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Effects of density, season and weather on use of an altitudinal gradient by sheep

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Abstract

The distribution of high-quality forage is an important determinant for foraging patterns of ruminants. It has been suggested that herbivores should gradually increase the use of higher altitudes as new, high-quality forage emerges. Further, the ideal-free distribution (IFD) theory predicts a more even use of habitats (i.e., altitudes) at high population (stocking) density. We tested these predictions by following individually marked sheep within a landscape-scale experiment with high (80 km^2) and low (25 km^2) sheep population density, covering altitudes from 1050 to 1300 m a.s.l. on alpine ranges of Norway. Sheep used all altitudes from the beginning to the end of the summer grazing season. Contrary to prediction from the IFD theory, there was no effect of population density on the use of the altitudinal gradient. As predicted, sheep used lower altitudes more often during the early season than during the middle of the grazing season. However, contrary to prediction, there was a decline in average altitude used during the last part of the season. There was also a strong effect of prevailing weather. Early in the season, sheep used higher altitudes more during warm than cold weather both during grazing and resting. As the season progressed, the effect of temperature decreased and the altitude difference between resting and grazing increased. Sheep used higher altitudes more during clear weather than during cloudy weather, and used the lowest altitudes when there were clouds and no wind. Sheep were more often at high altitude when there was wind, especially during the first part of the grazing season, and tended to be at a lower altitude during grazing than resting when there was no wind. We conclude that movements in the altitudinal gradient were to a large degree determined by factors other than population density.

Keywords: Ideal-free distribution; Foraging; Norway; Seasonality; Ungulates

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1. Introduction

Strategies of foraging animals typically involve a number of decisions regarding the optimal diet composition, foraging space and how to distribute foraging between time periods (Schoener, 1971). The ideal-free distribution (IFD) theory predicts how animals optimally should exploit resource patches differing in value (Fretwell and Lucas, 1969). At low population density with no competition, animals should use the highest quality patches only, with increasing use of low quality patches as population density and level of exploitation competition increases (Tyler and Hargrove, 1997; Weber, 1998). No study has used IFD to predict use of altitudinal gradients by ruminants during summer depending on population density. IFD predicts (H1a) a more even use of an altitudinal gradients over the grazing season with an increase in population density. Further, if plant biomass decreases with increasing altitude due to harsher climate, we may predict (H1b) sheep at high population density, being more biomass limited, to be using on average lower altitudes to a greater extent. To our knowledge these predictions are untested.

Distribution of high-quality forage is regarded as the most central factor affecting ruminant foraging patterns (see Hanley, 1997 for a review). Eating high-quality forages allows ruminants to increase energetic efficiency by reducing the energetic cost of foraging per unit of nutrient gain. Early phenological stages of plants generally have greater nutritional quality in terms of available energy and protein (Albon and Langvatn, 1992; Van Soest, 1994). During the summer, phenological development is typically delayed at higher altitudes (Albon and Langvatn, 1992; Pettorelli et al., 2005). Therefore, it is generally agreed that (H2) ruminants should forage at increasingly higher altitudes as summer progresses. A number of studies examine the migration of free-ranging wild ungulates report the existence of low altitude winter range, and a high altitude summer range (e.g., Albon and Langvatn, 1992; Mysterud, 1999; Oosenbrug and Theberge, 1980). For these studies, animal movements are also related to differences in snow depth during winter irrespective of forage quality. While optimal foraging theory and food quantity and quality has been quite successful in predicting distribution patterns at fine spatial scales, movements at coarser scales are often more strongly influenced by factors such as climate (Bailey et al., 1996; Bailey, 2005; Senft et al., 1987). There is limited theory to predict the direction of such effects. We thus aimed at testing the general prediction that (H3) prevailing weather affected movement in an altitudinal gradient.

Within a landscape-scale experiment (sensu Senft et al., 1987), we tested the above hypotheses regarding how population density and climate affect the particular altitude at which sheep choose to graze as the summer progresses.

2. Material and methods

2.1. Study area

The study was conducted in southern Norway (60°40′N, 7°55′WE) in the Hol municipality of Buskerud county. The area has a subcontinental, alpine climate with annual precipitation ranging from 7 to 800 mm (Førland, 1993). Altitude ranges from 1050 to 1300 m. The lower border was close to the upper reaches of the forest boundary, mainly in the lower alpine zone and up to the middle alpine zone. This area contained only a few scattered birch (*Betula* sp.) trees in the lowest areas. The vegetation was dominated by low shrubs interspersed with grass-dominated meadows (Rekdal, 2001, Fig. 1). A detailed description of the vegetation is given elsewhere (Austrheim et al., 2005a,b; Evju et al., 2006).

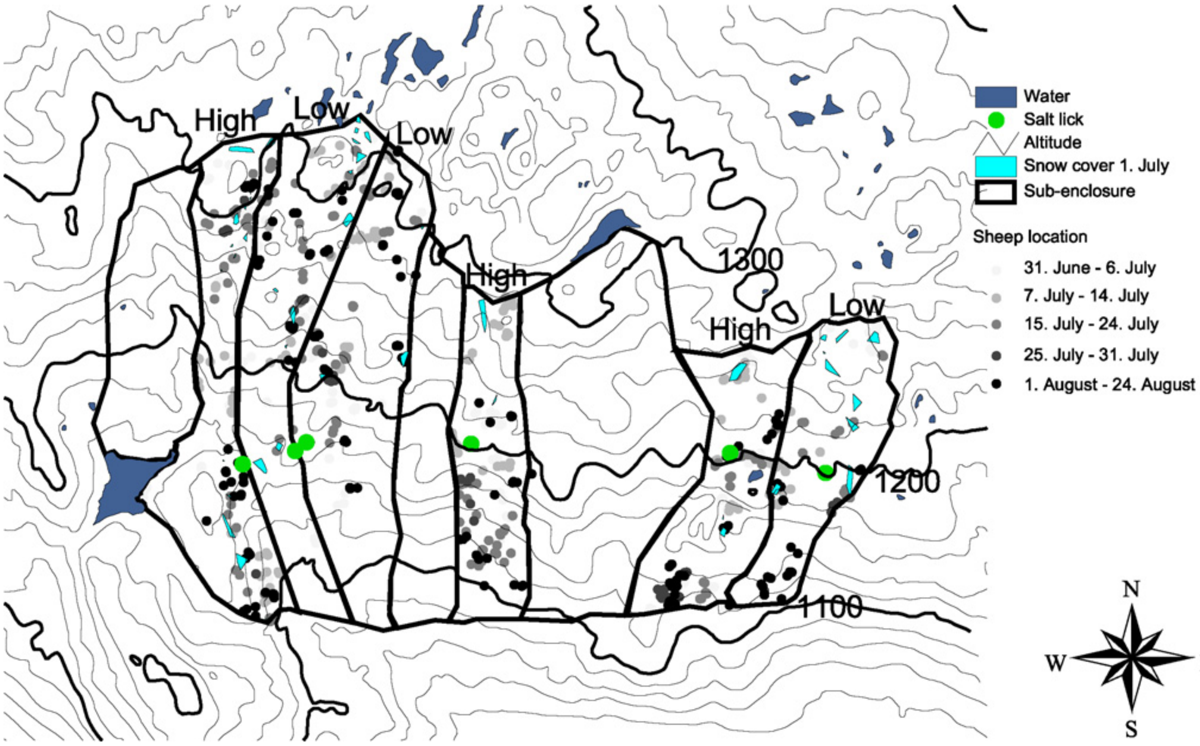

Fig. 1. The sheep use of the altitudinal gradient throughout the season and the snow distribution that was documented on 1st of July 2003. The ‘‘low’’ and ‘‘high’’ above sub-enclosure refer to low and high population density of sheep. The number refers to altitude.

2.2. Experimental design

A large enclosure covering 2.7 km^2 and with a total of 17.3 km of standard sheep fencing (110 cm high) was established in the summer of 2001, and grazed by sheep during summer from 2002 and onwards (Mysterud et al., 2005; Steen et al., 2005). The large enclosure consisted of nine sub-enclosures (Fig. 1). Distribution of main habitat types used by sheep was similar among the sub-enclosures, and each sub-enclosure also contained about the same altitudinal range and on a generally south-facing slope. For each of three adjacent sub-enclosures, we randomly assigned the treatments low and high population density of sheep and one remained a control with no sheep, i.e., a block-wise randomization design. The experiment was designed to assess both foraging ecology of sheep as well as grazing impact of sheep on the ecosystem (Austrheim et al., 2005a,b; Mysterud et al., 2005; Steen et al., 2005). Average size of the six sub-enclosures with sheep was 0.288 km^2, but there was some size variation (0.22–0.38 km^2) due to practical problems in putting up fence in areas with bare rock visible (Fig. 1).

In 2001, the vegetation of the area was mapped and its value for grazing by sheep was assessed (Rekdal, 2001). Based on the resulting recommendations, we used 25 sheep per km^2 as a low density treatment and 80 sheep per km^2 as a high density treatment, which covers most of the variation in densities of sheep on mountain pastures in Norway (further details in Kausrud et al., 2006). Twenty-four ewes and 45 lambs were used. Ewe live weight averaged 87 kg (63–110 kg) in spring and lambs averaged 20 kg (11–32 kg) in spring and 40 kg (27–57 kg) in autumn. Water is naturally available as small streams within all sub-enclosures. In the middle of each sub-enclosure, a salt lick with minerals was provided. All sheep were of the ‘‘Kvit norsk sau’’ breed (often called ‘‘Dala breed’’), the most common breed in Norway (Drabløs, 1997), coming for one single sheep farmer (Knut-Eirik Sveingard). The grazing season was from the last week of June through the last week of August, which is a typical grazing season for mountain regions of southern Norway.

2.3. Data collection

Data were collected throughout the 2003 grazing season, extending from 31 June to 24 August. Sheep behavior was assessed by direct observation using binoculars. All sheep were individually numbered with ear tags and neck bands. Color coded neck bands were used to facilitate identification of individual animals from distances of 20–50 m. As sheep are kept indoors during winter, they are used to human contact, and they were quickly habituated to the observer. The location of each ewe and her lamb(s), within the sub-enclosure was located and recorded by GPS. We termed each ewe and her lamb(s) as a family group (24 in total) and defined that as the sampling unit (Kausrud et al., 2006). We used two working cycles randomly throughout the season, from 0900 to 1700 or from 1400 to 2200. To ensure unbiased sampling, we randomly selected whether the eastern or western part of the area should be covered each day, and then which sub-enclosure in that part to start in, and from which direction within the sub-enclosure (from above or below, i.e., a stratified randomization). After data on all ewes in a specific sub-enclosure had been recorded, we randomly selected a new sub-enclosure in the chosen half of the research area. As there are more sheep in high population density sub-enclosures (by definition), we sampled low population density sub-enclosures twice as frequent to partly compensate for this. Therefore, each ewe and lamb was recorded 50–52 and 25–29 number of occasions within, respectively, the low and high density sub-enclosures. Each low and high density sub-enclosure was visited on 31–32 and 25–26 days, respectively. A total of 798 registrations were obtained during the entire summer for all ewes pooled.

Each location was mapped with GPS, so that altitude was known directly from the GPS. We noted whether the ewe was resting (lying down) or active (grazing), and measured air temperature with a (shaded) thermometer right above ground and wind speed standing with a handheld wind speed measurer. We also qualitatively judged whether it was cloudy, clear or rain in the air, without providing an explicit quantitative measure of precipitation.

On the 1st of July, we mapped all laying snow manually with the aid of GPS. Most snow is melted at this time, while the latest snow patches usually melt in late July. These late thawing patches usually have snow bed vegetation types. Plant growth does not start before snow is melted away. Information about snow cover thus gives a picture of the areas with the latest plant phenology for a given year.

2.4. Statistical analyses

All analyses were conducted using S-Plus (Crawley, 2003).

We used a combination of linear models (LM), linear effects mixed models (LME) and additive models (AM) to analyze variation in sheep use of vegetation within an altitudinal gradient. Factors including: day within the grazing season, sheep population density, animal activity, atmospheric temperature, presence of cloud cover, rainfall, wind speed, and subsequent interactions among these attributes affecting where the sheep were located were included in the models. We first screened our variables for possible collinearity. In our study area, it is always cloudy when it is raining. Using plots of AM we did not detect visible differences in use of different altitudes gradients different as affected by rain or degree of cloudiness. Therefore, we continued the analyses using only cloud cover as a covariate, since rain and cloud cover are correlated and should therefore not be in the same model. We also used AM with smoothing splines to assess possible non-linearity (Hastie and Tibshirani, 1990), and then chose adequate polynomials for the LM and LME. For wind speed, there was a clear distinction between windy ($\geq$1 m/s) and non-windy days, and we therefore used a categorical rather than a continuous covariate for wind. This is also a sound decision since exact wind speed in the mountains is very variable even at short time intervals. Therefore, the difference between 3 and 5 m/s can occur in seconds, while the difference between 0 and 1 m/s is more stable justifying this lumping into categories (which also makes it easier to look at interactions with other factors).

We used ''ewe identity'' nested within ''sub-enclosure'' as a random effect, so that pseudoreplication due to repeated measures of the same ewe were removed, and so that when it comes to the population density effect, we have three replicates. As activity is known to be a major factor for habitat selection in ruminants, we also analyzed data separately for grazing and resting.

We used model selection for selecting an appropriate model for hypotheses testing. The model with the lowest Akaike Information Criteria (AIC) value is considered to be the most parsimonious model (Burnham and Anderson, 1998; Johnson and Omland, 2004), i.e., the best compromise between explaining most of the variation and simultaneously using as few parameters as possible. Model selection was done with LM, since AIC cannot be used based on Restricted Maximum Likelihood (REML) as in LME (Crawley, 2003). The model with the lowest AIC value was then used to estimate the parameters for hypothesis testing. We did not use automatic selection procedures as, for example, a third-order term may give a much better fit than a first-order term, but a second-order may not. We therefore systematically explored models with higher order polynomials, as well as interaction terms. The detailed strategy when selecting models is given in electronic appendix for the total material. A similar strategy was used when splitting data into grazing and resting.

For the population density effect, one may argue that variability in use of different altitude is a more appropriate measure than altitude per see (cfr. H1a). We therefore also calculated variance in the use of altitudes for each sub-enclosure over the season, and ran a *t*-test to test whether variance varied depending on population density.

3. Results

Sheep used all parts of the altitudinal gradient during the grazing season (Fig. 1). We detected differences in the proportional use of the gradient during the grazing season. The most parsimonious linear model of the spatial use of the altitudinal gradient included the factors date (up to a second-order term), population density, activity type, temperature (up to a third-order term), wind speed category, cloud cover category, and interactions between date and temperature, date and activity type, date and cloud cover category, date and wind speed category, population density and activity type, activity type and wind category, temperature and wind category and finally cloud cover category and wind category ($n = 798$, $R^2 = 0.366$, AIC weight = 0.409, see electronic appendix for details).

Overall, sheep used lower altitudes earlier in the grazing season and moved up the altitudinal gradient as the grazing season progressed (Table 1). However, contrary to prediction, there was a decline in average altitude used during the last part of the season. Generally, sheep used higher altitudes with increasing temperature; the third-order term entering the global and grazing model was due to a stronger effect of temperature below than above average temperature. The effect of date interacted with both temperature and type of activity (Fig. 2). Early in the season, sheep used higher altitudes during warm than cold weather both during grazing and resting. As the season progressed, the effect of temperature decreased and the altitude difference between resting and grazing increased. Sheep used on average higher altitudes during clear weather than during cloudy weather, and used the lowest altitudes when there were clouds and no wind (often foggy weather in the area). Sheep were more often at high altitudes when there was wind, especially during the first part of the grazing season, and tended to be at a lower altitude during grazing than resting when there was no wind (Table 1).

Contrary to prediction, there was no effect of population density on the use of the altitudinal gradient. The interaction term ‘‘density × activity’’ entered the final model, but there was no population density effect when running separate models for grazing ($T = 1.998$, $P = 0.116$) and resting ($T = 1.922$, $P = 0.127$). There was no difference in variance in the use of altitudes over the grazing season either ($T = -1.216$, $P = 0.291$).

As can be evident from Fig. 1, the pattern of snow cover on 1st of July confirmed that there was more snow at high altitudes. These snow beds thaw during July and plant growth starts; while plant growth has already started in areas free of snow on 1st of July. Thus, on average, plant phenology is delayed at high altitude due to later thawing of snow.

Table 1
Parameter estimates and test statistics for analysis of which parameters affected the sheep grazing pattern on the study area 2003, based on the model from the total material with the lowest AIC value

Parameter	Total material					Grazing			Resting		
	L.s. mean	SE	d.f.	*T*	*P*	L.s. mean	*T*	*P*	L.s. mean	*T*	*P*
Intercept	1166.3260	14.6471	754	79.629	<0.001	1165.6280	78.335	<0.001	1149.1600	67.651	<0.001
st(Date)	−15.1170	4.3714	754	−3.458	0.001	−15.8980	−3.764	0.000	−41.5020	−3.953	0.000
st(Date)^2	−15.3640	2.2513	754	−6.824	<0.001	−15.8840	−6.046	<0.001	−20.9560	−4.177	<0.001
Density (low vs. high)	40.3640	19.7327	4	2.046	0.110	40.0850	1.998	0.116	16.1720	2.919	0.004
Activity (Resting vs. grazing)	−8.4800	8.1079	754	−1.046	0.296						
st(Temp)	26.4470	6.4134	754	4.124	<0.001	24.0010	4.626	<0.001	37.0440	1.922	0.127
st(Temp)^2	3.3530	2.2438	754	1.495	0.136	2.6010	1.038	0.300	−11.7520	−0.742	0.459
st(Temp)^3	−4.2610	1.3163	754	−3.237	0.001	−5.6390	−3.743	0.000			
Cloud cover (“clear” vs. “cloudy”)	37.7310	12.7766	754	2.953	0.003	51.1240	4.322	<0.001	86.4850	2.932	0.004
Cloud cover (“variable” vs. “cloudy”)	17.9010	8.7761	754	2.040	0.042	22.8710	2.420	0.016	28.9340	1.618	0.107
Wind (“wind” vs. “no wind”)	31.8110	6.5792	754	4.835	<0.001	37.8320	5.774	<0.001	42.4390	4.126	0.000
st(Date) × st(Temp)	−19.7910	3.6530	754	−5.418	<0.001	−20.2700	−4.868	<0.001	−11.5870	−2.281	0.024
st(Date) × Activity (resting vs. grazing)	−11.7240	3.8207	754	−3.068	0.002						
st(Date) × Cloud cover (“clear” vs. “cloudy”)	21.8630	6.1827	754	3.536	0.000	33.2440	4.961	<0.001			
st(Date) × Cloud cover (“variable” vs. “cloudy”)	5.4840	5.0415	754	1.088	0.277	18.1160	3.574	0.000			
st(Date × Wind)	8.5040	4.8961	754	1.737	0.083						
Density × Activity	−12.2250	7.1207	754	−1.717	0.086						
Activity × Wind	19.2180	8.3757	754	2.295	0.022						
st(Temp) × Wind	−8.3500	6.6183	754	−1.262	0.208				5.8650	0.423	0.673
Cloud cover (“clear” vs. “cloudy”) × Wind	−40.3040	14.4802	754	−2.783	0.006	−65.0580	−4.922	<0.001	−50.6490	−1.727	0.086
Cloud cover (“variable” vs. “cloudy”) × Wind	−8.8940	10.4977	754	−0.847	0.397	−16.0600	−1.380	0.168	−5.4140	−0.302	0.763
Density × Cloud cover (“clear” vs. “cloudy”)									−20.5860	−1.531	0.127
Density × Cloud cover (“variable” vs. “cloudy”)									−15.3860	−1.203	0.230
st(Temp) × Cloud cover (“clear” vs. “cloudy”)									3.9000	0.263	0.793
st(Temp) × Cloud cover (“variable” vs. “cloudy”)									26.1390	1.990	0.048

These estimates are the one used for drawing Fig. 2.

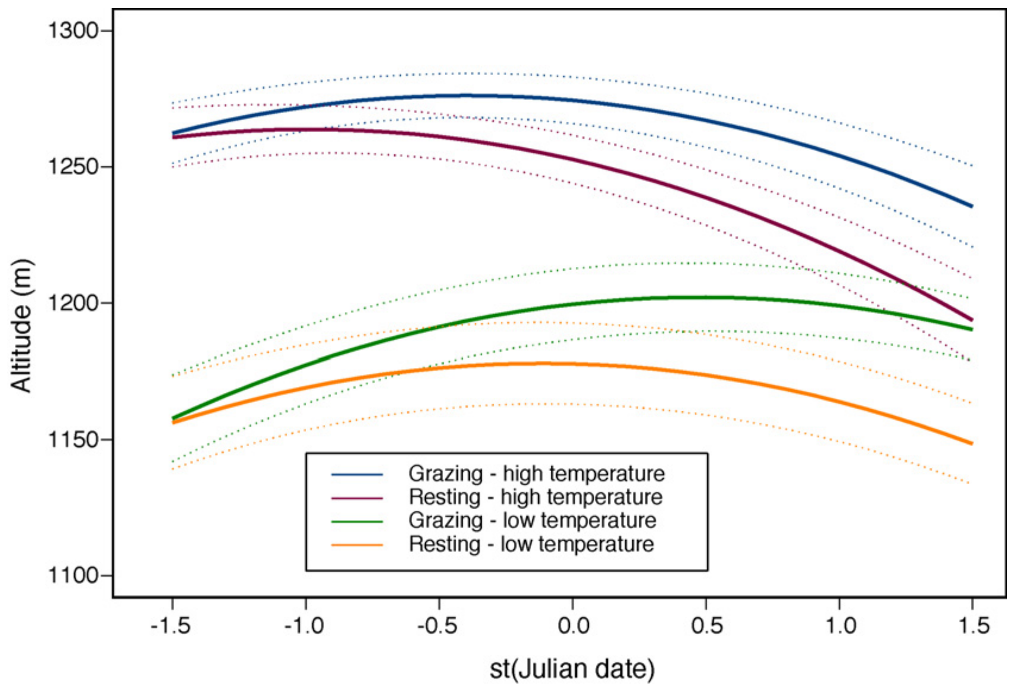

Fig. 2. Models showing how the sheep used the altitudinal gradient on the study area through the summer, depending on whether the sheep were grazing or resting and whether ambient temperature was high or low.

4. Discussion

Our study demonstrated that the sheep used all altitudes from the beginning to the end of the grazing season. Movement within any enclosure is clearly somewhat constrained. However, the scale of the sub-enclosures is so large – around 1 km long encompassing altitudes from 1050 to 1300 m a.s.l. – that patterns observed most likely reflect some general aspect of large herbivore movement in altitudinal gradients on alpine ranges.

4.1. The absence of density dependence

From the IFD theory (Fretwell and Lucas, 1969), we predicted that sheep use of the altitudinal gradient should (H1a) be more even at high population density. Further, we predicted that (H1b) sheep at high population density, being more biomass limited, to be using on average lower altitudes to a greater extent. Our experimental scale is theoretically suitable for an IFD, which is the daily movement scale (Tyler and Hargrove, 1997), but we found no density effect. In our study area, lambs were about 1 kg lighter at high than low population density after the grazing season (Mysterud and Austrheim, 2005), so there is likely resource limitation at high population density. Finding an absence of an effect is always difficult as this will be a function of sample size. But at least we can conclude that population density is a less important factor for the movement of sheep in the altitudinal gradient compared to the effect of season (linked to plant phenology) and weather.

4.2. The seasonal pattern

In the alpine zone, the vegetation season is short (~74 days with over 5 °C at 1222 m a.s.l., cfr. Karlsson and Nordell, 1996), and domestic sheep are released in late June when the first new vegetation has emerged, and they are gathered by the end of August or in early September when frost during night make the vegetation less nutritious and growth of lambs ceases. Most studies of wild large herbivores have looked at migration pattern between winter and summer ranges, typically situated at low and high altitude, respectively (e.g., Mysterud et al., 1997 and references therein). Whereas deer during winter are ‘‘forced’’ to low altitude by snow depth (Mysterud, 1999; Nelson, 1995), the increased use of higher altitudes in summer have been linked to the later plant phenology at high altitudes (Albon and Langvatn, 1992). However, this corresponds to quite large-scale movements in the case of the red deer (*Cervus elaphus*), up to about 50 km, and the movement to the summer range was for a fairly short time span—only about 3 weeks (Albon and Langvatn, 1992). In roe deer (*Capreolus capreolus*) movement from winter to summer is even quicker (200–600 m, range of 3–20 km), happening within less than a week (Mysterud, 1999), making it unlikely that plant phenology is largely affecting the altitudinal movement. Indeed in our case, with a gradient from around 1050 m up to slightly above 1300 m, sheep found forage at all altitudes from the start to the end of the vegetation season, even though snow was typically lying more frequently at high altitudes (Fig. 1). On average, we found the predicted increase in use of higher altitudes from early to mid grazing season, but the pattern was reversed towards the end of the season. The migration down slopes at the end of the season could have a relation to a higher biomass of forage plants at lower altitudes. The decline in crude protein towards the end of the grazing season may give the sheep a different trade-off between quality and quantity than early in the season, thus ‘‘forcing’’ the sheep to low altitude.

4.3. *Effects of activity and weather*

Animals may avoid attractive feeding areas to escape discomfort, for example, by selecting favourable microclimates under adverse weather conditions (Bailey et al., 1996; Senft et al., 1987). The movement of sheep along the altitudinal gradient was quite strongly affected by type of activity and weather. In the beginning of the season the sheep kept at the same altitudes both when resting and grazing, but with a considerable difference between high and low temperature. The difference in use of altitude between areas for grazing and resting increases later in the season, the sheep rested at lower altitudes compared to when they were grazing, at both high and low temperatures (Fig. 2). There were salt licks placed in the middle of each sub-enclosure (Fig. 1), and these sites were often visited when resting explaining some of the difference between resting and grazing. However, sheep also used lichen heaths situated on ridges more often when resting (Kausrud et al., 2006), irrespective of salt licks. For reindeer (Colman et al., 2001) and bighorn sheep (*Ovis canadensis*) (Mooring et al., 2003), increased use of higher altitudes during high temperature during summer is linked to increasing insect harassment. The numbers of midges and other biting insects increased in association with rising temperature and decreased with increasing wind speed (Mooring et al., 2003).

5. Conclusion

We conclude that predictions derived from IFD theory was rejected, and that those from pattern of plant phenology could only partly explain the sheep foraging pattern in the altitudinal gradient, and that movement to a large degree were determined by other factors such as prevailing weather.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.applanim.2006.10.017.

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