD means are in the mid-range of mean home ranges (3.0–24.4 km^2) reported by Gautestad et al. (1996) from four locations in Norway. However, the sizes of the UDs found in this study are not directly comparable to what Gautestad et al. (1996) reported, as the methods for obtaining animal locations as well estimating UD differ greatly. Their traditional geometric shape home range estimate, using minimum convex polygon (MCP), as compared to our dynamic DBBMM method, normally yield bigger estimates, including areas that have not seen actual use by animals. UD calculated using DBBMM sums up smaller patches of intensively used areas, leaving out travelling paths and less frequently used areas, and gives a sounder biological picture of area use as compared to a MCP-based geometric shape that ignores the temporal aspect of movement (Kranstauber, 2012). Compared to MCP, using DBBMM should thus reduce estimated area used more in Spekedalen than in Vingelen, as animals in Spekedalen are likely to have travelled more between discrete forage patches.

SP showed a tendency to utilise larger mean area (10.09 km^2; range 2013: 4.64–21.06 km^2 and 2014: 1.69–49.42 km^2) compared to NWS (4.74 km^2; range 2013 1.08–27.63 km^2 and 2014: 0.75–17.05 km^2) across area. However, the individual variation in UD was large, especially for SP, and given the UD means and variances it would take more animals (refer to individual variation in area UD discussion) for the observed breed difference to emerge as significant. The difference between breeds in variation is largely caused by two SP ewes that behaved untypically, travelling long distances in an, according to farmers, unusual manner. It is not surprising that individuals in general vary in terms of area use: the areas ewes inherit from their dams vary strongly in topography and other characteristics; animals will also have individual experiences that shape their behaviours. The large individual variation differences between individual give the possibity for phenotypic selection against large area use should that be desirable in a management setting, for example, if grazing right violations is a reoccurring issue. Using larger grazing areas might prone individuals to exceed legal grazing rights' boundaries and increase local socioeconomic conflicts.

The SP form larger groups compared to NWS, and is more selective in diet choice than the "bulk feeder" NWS. We thus expected SP to be more exposed to within-species competition, and that it may deplete forage patches quicker, both of which should lead to use of larger areas. The NWS being around 20% heavier than SP (Drabløs, 1997), and thus having higher energy demands, may lead to use of larger areas; this, however, is not supported by van Beest et al. (2011), who stated that only interspecific studies report that body size is a major factor in determining home range size.

We found no support for the predictions that (1) sheep on low-quality habitat (Spekedalen) utilise larger area compared to sheep on good-quality habitat (Vingelen) and that (2) SP utilise larger area than NWS. We appreciate that in our study the large individual variation may have overshadowed the effects of the intrinsic and extrinsic determinants. Individual variation is in itself important when area use of animals is to be described and understood. More work should be done to elucidate how area use might have implication for production output.

Acknowledgements

We thank Michael Angeloff, NIBIO, Rune Granås at NLR Nord-Østerdal and the farmers of Sølendalen beitelag and Brathøa sauhavnelag for lending us research animals in the two summer grazing season 2013 and 2014.

Funding

This project was supported by the Norwegian Research Council project "Sheep in motion" [grant number NFR 208036] and the Regional Småfefondet.

References

Aaby, B. A., Kantanen, J., Aass, L. & Meuwissen, T. (2014) Current status of livestock production in the Nordic countries and future challenges with a changing climate and human population growth. *Acta Agriculturae Scandinavica Section A-Animal Science*, 64(2), 73–97.

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

van Beest, F. M., Rivrud, I. M., Loe, L. E., Milner, J. M. & Mysterud, A. (2011) What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology*, 80, 771–785.

Borger, L., Franconi, N., Ferretti, F., Meschi, F., De Michele, G., Gantz, A. & Coulson, T. (2006) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *The American Naturalist*, 168, 471–485.

Clapp, J. G. & Beck, J. L. (2015) Evaluating distributional shifts in home range estimates. *Ecology and Evolution*, 5, 3869–3878.

Drabløs, D. (1997) *Soga om smalen: jubileumsskrift Norsk sau-og geitalslag 1947±1997 (The Tale of the Sheep: Festschrift for the Norwegian Sheep and Goat Breeders' Association 1947–1997)* (Oslo: Norwegian Sheep and Goat Breeders).

Dussault, C., Ouellet, J. P., Courtois, R., Huot, J., Breton, L. & Jolicoeur, H. (2005) Linking moose habitat selection to limiting factors. *Ecography*, 28, 619–628.

Dwyer, C. M. & Lawrence, A. B. (1999) Ewe-ewe and ewe-lamb behaviour in a hill and a lowland breed of sheep: A study using embryo transfer. *Applied Animal Behaviour Science*, 61, 319–334.

Dwyer, C. M. & Lawrence, A. B. (2005) A review of the behavioural and physiological adaptations of hill and lowland breeds of sheep that favour lamb survival. *Applied Animal Behaviour Science*, 92, 235–260.

Dwyer, C. M., McLean, K. A., Deans, L. A., Chirnside, J., Calvert, S. K. & Lawrence, A. B. (1998) Vocalisations between mother and young in sheep: Effects of breed and maternal experience. *Applied Animal Behaviour Science*, 58, 105–119.

Fretwell, S. D. & Lucas, H. L. (1970) On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, 19, 16–36.

Gautestad, A. O., Mysterud, I. & Mysterud, I. (1996) *Carnivores and sheep farming in Norway*. 2. Evaluation of current knowledge concerning preventive measures against carnivore damage. (In Norwegian, English summary). UoO, Department of Biology.

Hansen, I., Christiansen, F., Hansen, H. S., Braastad, B. & Bakken, M. (2001) Variation in behavioural responses of ewes towards predator-related stimuli. *Applied Animal Behaviour Science*, 70, 227–237.

Hemsing, L. Ø. & Bryn, A. (2011) Changes in landscape and vegetation heterogeneity of rural Norway. In L. Nesheim (ed.) *Biodiversity in Agriculture - Lessons Learned and Future Directions*. NJF Report Vol. 7, No. 1 (Stockholm: Nordic Association of Agricultural Scientists), pp. 33–38.

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

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., Gaillard, J. M. & Moorcroft, P. R. (2010) The home-range concept: Are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2221–2231.

Kranstauber, B., Cameron, A., Weinzerl, R., Fountain, T., Tilak, S., Wikelski, M. & Kays, R. (2011) The Movebank data model for animal tracking. *Environmental Modelling & Software*, 26, 834–835.

Kranstauber, B., Kays, R., LaPoint, S. D., Wikelski, M. & Safi, K. (2012) A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology*, 81, 738–746.

Kranstauber, B. & Smolla, M. (2016) Move: Visualizing and Analyzing Animal Track Data. R package version 2.0.0. https://CRAN.R-project.org/package=move.

Langley, R. B. (1999) Dilution of precision. *GPS World*, 10, 52–59.

Mysterud, A., Langvatn, R., Yoccoz, N. G. & Stenseth, N. C. (2001) Plant phenology, migration and geographical variation in body weight of a large herbivore: The effect of a variable topography. *Journal of Animal Ecology*, 70, 915–923.

Ortega-Reyes, L. & Provenza, F. D. (1993) Amount of experience and age affect the development of foraging skills of goats browsing blackbrush (*Coleogyne ramosissima*). *Applied Animal Behaviour Science*, 36, 169–183.

Owen-Smith, N., Fryxell, J. M. & Merrill, E. H. (2010) Foraging theory upscaled: The behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2267–2278.

Parkinson, B. W. & Spilker, J. J. (1996) *Global Positioning System: Part 1 GPS fundamentals, part 2 GPS performance and error effects; vol. 2, part 3 differential GPS and integrity monitoring, part 4 integrated navigation systems, part 5 GPS navigation applications, part 6 special applications*: Aiaa.

Powell, R. A. & Mitchell, M. S. (2012) What is a home range? *Journal of Mammalogy*, 93, 948–958.

Provenza, F. D. (1995) Tracking variable environments: There is more than one kind of memory. *Journal of Chemical Ecology*, 21, 911–923.

Rekdal, Y. (2007) Vegetasjon og beite i Rendalen østfjell. *Skog og Landskap*, 11, 1–68.

Rekdal, Y. (2009) Vegetasjon og utmarksbeite i Vingelen. *Skog og Landskap*, 13, 1–82.

Ryder, M. L. (1964) The history of sheep breeds in Britain (Continued). *The Agricultural History Review*, 12, 65–82.

Ryder, M. L. (1984) Medieval sheep and wool types. *Agricultural History Review*, 32, 14–28.

Said, S., Gaillard, J. M., Duncan, P., Guillon, N., Guillon, N., Servanty, S., Pellerin, M., Lefeuvre, K., Martin, C. & Van Laere, G. (2005) Ecological correlates of home-range size in spring-summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. *Journal of Zoology*, 267, 301–308.

Said, S., Gaillard, J. M., Widmer, O., Debias, F., Bourgoin, G., Delorme, D. & Roux, C. (2009) What shapes intra-specific variation in home range size? A case study of female roe deer. *Oikos*, 118, 1299–1306.

Seagle, S. W. & Mcnaughton, S. J. (1992) Spatial variation in forage nutrient concentrations and the distribution of serengeti grazing ungulates. *Landscape Ecology*, 7, 229–241.

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E. & Swift, D. M. (1987) Large herbivore foraging and ecological hierarchies. *Bioscience*, 37, 789–799.

Steinheim, G., Weladji, R. B., Skogan, T., Adnoy, T., Skjelvag, A. O. & Holand, O. (2004) Climatic variability and effects on ungulate body weight: The case of domestic sheep. *Annales Zoologici Fennici*, 41, 525–538.

Steinheim, G., Nordheim, L. A., Weladji, R. B., Gordon, I. J., Adnoy, T. & Holand, O. (2005) Differences in choice of diet between sheep breeds grazing mountain pastures in Norway. *Acta Agriculturae Scandinavica Section A – Animal Science*, 55, 16–20.

Steinheim, G., Odegard, J., Adnoy, T. & Klemetsdal, G. (2008) Genotype by environment interaction for lamb weaning weight in two Norwegian sheep breeds. *Journal of Animal Science*, 86, 33–39.

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G. & Bates, K. K. (2010) Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B*, 365, 2163–2176.

Tufto, J., Andersen, R. & Linnell, J. D. C. (1996) Habitat use and ecological correlates of home range size in a small cervid: The roe deer. *The Journal of Animal Ecology*, 65, 715–724.

Wal, E., Laforge, M. P. & McLoughlin, P. D. (2013) Density dependence in social behaviour: Home range overlap and density interacts to affect conspecific encounter rates in a gregarious ungulate. *Behavioral Ecology and Sociobiology*, 68, 383–390.

WallisDeVries, M. F. (1996) Effects of resource distribution patterns on ungulate foraging behaviour: A modelling approach. *Forest Ecology and Management*, 88, 167–177.

Paper II

Rangeland Ecology & Management xxx (2018) xxx–xxx

Contents lists available at ScienceDirect

Rangeland Ecology & Management

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

Original Research

Does Scale Matter? Variation in Area Use Across Spatiotemporal Scales of Two Sheep Breeds in Two Contrasting Alpine Environments☆

N.H. Jørgensen *, G. Steinheim, Ø. Holand

Department of Animal and Aquacultural Sciences at Faculty of Biosciences, Norwegian University of Life Sciences, Aas, Norway

ARTICLE INFO

Article history:
Received 18 November 2016
Received in revised form 16 October 2017
Accepted 6 November 2017
Available online xxxx

Keywords:
core areas
dBBMM
home ranges
pasture
utilization distribution

ABSTRACT

Animal-by-environment interaction creates space use patterns, which characterize an animal's utilization distribution (UD) area. We fitted 51 ewes of the two Norwegian breeds Norwegian White Sheep (NWS) and Spælsau (SP) with Global Positioning System collars in two contrasting environments (Spekedalen; poor pasture and Bratthøa; rich pasture) during the 2013 and 2014 summer grazing seasons. We explored effects of spatiotemporal scales on UD sizes of the sheep in these environments. We defined the temporal scales as 5-, 10-, 15-, 20-, 30-, and 60-d intervals and spatial scales as 95% and 50% UD using the dynamic Brownian Bridge Movement Model. Our results showed that, in general, sheep had larger UDs in the poor area compared with the rich area and the SP had larger UDs compared with the NWS. We found 95% UD differences between the two environments at all temporal scales, except 60 d, whereas differences were found between breeds at all but the finest temporal scale. The 50% UD differed between breeds and environments on all temporal scales except between-study areas at the 5-d scale. The lack of environment by breed interactions suggest that the two breeds respond equally to range quality at all spatiotemporal scales. We conclude that scale has to be considered when comparing UD differences across spatial and temporal scales in contrasting environments and between sheep genotypes. Our findings are thus important for management of grazing resources in multipurpose land use planning.

Introduction

Animal-by-environment interplay creates space use patterns (Morales et al., 2010). This can be used to characterize how an animal utilizes its surroundings (Tufto et al., 1996). Animals often restrict themselves to a certain area, their home range, and are likely to increase their forage efficiency and subsequent fitness as familiarity with that area increases (Van Moorter et al., 2009). Animals operate on different functional scales, and causes for variation in home range size may differ within and between species. Differences between species are generally driven by body mass (Carbone et al., 2005). Intraspecific variation may be caused by a number of intrinsic factors such as age (Saïd et al., 2005, 2009), sex (Main and Coblentz, 1996), body mass (van Beest et al., 2011), and reproductive status (Tufto et al., 1996), as well as social organization (Wronski et al., 2006) and activity patterns (Owen-Smith et al., 2010). Indeed, extrinsic factors such as range quality and population density (Dussault et al., 2005; Saïd et al., 2005, 2009) may also cause variation.

Landscape characteristics including heterogeneity (Bartlam-Brooks et al., 2013), topography (Mysterud et al., 2001), and elevation (Killeen et al., 2014) can influence how individuals in spatially structured populations interact with the environment. However, studies that address spatiotemporal processes affecting area use are scarce (Bjørneraas et al., 2012), but see van Beest et al. (2011) that aimed to quantify the relative effect of various individual, forage, and climatic determinants of variation in home range size across multiple spatiotemporal scales in moose *(Alces alces)*. Because spatial and temporal scales may co-vary (Wiens, 1989), it is imperative to include both when analyzing ecological processes and to select the most informative scales of analysis (Dayton and Tegner, 1984; Mayor et al., 2009). Indeed, a multiscale approach is often imperative to unravel scale-sensitive ecological processes (e.g., an animal's area use and at which spatiotemporal scales it is operating on).

An animal's space use can be characterized by its utilization distribution (UD), which can be calculated using statistical methods like kernel density estimation (Worton, 1989) and Brownian bridge movement models (Horne et al., 2007) or variations thereof

---

☆ This work was supported by Småfefondet, NMBU and Norwegian Research Council (NFR 208036/010).

* Correspondence: N. H. Jørgensen, Dept of Animal and Aquacultural Sciences at Faculty of Biosciences, Norwegian University of Life Sciences, Box 5003, NO-1432, Aas, Norway. Tel.: +47 67232624
E-mail address: nicolai.jorgensen@nmbu.no (N.H. Jørgensen).

https://doi.org/10.1016/j.rama.2017.11.001

Please cite this article as: Jørgensen, NH., et al., Does Scale Matter? Variation in Area Use Across Spatiotemporal Scales of Two Sheep Breeds in Two Contrasting Alpine Environments, Rangeland Ecology & Management (2018), https://doi.org/10.1016/j.rama.2017.11.001

(i.e., dynamic Brownian bridge movement model) (Kranstauber et al., 2012). The 95% and 50% areas used represent the most commonly used spatial estimators (see e.g., van Beest et al., 2011). Both of these UD estimates may vary in extension and overlap both spatially and temporally. However, the two spatial scales need not conform to a certain percentage of the estimated UD, per se, and may depend on the species' or breed's range behavioral patterns. Animals may thus have the same home range sizes, but with different ratios of intensively used foraging patches because resources are distributed differently within the areas (Vander Wal and Rodgers, 2012). Indeed, core areas may be more important within heterogeneous home ranges with greater forage availability or quality than in areas with fewer or homogeneously distributed resources (McLoughlin and Ferguson, 2000). One would thus expect that differences in UDs, at any temporal scale, between the homogeneous Spekedalen and the heterogeneous Bratthøa study area would be more pronounced at a finer spatial scale (e.g., 50% UD). Further, an animal's use of space within a short time-span should intuitively be smaller than the area used during a longer period within a specific environment (WallisDeVries et al., 1999; Fortin et al., 2003).

It is well documented that herbivores that use sparsely distributed resources are likely to operate on a larger spatial scale than those using richer environments (Searle et al., 2006). Further, differences between animal genotypes may exist—it is known that the Spælsau (SP) is more gregarious and active and should thus use larger areas compared with the Norwegian White Sheep (NWS) (http://www.nsg.no), which spread out in small groups. However, Jørgensen et al. (2016) were not able to show that sheep used larger home ranges (95% UD) in Spekedalen, a poor grazing area, as compared with Bratthøa, a rich area, or that SP used larger home ranges than NWS on a full summer season scale. We therefore set out to study:

1. how temporal scales affect sheep area use on 50% UD and 95% UD spatial scales in Spekedalen compared with Bratthøa;
2. how temporal scales affect breed area use on 50% UD and 95% UD spatial scales in Spekedalen compared with Bratthøa; and
3. if there is a genotype by environment interaction effect on area use across spatiotemporal scales.

Materials and methods

Study Area

Spekedalen study area (Fig. 1), a part of the Sølendalen grazing commons (hereafter called Spekedalen), is situated in the northern part of Rendalen municipality, Hedmark County, in southeastern Norway (11°21′E, 62°4016′N). Spekedalen covers 97 km^2 and reaches from 688 to 1604 m above sea level (m.a.s.l.). Pasture quality is generally poor (Rekdal, 2007) in terms of sheep grazing quality, with 1% classified as "Very Good," 21% as "Good," and 78% as "Less Good." Bratthøa commons study area (hereafter called Bratthøa) (see Fig. 1) in Vingelen (northern part of Tolga municipality) covers approximately 62 km^2 spanning from 790 to 1229 m.a.s.l. and has in general higher pasture quality (Rekdal, 2009): 12% "Very Good," 48% "Good," and 40% "Less Good." The difference in pasture quality is reflected in the mean lamb autumn weights (1993 — 2013) of 47 kg in rich Bratthøa as compared with 40 kg in poor Spekedalen (Animalia, 2017).

The total density of sheep in the Spekedalen study area was approximately 3 sheep per km^2 in both 2013 and 2014, while in Bratthøa density it was 38 and 40 sheep per km^2 in 2013 and 2014, respectively (www.nibio.no), below their estimated grazing capacities, especially in Spekedalen (Rekdal, 2007). See Jørgensen et al. (2016) for further details regarding the two study areas.

Study Animals

The free-range summer outfield grazing started on 23 June and lasted to 2 September in both 2013 and 2014. Fifty-one lactating ewes of the SP and NWS breeds, of known age and with two lambs at foot, were released into the two study areas, 23 and 28 ewes in Spekedalen (SP: 10, NWS: 13) and Bratthøa (SP: 13, NWS: 15), respectively. The study animals were recruited from six sheep farms that had used the study areas for summer grazing during several years before the study.

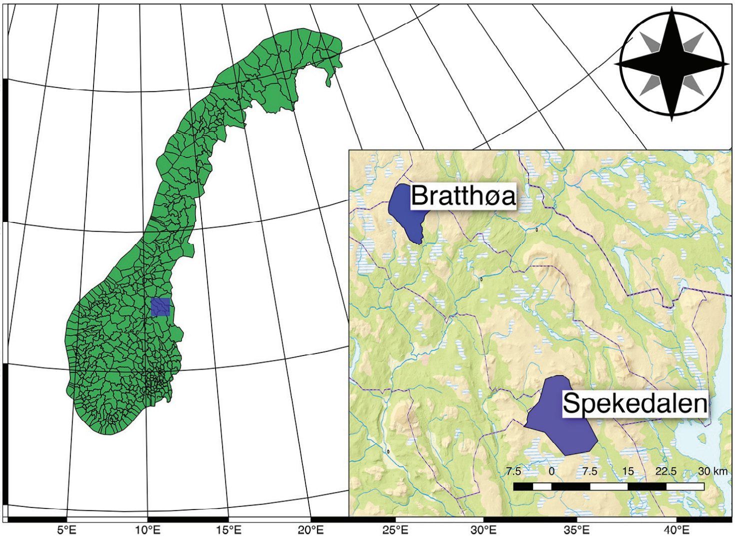


Figure 1. Study areas: Bratthøa study area in the northern part of Tolga municipality and Spekedalen study area in northern part of the Rendalen municipality, both in Hedmark County, Norway (Source: Statens Kartverk 2015). Map was generated using the QGIS version 2.16.3 print composer (QGIS Development Team, 2016).

Please cite this article as: Jørgensen, NH., et al., Does Scale Matter? Variation in Area Use Across Spatiotemporal Scales of Two Sheep Breeds in Two Contrasting Alpine Environments, Rangeland Ecology & Management (2018), https://doi.org/10.1016/j.rama.2017.11.001

The NWS, a relatively new composite breed, is prolific and with heavy lambs and adults (adult ewes often > 90 kg) and is by far the most used breed in Norway. The SP is a short-tailed breed with many of the old Nordic breeds' characteristics; it is smaller than the NWS but with similar litter size. The SP is agile and more gregarious than the NWS. According to NGS (http://www.ngs.no), the NWS and the SP constitute approximately 80% and 13%, respectively, of the registered Norwegian sheep population.

Data Collection

Global Positioning System (GPS) Collars

During the summer grazing seasons of 2013 − 2014, ewes were fitted with Followit Tellus Wildlife Tracking GPS collars that registered their position every 60 min. For the GPS-tracking data a proportion of the data points were removed from the dataset due to a high DOP (dilution of precision). We set the DOP data inclusion criteria to a maximum of 2.0, which is considered “good” (Parkinson et al., 1996). GPS fixes from days around the release and capture were removed, as were unsuccessful GPS fixes (time-out after 90-sec acquisition time). Six collars failed during 2014, and one failed during 2013; the incomplete data from these seven animals were not included. The estimated error rate of the GPS collars is ± 20 m.

The total usable GPS-positions accounted to 73.7% in 2013 (60701 of 82396) and 95.4% in 2014 (70965 of 74400). The information was uploaded to the movebank.org website and mapped according to the movebank.org guidelines (see also Kranstauber et al., 2011). The data were divided into yr (2013 or 2014), area (Spekedalen or Bratthøa), and breed (SP or NWS) for further analyses. In 2013 several of the study animals in Spekedalen were collected before general sheep gathering in September and kept temporarily on seminatural pastures; to avoid data from this period, the study period was reduced to 60 d for both 2013 and 2014 (23 June–23 August) for across-year comparisons.

Area Use Modeling

Dynamic Brownian Bridge Movement Model

The dynamic Brownian Bridge Movement Model method (dBBMM) was used to calculate the UD area, following the guidelines in the Move package (Kranstauber and Smolla, 2016), incorporating the temporal characteristics of the movement paths. Before the calculation of the UD for temporal variation comparisons, the grazing season was divided into intervals of 5, 10, 15, 20, 30, and 60 d. A window size of 24 locations (1 d), a margin of 3 locations, location error of 20 m, raster size of 20 × 20 m, extension of 0.25 and a 60-min time step were used when calculating the dBBMM for each animal. For the spatiotemporal variation analyses, a total of 28 576 UDs were calculated by year, area, breed, UD sizes, interval, and period. Each UD was calculated from the dBBMM UDs summarizing the number of raster cells for each spatial scale (50% and 95%) and temporal scale (interval: 5, 10, 15, 20, 25, 30, and 60 d) (Kranstauber et al., 2011, 2012).

The 5-d minimum for the temporal scales was based on a mean variogram function from the ctmm R package (Fleming and Calabrese, 2016). The mean population variogram leveled out at approximately 5 d, which can thus be considered as the lower temporal limit of where the data are not autocorrelated.

Statistical Analyses

Since all ewes had two lambs at foot, the number of lambs was not included in the analyses. Preliminary analyses showed that distribution of ewes in age classes (3 age classes; 1-yr-old, 2 − 3 yr old, and ≥ 4 yr old) was similar among years, areas, and breeds, and the effects were thus excluded from analyses. The independent variable farm was also initially fitted in the model but contributed little and was thus excluded.

To analyze effects on UD, we used a general linear mixed model (employing the SAS University Edition 3.4 Inc. 2015) mixed procedure:

$$UD = \text{environment} + \text{breed} + \text{yr} + \text{environment} \cdot \text{breed} + \text{ID} + \text{error} \tag{1}$$

where *UD* area (in km^2) is the dependent variable and environment (Spekedalen or Bratthøa), *breed* (NWS or SP), and *yr* (2013 or 2014) are independent variables (Eq. 1). The interaction between environment and breed (environment · breed) was added to the model to account for potential breed-specific responses to changes in environment. Individual ewe ID was fitted as a random effect to account

Table 1
Summary of type 3 *F* tests of fixed-effects breed (Norwegian White Sheep and Spælsau), environment (env: Spekedalen and Bratthøa), and yr (2013 and 2014). Results for each temporal (5-, 10-, 15-, 20-, 30-, and 60-d intervals) and spatial (50% utilization distribution [UD] and 95% UD) scale. Significant probability values *(P)* at the 10% level are shown in bold. *N* denotes number of observations, and *df* denotes Satterthwaite corrected degrees of freedom.

Interval	Fixed effect	50%, *N*	50%, *df*	50%, *F*	50%, *P*	95%, *N*	95%, *df*	95%, *F*	95%, *P*
5 d	Env	588	37.7	8.77	**0.0050**	588	37.5	4.62	**0.0375**
	Breed	588	37.7	2.19	0.1468	588	37.6	2.33	0.1343
	Yr	588	37.9	14.61	**0.0004**	588	37.7	9.92	**0.0030**
	Env · Breed	588	37.7	0.81	0.3736	588	37.6	0.61	0.4388
10 d	Env	304	38	11.49	**0.0015**	304	38	7.67	**0.0083**
	Breed	304	38	5.02	**0.0304**	304	38.1	4.01	**0.0518**
	Yr	304	38	0.34	0.5615	304	38	0.83	0.3664
	Env · Breed	304	38.1	0.00	0.9805	304	38.1	0.18	0.6762
15 d	Env	204	38	11.36	**0.0016**	204	38	5.71	**0.0215**
	Breed	204	38	4.75	**0.0350**	204	38	4.42	**0.0415**
	Yr	204	38	0.44	0.5101	204	38	0.73	0.3977
	Env · Breed	204	38	0.00	0.9692	204	38	0.15	0.7030
20 d	Env	153	38	10.12	**0.0028**	153	38	5.88	**0.0197**
	Breed	153	38	5.44	**0.0245**	153	38	3.77	**0.0589**
	Yr	153	38	0.42	0.5209	153	38	1.17	0.2684
	Env · Breed	153	38	0.00	0.9660	153	38	0.13	0.7241
30 d	Env	102	38	8.40	**0.0059**	102	38	3.90	**0.0550**
	Breed	102	38	5.77	**0.0208**	102	38	3.51	**0.0681**
	Yr	102	38	0.81	0.3734	102	38	1.14	0.2919
	Env · Breed	102	38	0.00	0.9691	102	38	0.12	0.7340
60 d	Env	51	38	6.63	**0.0136**	51	38	1.89	0.1768
	Breed	51	38	4.49	**0.0400**	51	38	3.07	**0.0871**
	Yr	51	38	0.08	0.7794	51	38	1.33	0.2551
	Env · Breed	51	38	0.17	0.6837	51	38	0.33	0.5702

Please cite this article as: Jørgensen, NH., et al., Does Scale Matter? Variation in Area Use Across Spatiotemporal Scales of Two Sheep Breeds in Two Contrasting Alpine Environments, Rangeland Ecology & Management (2018), https://doi.org/10.1016/j.rama.2017.11.001

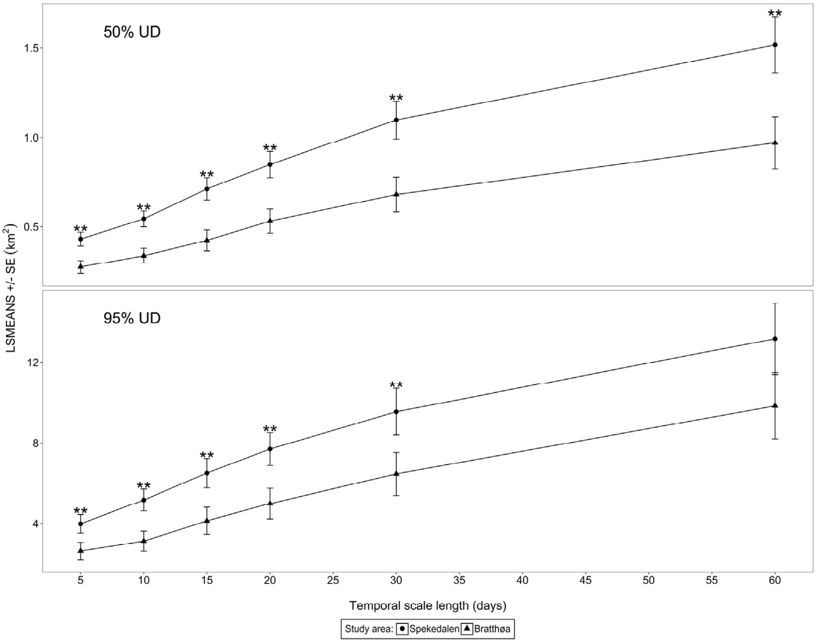


Figure 2. Spatial and temporal least square means (LSMEANS) of utilization distribution (UD) in km^2 for Spekedalen and Bratthøa study areas. 50 denotes 50% UD and 95 denotes 95% UD. Note the different LSMEANS scales in the two panels. The asterisks denote where the study areas differ in terms of UD within a temporal scale (**: 10% level). The model was run separately for each temporal scale for the 50% and 95% UDs. Generated using R version 3.2.0 (R Core Team, 2016), ggplot2 (Wickham, 2009), ggExtra (Attali, 2016), and ggthemes (Arnold, 2016).

for repeated observations of the same animal, and the Satterthwaite option was used to achieve correct degrees of freedom.

The model was repeated across the six temporal scales and for the two spatial scales (i.e., it was run a total of 12 times). Significance level was set to 10%.

Least square means (LSMEANS) for the main fixed effects (Table 1) were calculated for all model repetitions (Figs. 2 and 3).

We chose to perform the analyses using linear models, even with the assumption of normal distributions of the response variables not being met. Various transformations were tested and log-transformation did bring us closer to a normal distribution, but as using transformed variables did not affect results (significance levels), we used nontransformed data for direct interpretability.

Results

Type 3 F-tests of fixed effects for the 50% UDs showed differences between the environment for all temporal scales, while differences for the 95% UDs were found for all but the 60-d temporal scale (see Table 1). Breed differences were found for all but the 5-d intervals' temporal scales for both the 50% UDs and 95% spatial scales (see Table 1). The environment-by-breed interaction term was not significant on any spatial or temporal scale (see Table 1).

UD area estimates (LSMEANS) on both spatial scales showed an increase with coarser temporal scales, with considerable variation within each spatial scale (see Figs. 2 and 3).

In general, SP used larger areas compared with NWS and sheep used larger areas in Spekedalen compared with Bratthøa, on all temporal and on both spatial scales, although not significantly on all spatiotemporal scales (see Figs. 2 and 3).

Discussion

Using the dBBMM to estimate UD enabled us to assess patterns of area use of the two sheep breeds in the two contrasting environments at two spatial and across multiple temporal scales during the summer grazing season. Sheep used larger areas at the 95% UD scale in the poor Spekedalen environment as compared with the rich Bratthøa across all temporal scales, except at the coarsest, and SP had larger UD than NWS at all temporal scales but the finest. At the 50% UD scale, sheep used larger areas in the poor as compared with the rich environment at all temporal scales, whereas SP used larger areas than NWS, at all except the finest temporal scale. No environment-by-breed interactions were found at any spatiotemporal scales.

We found that sheep, in general, used larger areas at the 95% UD scale in Spekedalen compared with Bratthøa, with differences at the 5, 10, 15, 20, and 30-d temporal scales (see Fig. 2). These findings are in line with general optimal foraging theory (Charnov et al., 1976), which predict that herbivores' home range sizes are larger in poor as compared with rich foraging quality environments (e.g., Tufto et al., 1996; Saïd and Servanty, 2005; van Beest et al., 2011). However, the number of sheep released in Bratthøa is closer to the areas' grazing capacity as compared with Spekedalen and should work in the opposite direction. The lack of 95% UD differences between the two environments at the coarsest temporal scale (60 d) could therefore indicate that the density effect first sets in at the seasonal scale, when the resources are starting to be depleted late in the season in Bratthøa.

Indeed, population density is known to affect individual distribution (see review by Bowler and Benton, 2005). In Spekedalen the grazing capacity was estimated to be 50 sheep (including ewes and lambs) per km^2 suitable for sheep grazing (Rekdal, 2007), whereas in Bratthøa the capacity was estimated to be 80 sheep per km^2 suitable for sheep grazing (Rekdal, 2009). The estimated area a ewe and her two lambs

Please cite this article as: Jørgensen, NH., et al., Does Scale Matter? Variation in Area Use Across Spatiotemporal Scales of Two Sheep Breeds in Two Contrasting Alpine Environments, Rangeland Ecology & Management (2018), https://doi.org/10.1016/j.rama.2017.11.001

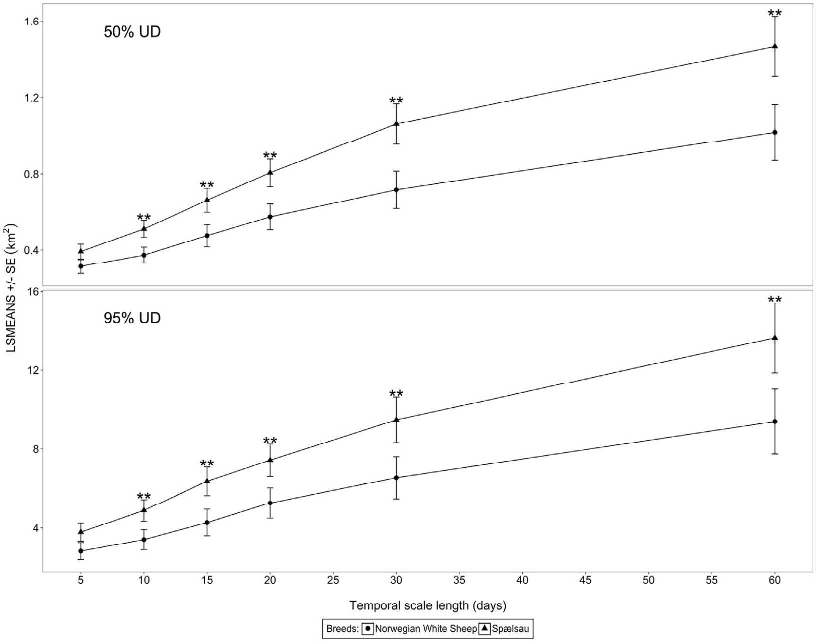


Figure 3. Spatial and temporal least square means (LSMEANS) of utilization distribution (UD) in km^2 for the NWS and SP breeds. 50 denotes 50% UD and 95 denotes 95% UD. Note the different LSMEANS scales in the two panels. The asterisks denote where the study areas differ statistically in terms of UD within a temporal scale (**: 10% level). The model was run separately for each temporal scale for the 50% and 95% UDs. Generated using R version 3.2.0 (R Core Team, 2016), ggplot2 (Wickham, 2009), ggExtra (Attali, 2016), and ggthemes (Arnold, 2016).

would need for maintenance and growth over a summer grazing season (normally 95 d, see Skurdal, 1997), based on Rekdal's grazing capacity estimates and estimated percentage suitable for grazing; 60.1% and 26.2%, in Bratthøa and Spekedalen, respectively, would thus amount to a total area of 0.062 km^2 and 0.23 km^2; that is, ≈48 and ≈12 sheep per km^2, in Bratthøa and Spekedalen, respectively (Rekdal, 2007, 2009). Thus, the total densities in both areas, approximately 3 sheep per km^2 in Spekedalen and 40 sheep per km^2, in Bratthøa (www.nibio.no), were well below the estimated grazing capacities for the two areas, especially in Spekedalen.

Several herbivore studies (Post and Stenseth, 1999; Pettorelli et al., 2011) at coarse temporal scales have underlined the importance of climatic (The North Atlantic Oscillation) and weather-related (winter snow accumulation and melting, as well as summer temperature) landscape processes connected to plant phenology, for the animals' area use pattern. Herbivores are known to follow the new vegetation growth along an altitudinal gradient (see e.g., Albon and Langvatn, 1992; Mysterud et al., 2001). Indeed, at this coarsest spatial and temporal scale the animals are exploring the resources by moving over relatively large areas, probably increasing the individual variations and hence masking the range quality effect. Moreover, the low total density in Spekedalen as compared with the large seasonal 95% UD of a ewe with two lambs (≈12 km^2) implies a high degree of between-sheep overlap in area use. Interestingly, also at the 5-d temporal scale with a mean 95% UD of (≈4 km^2) the spatial overlap is extensive. The pattern is even more apparent in Bratthøa, due to the much higher number of sheep released (≈40 sheep/km^2) and an estimated 95% UD of about 8 and 2 km^2 at seasonal and 5-d scales, respectively. At the 50% UD scale the same pattern appeared, being clearer at all temporal scales—even at the coarsest (see Table 1): UDs were always largest in the poor environment. The 50% UDs contain all intensively used foraging patches, and they will obviously be of general lower quality in Spekedalen as compared with Bratthøa. Accordingly, an animal should optimize the gain of energy at the lowest cost limited by constraining factors when foraging. The lower-quality, fewer, and larger used patches in Spekedalen as compared with Bratthøa (Jørgensen, unpublished results) will affect the residence time. Indeed, the exploratory range behavior seems weaker at the 50% UD scale as compared with the 95% UD scale and the consequence is larger 50% UDs in the poor Spekedalen as compared with the rich Bratthøa. This underlines the hierarchical spatiotemporal dimension and their interaction (Senft et al., 1987).

When comparing the two breeds (see Fig. 3), larger 95% UDs for SP were found at all temporal scales but the finest (5-d temporal scale) (see Table 1). This is counterintuitive, as the heavier NWS's higher metabolic requirement should result in larger UDs compared with SP. Other intrinsic factors may thus have a stronger effect on area use, as reported in several intraspecific studies (e.g., Saïd and Servanty, 2005; Wronski et al., 2006; Saïd et al., 2009). Since all ewes had equal maternal load, having two lambs at foot, we were able to rule out the effect of reproductive status. The same was apparent for ewe's age, which also reflect their within breed's body mass, as the age distribution was similar among years, areas, and breeds. We therefore suggest that the SP, being more gregarious, will deplete food patches faster as compared with NWS, inducing larger 95% UDs. The 95% UD encompasses a number of food patches varying in size and distribution that will affect the residence time. However, at the finest temporal scale there seems to be enough resources within the UD area leading to reduced exploratory movement and thus proportionally equal 95% UD size between breeds.

Larger 50% UD areas were found for SP as compared with NWS at all temporal scales, except at the 5-d temporal scale (see Fig. 3). This is consistent with our findings at the 95% UD scale, with the effects being even

Please cite this article as: Jørgensen, NH., et al., Does Scale Matter? Variation in Area Use Across Spatiotemporal Scales of Two Sheep Breeds in Two Contrasting Alpine Environments, Rangeland Ecology & Management (2018), https://doi.org/10.1016/j.rama.2017.11.001

clearer (see Table 1). SP's flocking behavior would lead to faster depletion of food patches and hence SP would have to move on to other patches within a shorter time-span as compared with NWS, inducing larger SP 50% UDs. Also, this may be amplified by SP preference for high-quality forage as compared with NWS (Steinheim et al., 2005).

At the finest temporal scale, we do not, however, find the previously mentioned patterns. It could be explained by breed-specific forage preferences; also, the effect of gregariousness may simply not have time to manifest at the 5-d temporal level at any of the two spatial scales.

We expected larger relative differences in area use for NWS as compared with SP in a poor versus a rich environment (i.e., we would expect breed-by-environment interactions at both spatial and for all temporal scales). As we did not find any such interactions, we suggest that breed differences in social organization and forage preferences may counterbalance the effect of body mass. The consistent curve patterns, with sheep UD being larger in Spekedalen compared with Bratthøa (see Fig. 2) and SP having larger UD areas than NWS (see Fig. 3) at both spatial scales across all temporal scales, suggest a similar response in both environments. This could explain the proportional consistent smaller 50% UDs; actually, the 50% UD amounted to around one tenth of the 95% UD-size across all temporal scales (see Fig. 3). The fact that the curves in Figures 2 and 3 seem to approach an asymptotic maximum at the coarsest temporal scale imply that an individual's UD overlap within each temporal scale. Had the UDs been shifting in space with no overlap, we would have expected a linear relationship between temporal scale and UD size.

It is known that home range areas in many mammals are handed down from mother to female offspring from generation to generation (Broad et al., 2006). Indeed, this is in line with our findings that year has no effect on either the 50% or the 95% UD size, the exception being at the finest temporal scale (see Table 1). In general, UDs were larger in 2014 as compared with 2013, although only significant at the finest temporal scale. This suggests that the quality of the 2014 grazing range in both environments was lower as compared with 2013. Indeed, Summer 2014 in the study areas was warmer than in 2013 (www.met.no), resulting in earlier plant maturity and reduced plant quality. This is further supported by lower autumn sheep weights found in 2014 as compared with 2013 (Steinheim, unpublished results). Indeed, the breeds foraging movement patterns at the finest temporal scale seem more sensitive to between-year habitat quality variations, as compared with coarser spatiotemporal scales.

Other factors than habitat quality, such as water (Rubenstein, 1989), mineral licks (Valdez and Krausman, 1999), predation (Kuijper et al., 2013), and disturbance (Buuveibaatar et al., 2016), may affect animal range distribution. Water is available throughout the study areas and is not regarded as an important factor in sheep range distribution and use in these two environments. This is a general environmental characteristic of northern alpine and subalpine environments, where summer pastures are moist and fresh, in contrast to arid (Rubenstein, 1989) and semiarid environments (Western, 1975).

We conclude that when comparing area use between contrasting environments and breeds, scales may matter. We notice that the effect of breed and environment on sheep area use is stronger at the 50% UDs as compared with the 95% UDs, at all temporal scales.

Management Implications

Increased competition with other area-extensive businesses challenges the sheep industry in the north Atlantic region (Ross et al., 2016). Our results are important for area use administrators and planners at different management levels, as well as for farmers and commons that need to highlight rangeland area demands. In our study, the estimated area use across temporal scales approached an asymptotic maximum at the coarsest temporal scale and could thus be used as a good estimate of how much space a sheep would use during a grazing season. Hence, when determining total need for grazing area, one have to consider the 95% UD at the seasonal scale. When establishing management plans, breed and environment differences should be taken into account.

Acknowledgments

We thank Michael Angeloff at NIBIO and Rune Granås at NLR Nord-Østerdal for important input and help with logistics, as well as the farmers of Sølendalen and Bratthøa grazing commons for providing us with study animals in the two summer grazing seasons, 2013 and 2014.

References

Albon, S.D., Langvatn, R., 1992. Plant Phenology and the Benefits of Migration in a Temperate Ungulate. Oikos 65:502–513. https://doi.org/10.2307/3545568.

Animalia [WWW Document], 2017. Årsmelding. URL. https://www.animalia.no/globalassets/sauekontrollen—dokumenter/arsmelding-2016-endelig.pdf.

Arnold, J.B., 2016. ggthemes: Extra Themes, Scales and Geoms for "ggplot2".

Attali, D., 2016. ggExtra: Add Marginal Histograms to "ggplot2", and More "ggplot2" Enhancements.

Bartlam-Brooks, H.L.A., Bonyongo, M.C., Harris, S., 2013. How landscape scale changes affect ecological processes in conservation areas: External factors influence land use by zebra (Equus burchelli) in the Okavango Delta. Ecology and Evolution 3:2795–2805. https://doi.org/10.1002/ece3.676.

van Beest, F.M., Rivrud, I.M., Loe, L.E., Milner, J.M., Mysterud, A., 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? The Journal of Animal Ecology 80:771–785. https://doi.org/10.1111/j.1365-2656.2011.01829.x.

Bjørneraas, K., Herfindal, I., Solberg, E.J., Sæther, B.-E.E., van Moorter, B., Rolandsen, C.M., 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. Oecologia 168: 231–243. https://doi.org/10.1007/s00442-011-2072-3.

Bowler, D.E., Benton, T.G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80:205–225. https://doi.org/10.1017/S1464793104006645.

Broad, K.D., Curley, J.P., Keverne, E.B., 2006. Mother-infant bonding and the evolution of mammalian social relationships. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 361:2199–2214. https://doi.org/10.1098/rstb.2006.1940.

Buuveibaatar, B., Mueller, T., Strindberg, S., Leimgruber, P., Kaczensky, P., Fuller, T.K., 2016. Human activities negatively impact distribution of ungulates in the Mongolian Gobi. Biological Conservation 203:168–175. https://doi.org/10.1016/j.biocon.2016.09.013.

Carbone, C., Cowlishaw, G., Isaac, N.J.B., Rowcliffe, J.M., 2005. How far do animals go? Determinants of day range in mammals. The American Naturalist 165:290–297. https://doi.org/10.1086/426790.

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129–136. https://doi.org/10.1016/0040-5809(76)90040-X.

Dayton, P.K., Tegner, M.J., 1984. The importance of scale in community ecology: A kelp forest example with terrestrial analogs. A New Ecology, Novel Approaches to Interactive Systems, pp. 457–481.

Dussault, C., Quellet, J.P., Courtois, R., Huot, J., Breton, L., Jolicoeur, H., 2005. Linking moose habitat selection to limiting factors. Ecography (Copenhagen) 28:619–628. https://doi.org/10.1111/j.2005.0906-7590.04263.x.

Fleming, C.H., Calabrese, J.M., 2016. ctmm: Continuous-Time Movement Modeling.

Fortin, D., Fryxell, J.M., O'Brodovich, L., Frandsen, D., 2003. Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. Oecologia 134:219–227. https://doi.org/10.1007/s00442-002-1112-4.

Horne, J.S., Garton, E.O., Krone, S.M., Lewis, J.S., 2007. Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363. https://doi.org/10.1890/06-0957.1.

Jørgensen, N.H., Steinheim, G., Holand, Ø., 2016. Area use of two sheep breeds in contrasting summer alpine grazing environments in southern Norway. Acta Agriculturae Scandinavica Section A Animal Science:1–7 https://doi.org/10.1080/09064702.2016.1215513.

Killeen, J., Thurfjell, H., Ciuti, S., Paton, D., Musiani, M., Boyce, M.S., 2014. Habitat selection during ungulate dispersal and exploratory movement at broad and fine scale with implications for conservation management. Movement Ecology 2:15. https://doi.org/10.1186/s40462-014-0015-4.

Kranstauber, B., Smolla, M., 2016. move: Visualizing and Analyzing Animal Track Data.

Kranstauber, B., Cameron, A., Weinzerl, R., Fountain, T., Tilak, S., Wikelski, M., Kays, R., 2011. The Movebank data model for animal tracking. Environmental Modelling and Software 26:834–835. https://doi.org/10.1016/j.envsoft.2010.12.005.

Kranstauber, B., Kays, R., LaPoint, S.D., Wikelski, M., Safi, K., 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. The Journal of Animal Ecology 81:738–746. https://doi.org/10.1111/j.1365-2656.2012.01955.x.

Kuijper, D.P.J., de Kleine, C., Churski, M., van Hooft, P., Bubnicki, J., Jędrzejewska, B., 2013. Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. Ecography (Copenhagen) 36:1263–1275. https://doi.org/10.1111/j.1600-0587.2013.00266.x.

Main, M.B., Coblentz, B.E., 1996. Sexual segregation in Rocky Mountain mule deer. Journal of Wildlife Management 60:497–507. https://doi.org/10.2307/3802067.

Please cite this article as: Jørgensen, NH., et al., Does Scale Matter? Variation in Area Use Across Spatiotemporal Scales of Two Sheep Breeds in Two Contrasting Alpine Environments, Rangeland Ecology & Management (2018), https://doi.org/10.1016/j.rama.2017.11.001

Mayor, S.J., Schneider, D.C., Schaefer, J.A., Mahoney, S.P., 2009. Habitat selection at multiple scales. Ecoscience 16:238–247. https://doi.org/10.2980/16-2-3238.

McLoughlin, P.D., Ferguson, S.H., 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. Écoscience (Sainte-Foy) 7:123–130. https://doi.org/10.2307/42902482.

Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R.A., Merrill, E.H., Haydon, D.T., 2010. Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 365:2289–2301. https://doi.org/10.1098/rstb.2010.0082.

Mysterud, A., Langvatn, R., Yoccoz, N.G., Stenseth, N.C., 2001. Plant phenology , migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. The Journal of Animal Ecology 70:915–923. https://doi.org/10.1046/j.0021-8790.2001.00559.x.

Owen-Smith, N., Fryxell, J.M., Merrill, E.H., 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 365:2267–2278. https://doi.org/10.1098/rstb.2010.0095.

Parkinson, B.W., Spilker, J.J., Axelrad, P., Enge, P., American Institute of Aeronautics and Astronautics, 1996. The global positioning system: theory and applications. Volume I. American Institute of Aeronautics and Astronautics.

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., Kausrud, K., 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46. https://doi.org/10.3354/cr00936.

Post, E., Stenseth, N.C., 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322–1339. https://doi.org/10.1890/0012-9658(1999)080[1322:CVPPAN]2.0.CO;2.

QGIS Development Team, 2016. QGIS Geographic Information System. Available at:. http://www.qgis.org.

R Core Team, 2016. R: A Language and Environment for Statistical Computing.

Rekdal, Y., 2007. Vegetasjon og beite i Rendalen østfjell. Skog og Landskap 11:1–68 http://www.skogoglandskap.no/filearchive/oppdrag11_07.pdf.

Rekdal, Y., 2009. Vegetasjon og utmarksbeite i Vingelen. Skog og Landskap 13:1–82 http://www.skogoglandskap.no/filearchive/oppdragsrapport_13_09_vegetasjon_og_utmarksbeite_i_vingelen.pdf.

Ross, L.C., Austrheim, G., Asheim, L.-J., Bjarnason, G., Feilberg, J., Fosaa, A.M., Hester, A.J., Holand, Ø., Jónsdóttir, I.S., Mortensen, L.E., Mysterud, A., Olsen, E., Skonhoft, A., Speed, J.D.M., Steinheim, G., Thompson, D.B.A., Thórhallsdóttir, A.G., 2016. Sheep grazing in the North Atlantic region: A long-term perspective on environmental sustainability. Ambio:551–566 https://doi.org/10.1007/s13280-016-0771-z.

Rubenstein, D.I., 1989. Life history and social organization in arid adapted ungulates. Journal of Arid Environments.

Saïd, S., Servanty, S., 2005. The influence of landscape structure on female roe deer home-range size. Landscape Ecology 20:1003–1012. https://doi.org/10.1007/s10980-005-7518-8.

Saïd, S., Gaillard, J.-M., Duncan, P., Guillon, N., Guillon, N., Servanty, S., Pellerin, M., Lefeuvre, K., Martin, C., Van Laere, G., 2005. Ecological correlates of home-range size in spring–summer for female roe deer (Capreolus capreolus) in a deciduous woodland. Journal of Zoology 267:301–308. https://doi.org/10.1017/S0952836905007454.

Saïd, S., Gaillard, J.-M., Widmer, O., Débias, F., Bourgoin, G., Delorme, D., Roux, C., 2009. What shapes intra-specific variation in home range size? A case study of female roe deer. Oikos 118:1299–1306. https://doi.org/10.1111/j.1600-0706.2009.17346.x.

Searle, K.R., Vandervelde, T., Hobbs, N.T., Shipley, L.A., Wunder, B.A., 2006. Spatial context influences patch residence time in foraging hierarchies. Oecologia 148:710–719. https://doi.org/10.1007/s00442-005-0285-z.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., Swift, D.M., 1987. Large Herbivore Foraging and Ecological Hierarchies. Bioscience 37:789–799. https://doi.org/10.2307/1310545.

Skurdal, E., 1997. Beiting i utmark: i praksis og i plansamanheng. Norsk sau- og geitalslag. https://urn.nb.no/URN:NBN:no-nb_digibok_2009110600062.

Steinheim, G., Nordheim, L.A., Weladji, R.B., Gordon, I.J., Adnoy, T., Holand, O., 2005. Differences in choice of diet between sheep breeds grazing mountain pastures in Norway. Acta Agriculturae Scandinavica Section A Animal Science 55:16–20. https://doi.org/10.1080/09064700510009261.

Tufto, J., Andersen, R., Linnell, J., 1996. Habitat use and ecological correlates of home range size in a small cervid: The roe deer. The Journal of Animal Ecology 65:715–724. https://doi.org/10.2307/5670.

Valdez, R., Krausman, P.R., 1999. Mountain sheep of North America. University of Arizona Press.

Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M.S., Gaillard, J.M., 2009. Memory keeps you at home: A mechanistic model for home range emergence. Oikos 118:641–652. https://doi.org/10.1111/j.1600-0706.2008.17003.x.

Vander Wal, E., Rodgers, A.R., 2012. An individual-based quantitative approach for delineating core areas of animal space use. Ecological Modelling 224:48–53. https://doi.org/10.1016/j.ecolmodel.2011.10.006.

WallisDeVries, M.F., Laca, E.A., Demment, M.W., 1999. The importance of scale of patchiness for selectivity in grazing herbivores. Oecologia 121:355–363. https://doi.org/10.1007/s004420050939.

Western, D., 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. African Journal of Ecology 13:265–286. https://doi.org/10.1111/j.1365-2028.1975.tb00139.x.

Wickham, H., 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Wiens, J.A., 1989. Spatial scaling in ecology. Functional Ecology 3:385–397. https://doi.org/10.2307/2389612.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology https://doi.org/10.2307/1938423.

Wronski, T., Apio, A., Plath, M., 2006. Activity patterns of bushbuck (Tragelaphus scriptus) in Queen Elizabeth National Park. Behavioural Processes 73:333–341. https://doi.org/10.1016/j.beproc.2006.08.003.

Please cite this article as: Jørgensen, NH., et al., Does Scale Matter? Variation in Area Use Across Spatiotemporal Scales of Two Sheep Breeds in Two Contrasting Alpine Environments, Rangeland Ecology & Management (2018), https://doi.org/10.1016/j.rama.2017.11.001

Paper III

SCALE MATTERS - HABITAT USE AND SELECTION BY TWO SHEEP BREEDS IN TWO CONTRASTING ALPINE ENVIRONMENTS

N.H. Jørgensen[1*], G. Steinheim[1], & Ø. Holand[1]

[1] *Department of Animal and Aquacultural Sciences at Faculty of Biosciences, Norwegian University of Life Sciences, Aas, Norway.*
[*] N.H. Jørgensen, Department of Animal and Aquacultural Sciences at Faculty of Biosciences, Norwegian University of Life Sciences, Box 5003, NO-1432 Aas, Norway. Tel: +47 67232624. E-mail: nicolai.jorgensen@nmbu.no

SCALE MATTERS - HABITAT USE AND SELECTION BY TWO SHEEP BREEDS IN TWO CONTRASTING ALPINE ENVIRONMENTS

N.H. Jørgensen[1*], G. Steinheim[1], & Ø. Holand[1]

[1] *Department of Animal and Aquacultural Sciences at Faculty of Biosciences, Norwegian University of Life Sciences, Aas, Norway.*

[*] N.H. Jørgensen, Department of Animal and Aquacultural Sciences at Faculty of Biosciences, Norwegian University of Life Sciences, Box 5003, NO-1432 Aas, Norway. Tel: +47 67232624. E-mail: nicolai.jorgensen@nmbu.no

ABSTRACT

We investigated summer foraging vegetation (divided into three quality classes) use and selection by free-ranging sheep at three temporal (season, 5 days, and hourly) and three spatial (95%, 50%, and 20% utilization distribution (UD)) scales. We fitted 51 ewes of the Norwegian breeds, Norwegian White Sheep (NWS) and Spælsau (SP), with GPS collars in two environments, one poor (Spekedalen) and one rich (Bratthøa), during the grazing seasons 2013-14. Habitat use was affected by vegetation class and environment, but not by breed, at all temporal and spatial scales. In Spekedalen, at all temporal scales, the use of “Less Good” vegetation decreased and “Very Good” increased with finer spatial scales, while the use of “Good” was fairly constant. In Bratthøa, at all temporal scales, the use of “Good” dominated at the coarsest spatial scale, whereas the use of “Very Good” increased and almost equaled the use of “Good”, at the two finest spatial scales. Habitat selection was affected by vegetation class at all temporal scales, by environment at the two finest temporal scales but not by breed. In Spekedalen, both breeds selected for “Very Good”, with increasing intensity with finer temporal scales, while “Good” and “Less Good” were in general selected against. In Bratthøa, the selection for “Very Good” decreased towards neutral and the selection against “Less Good” approached neutral with finer temporal scales, while “Good” was selected weakly against at the two finest scales. The sheep habitat use and selection seem to be affected by the proportion and spatial heterogeneity of the vegetation classes. Indeed, in Spekedalen sheep were able select for the scarce “Very Good” patches at all temporal scales, increasing in intensity with finer temporal scales, while sheep in the rich Bratthøa showed a neutral selection for the two best and most abundant vegetation classes at finer temporal scales. Surprisingly, no breed specific effects were found. Our findings highlight the importance of the scarce “Very Good” patches, at fine scales, in poor Spekedalen. Indeed, this high quality and productive class is probably more important for nutrient extraction and acquisition than the use indicates.

Keywords: grazing, temporal scales, spatial scales, spatiotemporal scales, heterogeneity, dBBMM.

INTRODUCTION

Quantifying livestock foraging habitat use and selection is important for grazing management (Belsky and Blumenthal, 1997; Schuman et al., 1999). These complex behavioral processes are hierarchical, e.g. Johnson (1980), Senft et al. (1987), Mayor et al. (2009), as large herbivores operate on several spatial and temporal scales to maximize nutritional acquisition and hence their fitness (Gaillard et al., 2010). Senft et al. (1987) stated that at coarser spatial scales, the relative importance of plant-herbivore interactions declines and abiotic factors increase in importance. Even at finer scales, habitat use and selection is not purely a function of forage quality and quantity; there will be trade-offs with other fitness related factors, e.g. escape from predators (Lima and Dill, 1990; Mount, 1979; Mysterud and Ims, 1998) and thermoregulation (Dwyer, 2008; Mysterud et al., 1999).

Natural environments are heterogeneous on many temporal and spatial scales (González-Megías et al., 2007; Wiens, 1989). Therefore, on what spatial and temporal scales habitat traits are measured, do matter. At fine scales, (optimal) foraging theory (Charnov, 1976; Rosenzweig, 1981) has been used to predict large herbivores' foraging behavior, see e.g. Bazely (1988), Illius et al. (1992), and Langvatn and Hanley (1993). Given complete information of resources available, an animal should use a food patch until the harvest rate falls below the rates of the averages of all patches. The forager will accordingly spend a higher proportion of foraging time in high versus low quality patches. The utilization will depend on patch distribution and size within the animal's known environment, as movement between patches and exploratory behavior to keep track of the environmental variation are costly time and energy wise (Fagan et al., 2013; Russell et al., 2003) and cognitively challenging (Dall et al., 2005).

Selection is the process where an animal preferentially uses a set of available resources (Morris, 2003). Often the (seasonal) home range is regarded as known by the animal and hence available to choose from in daily foraging, called third-order selection (Johnson, 1980). As pointed out by Johnson (1980) and reviewed by Ofstad et al. (2016) this "depend on the investigator's notion of what components are available to the animals". The choice of scale for defining use and availability is therefore crucial (Aebischer et al., 1993; Börger et al., 2008) and may have implications for understanding the dynamic use and functional selection (Arthur et al., 1996; Mysterud and Ims, 1998).

Animal by environment interaction creates space use patterns (Morales et al., 2010). Jørgensen et al. (2017) concluded that the environment quality affects sheep utilization distribution (UD), resulting in larger UDs in poor environments, at several spatiotemporal scales. Patch use and selection result from complex interactions between an individual and its environment, and is, largely, constrained by the individuals' ability to detect and utilize the spatial heterogeneity (Doligez and Boulinier, 2008). In a poor, homogenous environment, the expected payoff will be about equal in most patches. Indeed, large herbivores would be expected to make the best out of a bad job by utilizing the dominating low quality patches (Witt et al., 2012). Thus, even at low densities, they may not able to fully express their plastic foraging response and hence their selection of specific vegetation patches appear weak. However, what is apparent at a coarse scale can mask utilization of less dominating patches of high quality at finer temporal and spatial scales (Kotliar et al., 1990). Contrastingly, in heterogeneous, rich environments, herbivores may not need to fully realize their selection potential. Thus habitat utilization of dominating patches of high quality, would be rather similar across spatiotemporal scales and preference appear neutral (Mayor et al., 2009).

How, and on what scales, large herbivores are able to respond to environmental variation in time and space is species specific (Fahrig, 1992). On a finer genetic resolution, breeds are tailored to cope with specific environmental conditions (reviewed by

Hoffmann (2013)) and the sheep breeds are seen to respond differently to environmental and climate fluctuations (Nielsen et al. 2013; Bowles et al., 2014; Carson et al., 2009)). Indeed, body size, anatomy and behavior will often vary substantially between breeds, and may result in differences in foraging behavior (Hessle et al., 2008; Steinheim et al., 2005). Interestingly, Jørgensen et al. (2018) found that the smaller Spælsau (SP) responded to a poor environment by utilizing larger areas as compared to the heavier

Norwegian White Sheep (NWS). This is counterintuitive, as the heavier NWS' higher metabolic requirement, should result in larger UDs compared to SP, but they accounted that to foraging and flocking behavior differences between the two breeds.

Our objective was to investigate sheep summer foraging habitat use and selection, and to explore potential breed differences in different environments at different spatiotemporal scales. We selected two alpine sheep grazing environments of different pasture quality: Spekedalen (poor) and Bratthøa (rich) (Rekdal, 2009, 2007). In both environments, the two dominating Norwegian sheep breeds (SP and NWS)), which vary in foraging behavior and diet selection (Steinheim et al., 2005), digestive anatomy (Steinheim et al. 2003), body mass (Drabløs, 1997) and flocking behavior (Hansen et al., 2001), were studied. This enables us to investigate habitat use and selection at different spatiotemporal scales by asking:

- Do sheep differ in use and selection of vegetation classes?
- Does large-scale environment affect the sheep's use and selection of vegetation classes?
- Do breeds differ in use and selection of vegetation classes?
- Is there a breed by environment effect on the use and selection of vegetation classes?

MATERIALS AND METHODS

Study area

The two study areas are situated 62 km apart, in Hedmark County in southeastern Norway (Fig. 1). The Spekedalen area is part of the Sølendalen grazing commons, and situated in the northern part of Rendalen municipality (11°21’ E, 62°4016’ N). Spekedalen covers 97 km^2 and range from 688 to 1604 meters above sea level (m.a.s.l.); habitat quality in Spekedalen is in general poor (Rekdal, 2007). Bratthøa sauhavnelag (hereafter called Bratthøa) (Fig. 1) is a grazing commons in the northern part of Tolga municipality; it covers 62 km^2, between 790 and 1229 m.a.s.l., with in general rich vegetation types, with high habitat quality (Rekdal 2009). The density of sheep in Spekedalen was approximately 3 sheep per km^2 in both 2013 and 2014, whilst in Bratthøa density was 38 and 40 sheep per km^2 in 2013 and 2014 respectively (Angeloff , pers. comm.). For further details on the areas, see Jørgensen et al. (2018, 2016) and Rekdal (2007, 2009).

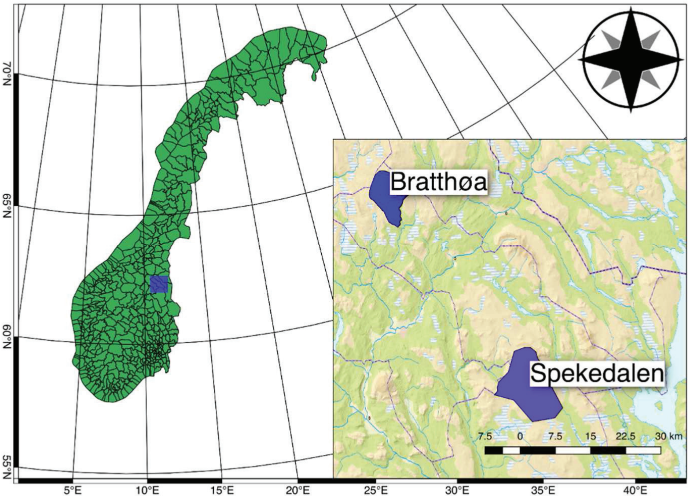


Figure 1. Study areas. Bratthøa in Tolga municipality and Spekedalen in Rendalen municipality, both in Hedmark county, Norway (Source: Statens Kartverk, 2015).

Vegetation classes

We classified the 24 vegetation types present into three classes: “Less Good”, “Good”, or “Very Good”, following the vegetation classification system of (Rekdal, 2007) (Appendix 1). Areas of no grazing values (impediments, water bodies, boulder fields) were omitted from all analyses. Figure 2 shows the distribution and proportion of the vegetation classes in the two study areas. The mean polygon size for each vegetation class in Bratthøa and Spekedalen were: “Very Good”: 0.03 and 0.02 km^2, “Good”: 0.06

and 0.04 km^2, “Less Good”: 0.05 and 0.08 km^2, respectively. We calculated the Shannon Diversity Index (H’) (Morris et al., 2014) for each study area, based on the number of patches of the three grazeable vegetation classes to assess the heterogeneity (Fig. 2).

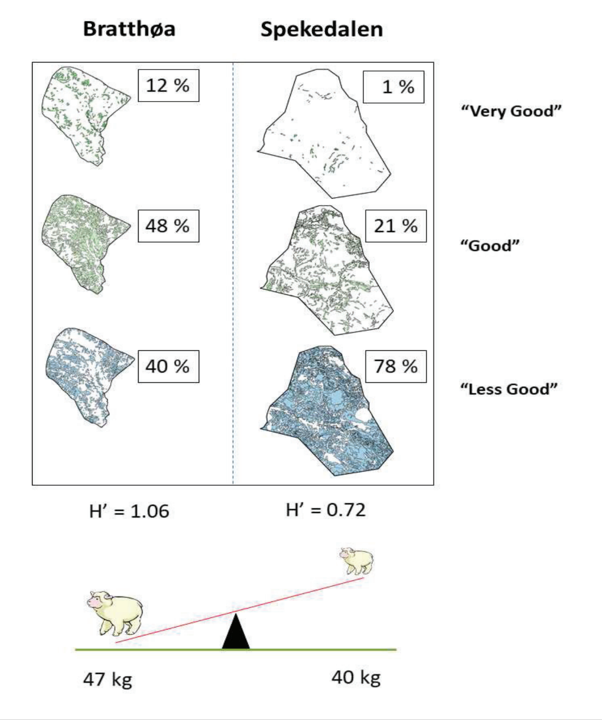


Figure 2. Distribution and proportion of vegetation classes ("Very Good", "Good" and "Less Good") in the two study areas. The percentages denote the proportional total amount of a vegetation class. Shannon Diversity Index (H') denotes the vegetation heterogeneity. The mean autumn lamb live weights (Steinheim et al. unpublished data) are given in the bottom of the figure.

Study animals

The 51 ewes started their free-range outfield grazing season on the 23rd of June and were collected on the 2nd of September in both 2013 and 2014. The lactating ewes of breeds Norwegian White Sheep (hereafter NWS) and Spælsau (hereafter SP), of known age and with two lambs at foot, were released into the study areas, 23 in Spekedalen and 28 in Bratthøa (Table 1). The animals were recruited from six sheep farms that had used the study areas for summer grazing during several years before the study.

Table 1. Number and distribution of study animals by breed (NWS is Norwegian White Sheep; SP is Spælsau) in the two study areas, Spekedalen and Bratthøa, in 2013 and 2014.

	Breed	**2013**	**2014**
Spekedalen	**NWS**	**7**	**6**
	SP	**7**	**3**
Bratthøa	**NWS**	**9**	**6**
	SP	**7**	**6**

The NWS, a relatively new composite breed, is prolific with ≈2.2 in litter size at birth and with heavy lambs and adults (adult ewes often > 90 kg), and is by far the most used breed in Norway. The SP sheep is a short-tailed breed with many of the old Nordic breeds' characteristics, it is smaller than the NWS with a similar (≈ 2.0) litter size. The SP is more gregarious than the NWS and seems to choose a diet with more woody plant species (Steinheim et al., 2005). The NWS and the SP constitute approximately 80% and 13% of the registered Norwegian sheep population, respectively (Sauekontrollen, 2016).

Data collection

GPS collars

Ewes were fitted with Followit Tellus GPS-collars that registered positions every 60 min. The location error of the collars is 20 meters. Some positions were removed from the dataset due to inaccuracy: we set a DOP (dilution of precision) criteria for data inclusion to ≤ 2.0, which is considered "good quality data" (Parkinson et al., 1996). Unsuccessful GPS-fixes (time-out after 90 sec acquisition time) were also removed. One collar failed during 2013 and six failed during 2014; all data from these seven animals were excluded.

In 2013, several of the study animals in Spekedalen were collected prior to general sheep gathering in September, and kept temporarily on semi-natural pastures; thus, only data between 23th June and 23th August were included for both 2013 and 2014, leaving a total of 60 days of observations. Usable GPS-positions accounted to 73.7 % in 2013 (60701 of 82396) and 95.4 % in 2014 (70965 of 74400).

The GPS collars also recorded collar movements in the horizontal (x) and vertical (y) plane in the time the GPS used to get a fix from at least 3 satellites (Time-to-fix: TTF); For each location, activity was calculated as $ACTSUM = \left(\frac{Act\_x}{TTF} + \frac{Act\_y}{TTF}\right)$, where Act_y and Act_x is number of times the activity sensor is triggered during the TTF. Based on calibration tests (Jørgensen unpublished results) animals were defined as inactive at the location if ACTSUM < 0.26 and active if ACTSUM was ≥ 0.26. Only locations where animals were active were included in the analyses.

Calculation

Dynamic Brownian Bridge movement model

The dynamic Brownian bridge movement model method (dBBMM) was used to calculate the utilization distribution (UD) area on the seasonal and the five days scales, following the guidelines in the Move package (Kranstauber et al. (2012)), incorporating the temporal characteristics of the movement paths (Kranstauber et al., 2011; Kranstauber and Smolla, 2016). A window size of 13 locations, a margin of 3 locations, location error of 20 meters, raster size of 20 by 20 meters, extension of 0.35 and a 60 min time step were used when calculating the dBBMM for each animal. We extracted the compound 95, 50 and 20% contours of the dBBMM UDs for the two coarsest temporal scales (seasonal and 5 days' intervals), for each animal.

Moveud

Following Byrne et al. (2014) we used the *moveud* R package (Collier, 2016) to estimate the 95, 50 and 20% UD for each time-step between (hourly scale) relocations, for each sheep. Each time-step was indexed by the time of the first location in each pair of locations. Time-steps with extreme movement variances (DBMvar > 10000), indicating unrealistic large time-step UD size (> ≈ 5 km^2 95% UD), were also omitted; these accounted for some 5% of the time-steps.

Vegetation class extraction and recoding

The three temporal dBBMM UD compound contours were intersected with digital vegetation maps covering both study areas (QGIS Development Team, 2016), and vegetation class (Appendix 1) coverage within the individual UD contours were extracted. We then calculated the corrected mean proportional use of each vegetation class at the seasonal, 5 days' intervals and hourly temporal scales (mean per day) at the three spatial scales (20, 50 and 95% dBBMM UDs).

Data from study animals roaming outside the (unfenced) study areas was included, provided that their UDs intersected the vegetation maps.

Habitat use and selection

To assess the habitat use at three temporal and three spatial scales we prepared three datasets, with data on: 1) the total grazing season, 2) 5 days intervals and 3) hourly (mean daily time-steps).

Within each temporal scale, we defined the mean proportion of each vegetation class within the 95% spatial scale as available to the sheep, and the mean proportional use of each vegetation class within the 20% spatial scale as used (see e.g. Byrne et al. (2014). Habitat selection was calculated using the Manly-Chesson standardized Habitat Selection Index (Chesson, 1978; Manly et al., 1972), which quantifies the relative proportional use of each vegetation classes relative to its proportional availability. Only cases where all vegetation classes were available (95% level) were included in the analyses of habitat selection (Manly et al., 2002). The index formula is:

$$\alpha_i = \frac{{}^{r_i}/_{p_i}}{\sum_{i=1}^{m} {}^{r_i}/_{p_i}}$$

where r_i is the proportional use of vegetation class i, p_i is the proportion of available vegetation class i, and m in the number of vegetation classes. We thus obtained standardized selection ratios by scaling selection ratios between 0 and 1 for each vegetation class. A ratio of 0 would indicate total avoidance, a ratio of 1 total preference and a ratio of 1/m, here m = 3, (1/3) would indicate neutral selection.

Statistical analyses

For the analyses of effect of vegetation class on vegetation use (USE) and selection (SEL) we used general linear mixed models [employing the SAS (SAS University Edition 3.4 Inc. 2015) Mixed procedure]. The Satterthwaite option was used to achieve correct degrees of freedom. The models used were:

USE = V + B*V + E*V +L*V + B*E*V + L*E*V + L*B*V + L*E*B*V + error [1]

SEL = V + E*V + B*V + E*B*V + error [2]

Where **V** is vegetation class ("Very Good", "Good" and "Less Good") , **B** is breed (NWS or SP) , **E** is study area (Bratthøa or Spekedalen) and **L** is spatial level (20, 50, or 95% UDs). Finally, **error** is the residual variance not explained by the model. The interaction between environment (E: Spekedalen or Bratthøa) and vegetation class V (E*V) was included in the models to account for environment specific effects on habitat use and selection. To check for effects of breed (B) we also included B*V. Spatial level L was included to check for effects of spatial level on habitat use.

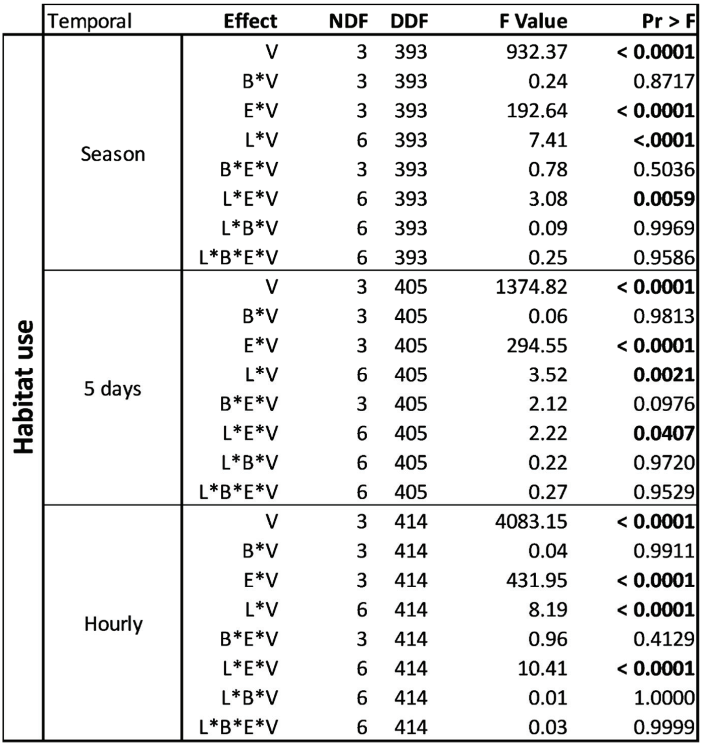
We estimated corrected (least squared) means for the model terms.

RESULTS

Habitat use

At all spatial and temporal scales, the effect of vegetation class and vegetation class-specific effects of environment and spatial level on habitat use were all highly significant ($p < 0.0001$), whereas breed specific effects vegetation class (B*V) and environment specific effects of vegetation class (B*V*E) did not affect the habitat use at any spatial or temporal scales ($p > 0.05$) (Table 2). The effect of vegetation class was in general stronger than the environment specific effect of vegetation class (Table 2.), but both seems to be enhanced with finer temporal scales.

Table 2. Summary of type 3 F tests of fixed effects for the seasonal, 5 days and daily (mean hourly per day) temporal scales for the habitat use. V denotes vegetation class, B denotes breeds, L denotes spatial level and E denotes environments.



	Temporal	Effect	NDF	DDF	F Value	Pr > F
Habitat use	Season	V	3	393	932.37	**< 0.0001**
		B*V	3	393	0.24	0.8717
		E*V	3	393	192.64	**< 0.0001**
		L*V	6	393	7.41	**<.0001**
		B*E*V	3	393	0.78	0.5036
		L*E*V	6	393	3.08	**0.0059**
		L*B*V	6	393	0.09	0.9969
		L*B*E*V	6	393	0.25	0.9586
	5 days	V	3	405	1374.82	**< 0.0001**
		B*V	3	405	0.06	0.9813
		E*V	3	405	294.55	**< 0.0001**
		L*V	6	405	3.52	**0.0021**
		B*E*V	3	405	2.12	0.0976
		L*E*V	6	405	2.22	**0.0407**
		L*B*V	6	405	0.22	0.9720
		L*B*E*V	6	405	0.27	0.9529
	Hourly	V	3	414	4083.15	**< 0.0001**
		B*V	3	414	0.04	0.9911
		E*V	3	414	431.95	**< 0.0001**
		L*V	6	414	8.19	**< 0.0001**
		B*E*V	3	414	0.96	0.4129
		L*E*V	6	414	10.41	**< 0.0001**
		L*B*V	6	414	0.01	1.0000
		L*B*E*V	6	414	0.03	0.9999

In Bratthøa, the breeds used in general the “Good” and “Very Good” the most, at all spatial and temporal scales. In Spekedalen, at all temporal scales the sheep’s’ dominating use of “Less Good” declined with finer spatial scales, whereas the use of “Good” and “Very Good” increased. (Fig. 3). It is noticeable that the use of “Very Good” increased with finer temporal scales (Fig. 3).

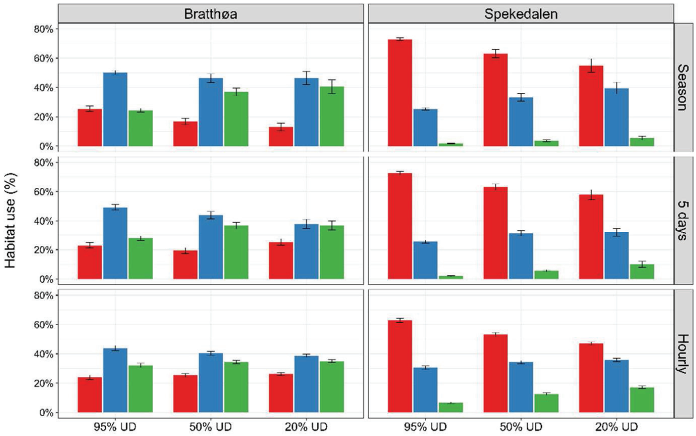


Figure 3. Corrected mean proportional vegetation class use at three temporal scales (seasonal, 5 days period and hourly), three spatial scales (95%, 50% and 20% dBBMM UD) of three vegetation classes suitable for sheep grazing (“Less Good” (red), “Good” (blue) and “Very Good” (green)) in the two study areas (Bratthøa and Spekedalen).

Habitat selection

At all temporal scales, the effect of vegetation class was highly significant ($p < 0.0001$) whereas environment specific effect of vegetation class was significant at the two finest scales. Breed and breed by environment specific effect of vegetation class never affected selection (Table 3).

Table 3. Summary of type 3 F tests of fixed effects for the seasonal, 5 days and daily (mean hourly per day) temporal scales for the habitat selection. V denotes vegetation class, B denotes breeds and E denotes environments.

	Temporal	**Effect**	**NDF**	**DDF**	**F Value**	**Pr > F**
Habitat selection	**Season**	V	3	135	129.67	**< 0.0001**
		B*V	3	135	0.40	0.7554
		E*V	3	135	0.64	0.5914
		E*B*V	3	135	1.22	0.3036
	5 days	V	3	138	215.20	**< 0.0001**
		B*V	3	138	1.52	0.2125
		E*V	3	138	24.89	**< 0.0001**
		E*B*V	3	138	2.00	0.117
	Daily	V	3	138	1187.14	**< 0.0001**
		B*V	3	138	0.74	0.5276
		E*V	3	138	20.42	**< 0.0001**
		E*B*V	3	138	0.72	0.5399

In general, both breeds selected for “Very Good” at all temporal scales in both study areas, while “Good” was generally selected against, expect at the seasonal scale. In Bratthøa, the selection for

"Very Good" and against "Less Good" approached neutral selection with finer temporal scales, while the selection against "Good" remained fairly constant. In Spekedalen, both breeds selected strongly for "Very Good" and in general strongly against both "Good" and "Very Good", at all temporal scales, with the exception of the neutral selection for "Good" (Fig. 4) at the seasonal scale.

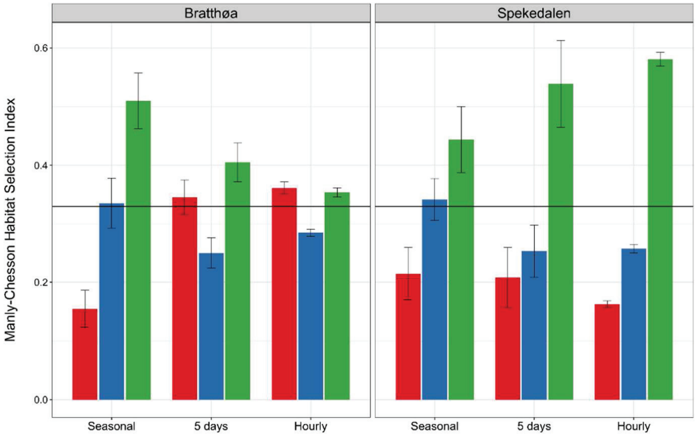


Figure 4. Mean vegetation class ("Less Good" (red), "Good" (blue) and "Very Good" (green)) selection at three temporal scales (seasonal, 5 days period and hourly) in two study areas (Bratthøa and Spekedalen). The black solid horizontal line (33%) represent neutral selection.

DISCUSSION

At three temporal and three spatial scales, we estimated UD. Combined with information from vegetation maps this enabled us to assess patterns of habitat use and selection of the two sheep breeds in the two contrasting environments. As expected, we found an effect of environment and abundance of vegetation class on habitat use at all spatiotemporal scales. The use of “Very Good” was considerably higher in Bratthøa as compared to Spekedalen, whereas “Less Good” was used to a much higher degree in Spekedalen as compared to Bratthøa. Further, the “Good” vegetation class was generally used more in Bratthøa, than in Spekedalen at all scales. Indeed, the abundance of the vegetation classes is an important driver of the habitat use, especially in Spekedalen. It is noteworthy that spatial level within each temporal scale affected habitat use. In Spekedalen, the same habitat use pattern was seen at all temporal scales with a reduced use of “Lees Good” and increased use of “Very Good” being more pronounced at finer temporal scales. The same pattern was seen in Bratthøa at the coarsest temporal scale, to a lesser degree at the two finest temporal scales. Habitat selection was therefore affected by study area at the two finest temporal scales. Indeed, while the vegetation class specific selection in Bratthøa approached neutral selection, the selection pattern in Spekedalen was more pronounced, i.e. selection for “Very Good” and against the two other classes. Surprisingly we were not able to detect breed nor breed by environment differences in foraging behavior, in neither time nor space.

At the seasonal temporal scale, ewes were clearly able to express their plastic foraging response. This was amplified with finer spatial scales and resulted in strong selection for the “Very Good” and against the “Less Good”, especially in Bratthøa. In Spekedalen the estimated proportional use (20% UD) of vegetation classes, is close to their availability (95% UD). Thus, what appears to be making the best of a bad job by the sheep, at the coarsest spatial scale in Spekedalen (Fig. 3), masked a selection for the less abundant patches of high quality. Interestingly, the overall proportion of “Very Good” in Bratthøa amounts to 12% (Fig. 2), whereas the estimated proportional use of this vegetation class at seasonal 95% spatial scale is about 24% (Fig. 3), suggesting a clear selection for “Very Good” also at the landscape scale. The same landscape selection pattern for “Very Good” is also seen in Spekedalen, although here the overall availability is about 1% (Fig. 2) and the use (defined here as 95% UD at seasonal scale) around 2%. This demonstrates that a 12% percentage point difference in use compared to availability in Bratthøa, as compared to a 1% difference in Spekedalen, both results in a strong positive selection. Indeed, the implication of this positive selection for high quality habitats at these two highest spatial scales, within landscape and 95% UD, is much more pronounced area-wise, in Bratthøa as compared to Spekedalen, although the study area is larger and the 95% UDs seems to be somewhat larger in Spekedalen than in Bratthøa (Jørgensen et al. 2018).

At the 5 days' temporal scale we notice the same habitat use patterns as found on the seasonal scale. However, the ewes in Bratthøa were only partly realizing their selection potential, in contrast to in Spekedalen with its stronger selection for "Very Good" (Fig. 4). At the finest temporal (hourly) scale, the habitat use patterns across spatial scales in Bratthøa are rather similar, close to 40% for both "Very Good" and "Good". This results in approximately neutral selection for all vegetation classes (Fig. 4). The ewes do not have to travel that far to find good forage patches and can utilize the patches for a longer period before moving on to the next. This is supported by Jørgensen et al. (unpublished data) showing that sheep travelled shorter mean daily distances in Bratthøa as compared to Spekedalen (≈ 5.5 km vs ≈ 6.6 km). In Spekedalen, the use of "Very Good" clearly increased and the use of "Less Good" decreased with spatial scale. It appears that ewes in Spekedalen are more actively seeking out the "Very Good" quality class, at this hourly temporal scale.

These patches are magnets for the ewes, although they are smaller and more spread out as compared to in Bratthøa (Fig. 2), making them more costly to exploit, both time- and energy-wise. Some of the time used in the "Less Good" dominated matrix may therefore be connected to transportation legs between "Very Good" (and "Good") patches, as we were not able to distinguish between foraging and walking (Jørgensen et al., unpublished data).

Consequently, the time used in “Less Good” is somewhat higher than the actual time foraging in this vegetation class, especially at the 95% spatial scale, where most of these legs are included.

According to theory habitat selection across scales will occur hierarchically (Johnson, 1980), and the relative importance of plant-herbivore interactions will increase toward finer scale (Senft et al., 1987). Our findings are to some degree in accordance with this, at least in poor Spekedalen, where the habitat selection for the scarce “Very Good” patches is indeed getting stronger with finer temporal scale. Although the abundance of the vegetation classes is driving the habitat use, the animals are able to find and utilize “Very Good” patches at the finest spatial scale. In Bratthøa, however, the strongest habitat selection for “Very Good” is noticed at the two coarsest temporal scale, with a decline towards neutral with finer temporal scales. The strong selection for “Very Good” at landscape scale in Bratthøa is amplified by the selection at the “home range” scale and may be attributed to a more heterogeneous patch distribution (Fig. 2) (Kotliar et al., 1990).

Small non-mapped “Very Good” patches in association with moist run-offs and depressions within the “Less Good” and “Good” vegetation classes is of importance for sheep in Spekedalen (Rekdal pers. comm.). The current resolution of the vegetation map (scale 1:10000; Rekdal 2007) is not sufficient to depict these features. This may lead to an underestimation of the use of “Very Good”. For these non-mapped features to emerge, a vegetation mapping at a 1:1000 -

5000 scale would be needed (Rekdal pers. comm.). However, these small patches accounts for less than half a percentage of the total area (Rekdal, pers. comm.). Obviously, the resource resolution will influence our results. In theory, we could have analyzed the use and selection of all the 24 vegetation types. However, some of them have a minor appearance and not all are found in both areas (Appendix 1). We have therefore chosen Rekdal's coarse three level vegetation classification as this is the only empirical based and functional grazing classification system available.

Indeed, the choice of scale for defining habitat use and availability is important (Aebischer et al., 1993; Börger et al., 2008), when assessing how an animal select available resources (Morris, 2003). Several studies assessing habitat selection (see e.g. Byrne et al. 2014) have used estimates of 95% UD as available and 50 % UD as the used resources. But, since a higher contrast between estimates of availability and use can give a clearer result, when assessing habitat preferences (Kauhala and Auttila, 2010), we used the 95% UD as available and 20% UD as use at all three temporal scales. Indeed, based on the habitat use seen in Fig. 3, a choice of 50% UD instead of 20% UD would result in a weaker selection for "Very Good" and against "Less Good" in Spekedalen, whereas the selection in Bratthøa would be affected to a lesser degree. Thus, analyses of habitat use and selection in poor homogeneous Spekedalen seem more sensitive to choice of scale than in the heterogeneous rich Bratthøa. This is also reflected in an increasing mean UD heterogeneity in Spekedalen with finer spatiotemporal scales, in contrast to Bratthøa with a higher and constant heterogeneity index (H') (Appendix 2).

Breed and breed by environment did not affect habitat use nor habitat selection at any temporal nor spatial scales (Table 2, 3). This is somewhat surprising: SP and NWS differ in body size, their digestive system (Steinheim et al., 2003), flocking behavior (Hansen et al., 2001) and are known to differ in forage preferences (Steinheim et al., 2005) and in their area use (Jørgensen et al., 2018). Further, this suggests that the breeds' plastic foraging response to the proportion and spatial distribution of the vegetation classes in the two environments was similar. This is in line with (Rook and Tallowin, 2003) who claimed that there is limited evidence of breed differences in vegetation and dietary choice. However, (Sæther et al., 2006) reported differences in vegetation and plant preferences in a poor environment between high and moderate yield Norwegian dairy cattle breeds, whereas no differences was found in a rich environment indicating a breed by environment interaction. Indeed, the UK stratified sheep system is partly based on breeds differences in their utilization of pasture gradients (Parkin, 2015).

Little information is available how density may affect habitat use and selection of sheep (but see Mobaek et al. (2009)). Sheep can graze down the swards heights to a minimum and are known to withstand rather high densities before density effects are seen (Armstrong et al., 1997). Rekdal (2007, 2009) estimated the grazing capacity to be 4 times higher in Bratthøa than in Spekedalen, i.e. ≈

48 and ≈ 12 sheep per km^2 respectively, both above the actual density seen, especially in Spekedalen. We therefore conclude that density plays a minor role in relation to habitat use and selection in the two areas.

Salt blocks are known to influence sheep's spatial distribution (Arnold and Dudzinski, 1978). In Bratthøa 11 salt blocks were distributed, whereas in Spekedalen only three were put out (Granås, pers. comm.). A ewe, on average, visited a salt block every 15 days during the grazing season in Bratthøa, as compared every six days in Spekedalen. The lower salt block density and the higher visiting rate in Spekedalen as compared to Bratthøa may contribute to explain the longer daily walking distance and larger UD seen in Spekedalen (Jørgensen et al., 2018). However, based on the distribution and time spent at the salt blocks, we feel confident that they did not influence the habitat use and selection differences seen between the two study areas largely.

The landscape of fear may influence how preys are utilizing their resources (Laundré et al., 2010). The estimated losses of sheep to predators in Spekedalen in 2013 and 2014 amounted to less than 10% (Granås, pers. comm.), whereas in Bratthøa these losses were neglectable. Obviously, the predator pressure was highest in Spekedalen, but none of the GPS collared ewes was lost. Further, based on the activity and movement patterns of the GPS ewes in Spekedalen we have no indication that any of them were exposed to predator attacks. The predator losses in Spekedalen were occasionally very high in the late 1990s and the early 2000s (http://www.rovbase.no/). This could influence learning and transfer of knowledge over generation and may influence foraging behavior (Laundré et al., 2010), but we conclude that the study animals' habitat use and selection in Spekedalen were not heavily influenced by predators.

In general, daily intake is considered a function of time spent grazing (Newman et al., 1995). Nevertheless, time foraging does not necessarily reflect a vegetation class' importance for nutrient extraction and acquisition, as forage intake rate and quality is expected to be higher in high quality patches (Van Soest, 1994). Indeed, vegetation type productivity, biomass quality and degree of utilizable are the key factors to estimate a vegetation type's grazing value for sheep (see Rekdal (2001)) and form the backbone to classify pasture quality of consolidated broader vegetation classes such as the ones used here. We therefore conclude that although the sheep in Spekedalen spend more than half of their time foraging in the "Less Good" vegetation class and their use of "Very Good" does not exceed 20% even at the finest spatiotemporal scale, the energy extraction and acquisition from the two classes are closer to each other than simple time-budget interpretations might indicate. This point to the obvious fact, that "Very Good" is more important for "harvesting" net energy for growth in poor environment than reflected in use.

While White (1983) assumed the same energy costs for animals foraging selectively or not, we argue that energy expenditure for transportation between as well as searching for “Very Good” patches is higher in Spekedalen as compared to Bratthøa. The lower lamb autumn weight, in Bratthøa as compared to Spekedalen (47 kg versus 40 kg, see Fig. 2), can be explained by the cost of being selective.

Conclusion

Study area, vegetation class within study area and spatial level affected habitat use at all temporal scales. In poor Spekedalen at the 95% spatial scale both breeds seem to make the best of a bad job. However, they are able to find and use the sparsely distributed “Very Good” patches at finer spatial scales. This result in a clear and increasing selection, at finer temporal scales, for “Very Good” at the expense of selection for “Less Good” and “Good”, in spite of the two latter being clearly used the most. “Very Good” seems more important for the sheep in terms of net energy harvested in a poor environment, than reflected in actual use. In Bratthøa, both breeds respond to the more numerous, larger and more widely distributed patches of “Very Good”, typical for a rich and diverse resource base, by clear selection at the coarsest temporal scale. Thus, even if sheep in Bratthøa do not select strongly for “Very Good” at the two finest temporal scales, as in Spekedalen, the vegetation class together with “Good” are used the most, and are the stable part of their diet.

Clearly, sheep, although not breed specific, showed a plastic response to the spatiotemporal distribution of the foraging resources.

Management implications

Scale in time and space is important to understand the ewes' grazing behavior and can provide insight into how and which vegetation classes they use and prefer on rich and poor grazing pastures. Indeed, they do respond differently. It is therefore imperative to convey the importance of scale, when one speaks of land use. We have shown that breed as such in a management perspective, may not be crucial for use and vegetation class selection in areas with clearly different grazing quality. What matters is the landscape heterogeneity, its overall range quality and especially the proportion and distribution of high quality resources. The results are not necessarily directly transferrable to other pastures in other regions, but they are an important contribution to understanding sheep's plastic foraging capabilities in contrasting environments.

Acknowledgements

This work was supported by Småfefondet, NMBU and Norwegian Research Council (NFR 208036/010). We thank Michael Angeloff, Yngve Rekdal and Jørgen Todnem, NIBIO, Rune Granås at NLR Nord-Østerdal, and the farmers of Sølendalen and Bratthøa grazing areas for lending us research animals in the two summer grazing season 2013 and 2014. In addition, we thank Bret Collier for valuable input and suggestions.

REFERENCES

Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional Analysis of Habitat Use From Animal Radio-Tracking Data. Ecology 74, 1313–1325. https://doi.org/10.2307/1940062

Armstrong, H.M., Gordon, I.J., Hutchings, N.J., Illius, A.W., Milne, J.A., Sibbald, A.R., 1997. A Model of the Grazing of Hill Vegetation by Sheep in the UK. II. The Prediction of offtake by Sheep. J. Appl. Ecol. 34, 186. https://doi.org/10.2307/2404858

Arnold, G.W., Dudzinski, M.L., 1978. Ethology of free-ranging domestic animals. Amsterdam, Elsevier Sci. 1–125.

Arthur, S.M., Manly, B.F.J., McDonald, L.L., Garner, G.W., 1996. Assessing Habitat Selection when Availability Changes. Ecology 77, 215–227. https://doi.org/10.2307/2265671

Bazely, D.R., 1988. Foraging behaviour of sheep (Ovis aries L.) grazing on swards of perennial ryegrass (Lolium perenne L.). Dr Leonard Pol. thesis Digit.

Belsky, A.J., Blumenthal, D.M., 1997. Effects of Livestock Grazing on Stand Dynamics and Soils in Upland Forests of the Interior West. Efectos del Pastoreo sobre la Dinamica de Arboles y Suelos en Bosques en el Altiplano del Occidente Interior. Conserv. Biol. 11, 315–327. https://doi.org/10.1046/j.1523-

1739.1997.95405.x

Bowles, D., 2015. Recent advances in understanding the genetic resources of sheep breeds locally-adapted to the UK uplands: opportunities they offer for sustainable productivity. Front. Genet. 6, 24. https://doi.org/10.3389/fgene.2015.00024

Byrne, M.E., Clint McCoy, J., Hinton, J.W., Chamberlain, M.J., Collier, B.A., 2014. Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. J. Anim. Ecol. 83, 1234–1243. https://doi.org/10.1111/1365-2656.12205

Börger, L., Dalziel, B.D., Fryxell, J.M., 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecol. Lett. 11, 637–650. https://doi.org/10.1111/j.1461-0248.2008.01182.x

Charnov, E.L., 1976. Optimal Foraging: Attack Strategy of a Mantid. Am. Nat. 110, 141. https://doi.org/10.1086/283054

Chesson, J., 1978. Mesuring preference in selective predation. Ecology 59, 211–215. https://doi.org/10.2307/1936364

Collier, B., 2016. moveud: moveud: Dynamic brownian bridge movement model individual time-step utilization distributions (R 3.2.5 Build).

Dall, S., Giraldeau, L., Olsson, O., McNamara, J., Stephens, D.,

2005. Information and its use by animals in evolutionary ecology. Trends Ecol. Evol. 20, 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Doligez, B., Boulinier, T., 2008. Habitat Selection and Habitat Suitability Preferences. Encycl. Ecol. 1810–1830. https://doi.org/doi: DOI: 10.1016/B978-008045405-4.00015-X

Drabløs, D., 1997. Soga om smalen: jubileumsskrift Norsk sau-og geitalslag 1947±1997 (The tale of the sheep: festschrift for the Norwegian sheep and goat breeders' association 1947 -1997). Norwegian Sheep and Goat Breeders., Oslo.

Dwyer, C.M., 2008. Environment and the Sheep, in: The Welfare of Sheep. Springer Netherlands, Dordrecht, pp. 41–79. https://doi.org/10.1007/978-1-4020-8553-6_2

Fagan, W.F., Lewis, M.A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U.E., Tang, W., Papastamatiou, Y.P., Forester, J., Mueller, T., 2013. Spatial memory and animal movement. Ecol. Lett. 16, 1316–1329. https://doi.org/10.1111/ele.12165

Fahrig, L., 1992. Relative importance of spatial and temporal scales in a patchy environment. Theor. Popul. Biol. 41, 300–314. https://doi.org/10.1016/0040-5809(92)90031-N

Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., Van Moorter, B., 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 365, 2255–2265. https://doi.org/10.1098/rstb.2010.0085

González-Megías, A., María Gómez, J., Sánchez-Piñero, F., 2007. Diversity-habitat heterogeneity relationship at different spatial and temporal scales. Ecography (Cop.). 30, 31–41. https://doi.org/10.1111/j.2006.0906-7590.04867.x

Hansen, I., Christiansen, F., Hansen, H.S., Braastad, B., Bakken, M., 2001. Variation in behavioural responses of ewes towards predator-related stimuli. Appl. Anim. Behav. Sci. 70, 227–237. https://doi.org/10.1016/S0168-1591(00)00155-6

Hessle, A., Wissman, J., Bertilsson, J., Burstedt, E., 2008. Effect of breed of cattle and season on diet selection and defoliation of competitive plant species in semi-natural grasslands. Grass Forage Sci. 63, 86–93. https://doi.org/10.1111/j.1365-2494.2007.00616.x

Hoffmann, I., 2013. Adaptation to climate change – exploring the potential of locally adapted breeds. animal 7, 346–362. https://doi.org/10.1017/S1751731113000815

Illius, A.W., Clark, D.A., Hodgson, J., 1992. Discrimination and Patch Choice by Sheep Grazing Grass-Clover Swards. J. Anim. Ecol. 61, 183. https://doi.org/10.2307/5521

Johnson, D.H., 1980. The Comparison of Usage and Availabilty Measurements for Evaluating resource Preference. Ecology 61, 65–71. https://doi.org/10.2307/1937156

Jørgensen, N.H., Steinheim, G., Holand, Ø., 2018. Does Scale Matter? Variation in Area Use Across Spatiotemporal Scales of Two Sheep Breeds in Two Contrasting Alpine Environments. Rangel. Ecol. Manag. https://doi.org/10.1016/j.rama.2017.11.001

Jørgensen, N.H., Steinheim, G., Holand, Ø., 2017. Does scale matter? Variation in area use across spatiotemporal scales of two sheep breeds in two contrasting alpine environments. Rangel. Ecol. Manag. 11. https://doi.org/10.1016/j.rama.2017.11.001

Jørgensen, N.H., Steinheim, G., Holand, Ø., 2016. Area use of two sheep breeds in contrasting summer alpine grazing environments in southern Norway. Acta Agric. Scand. Sect. A — Anim. Sci. 1–7. https://doi.org/10.1080/09064702.2016.1215513

Kauhala, K., Auttila, M., 2010. Estimating habitat selection of badgers - A test between different methods. Folia Zool. 59, 16–25.

Kotliar, N.B., Wiens, J.A., Wiens Kotliar, J.A., Wiens, N.B., Kotliar, N.B., Wiens, J.A., 1990. Multiple Scales of Patchiness and Patch Structure: A Hierarchical Framework for the Study of Heterogeneity Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Source: Oikos OIKOS 59, 253–260.

Kranstauber, B., Cameron, A., Weinzerl, R., Fountain, T., Tilak, S., Wikelski, M., Kays, R., 2011. The Movebank data model for animal tracking. Environ. Model. Softw. 26, 834–835. https://doi.org/10.1016/j.envsoft.2010.12.005

Kranstauber, B., Kays, R., LaPoint, S.D., Wikelski, M., Safi, K., 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. J. Anim. Ecol. 81, 738–746. https://doi.org/10.1111/j.1365-2656.2012.01955.x

Kranstauber, B., Smolla, M., 2016. move: Visualizing and Analyzing Animal Track Data.

Langvatn, R., Hanley, T.A., 1993. Feeding-patch choice by red deer in relation to foraging efficiency - An experiment. Oecologia 95, 164–170. https://doi.org/10.1007/BF00323486

Laundré, J.W., Hernández, L., Ripple, W.J., 2010. The Landscape of Fear: Ecological Implications of Being Afraid. Open Ecol. J. 3, 1–7.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640. https://doi.org/10.1139/z90-092

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource selection by animals: statistical design and analysis for field studies. Technology 221. https://doi.org/10.1007/0-306-48151-0

Manly, B.F.J., Miller, P., Cook, L.M., 1972. Analysis of a Selective Predation Experiment. Am. Nat. 106, 719–736. https://doi.org/10.1086/282808

Mayor, S.J., Schneider, D.C., Schaefer, J.A., Mahoney, S.P., 2009. Habitat selection at multiple scales. Écoscience 16, 238–247. https://doi.org/10.2980/16-2-3238

Mobaek, R., Mysterud, A., Egil Loe, L., Holand, Ø., Austrheim, G., 2009. Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach. Oikos 118, 209–218. https://doi.org/10.1111/j.1600-0706.2008.16935.x

Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R.A., Merrill, E.H., Haydon, D.T., 2010. Building the bridge between animal movement and population dynamics. Philos. Trans. R. Soc. B Biol. Sci. 365, 2289–2301. https://doi.org/10.1098/rstb.2010.0082

Morris, D.W., 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136, 1–13. https://doi.org/10.1007/s00442-003-1241-4

Morris, E.K., Caruso, T., ßois Buscot, F., Fischer, M., Hancock, C., Maier, T.S., Meiners, T., M€ Uller, C., Obermaier, E., Prati, D., Socher, S.A., Sonnemann, I., W€ Aschke, N., Wubet, T., Wurst, S., Rillig, M.C., Morris, C.E.K., 2014. Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. Ecol. Evol. 4, 3514–3524. https://doi.org/10.1002/ece3.1155

Mount, L.E., 1979. Adaptation to thermal environment. Man and his productive animals. Adapt. to Therm. Environ. Man his Product. Anim.

Mysterud, A., Ims, R.A., 1998. Functional responses in habitat use: Availability influences relative use in trade-off situations. Ecology 79, 1435–1441. https://doi.org/10.1890/0012-9658(1998)079[1435:FRIHUA]2.0.CO;2

Mysterud, A., Lian, L.-B., Hjermann, D.Ø., 1999. Scale-dependent trade-offs in foraging by European roe deer (Capreolus capreolus) during winter. Can. J. Zool. 77, 1486–1493. https://doi.org/10.1139/z99-118

Newman, J.A., Parsons, A.J., Thornley, J.H.M., Penning, P.D., Krebs, J.R., 1995. Optimal Diet Selection by a Generalist

Grazing Herbivore. Funct. Ecol. 9, 255. https://doi.org/10.2307/2390572

Nielsen, A., Steinheim, G., Mysterud, A., 2013. Do different sheep breeds show equal responses to climate fluctuations? Basic Appl. Ecol. 14, 137–145. https://doi.org/10.1016/j.baae.2012.12.005

Ofstad, E.G., Herfindal, I., Solberg, E.J., Sæther, B.-E., 2016. Home ranges, habitat and body mass: simple correlates of home range size in ungulates. Proc. R. Soc. B Biol. Sci. 283, 20161234. https://doi.org/10.1098/rspb.2016.1234

Parkin, S.R., 2015. British sheep breeds. Shire Publications.

Parkinson, B.W., Spilker, J.J., Axelrad, P., Enge, P., American Institute of Aeronautics and Astronautics., 1996. The global positioning system : theory and applications. Volume I. American Institute of Aeronautics and Astronautics.

QGIS Development Team, 2016. QGIS Geographic Information System.

Rekdal, Y., 2009. Vegetasjon og utmarksbeite i Vingelen. Skog og Landsk. 13, 1–82. https://doi.org/http://www.skogoglandskap.no/filearchive/oppdragsrapport_13_09_vegetasjon_og_utmarksbeite_i_vingelen.pdf

Rekdal, Y., 2007. Vegetasjon og beite i Rendalen østfjell. Skog og

Landsk. 11, 1–68. https://doi.org/http://www.skogoglandskap.no/filearchive/oppdrag11_07.pdf

Rekdal, Y., 2001. Husdyrbeite i fjellet. Vegetasjonstypar og beiteverdi.

Rook, A.J., Tallowin, J.R.B., 2003. Grazing and pasture management for biodiversity benefit. Anim. Res 52, 181–189. https://doi.org/10.1051/animres:2003014

Rosenzweig, M.L., 1981. A Theory of Habitat Selection. Ecology 62, 327. https://doi.org/10.2307/1936707

Russell, R.E., Swihart, R.K., Feng, Z., 2003. Population consequences of movement decisions in a patchy landscape. Oikos 103, 142–152. https://doi.org/10.1034/j.1600-0706.2003.12418.x

Sauekontrollen, 2016. Årsmelding.

Schuman, G.E., Reeder, J.D., Manley, J.T., Hart, R.H., Manley, W.A., 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecol. Appl. 9, 65–71. https://doi.org/10.1890/1051-0761(1999)009[0065:IOGMOT]2.0.CO;2

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., Swift, D.M., 1987. Large Herbivore Foraging and

Ecological Hierarchies. Bioscience 37, 789–799. https://doi.org/10.2307/1310545

Steinheim, G., Nordheim, L.A., Weladji, R.B., Gordon, I.J., Adnoy, T., Holand, O., 2005. Differences in choice of diet between sheep breeds grazing mountain pastures in Norway. Acta Agric. Scand. Sect. A Anim. Sci. 55, 16–20. https://doi.org/10.1080/09064700510009261

Steinheim, G., Nordheim, L., Weladji, R., Holand, Ø., Ådnøy, T., 2003. Digestive Tract Anatomy of Norwegian Sheep: Difference Between Breeds. Acta Agric. Scand. Sect. A - Anim. Sci. 53, 155–158. https://doi.org/10.1080/09064700310012999

Sæther, N.H., Sickel, H., Norderhaug, A., Sickel, M., Vangen, O., 2006. Plant and vegetation preferences for a high and a moderate yielding Norwegian dairy cattle breed grazing semi-natural mountain pastures. Anim. Res. 55, 367–387. https://doi.org/10.1051/animres:2006033

Van Soest, P.J., 1994. Nutritional ecology of the ruminant. Comstock Pub.

White, R.G., 1983. Foraging Patterns and Their Multiplier Effects on Productivity of Northern Ungulates. Oikos 40, 377. https://doi.org/10.2307/3544310

Wiens, J.A., 1989. Spatial scaling in ecology. Funct. Ecol. 3, 385–397. https://doi.org/10.2307/2389612

Witt, J.C., Webster, C.R., Froese, R.E., Drummer, T.D., Vucetich, J.A., 2012. Scale-dependent drivers of ungulate patch use along a temporal and spatial gradient of snow depth. Can. J. Zool. 90, 972–983. https://doi.org/10.1139/z2012-065

APPENDIX

Appendix 1.

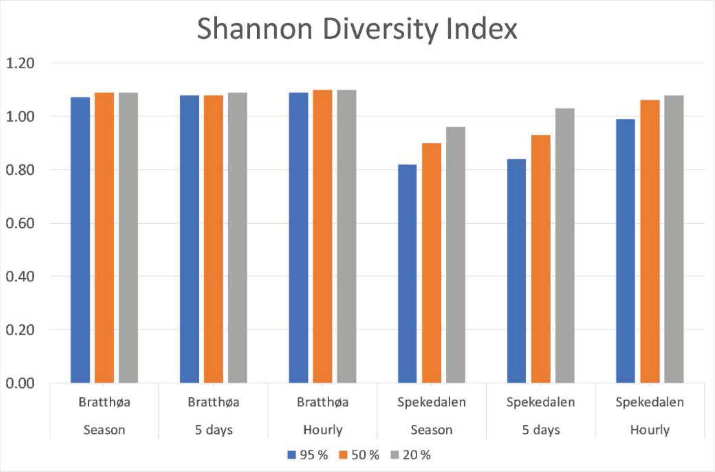
Vegetation classes based on 24 vegetation types. % is the percentage of area a given vegetation type covers in Spekedalen and Bratthøa study areas, respectively (Rekdal, 2009). Bold font type indicates the vegetation class where a given vegetation type is pronounced if classified in more than one vegetation class.

Vegetation type		Spekedalen		Bratthøa	
		%	Class	%	Class
1a	Moss snow-bed	0.12	LG	0.55	LG
1b	Sedge and grass snow-bed	0.48	**G**/LG	3.78	**G**/LG
1c	Stone polygon	2.11	LG	0.29	LG
2b	Dry grass heath	11.30	**LG**/G	2.30	LG
2c	Lichen heath	32.53	LG	20.39	LG
2d	Mountain avens heath	-	-	0.14	LG
2e	Dwarf shrub heath	22.68	**G**/LG	29.26	**G**/LG
2f	Alpine heather heath	3.32	LG	-	-
3a	Low herb meadow	0.03	VG	4.49	VG
3b	Tall forb meadow	0.62	VG	5.20	VG
4a	Lichen- and heather birch forest	9.63	LG	-	-
4b	Bilberry birch forest	4.68	**G**/VG	11.99	G
4c	Meadow birch forest	0.55	VG	2.45	VG
6a	Lichen- and heather pine forest	3.04	LG	-	-

8b	Bog forest	-	-	0.01	LG
8c	Poor swamp forest	0.02	LG	0.05	LG
8d	Rich swamp forest	0.06	G	0.56	G
9a	Bog	3.51	LG	0.64	LG
9b	Deer-gras fen	0.00	LG	-	-
9c	Fen	5.18	LG	17.48	**LG**/G
9d	Mud-bottom fens and bogs	0.02	LG	0.06	LG
9e	Sedge marsh	0.06	LG	0.08	LG
11a	Fully cultivated land	0.01	VG	0.02	VG
11b	Cultivated pastures	0.04	VG	0.26	VG

Appendix 2.

Mean Shannon Diversity Index (H') (Morris et al., 2014) based on the number of patches of the three grazeable vegetation classes for each individual 95%, 50% and 20% dBBMM UDs at three temporal scales (seasonal, 5 days period and hourly) in two study areas (Bratthøa and Spekedalen), to assess the heterogeneity.



20.04.2017

FORM 4.7 Errata

Correcting formal errors in the PhD thesis (cf. section15.3-2 in the PhD regulations)

The PhD candidate may after submitting the thesis apply to correct formal errors in the thesis. An application to correct formal errors must be submitted no less than four (4) weeks before the disputation. Such an application can be made only once.

Thesis title:	Sheep breeds in contrasting environments - pasture utilization at different spatiotemporal scales

Changes are in bold font

Page number	Paragraph	Change from	Change to
III	2	Using general mixed models I was thus able to infer area use across spatiotemporal scales, when both active and inactive, (papers I and II), habitat use across spatiotemporal scales and habitat selection, when active, (paper III) for both breeds in both environments, using a resource selection function (RSF) approach.	Using **general linear models and general linear mixed models** I was thus able to infer area use across spatiotemporal scales, when both active and inactive, (papers I and II), **and habitat use and selection when active, across spatiotemporal scales** for both breeds in both environments, using a resource selection function (RSF) approach **(paper III).**
30	2	4.6. Statistical analyses To analyze effects on UD (papers I and II) and effect of vegetation class on vegetation use and selection (paper III), I used a general linear mixed models (employing the SAS University Edition 3.4 Inc. 2015) with restricted maximum likelihood estimates and asymptotic standard errors.	4.6. Statistical analyses To analyze effects on UD (papers I and II) **and on** vegetation use and selection (paper III), **I used general linear models, in paper II including general linear mixed models** with restricted maximum likelihood estimates and asymptotic standard errors **(employing the SAS University Edition 3.4 Inc. 2015).**

20.04.2017

This form will be signed by the PhD candidate and the main supervisor and must be sent to the faculty for approval. The approved errata must be archived in the PhD candidate's doctoral archive and must be attached to the final thesis print version as the last page of the thesis.

Date and signature:

PhD candidate (Author):	03.04.2018

Main supervisor:	

Errata approved by the faculty: Yes ☒ No ☐

For the faculty:	, FUU 3.4.2018

ISBN: 978-82-575-1503-4
ISSN: 1894-6402

Norwegian University
of Life Sciences

Postboks 5003
NO-1432 Ås, Norway
+47 67 23 00 00
www.nmbu.no

97853 / ANDVORDGRAFISK.NO