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Source: Rangeland Ecology and Management, 71(2) : 189-195

Published By: Society for Range Management

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

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Rangeland Ecology & Management 71 (2018) 189–195

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☆

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ARTICLE INFO

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

Key Words:
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.

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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).

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

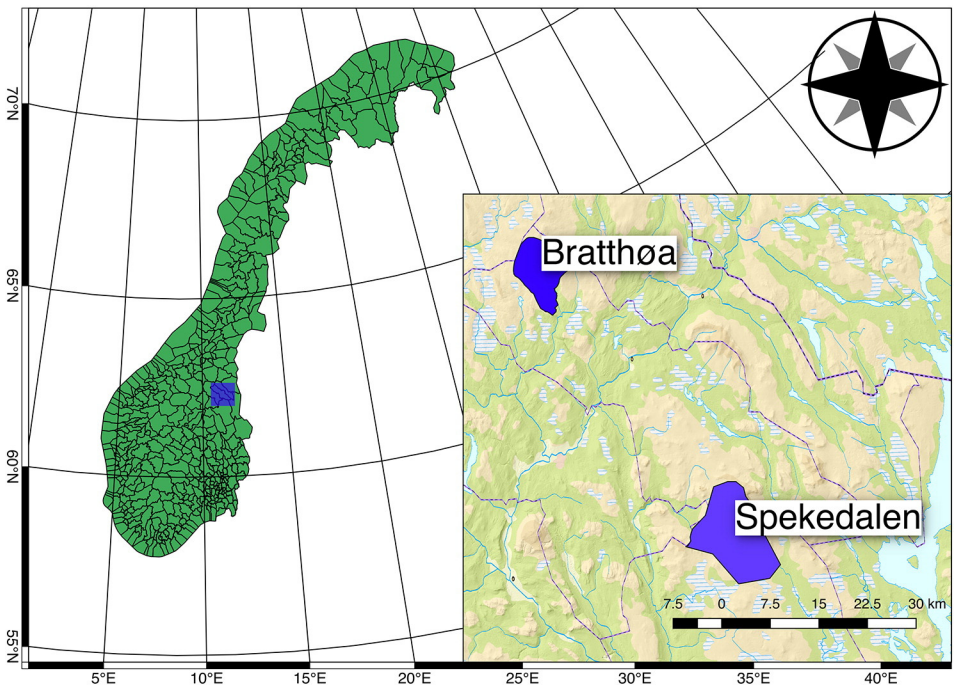


Figure 1. Study areas: Bratthøa study area in the northern part of Tolga municipality and Spekedalen study area in northern part of the Rendalen municipality, both in Hedmark County, Norway (Source: Statens Kartverk 2015). Map was generated using the QGIS version 2.16.3 print composer (QGIS Development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

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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:

$$\mathrm{UD} = \mathrm{environment} + \mathrm{breed} + \mathrm{yr} + \mathrm{environment} \cdot \mathrm{breed} + \mathrm{ID} + \mathrm{error} \quad (1)$$

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

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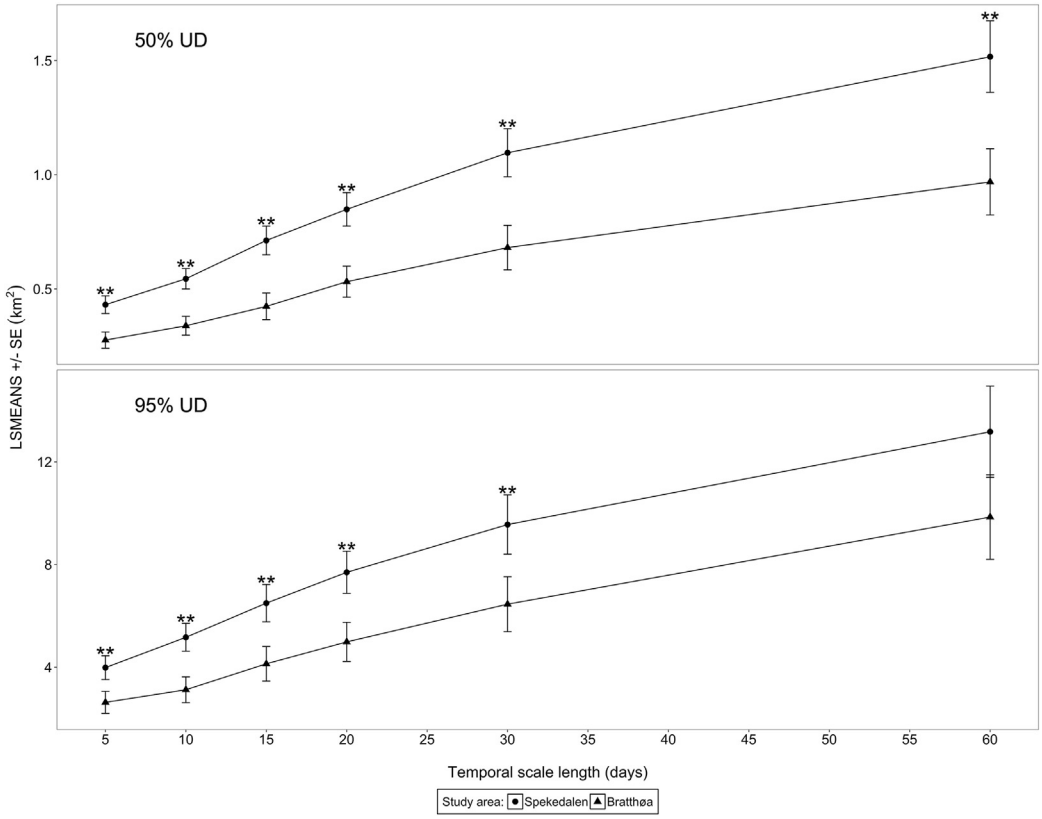


Figure 2. Spatial and temporal least square means (LSMEANS) of utilization distribution (UD) in km^2 for Spekedalen and Bratthøa study areas. 50 denotes 50% UD and 95 denotes 95% UD. Note the different LSMEANS scales in the two panels. The asterisks denote where the study areas differ in terms of UD 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

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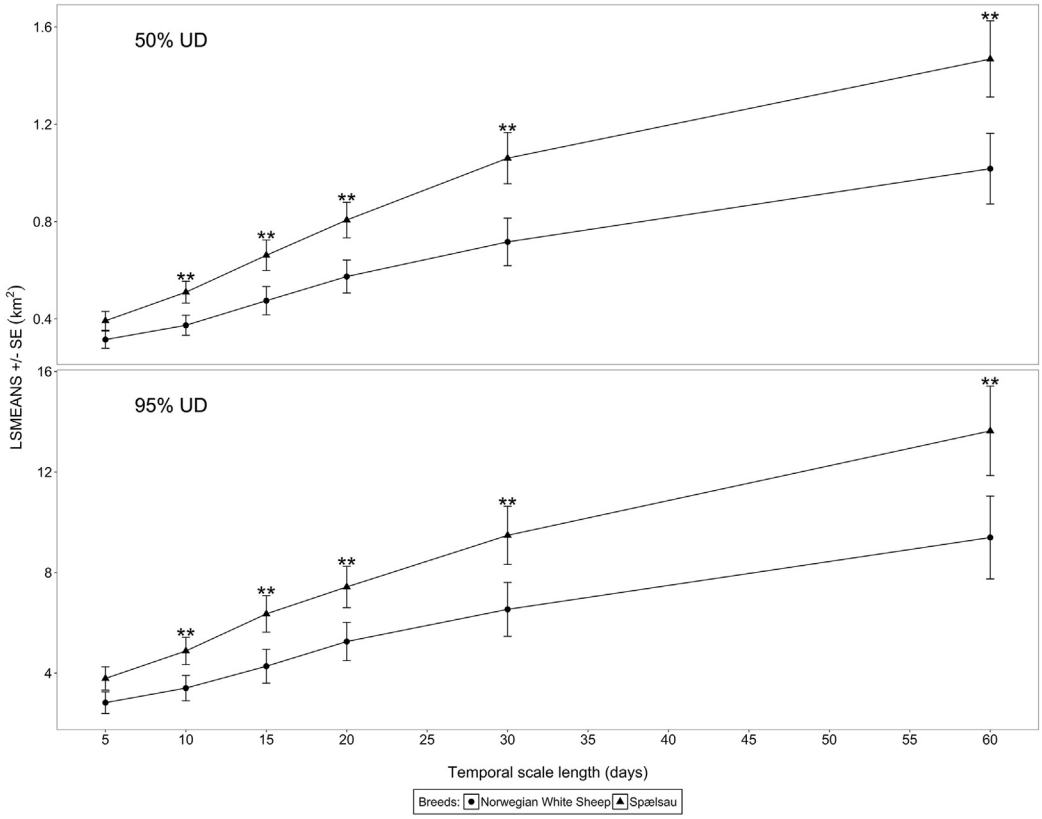


Figure 3. Spatial and temporal least square means (LSMEANS) of utilization distribution (UD) in km^2 for the NWS and SP breeds. 50 denotes 50% UD and 95 denotes 95% UD. Note the different LSMEANS scales in the two panels. The asterisks denote where the study areas differ statistically in terms of UD 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

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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.

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