Density-dependent foraging behaviour of sheep on alpine pastures: effects of scale

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Abstract

Foraging patterns of large herbivores may give important clues as to why their life history varies depending on population density. In this landscape-scale experiment, domestic sheep *Ovis aries* were kept at high ($80\,\mathrm{sheep\,km^{-2}}$) and low ($25\,\mathrm{sheep\,km^{-2}}$) population densities during summer in high mountain pastures in Hol, Norway. We predicted an increasing use of less preferred plant species or habitat types with increasing sheep population density. Foraging behaviour was investigated by direct observations of individually marked sheep on different spatial scales, and diet composition was also assessed with microhistological analysis of faecal samples from known individuals. We found that the effects of density on foraging behaviour depended on scale and were only detected at the scale of diet choice. Use of the common grass species *Deschampsia flexuosa*, which provided the bulk forage (10–65% of the diet), remained constant throughout the season at low densities, but increased significantly over time at high densities. On a coarser spatial scale, neither within vegetation type nor between vegetation types, selection was affected by density, but vegetation type selection differed depending on whether the sheep were grazing or resting. Our study provides evidence of density dependence in foraging behaviour, but only at the finest spatial scale (diet choice).

Introduction

How foraging patterns of large herbivores vary depending on their population density is important for two main reasons. First, large herbivores may have huge impacts on ecosystem processes (reviews in Jefferies, Klein & Shaver, 1994; Hobbs, 1996) and how foraging behaviour varies depending on density is a central key to predicting their ecological effects when densities increase (Armstrong *et al*., 1997). Second, density-dependent responses in life-history traits are the key to understanding population regulation (*sensu* Messier, 1991) in wild mammals (reviews in Sæther, 1997; Gaillard *et al*., 2000). Despite this, we still have a limited understanding of the underlying behavioural causes of density dependence in demographic rates, partly because such data are difficult to obtain. Arguably, density dependence in foraging is the single most important key to understanding these processes (Choquenot, 1991), although other factors such as territorial behaviour, social stress or higher loads of disease or parasites (Stanko *et al*., 2002) may play a role in population regulation.

A central issue in foraging theory is that processes may operate at different spatial (and temporal) scales, often viewed as a hierarchy from diet selection at the finest scale, via patch and habitat selection at intermittent scales and up to landscape level (Johnson, 1980; Senft *et al*., 1987). Indeed, sheep are capable of discriminating between food items on a fine spatial scale as well as responding to aggregation of differing forage quality on larger scales (Edwards *et al*., 1994). From the demographic literature on density dependence, it is evident that the processes involved may well be dependent on scale (Ray & Hastings, 1996; Mysterud *et al*., 2000). At a coarse scale, up to about the scale of daily movement by herbivores (Tyler & Hargrove, 1997), density-dependent patterns of foraging are predicted by the ideal free distribution theory (IFD; Fretwell & Lucas, 1970). Several studies on ungulates have tested whether they conform to these predictions, and results usually suggest rather strong spatial structuring (Conradt, Clutton-Brock & Guinness, 1999; Pettorelli *et al*., 2001, 2002), that is spatially variable demographic rates, and therefore a violation of the IFD (but see Wahlström & Kjellander, 1995 for roe deer *Capreolus capreolus* and Ramp & Coulson, 2002 for grey kangaroos *Macropus giganteus*). In white-tailed deer *Odocoileus virginianus*, deviations were found around IFD in an experimental setting with two artificial patches (Kohlmann & Risenhoover, 1997). Only a few studies, none of them fully experimental, have shown that selection of food items

is indeed density dependent (Freeland & Choquenot, 1990; Choquenot, 1991; Mellado *et al.*, 2003). Feral donkeys *Equus asinus* in Australia ingested an increasingly species-poor diet dominated by a single species of grass *Sehima nervosa* with increasing density, thus elevating intake of crude fibre and getting less nitrogen and mineral nutrients (Freeland & Choquenot, 1990). Similar effects from density on diet and demographic variables have been found for domestic goats on heavily grazed pastures in arid grasslands (Mellado *et al.*, 2003). Despite this, no single study has explicitly addressed whether any density dependence in the foraging behaviour of large ungulates is scale dependent or not. Such information is critical in order to predict the impact of grazers on the ecosystem.

Diet choice and aspects of foraging of sheep is well known from the UK (e.g. Hunter, 1964; Grubb & Jewell, 1974; Grant *et al.*, 1985; Hodgson *et al.*, 1991; Crawley *et al.*, 2004), but few studies come from alpine areas of Scandinavia. In this fully replicated experimental study at a landscape scale in the alpine habitats of Norway, we aimed to test whether sheep foraging behaviour is density dependent at three levels of scale: from diet selection, via intermediate-scale selection (within vegetation type selection) to coarse scaled habitat selection (between vegetation type selection). At the three scales considered, foraging processes are likely to dominate, whereas the landscape scale (i.e. dispersal processes) was not relevant because of our experimental setting. We predict a general inclusion of plant species (and habitats) of poorer nutritional quality (Borkowski, 2000), and therefore also a wider diet with an increase in sheep population density (stocking rate).

Materials and methods

Study area

The experimental area – a 2.7 km^2 large enclosure is situated in the Hol municipality in Buskerud County, southern

Figure 1 Proportion of *Deschampsia flexuosa* in the diet (based on faecal samples) over the summer grazing season for ewes and lambs at high and low density.

Norway (between 60°40′–60°45′ and 7°55′–8°00′). There is a sub-continental alpine climate with low to moderate precipitation (7–800 mm; Førland, 1993). The bedrock consists of metaarkose (Sigmond, 1998), and the soil is moderately base-rich especially in landscape depressions with seepage water (Austrheim, Evju & Mysterud, 2005). The enclosure is situated in an alpine environment, from 1050 to 1300 m above sea level, with a terrain typical of the alpine environment commonly in use for summer pastures in much of southern Norway. The enclosure is mainly in the lower alpine zone, with a lower border close to the forest line extending upwards into the middle alpine zone. Low shrubs interspersed with grass-dominated meadows dominate the vegetation, and there are only a few scattered birch (*Betula* sp.) trees in the lowest areas.

The area is rich in vascular plant species (i.e. 104 recorded in 180 quadrats each of 0.25 m^2) and herbs dominate (53%; Austrheim *et al.*, 2005). The total standing crop for dwarf shrubs and grassland communities was 207.6 ($n = 54$, year 2002) and 100.2 g m^{-2} ($n = 54$, year 2001) dry weight. Dwarf shrub communities are dominated by woody species (85%) such as *Betula nana*, *Vaccinium myrtillus*, *Empetrum hermaphroditum* and *Phyllodoce caerulea*, whereas graminoids (6%), bryophytes and lichens (8%), and herbs (1%) are rarer. Annual productions of graminoids and herbs are 13.1 and 1.3 g m^{-2}, respectively. Grasslands are dominated by graminoids (47%) such as *Carex bigelowii* and *Deschampsia flexuosa*, woody species (31%), herbs (12%), and bryophytes and lichens (9%). Annual productions of graminoids and herbs are 47.3 and 12.1 g m^{-2}, respectively. Thus production varies between vegetation types, which is important to consider in habitat selection studies (cf. Morris, 1994).

Before fencing (summer 2001), grazing pressure by domestic sheep was low (<10 sheep km^{-2}). Other herbivores such as reindeer *Rangifer tarandus*, moose *Alces alces* and roe deer *C. capreolus* can occasionally use part of the area, but are likely to have a negligible effect on the system.

Experimental design and treatment

This study is part of a larger study of the foraging ecology of sheep and the ecological impact of grazing on the alpine ecosystem (e.g. Mysterud *et al.*, 2005; Steen, Mysterud & Austrheim, 2005). The enclosure consisted of a total of 17.3 km standard sheep fencing (110 cm high). The area was split into nine sub-enclosures of about 0.3 km^2 (some size variation due to practical problems in putting up fencing in areas with bare rock visible), and each of three adjacent sub-enclosures was randomly assigned as controls, low-density and high-density areas, respectively, to obtain a blockwise randomized design with three replications. Each sub-enclosure contains a quite similar amount of vegetation types (Table 1).

On the basis of a vegetation map made in 2001, and knowledge of approximate grazing value to the sheep (Rekdal, 2001*a*), low-density sub-enclosures were assigned treatments of 25 sheep km^{-2} (C, D and I) and high density
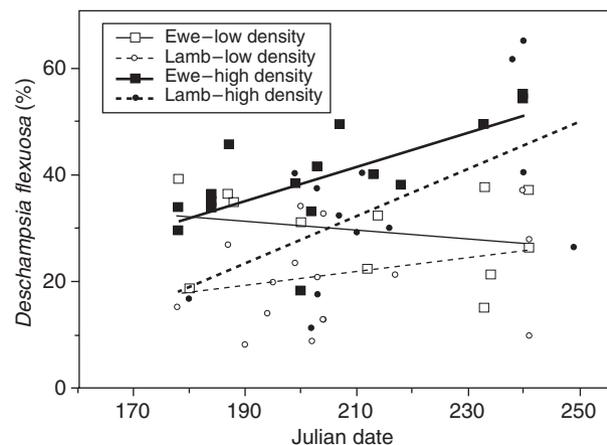
Table 1 Distribution of vegetation types over the sub-enclosures containing sheep (C, D and I with a low density of sheep; B, F and H with a high density of sheep)

Sub-enclosure	B		C		D		F		H		I	
Net density of sheep per km^2	80		25		25		80		80		25	
Number of sheep	18		6		8		16		17		4	
Vegetation type	daa	%	daa	%	daa	%	daa	%	daa	%	daa	%
Snow bed	51.2	16.2	89.1	26.2	35.7	9.3	17.5	7.9	17.3	7.1	42.1	18.2
Lichen heath	72	22.9	62.6	18.5	62.3	16.2	21.2	9.6	32.5	13.4	54.9	23.8
Dwarf shrub heath	152.9	48.6	143.3	42.2	213.6	55.6	122.9	55.7	161.5	66.7	117.6	50.9
Meadow	19	6	15.6	4.6	50.8	13.2	48.6	22	14.6	6	13.7	5.9
Bog	10.5	3.3	28.6	8.4	21.8	5.7	10.6	4.8	14.6	6	2.8	1.2
Boulder field	8	2.5										
Water bodies	1	0.3							1.6	0.7		
Total	305.6	100	339.2	100	384.2	100	220.8	100	240.5	100	231.1	100

Note that not all vegetation types were recorded by the survey in all areas (resolution 2 h explaining the missing values), but smaller patches could still be found during observation of forage selection in each of the sub-enclosures (daa = 0.001 km^2).

80 sheep km^{-2} (B, F and H) covering the most typical density range on alpine pastures of Norway (Warren & Mysterud, 1995; Mysterud & Mysterud, 1999; Mysterud et al., 2002). Habitats with little or no forage (such as water bodies and areas dominated by mosses, rocks, lichens and bogs) were excluded when calculating densities. Population density should always be considered relative to resource levels (Van Horne, 1983), so that it is important to know the grazing pressure. In other studies, low grazing pressure averaged 32% degree of utilization of forage plants, moderate grazing pressure 43%, whereas heavy grazing pressure was 57% degree of utilization of the most important forage plants (Holechek et al., 1999). Grazing pressure estimated from the most heavily used herbs (proportion eaten) in our area indicated that levels were low and moderate (Evju et al., 2006), which is consistent with the evaluation based on vegetation types carried out before the study (Rekdal, 2001b).

All sheep were of the most common breed used in Norway, the 'Kvit norsk sau' often refereed to as the 'Dala' breed, and from the same sheep farmer (Knut-Eirik Sveingard) to ensure a similar treatment of all sheep. Ewes averaged 83 kg in live weight in spring, whereas lambs grew from an average of 20 kg to an average of 44 kg during summer foraging (Mysterud & Austrheim, 2005). All sheep were individually tagged with coloured and numbered neckbands. The alpine pasture grazing season lasted from the last week of June to the first part of September, similar to what is used for most mountain regions in southern Norway. No data were collected the first few days, allowing the sheep to habituate to the setting.

Methods

Sheep were followed by direct observation using binoculars from 28 June to 29 August 2002, yielding a total of 383 observations on 41 days. To ensure an unbiased sample without losing too much in sampling efficiency, we used a stratified randomization of the sequence of registration of individual sheep. The family group was considered to be the smallest independent unit, as the bonds between ewe and lambs are stable, while this breed does not form stable, large herds – rather herd size usually is small and composition varies over short temporal scales. Enclosures were so large that observed behaviour was not influenced by fences. At the beginning of each day, we randomly selected whether the eastern or western part of the area should be covered, and then which sub-enclosure within that part to start in, and from which direction (from above or below). After all ewes in a sub-enclosure had been recorded, we randomly selected a new sub-enclosure in the chosen half of the research area. Identification of sheep at foraging sites was usually done within 20–50 m, to ensure correct identification of the individual sheep.

At each location (mapped with geographic positioning system), we first noted whether the sheep was resting (lying down) or active (grazing), and registered the vegetation type (see below). If the sheep was foraging, we obtained further data on dietary choice.

Fine-scale foraging: diet

Determining the diet of ungulates in field studies is difficult, as all methods have their different biases (e.g. Gaare, Sørensen & White, 1977; Kessler, Kasworm & Bodie, 1981; Henley, Smith & Raats, 2001). We therefore used two methods (direct observation and faecal analysis) to assess dietary choice. When the sheep was grazing, we used the binoculars to pinpoint us to the specific location of foraging. A 1 m^2 aluminium square was placed where the observed grazing had taken place – later referred to as a forage site. To obtain an index of local plant availability, all vascular plants were identified to species, except for Salix spp. (Salix glauca, Salix lapponum, Salix lanata with their possible hybrids) and some graminoids (Poaceae, Juncaceae, Cyperaceae) that could only be determined at plant group level. Their respective coverages were estimated on an ordinal scale by the same observer (K. K.). To obtain an

index of use, we noted whether bite marks could be observed on any given species. We also obtained faecal samples ($n = 58$) from known individuals collected over the season to ensure equal representation of densities ($n = 29$ for each density), ages [lamb ($n = 30$) vs. adult ($n = 28$)] and time periods. The samples were frozen, and later used for micro-histological analysis (e.g. Stewart & Stewart, 1970; Cortés *et al.*, 2003; Takatsuki, 2003) using a standard procedure (1 mL of faeces was boiled in 4 mm of nitric acid). For each sample, two parallel sub-samples from the same faeces were processed independently.

Intermediate-scale foraging: within vegetation type

For every third foraging site ($n = 102$), we placed a quadrate 10 m away in a random direction and estimated plant availability (coverage). If the placement procedure would have taken the random site across a fence or into open water, a new (random) direction was taken from the same foraged site until a valid location was obtained. We term the comparison of the actual foraging site and these 'constrained random sites' as intermediate-scale or within vegetation type selection (Mysterud, Lian & Hjermann, 1999).

Coarse-scale foraging: vegetation types

Vegetation was classified as belonging to one of five main types (snow bed, bog/fen, meadow, dwarf shrub heath and lichen heath), while a sixth category (water and boulder areas) was removed from the analysis. These vegetation types were usually fairly distinct, and mapped to a scale of about 2 ha during the summer of 2001 following procedures commonly used by the Norwegian Institute of Land Inventory (Table 1; Rekdal, 2001*b*).

Statistical analyses

Fine scale – plant use and selection

Diet composition was estimated as proportions. For direct observations, we used linear mixed effects models with sheep identity nested within sub-enclosure as a random effect to avoid pseudoreplication (Crawley, 2003), and tested whether there was any effect of density, age of sheep and date of observation. For faecal samples, we nested sub-sample within sheep identity within sub-enclosure as a random factor. Diet proportions were arcsine[sqrt(observed/100)] transformed before analysis to avoid unequal variances (heteroscedasticity; Crawley, 2003). We compared the dietary contribution of the two methods with Pearson correlation (r_{Pe}) at the finest scale of resolution (24 plant species or groups).

Diet breadth was calculated both overall and separately for each family group using the normalized Levin's measure of diet breadth (Hanski, 1978). We tested for density effects with linear mixed models as above.

Selection is usually defined as use above availability (e.g. Thomas & Taylor, 1990), and a number of different methods exist to estimate selection. For direct observation, we compared use (whether or not a plant was recorded as grazed upon or not) with plant species or group coverage within the $1\,m^2$ square defined as the foraging site using a variant of Ivlev's E_i index (Ivlev, 1961); the difference was that we used a binomial measure of use for each site. Confidence intervals were obtained by bootstrapping with 5000 resamples (Efron & Tibshirani, 1993).

To test for density-dependent differences in use and selection at the species level, we used sub-enclosure as a random effect in linear mixed models (Crawley, 2003) and density, date and their interaction as candidate explanatory variables. Models using maximum likelihood were first used to select the most parsimonious model selected by minimizing Akaike's information criterion (AIC; Burnham & Anderson, 1998; Johnson & Omland, 2004). The small-sample correction $AIC_c = AIC + 2\,K(K+1)/(N-K+1)$, where N is the number of observations and K is the number of regression coefficients including the intercept, was applied when $N/K < 40$. Then final models were run with restricted maximum likelihood (cf. Crawley, 2003).

Intermediate-scale (within vegetation type) selection

To assess selection on an intermediate scale, the difference in coverage of various plant species and groups (and also 'grazing value' as defined below) between foraging sites and the attached random sites 10 m away were analysed with Wilcoxon rank sum test on the coverage data. We conducted four-way contrasts between forage sites and constrained random sites within and between densities. We restricted these analyses to main groups of plants (Table 2). Clearly, there is some heterogeneity within these groups. For example, herbs contain many highly preferred species and also some avoided species, but the groups were found adequate for illustrating the main patterns.

Coarse scale – selection of vegetation type

We assessed habitat (or vegetation type) selection with the compositional analysis method working on log ratios, and ranking habitats from most to least selected (Aebischer, Robertson & Kenward, 1993). We used borders of each sub-enclosure to delimit availability for individual family groups. We used the most common habitat as the denominator (dwarf shrub heath), and avoided problems of missing values by using fairly broad habitat categories (see above). We tested for effects of density (high/low), activity (foraging/resting) and season (early/late) within a MANOVA setting (Aebischer *et al.*, 1993).

To assess the role of forage quantity and quality to sheep as a factor in habitat selection, we estimated what we termed grazing value for the different vegetation types. This grazing value was calculated for each forage site (above) as the selection score multiplied by coverage for a given plant

Table 2 Diet composition of free-ranging sheep at high and low population density in Hol, Norway, summer 2002, estimated by microhistological analysis of faeces and by direct observation

Plant group/ species	Density	Diet (%) – faecal samples			Diet (%) – direct observation			Available (%) – forage sites; mean	Available (%) – random sites; mean	Intermediate scale selection (available forage site vs. random site)	
		Mean	95% lower CL	95% upper CL	Mean	95% lower CL	95% upper CL			Wilcox	P
Forbs	Low	24.3	21.7	26.8	34.5	29.9	42.8	32.0	19.2	5.562	<0.001
	High	20.1	18.0	23.1	27.5	23.0	32.8	34.2	18.6	4.826	<0.001
Deschampsia flexuosa	Low	24.8	22.3	27.0	15.0	10.6	19.8	15.2	12.4	0.321	0.748
	High	36.6	33.1	40.1	20.6	16.0	26.0	19.3	13.6	1.151	0.250
Carex spp.	Low	2.1	1.7	2.7	15.5	7.0	28.0	5.0	3.8	0.326	0.745
	High	3.3	2.5	4.4	11.7	6.5	18.4	5.1	7.9	−0.890	0.374
Graminoids	Low	18.8	16.9	21.1	18.7	16.0	23.0	16.8	16.1	1.920	0.055
	High	15.9	14.1	17.8	19.7	16.8	23.6	20.2	16.3	1.152	0.249
Salix sp.	Low	18.0	14.0	22.9	9.9	8.6	12.0	9.5	9.1	−0.618	0.537
	High	15.8	11.9	20.4	11.8	9.4	14.2	16.2	12.7	0.803	0.422
Woody plants	Low	11.1	9.3	12.8	5.5	4.8	6.7	52.3	54.0	−0.216	0.829
	High	7.5	6.1	9.4	4.4	3.7	5.1	48.6	53.4	−0.601	0.548
Other	Low	0.7	0.5	1.1	1.0	0.9	1.2	28.8	37.3	−0.938	0.348
	High	0.8	0.5	1.1	4.3	3.2	5.3	27.7	37.7	−0.358	0.720

Estimates of availability refer to ground coverage. A 95% confidence interval (CL) was established for faecal samples by bootstrapping. Intermediate scale selection is estimated by compared availability of forage in actual grazing sites compared with availability in a random site nearby.

species/group, and then summed for all species/groups (similar to that of Mysterud *et al.*, 1999). We then multiplied by the height of the vegetation to at least partly estimate the effects of increased biomass in taller vegetation.

All statistical analysis was performed with S-Plus (Crawley, 2003), except for the compositional analysis, which was performed in Microsoft Excel.

Results

Fine scale – plant species/group use and selection

An overview of the main components in sheep diet at low and high population density is given in Table 2. The most parsimonious model explaining 47.0% of the variation in the proportion of the most frequently eaten plant *D. flexuosa* included factors of age, date and density and interaction between density and date (Table 3). The use of the most used forage species *D. flexuosa* increased over the grazing season in high-density but not in low-density sub-enclosures, and use was higher in ewes than in lambs (Fig. 1). This change in use over the season may occur because of changes either in availability or in selectivity by the sheep. It turned out that sheep selectivity for *D. flexuosa* declined over time at low sheep density (interaction date × density; d.f. = 421, $t = 3.180$, $P = 0.022$). There was no correlation between sheep density and diet breadth ($r_{pe} = 0.06$, $P = 0.30$).

The (square-root transformed) proportion of plant species or groups in diet estimated from faeces and direct

observation was highly correlated ($n = 24$, $r_{pe} = 0.94$, $P < 0.001$). Woody plants such as *Salix* spp. were overrepresented in faeces. The parameter estimates were similar when performing the same analysis using data from the direct (bite) observations, except that the r^2 was lower (5%) and the age estimate was less than halved and not quite significant (Table 3).

Intermediate scale – within vegetation type selection

Sheep selected forage sites that contained a higher coverage of forbs than constrained random sites, whereas there was no selection with regard to other main plant species or groups (Table 2). There was no evidence that coverage of herbs or any of the other main plant groups (Table 2) differed depending on population density (all $P > 0.05$). Just 39 of the 102 random sites placed 10 m away from foraging sites fell within the same vegetation type. When only the 39 pairs within the same vegetation type were used, no single species showed a significant difference between random and foraging sites. There was also a high correlation ($r_{Pe} = 0.784$, $P < 0.001$) between plant species coverage at foraging sites and at random sites. This suggests little heterogeneity at this scale, and therefore no strong selection within vegetation types. Comparing grazing values in random and forage sites within each vegetation type suggests no difference between forage and random sites in the meadow (mean 1.04 vs. 1.02; d.f. = 99, $t = 0.18$, $P = 0.860$), lichen heath (mean 0.31 vs. 0.28; d.f. = 39, $t = 32$, $P = 0.698$) and snow beds (0.58 vs. 0.53; d.f. = 120, $t = 0.63$, $P = 0.528$), but significantly

Table 3 Results from linear mixed effects models analysing how the proportion of *Deschampsia flexuosa*, the dominant plant in the diet (estimated by faecal analysis and direct observation), changes as a function of age, density and date

Parameter	Least square mean	SE	d.f.	t	P	AIC$_c$	ΔAIC$_c$	AIC$_c$ weights
A. Faecal analysis								
Intercept	−0.2051	0.1269	44	−1.617	0.113			
Age	0.1032	0.0330	37	3.124	0.004	−185.710	37.011	0.000
Julian date	0.0038	0.0006	26	6.461	<0.001	−193.658	29.063	0.000
Density	0.7027	0.1559	4	4.508	0.011	−198.701	24.020	0.000
Density × date	−0.0039	0.0007	26	−5.365	<0.001	−222.721	0.000	0.599
Density × age						−220.556	2.165	0.203
Age × date						−220.497	2.224	0.197
B. Direct observation								
Intercept	−0.2021	0.1925	246	−1.050	0.295			
Age	0.0845	0.0344	57	2.453	0.017	−88.343	2.169	0.137
Julian date	0.0016	0.0009	246	1.762	0.079	−86.291	4.221	0.049
Density	0.7027	0.2918	4	2.408	0.074	−85.566	4.946	0.034
Density × date	−0.0032	0.0014	246	−2.377	0.018	−89.299	1.213	0.221
Density × age	−0.0899	0.0483	57	−1.859	0.068	−90.512	0.000	0.405
Age × date						−88.582	1.930	0.154

Note that AIC$_c$ was calculated when using ML, while the final model was run with REML. ΔAIC$_c$ is given relative to the best model. Each factor was added from above to below. The interactions were only included in the next model if lowering the AIC$_c$.
AIC$_c$, Akaike information criterion.

Table 4 Vegetation type selection (rank) by foraging sheep in Hol, Norway, during summer 2002, as determined by the compositional analysis (see text), and per cent direct observations (use) versus per cent available (mean for all three sub-enclosures of a given density)

Vegetation type	Vegetation type ranking		Use		Available		Selection	
	Grazing	Resting	Low	High	Low	High	Low	High
Low/tall herb meadow	1	3	24.5	28.7	7.9	11.4	3.1	2.52
Moss/grass snowbed/stone polygon land	2	4	34.6	25.6	17.9	10.5	1.93	2.44
Lichen heath	3	1	10.7	5.5	19.5	15.4	0.55	0.36
Bog/fen	4	5	4.4	4.9	5.1	4.7	0.86	1.03
Dwarf shrub heath	5	2	25.8	35.4	49.6	57.2	0.52	0.62

There was no effect of density (Low, low density; High, high density) on habitat ranking of sheep when they were grazing.

higher grazing values for forage than random sites in the less selected vegetation types dwarf shrub heath (mean 0.70 vs. 0.47; d.f. = 135, $t = 4.15$, $P<0.001$), bog/fen (mean 0.90 vs. 0.55; d.f. = 25, $t = 3.15$, $P = 0.004$) and others (0.39 vs. 0.04; d.f. = 6, $t = 9.37$, $P<0.001$).

Coarse-scale foraging: selection of vegetation types

Use of vegetation types by sheep in the experimental area differed between resting and foraging behaviour (Table 4; Pillai–Bartlett trace = 0.544, $P<0.001$). Sheep were selective in their use of vegetation types when foraging ($\chi^2 = 37.3$, $P<0.001$) and resting ($\chi^2 = 48.9$, $P<0.001$), but selectivity (when foraging) did not differ with sheep population density (Pillai–Bartlett trace = 0.179, $P = 0.147$) or season (early vs. late; Pillai–Bartlett trace = 0.165, $P = 0.189$), neither was there any interaction between period and density (Pillai–Bartlett trace = 0.073, $P = 0.678$). There was no relationship between forage quantity and overall habitat ranking by sheep ($n = 5$, $r = −0.12$, $P>0.8$).

Discussion

Although there is an extensive literature on density dependence in demographic variables for ungulates in general (see the Introduction), little is known about the proximate mechanisms behind these effects. In this study, we show that although foraging by sheep was non-random at all scales, the density-dependent response in foraging behaviour was scale dependent. At a coarse (vegetation type) and intermediate (within vegetation type) spatial scale, selection did not differ significantly depending on density. However at the finest scale, use of plant species was markedly density dependent. Use of the abundant grass *D. flexuosa* increased as the grazing season progressed in high-density sub-enclosures only (Fig. 1). Because there was no density dependence in the selection of vegetation type (see Burboa-Cabrera, Schacht & Anderson, 2003 for a similar result in cattle), the density-dependent food choice is likely a small-scale process. Sheep have been shown to act less selectively on a fine scale when less satiated (Edwards *et al.*, 1994), which may on a proximate level explain this change in diet with food

limitation at high density. The current study was short term (1 year of grazing in a previously lightly grazed area), and it remains to be determined whether the same conclusion applies to areas with a long-term difference in grazing pressure.

The density dependence observed in diet was robust to the methodology used, as both direct observation and microhistological analyses of diet composition yielded similar results. However, the absolute values obtained by these two methods differed, as faecal analyses tended to underestimate the proportion of easily digestible plants such as many forbs, whereas grasses and especially shrubs may be overestimated (Stewart & Stewart, 1970; Kessler *et al.*, 1981; Mofareh, Bech & Schneberger, 1997; Henley *et al.*, 2001). On the other hand, it can be very difficult to obtain unbiased estimates by direct observation, as some plants are removed completely, leaving no observable bite marks. Indeed, graze marks on *D. flexuosa* were often difficult to detect, whereas big-leaved forbs and grasses like *Geranium sylvaticum* and *A. odoratum* probably represent the other extreme. Nonetheless, in general, the selection scores from the direct observation method were rather closely correlated with those obtained from faecal analysis (Table 2).

For the total material, sheep showed a selection of foraging sites with a high coverage of herbs, and this was similar at both high and low population density. However, selection at the intermediate (within vegetation type) scale seemed to occur only in heterogeneous vegetation types. There were no differences between grazing values in grazed and random sites (10 m away) in meadow, lichen heath and snow bed vegetation types, but significant differences in the vegetation types less frequently used for foraging, namely dwarf shrub heath, bog/fen and boulder fields. This suggests a more patchy distribution of selected food items in poorer vegetation types, resulting in within vegetation type selection.

At the coarsest spatial scale, selection differed depending on activity. Meadow was clearly the most highly selected vegetation type for foraging by sheep, and the estimated grazing values can account for the high selection of the meadow types – this is typically the best grazing area in the mountains (Rekdal, 2001*a*). If sheep were distributed only according to an IFD, we would expect the grazing pressure to be proportional to the amount of forage available in each vegetation type and/or density-dependent selection. The experimental scale is theoretically suitable (i.e. scale of daily movements) for an IFD to be observed (Tyler & Hargrove, 1997). However, selection of vegetation types was not density dependent, as predicted from the IFD. Further, snow beds were grazed considerably more than their proportions of available forage indicated in, and dwarf shrub heath less than expected from the grazing value. Differences in plant quality, which likely are very high in snow beds as newly emergent forage may be available as snow melts later here, may partly account for this. Note that this mainly applies to the grass snow beds, while there is very little forage in the moss snow beds, but the latter were rare in the area. Lichen heath, containing little forage, was observed to

be highly preferred for resting. Lichen heaths are typical on ridges, and the choice of such a position for resting has been suggested to be the remnant of an antipredator tactic (Warren & Mysterud, 1991; Warren *et al.*, 1993), as for example bighorn sheep *Ovis canadensis* show a similar behaviour (Geist, 1971). Similarly, mouflon sheep *Ovis gmelini* remained near escape terrain even in the absence of predators, and this was interpreted as phylogenetic inertia (Bon, Joachim & Maublanc, 1995).

Sheep have the ability to utilize grass forage resources in landscapes too poor to use for more intensive agricultural purposes, and sheep husbandry is a cornerstone of the economy in many rural areas of Norway (Drabløs, 1997). During the summer months, about 2–2.5 million sheep are released onto outlying pastures in Norway, making it by far the most common large herbivore. Alpine habitats constitute about 50% of the area of Norway and have been used for grazing since the Bronze Age (Kvamme, 1988). Despite this, the knowledge of the foraging ecology of domestic sheep is poor, and no study has earlier addressed whether or how population density may affect this. Densities in our experiment are within the density range for sheep grazing in similar alpine habitats of Norway (Mysterud & Mysterud, 1999), and are considered sustainable by sheep farmers in the sense that any loss from lower individual meat yield or higher mortality is expected to be more than offset by the benefit of increased total yield when increasing density within this range. This suggests that eventual density-dependent effects on foraging behaviour are non-extreme and may be hard to detect, but will have direct relevance to management of the commons used for sheep forage. Our study provides evidence that density dependence in foraging behaviour occurs, but only at the finest spatial scale (diet choice). With an increase in sheep density, not only is an increasing number of sheep eating more but they also eat a larger proportion of *D. flexuosa*. This thus provides a case showing that the ecological impact of grazers on plant population may not be linearly related to herbivore density, which is a result with broad implications for both basic and applied ecology.

Acknowledgements

References

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**, 1313–1325.

Armstrong, H.M., Gordon, I.J., Hutchings, N.J., Illius, A.W., Milne, J.A. & Sibbald, A.R. (1997). A model of the grazing of hill vegetation by sheep in the UK. II. The prediction of offtake by sheep. *J Appl. Ecol.* **34**, 186–207.

Austrheim, G., Evju, M. & Mysterud, A. (2005). Herb abundance and life history traits in two contrasting alpine habitats in southern Norway. *Plant Ecol.* **179**, 217–229.

Bon, R., Joachim, J. & Maublanc, M.L. (1995). Do lambs affect feeding habitat use by lactating female mouflons in spring in areas free of predators? *J. Zool. (Lond.)* **235**, 43–51.

Borkowski, J. (2000). Influence of the density of a sika deer population on activity, habitat use, and group size. *Can. J. Zool.* **78**, 1369–1374.

Burboa-Cabrera, F.R., Schacht, W.H. & Anderson, B.E. (2003). Utilization and grazing distribution of cattle at 4 stocking densities. *J. Range Mgmt.* **56**, 328–333.

Burnham, K.P. & Anderson, D.R. (1998). *Model selection and inference: a practical information-theoretic approach*. New York: Springer.

Choquenot, D. (1991). Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. *Ecology* **72**, 805–813.

Conradt, L., Clutton-Brock, T.H. & Guinness, F.E. (1999). The relationship between habitat choice and lifetime reproductive success in female red deer. *Oecologia* **120**, 218–224.

Cortés, A., Miranda, E., Rau, J.R. & Jiménez, J.E. (2003). Feeding habits of guanacos *Lama guanicoe* in the high Andes of north-central Chile. *Acta Theriol.* **48**, 229–237.

Crawley, M.J. (2003). *Statistical computing. An introduction to data analysis using S-plus*. Chichester, West Sussex, UK: John Wiley and Sons.

Crawley, M.J., Albon, S.D., Bazely, D.R., Milner, J.M., Pilkington, J.G. & Tuke, A.L. (2004). Vegetation and sheep population dynamics. In *Soay sheep: dynamics and selection in an island population*: 89–112. Clutton-Brock, T.H. & Pemberton, J.M. (Eds). Cambridge: Cambridge University Press.

Drabløs, D. (1997). *The story of the Norwegian sheep. Anniversary review of the Norwegian sheep and goat breeders 1947–1997*. Oslo: Norwegian Sheep and Goat Breeders.

Edwards, G.R., Newman, J.A., Parsons, A.J. & Krebs, J.R. (1994). Effects of the scale and spatial distribution of the food resource and animal state on diet selection: an example with sheep. *J. Anim. Ecol.* **63**, 816–826.

Efron, B. & Tibshirani, R.J. (1993). *An introduction to the bootstrap*. London: Chapman & Hall.

Evju, M., Mysterud, A., Austrheim, G. & Økland, R.H. (2006). Selecting herb species and traits as indicators of sheep grazing pressure in a Norwegian alpine habitat. *Ecoscience* in press.

Førland, E.J. (1993). Precipitation normals, period 1961–1990. *Norw. Metrol. Inst.* **39**, 1–63.

Freeland, W.J. & Choquenot, D. (1990). Determinants of herbivore carrying capacity: plants, nutrients, and *Equus asinus* in northern Australia. *Ecology* **71**, 589–597.

Fretwell, S.D. & Lucas, H.L.j. (1970). On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* **19**, 16–36.

Gaare, E., Sørensen, A. & White, R.G. (1977). Are rumen samples representative of the diet? *Oikos* **29**, 390–395.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* **31**, 367–393.

Geist, V. (1971). *Mountain sheep: a study in behavior and evolution*. Chicago and London: The University of Chicago Press.

Grant, S.A., Suckling, D.E., Smith, H.K., Torvell, L., Forbes, T.D.A. & Hodgson, J. (1985). Comparative studies of diet selection by sheep and cattle: the hill grasslands. *J. Ecol.* **73**, 987–1004.

Grubb, P. & Jewell, P.A. (1974). Movement, daily activity and home range of soay sheep. In *Island survivors: the ecology of the soay sheep of St Kilda*: 160–194. Jewell, P.A., Milner, C. & Boyd, J.M. (Eds). London: The Athlone Press.

Hanski, I. (1978). Some comments on the measurement of niche metrics. *Ecology* **59**, 168–174.

Henley, S.R., Smith, D.G. & Raats, J.G. (2001). Evaluation of 3 techniques for determining diet composition. *J. Range Mgmt.* **54**, 582–588.

Hobbs, N.T. (1996). Modification of ecosystems by ungulates. *J. Wildl. Mgmt.* **60**, 695–713.

Hodgson, J., Forbes, T.D.A., Armstrong, R.H., Beattie, M.M. & Hunter, E.A. (1991). Comparative studies of the ingestive behaviour and herbage intake of sheep and cattle grazing indigenous hill plant communities. *J. Appl. Ecol.* **28**, 205–227.

Holechek, J.L., Gomez, H., Molinar, F. & Galt, D. (1999). Grazing studies: what we've learned. *Rangelands* **21**, 12–16.

Hunter, R.F. (1964). Home range behaviour in hill sheep. In *Grazing in terrestrial and marine environments*: 155–171. Crisp, D.J. (Ed.). Oxford: Blackwell Scientific Press.

Ivlev, V.S. (1961). *Experimental ecology of the feeding fishes*. New Haven, CT: Yale University Press.

Jefferies, R.L., Klein, D.R. & Shaver, G.R. (1994). Vertebrate herbivores and northern plant communities: reciprocal influences and responses. *Oikos* **71**, 193–206.

Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**, 65–71.

Johnson, J.B. & Omland, K.S. (2004). Model selection in ecology and evolution. *Trends Ecol. Evol.* **19**, 101–108.

Kessler, W.B., Kasworm, W.F. & Bodie, W.L. (1981). Three methods compared for analysis of pronghorn diets. *J. Wildl. Mgmt.* **45**, 612–619.

Kohlmann, S.G. & Risenhoover, K.L. (1997). White-tailed deer in a patchy environment: a test of the ideal-free-distribution theory. *J. Mammal.* **78**, 1261–1272.

Kvamme, M. (1988). Pollen analytical studies of mountain summer farming in western Norway. In *The cultural landscape, past, present and future*: 349–367. Birks, H.H., Birks, H.J.B., Kaland, P.E. & Moe, D. (Eds). Cambridge: Cambridge University Press.

Mellado, M., Valdez, R., Lara, L.M. & Lopez, R. (2003). Stocking rate effects on goats: a research observation. *J. Range Mgmt.* **56**, 167–173.

Messier, F. (1991). The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *J. Anim. Ecol.* **60**, 377–393.

Mofareh, M.M., Bech, R.F. & Schneberger, A.G. (1997). Comparing techniques for determining steer diets in northern Chihuahuan Desert. *J. Range Mgmt.* **50**, 27–32.

Morris, D.W. (1994). Habitat matching: alternatives and implications to populations and communities. *Evol. Ecol.* **8**, 387–406.

Mysterud, A. & Austrheim, G. (2005). Ecological effects of sheep grazing in alpine habitats. Shortterm effects. *Utmarksnæring i Norge* **1-05**, 1–91.

Mysterud, A., Hansen, L.O., Peters, C. & Austrheim, G. (2005). The short-term effect of sheep grazing on selected invertebrates (Diptera and Hemiptera) relative to other environmental factors in an alpine ecosystem. *J. Zool. (Lond.)* **266**, 411–418.

Mysterud, A., Langvatn, R., Yoccoz, N.G. & Stenseth, N.C. (2002). Large-scale habitat variability, delayed density effects and red deer populations in Norway. *J. Anim. Ecol.* **71**, 569–580.

Mysterud, A., Lian, L.-B. & Hjermann, D.Ø. (1999). Scale-dependent trade-offs in foraging by European roe deer (*Capreolus capreolus*) during winter. *Can. J. Zool.* **77**, 1486–1493.

Mysterud, A. & Mysterud, I. (1999). Bærekraftig bruk og forvaltning av Setesdals Vesthei og Ryfylkeheiene. En utredning med spesiell vekt på økologiske effekter av husdyrbeiting i utmark. *Utmarksnæring i Norge* **1-99**, 1–197.

Mysterud, A., Yoccoz, N.G., Stenseth, N.C. & Langvatn, R. (2000). Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *J. Anim. Ecol.* **69**, 959–974.

Pettorelli, N., Gaillard, J.-M., Duncan, P., Ouellet, J.-P. & Van Laere, G. (2001). Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. *Oecologia* **128**, 400–405.

Pettorelli, N., Gaillard, J.-M., Van Laere, G., Duncan, P., Kjellander, P., Liberg, O., Delorme, D. & Maillard, D. (2002). Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. *Proc. Roy. Soc. Lond. Ser. B* **269**, 747–753.

Ramp, D. & Coulson, G. (2002). Density dependence in foraging habitat preference of eastern grey kangaroos. *Oikos* **98**, 393–402.

Ray, C. & Hastings, A. (1996). Density dependence: are we searching at the wrong spatial scale? *J. Anim. Ecol.* **65**, 556–566.

Rekdal, Y. (2001*a*). *Husdyrbeite i fjellet: vegetasjonstypar og beiteverdi*. NIJOS-rapport; 7/01, Norsk institutt for jord-og skogkartlegging, Ås.

Rekdal, Y. (2001*b*). Vegetation and forage at Minnestølen. *NIJOS-dokument* **23/01**, 1–21.

Sæther, B.-E. (1997). Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends Ecol. Evol.* **12**, 143–149.

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

Sigmond, E. (1998). *Odda map of rock; Odda; 1:250 000*. Trondheim: Norwegian Geological Surveys.

Stanko, M., Miklisová, D., de Bellocq, J.G. & Morand, S. (2002). Mammal density and patterns of ectoparasite species richness and abundance. *Oecologia* **131**, 289–295.

Steen, H., Mysterud, A. & Austrheim, G. (2005). Sheep grazing and rodent populations: evidence of negative interactions from a landscape scale experiment. *Oecologia* **143**, 357–364.

Stewart, D.R.M. & Stewart, J. (1970). Food preference data by faecal analysis for African plains ungulates. *Zool. Afr.* **15**, 115–129.

Takatsuki, S. (2003). Use of mires and food habits of sika deer in the Oze Area, central Japan. *Ecol. Res.* **18**, 331–338.

Thomas, D.L. & Taylor, E.J. (1990). Study design and tests for comparing resource use and availability. *J. Wildl. Mgmt.* **54**, 322–330.

Tyler, J.A. & Hargrove, W.W. (1997). Predicting spatial distribution of foragers over large resource landscapes: a modeling analysis of the ideal free distribution. *Oikos* **79**, 376–386.

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. *J. Wildl. Mgmt.* **47**, 893–901.

Wahlström, L.K. & Kjellander, P. (1995). Ideal free distribution and natal dispersal in female roe deer. *Oecologia* **103**, 302–308.

Warren, J.T. & Mysterud, I. (1991). Summer habitat use and activity patterns of domestic sheep on coniferous range in southern Norway. *J. Range Mgmt.* **44**, 2–6.

Warren, J.T. & Mysterud, I. (1995). *Sau, villrein og ressursbruk på Hardangervidda i tidligere tid og nå. En utredning med særlig vekt på dagens problemer for beitebruk og villreinforvaltning i lokalt og regionalt perspektiv*. Oslo: Biologisk Institutt, Universitetet i Oslo.

Warren, J.T., Mysterud, I., Stensli, O.M., Berg, M. & Movik, E. (1993). Use of forest vegetation by sheep as recorded by radio telemetry. *Acta Agr. Scand. Sec. A. Anim. Sci.* **43**, 190–192.