

Scale Matters Habitat Use and Selection by Two Sheep Breeds in Two Contrasting Alpine Environments

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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 Spaelsau (SP), with GPS collars in two environments, one poor (Spekedalen) and one rich (Bratthøa), during the grazing seasons 2013-2014. 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 to 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 even more important for nutrient extraction and acquisition than the use indicates.

Keywords: Grazing; Temporal scales; Spatial scales; Spatiotemporal scales; Heterogeneity

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Introduction

Quantifying livestock foraging habitat use and selection is important for grazing management [1,2]. These complex behavioral processes are hierarchical, as large herbivores operate on several spatial and temporal scales to maximize nutritional acquisition and hence fitness [3-6]. Sent 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, escape from predators and thermoregulation [9-11].

Natural environments are heterogeneous on many temporal and spatial scales [12,13]. Therefore, on what spatial and temporal scales habitat traits are measured, do matter. At fine scales, (optimal) foraging theory has been used to predict large herbivores' foraging behavior [14-18]. Given complete information

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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 and cognitively challenging [19-21].

Selection is the process where an animal preferentially uses a set of available resources. 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. As pointed out by Johnson and reviewed by Ofstad. This "depends 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 and may have implications for understanding the dynamic use and functional selection [9,22-27]. Animal by environment interaction creates space use patterns concluded that the environment quality affects sheep Utilization Distribution (UD), resulting in larger UDs in poor environments, at several spatiotemporal scales [28,29]. 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 [30]. 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. Thus, even at low densities, they may not be able to fully express their plastic foraging response and hence their selection of specific vegetation patches appears 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 [31]. 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 seem constant across spatiotemporal scales and preference appear neutral [5].

How, and on what scales, large herbivores are able to respond to environmental variation in time and space is species specific [32]. On a finer genetic resolution, sheep breeds tailored to cope with specific environmental conditions and the SP and NWS breeds may respond differently to climate fluctuations. Indeed, body size, anatomy and behavior will often vary substantially between breeds, and may result in differences in foraging behavior [33-38]. Interestingly, Jørgensen found that the smaller SP responded to a poor environment by utilizing larger areas as compared to the heavier 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: Spælsau (poor) and Bratthøa (rich) [39,40]. In both environments, the two dominating Norwegian sheep breeds (Spælsau and Norwegian White Sheep), which vary in foraging behavior and diet selection, digestive anatomy, body mass and flocking behavior, were studied. This enables us to investigate habitat use and selection at different spatiotemporal scales by asking [36,37,41]:

- 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 south-eastern Norway shown in **Figure 1**. The Spekedalen area is part of the Solendalen grazing commons, and situated in the northern part of Rendalen municipality (11°21' E, 62°40'16' N). Spekedalen covers 97 km² and range from 688 to 1604 Meters above Sea Level (MSL); habitat quality in Spekedalen is in general poor. Bratthøa sauhavnelag (hereafter called Bratthøa) is a grazing commons in the northern part of Tolga municipality; it covers 62 km², between 790 and 1229 MSL, with in general rich vegetation types, with high habitat quality. The density of sheep in Spekedalen was approximately 3 sheep per km² in both 2013 and 2014, whilst in Bratthøa density was 38 and 40 sheep per km² in 2013 and 2014 respectively.

Vegetation classes

We classified the 24 vegetation types present into four classes based on value for sheep grazing: "Not Suitable" (no grazing value or inaccessible), "Less Good", "Good", or "Very Good", following the vegetation classification system **Table 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. Bold font type indicates the vegetation class where a given vegetation type is pronounced if classified in more than one vegetation class.

The "Not Suitable" class was omitted from all analyses. The distribution and proportion of the vegetation classes in the two study areas shown in **Figure 2**. The mean polygon size for each vegetation class in Bratthøa and Spekedalen were: "Very good": 0.03 and 0.02 km², "Good": 0.06 and 0.04 km², "Less Good": 0.05 and 0.08 km², respectively. We calculated the Shannon Diversity Index (H') for each study area, based on the number of patches of the three grazable vegetation classes to assess the heterogeneity [42].

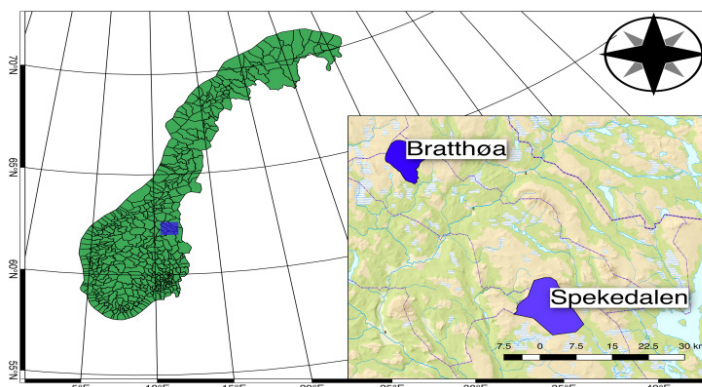
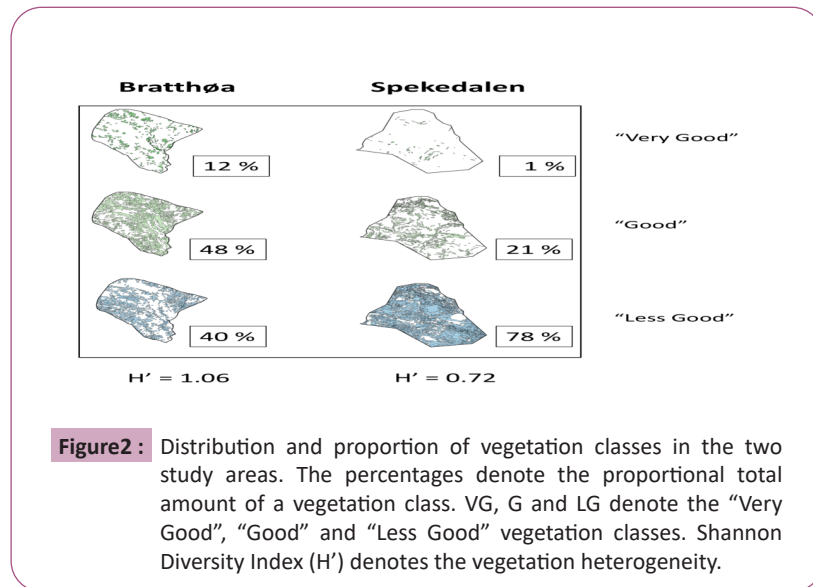


Figure1 : Study areas. Bratthøa in Tolga municipality and Spekedalen in Rendalen municipality, both in Hedmark county, Norway.

Table 1: Vegetation classes based on some vegetation types.

Vegetation type	Spekedalen		Bratthøa	
	%	Class	%	Class
1a)Moss snow-bed	0	LG	0.01	LG
1b)Sedge and grass snow-bed	0	G/LG	0.04	G/LG
1c)Stone polygon	0.02	LG	0	LG
2a)Dry grass heath	0.11	LG/G	0.02	LG
2b)Lichen heath	0.33	LG	0.2	LG
2c)Mountain avens heath	-	-	0	LG
2d)Dwarf shrub heath	0.23	G/LG	0.29	G/LG
2e)Alpine heather heath	0.03	LG	-	-
3a)Low herb meadow	0	VG	0.04	VG
3b)Tall forb meadow	0.01	VG	0.05	VG
4a)Lichen- and heather birch forest	0.1	LG	-	-
4b)Bilberry birch forest	0.05	G/VG	0.12	G
4c)Meadow birch forest	0.01	VG	0.02	VG
6a)Lichen- and heather pine forest	0.03	LG	-	-
8b)Bog forest	-	-	0	LG
8c)Poor swamp forest	0	LG	0	LG
8d)Rich swamp forest	0	G	0.01	G
9a)Bog	0.04	LG	0.01	LG
9b)Deer-grass fen	0	LG	-	-
9c)Fen	0.05	LG	0.17	LG/G
9d)Mud-bottom fens and bogs	0	LG	0	LG
9e)Sedge marsh	0	LG	0	LG
11a)Fully cultivated land	0	VG	0	VG
11b)Cultivated pastures	0	VG	0	VG
1. Yes	1. Yes	1. Yes	1. Yes	1. Yes



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 shown in **Table 2**. The animals were recruited from six sheep farms that had used the study areas for summer grazing during several years before the study. 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 [36]. The NWS and the SP constitute approximately 75% and 13% of the registered Norwegian sheep population, respectively.

Table 2: 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.

	2013 (SP)	2013 (NWS)	2014 (SP)	2014 (NWS)
Spekedalen	7	7	3	6
Bratthøa	7	9	6	6

GPS collars

Ewes were fitted with Follow it Tellus GPS-collars that registered positions every 60 minutes. 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” [43,44]. 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 23rd June and 23rd 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

$$\text{ACTSUM} = ((\text{Act}_x)/\text{TTF} + (\text{Act}_y)/\text{TTF}),$$

Where Act_y and Act_x are 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 $\text{ACTSUM} < 0.26$ and active if $\text{ACTSUM} \geq 0.26$. Only locations where animals were active were included in the analyses.

Dynamic brownianbridge movement model calculation

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, incorporating the temporal characteristics of the movement paths. 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 minutes 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 [45,46].

Moveud

Following Byrne we used the moveud R package 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 [47,48]. Time-steps with extreme movement variances (DBMvar>10000), indicating unrealistic large time-step UD size (> ≈ 5 km² 95% UD), were also omitted; these accounted for some 5% of the time-steps.

Vegetation class extraction and recoding

The three temporal dBMM UD compound contours were intersected with digital vegetation maps covering both study areas, and vegetation class coverage within the individual UD contours were extracted [49]. 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% dBMM 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

The total grazing season,

5 days intervals and

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 [47]. Habitat selection was calculated using the Manly-Chesson standardized Habitat Selection Index 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 [50-52]. The index formula is:

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

Where r_i the proportional use of vegetation is 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 analysis

For the analyses of effect of vegetation class on vegetation use and selection we used general linear mixed models. The Satterthwaite option was used to achieve correct degrees of freedom. The models used were:

$$USE = V + B \times V + E \times V + L \times V + B \times E \times V + L \times E \times V + L \times B \times V + L \times E \times B \times Error \quad [1]$$

$$SEL = V + E \times V + B \times V + E \times B \times Error \quad [2]$$

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 ($E \times V$) 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 $B \times V$. 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 and Discussion

Habitat use

At all spatial and temporal scales, the effect of vegetation class and vegetation class-specific effects of environment and spatial level on area use were all highly significant ($p < 0.0001$), whereas breed specific effects vegetation class ($B \times V$) and environment specific effects of vegetation class ($B \times V \times E$) did not affect the habitat use at any spatial or temporal scales ($p > 0.05$) shown in **Table 3**. The effect of vegetation class was in general stronger than the environment specific effect of vegetation class, but both seems to be enhanced with finer temporal scales. 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. It is noticeable that the use of "Very Good" increased with finer temporal scales shown in **Figure 3**.

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 environment specific effect of vegetation class never affected selection ($p > 0.5$) shown in **Table 4**. In general both breeds selected for "Very Good" at all temporal scales in both study areas, while "Good" was generally selected against. 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" at the seasonal scale shown in **Figure 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 use.

Habitat use	Tempora	Effect	NDF	DDF	F Value	Pr>F
	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	<0.0001
		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	0.972
		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
L*B*E*V		6	414	0.03	0.9999	

V denotes vegetation class, B denotes breeds, L denotes spatial level and E denotes environments, * denotes specific effects.

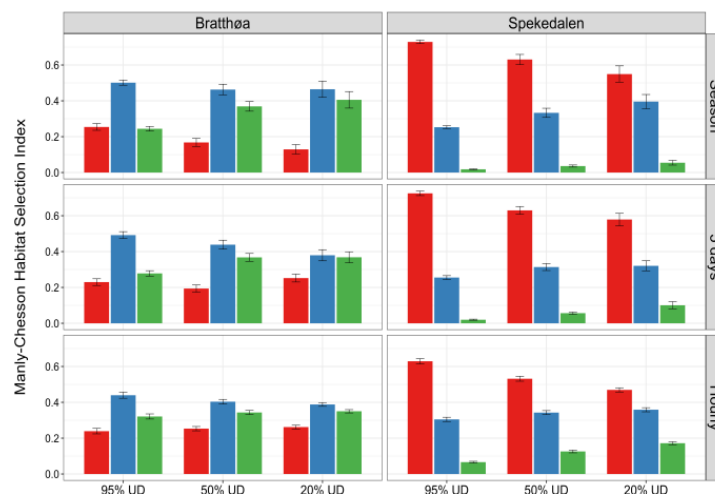


Figure 3: Distribution and proportion of vegetation classes in the two study areas. The percentages denote the proportional total amount of a vegetation class. VG, G and LG denote the “Very Good”, “Good” and “Less Good” vegetation classes. Shannon Diversity Index (H') denotes the vegetation heterogeneity.

Table 4: 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.

	NDF	Effect	NDF	DDF	F Value	Pr>F
	Habitat selection	Season	V	3	135	129.67
B*V			3	135	0.4	0.7554
E*V			3	135	0.64	0.5914
E*B*V			3	135	1.22	0.3036
5 days		V	3	138	215.2	<0.0001
		B*V	3	138	1.52	0.2125
		E*V	3	138	24.89	<0.0001
		E*B*V	3	138	2	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

V denotes vegetation class, B denotes breeds, L denotes spatial level and E denotes environments, * denotes specific effects.

At three spatial and three temporal scales, we estimated UD by the dBMM. Information from vegetation maps then enabled us to assess patterns of habitat use and selection of the two sheep breeds in the two environments. As expected we found an effect of environment 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. Further, the “Good” vegetation class was generally used slightly higher in Bratthøa at all temporal and spatial scales, than in Spekedalen. It is noteworthy that spatial level within each temporal scale affected habitat use. Breed did not affect habitat use at any temporal nor spatial scales. Habitat selection, in the two study areas, was affected by the available vegetation classes 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. Habitat selection was not affected by breed at any temporal scale.

We did not find breed difference in foraging behavior at any spatial temporal scale. This is somewhat surprising: SP and NWS differ in body size, their digestive system and are known to differ in forage preferences [36]. Jørgensen showed that the SP’s mean seasonal UD tended to be larger as compared to NWS and Jørgensen found that breed differences in UD size did occur at finer temporal and spatial scales [53]. Although the two breeds may differ in their spatial distribution and utilization of the ranges, we were not able to detect differences in use and selection of the vegetation classes, neither in time nor space. In addition, we did not find any breed by study area interaction.

The total density in Bratthøa is about 13 times higher than in Spekedalen, ≈ 39 sheep per km^2 for and ≈ 3 sheep per km^2 respectively. Rekdal (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, but especially in Spekedalen. The area of the “Very Good” vegetation class amounts to $\approx 7 \text{ km}^2$ (12% of 67 km^2) and $\approx 1 \text{ km}^2$ (1% of 97 km^2) in Bratthøa and Spekedalen, respectively. Interestingly, this

implies that the sheep density related to this class alone was in the same range in the two study areas, 5 sheep per km^2 and 3 sheep per km^2 , respectively. “Very Good” patches are magnets for the animals, especially in Spekedalen at fine scales, although these patches are smaller and more spread out as compared to in Bratthøa, making them more costly, both time and energy wise, to exploit. Actually, some of the time used in Spekedalen may be connected to transportation legs in this “Less Good” dominated matrix between “Very Good” (and “Good”) patches. We were not able to distinguish grazing from walking activity. In Bratthøa this seems less pronounced as “Less Good” accounted for 40% as compared to 70% in Spekedalen. However, this class, dominated by dry lichens ridges, is well suitable for cost efficient movements, observed in the well-developed path system in the two study areas. Consequently, the time used in “Less Good” is somewhat higher than the actual time foraging in this vegetation class in both study areas.

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.). However, the current resolution of the vegetation map (scale 1:10000) is not sufficient to depict these features [54]. This may lead to an underestimation of the use of “Very Good” and an overestimation of the use of the two other vegetation classes. For these non-mapped features to emerge, vegetation mapping at a 1:1000-5000 scale would be needed. Consequently, a vegetation mapping at this fine resolution, could lead to conclusions that the breeds had a higher use of the scarce “Very Good”, at least in Spekedalen. The effect on selection is more dubious, and would depend on the relative change in use at the 95% versus 20% spatial scales.

Indeed, the choice of scale for defining habitat use and availability is important, when assessing how an animal preferentially uses a set of available resources [22,24,25]. Several studies assessing habitat selection have used estimates of 95% UD as available and 50% UD as the used resources [47]. But, since a higher contrast between estimates of availability and use can give a clearer result, when assessing habitat preferences within the home range, we used the 95% UD as available and 20% UD as use, in our study [55].

A choice of 50% UD instead of 20% UD, as a measurement for use, would have had an impact on selection in Spekedalen, resulting in a weaker selection for “Very Good” and weaker selection against “Less Good”, whereas the selection in Bratthøa would be affected to a lesser degree shown in **Figure 3**. Thus, analyses of use and selection in poor homogeneous Spekedalen seem more sensitive to the choice of scale than in the heterogeneous rich Bratthøa.

At the seasonal temporal scale, in rich Bratthøa, both breeds selected strongly for the “Very Good” and strongly against the “Less Good”. Indeed, they were clearly able to express their plastic foraging response by utilizing the “Very Good” patches, at the expense of the “Less Good”. This was amplified with finer spatial scales. However, the use of “Good” at all spatial scales accounted for $\approx 50\%$ indicating that forage from this vegetation class makes up the staple part of the summer diet in Bratthøa. In poor Spekedalen the breeds used the vegetation classes according to the availability, 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. Thus, what appears to be making the best of a bad job by the sheep at the coarsest spatial scale, shifted to a clear selection for the less abundant patches of high quality (“Very Good”), with a clear aversion against the abundant areas of low quality (“Less Good”)?. Indeed, the proportional spatial differences (20% *versus* 95% spatial level) in vegetation class use are basically the same in the two study areas, resulting in the same vegetation class selection patterns. This is supported by the non-effect of environment by vegetation class on habitat selection at this coarsest temporal scale. These findings are in accordance with the general theory regarding second order selection (within seasonal home range) in contrasting environments. Although the abundance of the vegetation classes is driving the habitat use in poor and homogenous Spekedalen, the animals are able to find and utilize “Very Good” patches at the finest spatial scale.

This is also reflected in an increasing mean UD heterogeneity in Spekedalen with finer spatial scales, Mean Shannon Diversity Index (H') based on the number of patches of the three grazable 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, which is in contrast to Bratthøa with a higher and constant heterogeneity index (H') across spatial scales. Interestingly, the overall proportion of “Very Good” in Bratthøa amounts to 12%, whereas the estimated proportion use of this vegetation class at seasonal 95% spatial scale is about 24%, suggesting clear selection of high quality summer home range within Bratthøa study area. The strong selection for “Very Good” at this overall scale in Bratthøa is amplified by the selection at the seasonal scale and may be attributed to a more heterogenous and smaller patch size distribution. This is in contrast to Spekedalen where the estimated proportional use of “Very Good”, and also the two other classes, is close to their overall availability, 2% *versus* 1%, 25% *versus* 21% and 73% *versus* 78% respectively for “Very Good”, “Good” and “Less Good”. It seems that availability of the vegetation classes is driving the habitat use

in Spekedalen in contrast to Bratthøa. We did not find significant difference between environment and vegetation class in habitat selection at the seasonal scale, which could be explained by the fact, that the breeds' initially select similarly within their summer home ranges in the two study areas. However, it is important to keep in mind, that breeds used 24% and 2% of the “Very Good” as compared to the 12% and 1% overall availability, in Bratthøa and Spekedalen respectively.

At the 5 days' temporal scale we notice the same habitat use patterns as found on the seasonal scale in Bratthøa. The breeds used the “Very Good” vegetation class increasingly and “Good” decreasingly with finer spatial scales, whereas the use of “Less Good” was fairly constant. At this temporal scale, they were able to realize their selection potential to some degree, manifested in their weak positive preference of highest quality patches, at the expense of the more abundant “Good”. In Spekedalen, the breeds' vegetation class use pattern resembled what we observed at the seasonal scale, except from an increase in use of the “Very Good” with finer spatial scales. This resulted in a stronger selection for “Very Good” at the expense of selection for “Good”, as confirmed by the more heterogeneous UDs and increasingly so with finer spatial scales, as compared to at the seasonal scale. It seems, again, that the vegetation availability is driving the habitat use in Spekedalen.

At the finest temporal (hourly) scale, we notice that the habitat use patterns across spatial scales in Bratthøa are similar to what we found at the coarser temporal scales. This results in approximately neutral selection for all vegetation classes in Bratthøa, and could be explained by the available patches of “Good” and “Very Good” are as numerous, large and evenly distributed as at the 5 days temporal scale. 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 patch. This is supported by unpublished results showing that sheep travelled shorter mean daily distances in Bratthøa as compared to Spekedalen (≈ 5.5 km *versus* ≈ 6.6 km). It is possible that in Bratthøa the relative high availability at 95% UD of “Very Good” and high use at 25% UD means that the ewes could optimize the habitat use without showing a strong selection for any class. In Spekedalen, the vegetation class use pattern resembled what we observed at the two coarser temporal scales. However, the use of “Very Good” 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, as confirmed by the increase in H' index. However, exploiting these scarce and scattered patches is costly time- and energy-wise, and thus the animals are using the more abundant “Good” and “Less Good” as their staple food resources.

In general, daily intake is considered a function of time spent grazing [56]. Nevertheless, time foraging does not necessarily reflect a vegetation class' importance for nutrient extraction and acquisition. Indeed, vegetation type productivity, biomass quality and degree of utilizability are the key factors to estimate a vegetation type's grazing value for sheep and form the backbone to classify pasture quality of consolidated broader vegetation classes

such as the ones used here. The productivity, biomass quality and degree of utilizability is far lower in “Less Good” as compared to “Very Good”. In a (time) constraint setting, the opportunity for selection diminish when food quality and availability is low [57]. Fiber rich ingesta will slow down the turnover of the digesta. White in his seminal paper pointed out the importance of a selective foraging regime for the long term net energy for growth, which may have fitness consequences [58-61]. 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 scales, the energy extraction and acquisition from the two classes are closer to each other than simple time-budget interpretations might indicate. These points to the obvious fact that “Very Good” is even more important for “harvesting” net energy for growth in poor environment than reflected in use [62-65]. The lower lamb autumn weight, in Bratthøa as compared to Spekedalen (43kg *versus* 37kg, $p < 0.0001$, Jørgensen can be explained by the cost of being selective. While White 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 (as confirmed by distance movement data ≈ 5.5 km *versus* ≈ 6.6 km, is higher in Spekedalen as compared to Bratthøa. Thus, the energy requirement seems to be higher in Spekedalen as compared to Bratthøa.

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 clearly used the most. Sheep showed a strong plastic foraging response to Spekedalen’s spatial distribution of vegetation classes: few and small “Very Good” patches in a matrix dominated by “Less Good”. Indeed, “Very Good” is more important for the sheep in terms of net energy for production in a poor environment, than reflected in use. In Bratthøa both breeds respond to the more numerous, larger and more widely distributed patches of “Good” and “Very Good”, typical for a rich and diverse resource base, by using and selecting them at the coarsest temporal scale. Thus, even if sheep 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 the stable part of their diet.

Clearly, the abundance of vegetation classes suitable for sheep grazing is 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 Spekedalen is observed.

Management Implications

Scale in time and space is important to understand the ewes’

grazing behavior and can provide insight into how and when they use, and which vegetation classes they use and prefer on rich and poor grazing pastures. 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. It is therefore important to convey the importance of scale, when one speaks of the land use in time and space. We have shown that breed as such in a management perspective, may not be crucial for use and vegetation class selection in areas with different grazing quality. What matters is the landscape heterogeneity and scarce high quality resources in a homogenous environment.

The Dynamic Brownian Bridge Movement Model (dBBMM) was used to estimate utilization distribution (UD) at different scales. Fleming questioned the use of BBMM and dBBMM as methods for estimating UD. They argued that the methods quantify the occurrence distribution (the probability of where an animal have been at a given point in time?) rather than the UD (fraction of time an animal will occupy a given area in the long run). Preliminary analyses using the Animal Movement Tools (AMT) package, that would address the above concerns, show very similar habitat use and selection patterns across spatiotemporal scales. We are thus confident that the use of dBBMM elucidates the research questions in this paper. Further, we do realize that three UD-values (95%, 50% and 20%) are nested. This could have been circumvented by treating each UD-scale separately or by adding a random effect at the level of individual sheep. We do realize that the vegetation class cover fractions represent compositional data and that applying analytical procedures adapted to data in real space may be problematic. An approach using Dirichlet regression may also be considered.

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Author Declaration

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the

timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

We understand that the corresponding author is the sole contact for the Editorial process (including Editorial Manager and direct communications with the office). He is responsible for communicating with the other authors about progress, submissions of revisions and final approval of proofs.

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