

FEEDBACK PROCESSES
IN GRAZING ECOSYSTEMS:

*Are sheep grazing in alpine habitats
affecting long-term use and productivity?*



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ABSTRACT

Large herbivores and their grazing impact is an important subject in ecology. It is well known that grazing shapes the structure, diversity and functioning of terrestrial ecosystems, but how the level of density dependence on the herbivore might change due to the interaction between herbivore and habitat is less studied. In this thesis, I studied feedback processes in an alpine environment in Southern Norway. In a large scale, long term experimental setting, sheep have been kept at high and low grazing densities for ten consecutive grazing seasons. I investigated how density-dependent habitat selection by a large grazing herbivore, sheep (*Ovis aries*), develops over the time scale of a decade. By applying biomass cages I could study how contrasting grazing levels influence biomass production. I predicted that sheep habitat selection would be density dependent, affected by annual and seasonal variations, and show a trend in density dependent selection for given patches within the same vegetation type. With respect to effects on biomass, I predicted that biomass production would be highest at low grazing density for tolerant functional groups, and that resistant functional groups would decrease with increasing density. These predictions were investigated using generalized linear mixed effect models. I found that habitat selection was density dependent. Seasonal and annual variations had a significant impact on sheep habitat selection. Graminoid and herb biomass significantly changed with increasing sheep density. There was a trend in change in long-term within-patch use, but sheep habitat selection was more affected by seasonal and annual climatic variations. This study sheds light on the little studied interactive effects of herbivores and habitat. My findings increase the general comprehension of density dependent habitat selection and how this affects biomass production, and helps us understand how the habitat selection by herbivores is affecting the ecosystem productivity depending on the population density over longer time frames.

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INTRODUCTION

The impact large herbivores have on ecosystems is a subject of great interest in ecology (Augustine & McNaughton 1998; Côté et al. 2004; Jefferies et al. 1994). The grazing impact of large herbivores is a key mechanism that shapes the structure, diversity and functioning of terrestrial ecosystems (Gordon et al. 2004). Ruminants forage selectively (Hanley 1997), and generally choose plants and plant parts with the highest nutritional quality and/or digestibility. Plants have over time evolved different responses to grazing; either tolerance or resistance (Karban & Baldwin 1997; Strauss & Agrawal 1999). An example of tolerance is graminoids who have basal growth meristems, and can thus continue to grow after grazing events and cope even with heavy grazing. Resistance is any plant trait that reduces the preference or performance of herbivores (Karban & Baldwin 1997). Physical or chemical defenses are typical examples of the resistance-strategy. Elements that compose the physical and chemical defense in plants, like cellulose or alkaloids, reduces the edibility, growth rate and decomposing of the plant (Augustine & McNaughton 1998; Pastor & Naiman 1992). Tolerant plants respond to grazing by investing in protein-rich regrowth that increases the quality and digestibility for the herbivore (McNaughton 1984; Van der Graaf et al. 2005). Heavy grazing or browsing may over longer term therefore affect the productivity of the plant community. Nutrient-rich and nutrient-poor ecosystems may respond differently to grazing (Proulx & Mazumder 1998), and the most effective strategy against herbivores may thus vary in different settings. These processes are expected to yield long term feedback effects on herbivore performance (Simard et al. 2008).

When behaviour or life history traits of individuals in a population are affected by density, it is said to be density dependent (Hixon & Johnson 2009). Density dependence is a central and well-known part of life history theory. However, the amount of density dependent variation in life history traits caused by density dependent variation in grazing behaviour is less known (Mobæk et al. 2012b). Habitat use by herbivores is one example of a density depend-

ent process (Rosenzweig 1981). The selectivity towards the most nutrient rich patches is assumed to decrease as the density increases, because the competition for these patches is higher. This is predicted by the Ideal Free Distribution (IFD) (Fretwell & Lucas 1970), which states that animals will distribute themselves into patches proportional to the resources available so that equal fitness is obtained.

Most theories of density dependent processes have assumed that the level of competition at a given density is static. However, since herbivores affect their habitat, the level of competition is typically dynamic (Bayliss & Choquenot 2002; Noy-Meir 1975). It is indeed becoming apparent that the temporal scale of observation is crucial for the level of density dependence (Kuijper et al. 2008; Mønbæk et al. 2009; Ramp & Coulson 2002). Plant quality fluctuates during the season, as the nutritional value decreases when plants grow older and accumulate more fibers (Hebblewhite et al. 2008). Annual variation in climate affects vascular growth (Walker et al. 1994). It is generally hypothesized that seasonal and annual variation affects habitat use by herbivores (Bailey et al. 1996; Hebblewhite et al. 2008; Kausrud et al. 2006). To understand the relationship between herbivore performance and plant community development in the long term, we also need to know how the herbivores use of their habitat is affecting the ecosystem productivity depending on the population density over longer time frames.

Depending on whether grazing increase resistant or tolerant plants, ecosystem productivity and the expected effect on the herbivore in the long term may be either negative or positive. Grazing facilitation occurs when one herbivore by grazing improves the plant quality or increases the standing crop, which benefits another grazer (Arsenault & Owen-Smith 2002). Primary production may under some circumstances be stimulated by intermediate grazing levels (Dyer 1975; McNaughton 1976; McNaughton 1979; Pearson 1965), termed the grazing optimization hypothesis (Hilbert et al. 1981). This hypothesis states that grazing can stimulate aboveground primary production, so that it increases with increased grazing intensity up to a certain point, where over-exploitation of the resource leads to depletion. The hypothe-

sis of grazing optimization is controversial in the ecological community (Belsky et al. 1993) and further experimental work is required to determine its generality. High grazing levels may also induce a change in the plant species composition towards less palatable species (Augustine & McNaughton 1998). If grazing were negatively affecting the ecosystem production from a herbivore perspective, it would be expected to increase the level of competition as resource levels decline.

Habitat selection occurs on different spatial scales from landscape, via habitat to patch and at the smallest scale, plant and plant parts to include in diet (Senft et al. 1987). A landscape ecologist can define a patch as a discrete spatial unit which is distinguished from the surroundings by discontinuities in environmental variables (Wiens 1976). However, the terms patch and habitat are used rather loosely in the literature, and most studies of habitat selection often rely on habitat maps derived for other purposes such as forestry (e.g. Godvik et al. 2009). Typically, resource levels are either not measured, or they are averaged at the level of habitat or patch types so that the extent to which the types reflect the actual resource levels is uncertain (Dussault et al. 2005; McLoughlin et al. 2002; Ryan et al. 2006). With the surge of Geographic Information System (GIS) and increased availability of broad habitat maps, the actual resource level is often never measured or lost in the analyses. A neglected field in habitat selection studies is whether there is variation in use within a particular habitat or vegetation type, and what may explain such variation. It may be that if grazing improves the grazing value of a given patch, the use of this patch will increase over time due to past grazing (Augustine & Frank 2001; Frank 1998), but this has received little attention in the literature.

In this thesis, I study how density-dependent habitat selection by a large grazing herbivore, sheep (*Ovis aries*), develop over the time scale of a decade, and how contrasting grazing levels influence biomass production in an alpine environment in the northern hemisphere. In a large scale, long term experimental setting, sheep have been kept at high and low grazing densities for ten consecutive grazing seasons. By applying biomass cages to prevent grazing

in specific patches for the last grazing season, I can investigate the temporal effect of different levels of grazing on biomass production. The cages were placed in high productivity habitat and thus in nutrient-rich patches, in an ecosystem classified as nutrient rich (Mysterud & Austrheim 2005). Due to the nutrient richness of patches and system, I predict that biomass production will be highest at low density for tolerant functional groups, and that resistant functional groups will decrease with increasing density. These predictions, in addition to the following hypotheses (adjusted and extended from Mobæk et al. (2009)) regarding habitat use, are tested (summarized in Table 1):

H₁: DENSITY DEPENDENT HABITAT SELECTION

I predict a difference in habitat selection between sheep kept at high and low density. Sheep at high density will be less selective due to limited access to the productive habitat because of increased competition, as predicted by the IFD (Fretwell & Lucas 1970).

H₂: SEASONALITY

The quality of the plant material will be at its highest at the beginning of the grazing season, with a gradual decline towards the end of the season (Hebblewhite et al. 2008; Mysterud et al. 2011). I therefore predict the selection of the most productive habitat to decline during the grazing period, since the level of competition is expected to increase as forage senesce (H_{2a}). The selection of the most productive habitat will also decline more at high grazing levels, where the competition is higher (H_{2b}).

H₃: ANNUAL VARIATION

Plant production is influenced by inter-annual climatic fluctuations (Walker et al. 1994). The prediction is that habitat selection is influenced by annual variation, since the level of competition will increase in years of poor vegetation development (H_{3a}). Habitat selection for highly productive habitat will decrease with increased annual variation, and this decrease will be more explicit at high grazing levels (H_{3b}).

H₄: LONG TERM TREND

Grazing may affect the habitat over years (Augustine & McNaughton 1998). Due to grazing optimization, I predict an overall temporal trend in selection (H_{4a}), and that this selection is density dependent (H_{4b}). There is within vegetation type differences in selection; i.e., patches of the same vegetation type are used to different extents (H_{4c}). This leads to a temporal trend in density dependent selection for given patches within the same vegetation type (H_{4d}).

Table 1. An overview of hypotheses, their rationale and how they are interpreted in terms of parameters of interest in the generalized linear mixed effects model. Random slopes and intercepts are given in parenthesis “(slope|intercept)” (See Material and Methods for definition of parameters).

HYPOTHESES	RATIONALE	PARAMETER OF INTEREST
H1. Density dependence	Increased use of less productive habitat in high grazing levels because of competition	Density x Habitat production
H2. Seasonality		
H2a. Selection of the more productive habitat declines over the season	Habitat selection is affected by aging of plant material	Date x Habitat production
H2b. Habitat selection decline is more explicit in high density enclosures compared to low density enclosures	Decrease in selection is more explicit when competition is high	Date x Habitat production x Density
H3. Annual variation		
H3a. Habitat selection varies between years	Habitat selection is affected by differences in plant quality due to annual variations	(categorical) Year x Habitat production
H3b. Variation in habitat selection is more explicit in high density vs. low density enclosures	Competition is increased at high density	(categorical) Year x Habitat production (x Density)
H4. Long-term trend		
H4a. Temporal trend in habitat selection	Grazing affects plant community composition and production	Year (as trend) x Habitat production
H4b. Temporal trend in density dependent selection; overall	Grazing optimization leads to density dependent temporal trend in selection	Year (as trend) x Habitat production x Density
H4c. Patch scale selection	Difference in within vegetation type selection	Year (as trend) x Habitat production x Density + (1 patchID)
H4d. Temporal trend in density dependent selection for given patches	Grazing optimization leads to temporal trend in density dependent selection for patches within the same vegetation type.	Year (as trend) x Habitat production x Density + (year patchID)

MATERIAL AND METHODS

Study Area

This thesis is a part of the long-term, large-scale project “Ecological effects of sheep grazing in alpine habitats” (Mysterud & Austrheim 2005) which in 2001 established a large enclosure covering 2.7 km² (Fig. 1) in Hol municipality in Hallingdal, southern Norway (between 60°40’-60°45’N and 7°55’-8°00’E). This area is in the sub-continental alpine climatic zone, with low to moderate precipitation (Førland 1993). Metaarkose is dominant in the bedrock (Sigmond 1998), and the soil relatively dry, productive and moderately base-rich (Austrheim et al. 2005). The enclosure is situated on a mainly south-facing hillside (Mysterud & Austrheim 2005). The lowest part of the enclosure borders the forest line (1050 m a.s.l.), whereas the highest part (1320 m a.s.l.) reaches the middle alpine zone. Fencing was done with a total of 17.3 km of 110 cm tall standard sheep fencing. Most area covered in the enclosure is situated in the lower alpine zone. This terrain is a typical alpine environment commonly used for summer pastures in southern Norway (Kausrud et al. 2006). Grazing pressure in the area before fencing (<2001) was low with less than 10 sheep per km². Other herbivores like moose (*Alces alces*), reindeer (*Rangifer tarandus*) and roe deer (*Capreolus capreolus*) can occasionally cross the area, but are not likely to have any grazing effect (Kausrud et al. 2006).

Experimental Design and Treatment

The enclosure is divided into 9 sub-enclosures, each covering approximately 0.3 km², variation due to problems with setting up fence on bare rock (Mobæk et al. 2009). The sub-enclosures span the same altitudinal range and contain approximately the same amount of productive habitat. The 9 sub-enclosures are divided into three blocks. Each in a block of three adjacent sub-enclosures was randomly assigned to one of three treatments: control (no sheep), low density of sheep (25 sheep per km²) and high density of sheep (80 sheep per km²) (Mysterud & Austrheim 2005).

Grazing lasted from the last week in June to the last week in August or the first week in September every year in the summers from 2002 till 2011, as is common in most mountain regions in southern Norway (Evju et al. 2006). After release every year, the sheep were allowed to habituate to the setting for a few days before data collection started.

Every grazing season, 23-26 ewes and 44-50 lambs from the same sheep farmer (the Sveingard family) were released in the enclosure. The sheep were of the “Norsk Kvit Sau”-breed (formerly called “Dala”), the most common breed in Norway. This breed is relatively large, used for meat production, and has limited gregariousness. Ewes had 1-3 lambs, and ewes with different number of lambs were evenly distributed to the different sub-enclosures, to ensure a similar average reproductive status for the ewes in the two different treatments over time.

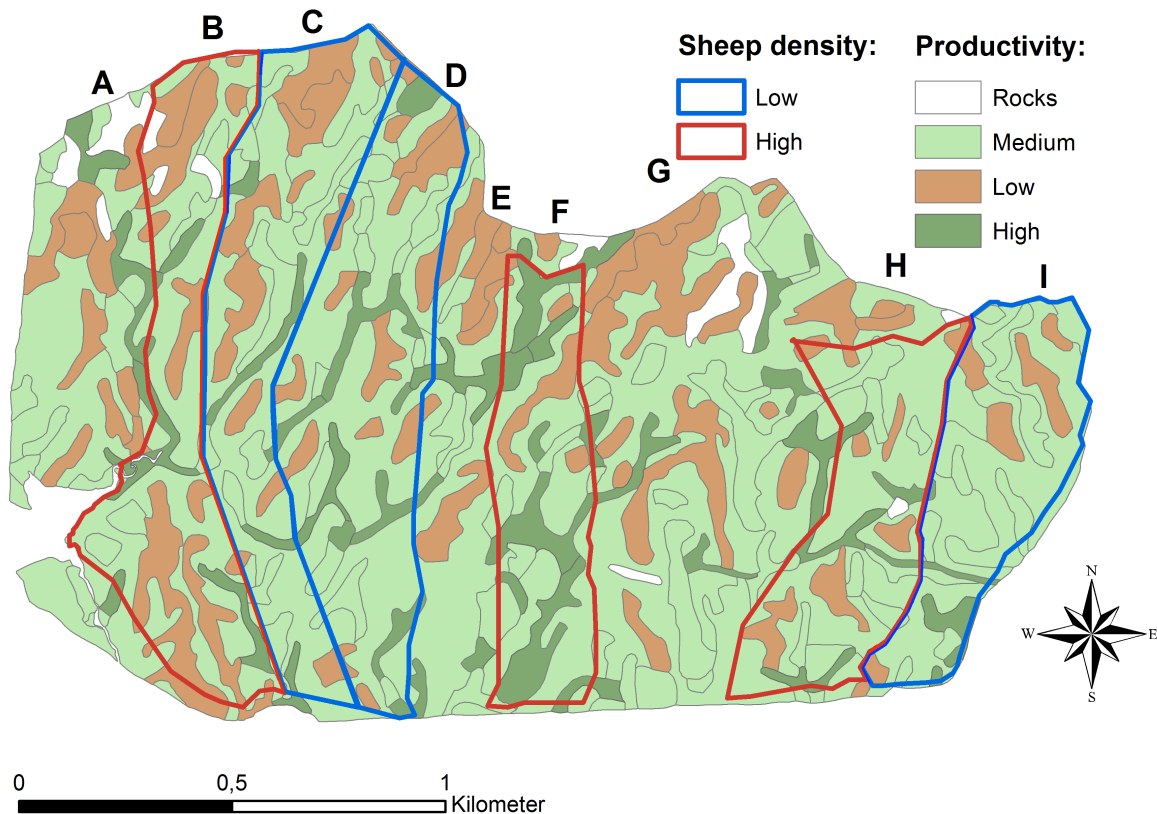


Figure 1. Map showing the experimental set-up and sub-enclosures (A-I) in Hol municipality, Norway. Habitat productivity is divided in three levels (low, medium and high) as well as bare rocks (excluded from the analyses).

Habitat productivity classification

Before grazing in the experimental field started, the distribution of vegetation types was mapped (Rekdal 2001b). This botanical survey also assessed the vegetation's grazing value for sheep mainly based on previous work (Rekdal 2001a), and thus made it possible to classify the nine vegetation types into two classes, with high productivity habitat in one class, and medium and low productivity habitat in the other. High productivity includes tall herb meadow and low herb meadow, whereas medium/low productivity includes grass snowbed, dwarf shrub heath, moss snowbed, lichen heath, bog, fen, and stone polygon land. This categorization of vegetation types into two classes highlights the effect of the most productive habitat, and avoids issues that arise when a particular vegetation type does not occur in all sub-enclosures, or when some vegetation types are recorded as used but not available (Mobæk et al. 2009).

Data collection

S H E E P H A B I T A T U S E

For ten consecutive summers, sheep activity was recorded through direct observations with binoculars in the field (Mobæk et al. 2009; Mobæk et al. 2012b). Data recording was modified and improved after the first field season, and the year 2002 is thus not included in the analyses. Prior to release in the field, every ewe and lamb was individually marked with ear tags and color/number coded neckbands. The observer used two working cycles randomly distributed through the season, one from 09:00 to 17:00, and the other from 14:00 to 22:00. The observer walked through a partly random selection of sub-enclosures each day, but with some stratification to ensure sampling efficiency. Because there were fewer ewes in the low density sub-enclosures, these were observed twice as often to balance samples with respect to the number of observations within each density level. Ewes were observed with binoculars at a distance of 20-50 meters. When individual identity of each ewe and lamb was confirmed, the observer approached the exact spot the ewe occupied. Here coordinates were marked on a hand-held Global Positioning System (GPS)-device, and sheep activity (grazing,

resting, walking) and vegetation type was recorded. Within a sub-enclosure, every ewe was observed before the procedure was repeated in the next sub-enclosure. The sampling unit was defined as a family group (an ewe and her lambs), because of the limited grouping behavior of this breed (Mobæk et al. 2012b).

B I O M A S S

To prevent grazing from rodents, sheep and other large herbivores during summer, biomass cages (Fig. 2a) were placed on predefined spots before sheep were released in the enclosures on 22nd of June 2011. 6 cages were placed in high productive habitat in each of the 9 sub-enclosures, a total of 54 cages. The cages were placed pair-wise, one in a preferred grazing spot, and one in a less preferred grazing spot within high productivity habitat, preference estimated from sheep use during earlier years. During three days in the middle of August same year (10th to 12th of August 2011), the biomass was harvested. Before harvesting, species amount and composition was estimated by the point intercept method (Jonasson 1988). A pin was inserted vertically in 16 points in the cage. By measuring which species touched the pin, and how many times, species composition and proportion was estimated in the spot. The points were equally distributed within the cage by use of a grid (Fig. 2b). Both harvesting and point intercept estimates were obtained for the possibility of running analyses on individual species, even if biomass at a whole was the main research interest. Due to different sizes of cages, the biomass within an area measuring 0.225 m² (0.5 x 0.45 m) was harvested from each cage. When this was not possible, due to shorter length on one side of the cage, all biomass within the cage was harvested, and dry biomass weight multiplied with a ratio to be comparable. The biomass was harvested at ground level using scissors (Fig. 2c), and stored in plastic bags in a dark, cool room for 3 to 10 days prior to processing. The harvested biomass was sorted into functional groups, and dried in paper bags in a drying cabinet at 60°C for 24 hours. Functional groups were based on growth forms and separated into graminoids, herbs, woody species and cryptogams. Dried biomass was stored at room tem-

perature until weighing. Weighing was done on a conventional electrical weight. Weight was measured in grams with two decimals.



Figure 2. Biomass data collection from 54 spots in high productivity habitat with three different grazing treatments in an alpine landscape in southern Norway, a: Biomass cage preventing grazing, b: grid used to estimate species composition with the point intercept method, c: after harvesting of biomass at ground level with scissors.

Statistical Analyses

SHEEP HABITAT SELECTION

Sheep habitat selection was analyzed with a use/availability design, where the use of resource units is compared to available units. The habitat selection corresponds to a type III design (Thomas & Taylor 1990) with repeated observations of known individuals, but due to the restrictions of being in a specific sub-enclosure, the availability will differ from individual to individual. The entire sub-enclosure was assumed available to all individuals in it, rather than a calculating of home ranges as is often done for free-ranging animals.

Generalized linear mixed-effect models (GLMM) (Pinheiro & Bates 2002) were fitted to address how habitat selection varies with habitat productivity (low/high), density (low/high), date (Julian date) and year (trend and categorical for years 2003-2011), as well as selected interactions according to predictions (Table 1). The outcome of a GLMM is a population level estimate of the logarithm of the odds for using a map pixel with a certain combination of predictor variable values (Mørbæk et al. 2009). Only the data where sheep was actively feeding was used, whereas data when sheep was inactive was discarded. The response variable “use” was assumed binomially distributed, with use as the actual points where sheep had been observed grazing. Available points are a random selection of points within the relevant sub-enclosure. Twenty times as many random available points as actually used points was selected for each individual and year. Since the “available” sites are a random selection, it is not known if they are truly unused. Therefore, the absolute values of log odds are meaningless (Keating & Cherry 2004). However, the log odds ratios can be directly interpreted from the model output. The exponent of a model estimate is the log odds ratio per unit (for a continuous variable) or compared to a reference level (for a categorical variable) to which this parameter influences the response variable.

To investigate both hypotheses regarding the effect of temporal trends and difference between years, separate models with year as trend or year as a categorical variable was used. Parameters included in the models are Use (binomial variable, used = 1, available = 0), Habitat productivity (factor variable with 2 levels, high and low), Density (factor variable with 2 levels, low and high), Year (factor variable with year 2003-2011 as levels), Year (trend; numeric variable), and Date (numeric variable). Year (trend) and Date were standardized (by subtracting the mean from each value) and centered (by dividing the standardized value on the standard deviation) so that parameter estimates are directly comparable. Individual and sub-enclosure was fitted as random factors in all models, to take account of repeated observations of individuals and variation in habitat use among sub-enclosures (i.e., variation in random intercept).

Backwards model selection was done using the Akaike Information Criterion (AIC) (Burnham & Anderson 2002). The Akaike Information Criterion finds the most parsimonious model as a balance between variation explained by the model (decreases value) and number of parameters included (increases value). All models were fitted using maximum likelihood (ML) estimation using the lmer-function in the R (R Development Core Team 2011) library lme4 (Bates et al. 2011). The most complex model included all the hypotheses as presented in table 1, as well as other potentially biologically reasonable interactions to prevent bias in the selection process. Model selection included the full model and all simpler combinations of this. AIC values of all models were compared (Table 2).

To test hypotheses 4a-d, the most parsimonious model was fitted with year as trend, and then used for model selection with different random effect parameters. Even if the variable Year (trend) did not enter the best model, there are biological reasons to estimate these effects, and models with year as trend will estimate if there is a trend in selection for given patches. Comparison of AIC of different models with the same fixed parameters but different random effects were possible by using restricted maximum likelihood (REML). The most parsimonious model was also tested with different random effect parameters, to see if difference in patch-use can explain more of the variation in the data.

B I O M A S S

Difference in biomass in total and for each functional group, as well as point intercept values for selected species was tested with generalized linear mixed effects models, using the lmer-function in the lme4-library in R (Bates et al. 2011). The primary explanatory variables of interest were density, altitude, and previous use in a radius of 25 m around the point of the cage for the former 8 grazing seasons. For all models, sub-enclosure was entered as a random effect. The R-library nlme (Pinheiro et al. 2011) was used to obtain p-values.

RESULTS

Sheep habitat selection

The most parsimonious model of sheep habitat selection included the factors Habitat productivity, Density, Date, Year (as factor), the second order interactions Year (factor) x Date, Habitat productivity x Density, Habitat productivity x Date and Habitat productivity x Year (factor), and the third order interaction Habitat productivity x Year (factor) x Date (Table 3). The variable Year fitted as factor (with years 2003-2011 as levels) explained the data better than Year fitted as a linear trend. Interactions not included in the most parsimonious model are presented in Table 2.

Sheep selected for the most productive habitat both at high and low population density, but there was higher selection at low density, as predicted by H1 (Table 3, the interaction Hab.prod x Density). Sheep selection for the most productive habitat was higher at the beginning of the grazing season than later, as predicted by H2a (Table 3, the interaction Hab.prod x Date). However, the effect of Date on selection was not influenced by density as predicted by H2b (the interaction Hab.prod x Date x Density did not enter the most parsimonious model, Table 2). Sheep habitat selection varied between years (Fig. 3, Table 3, the interaction Hab.prod x Year). The log odds ratio of choosing high productivity habitat at low density compared to high density in e.g. 2004 is 1.7 ($e^{(-1.45+1.98)}$), i.e. the probability of a “use” point to fall within high productivity habitat is 1.7 times higher at low compared to high density. The probability for low density sheep to use high productivity habitat compared with high density sheep is between 1.6 and 1.7 times higher all years.

Table 2. A priori generalized linear mixed effects models for sheep habitat use when actively grazing with three replicates of low and high density in an alpine environment over 9 years in southern Norway. x = term included in model. AIC = Akaike Information Criterion; Δ AIC = difference in AIC value for the model in the row and the most parsimonious model (marked in grey). Random effects are always individuals nested within sub-enclosure. Date and year (trend) was standardized prior to analysis.

Habitat productivity	Density	Date	Year (factor)	Year (trend)	Year (factor) x Density	Year (trend) x Density	Year (factor) x Date	Year (trend) x Date	Date x Density	Hab. Prod x Year (factor) x Date	Hab. Prod x Year (trend) x Date	Hab. Prod x Density H1	Hab. Prod x Date H2a	Hab. Prod x Date x Density H2b	Hab. Prod x Year (factor) H3a	Hab. Prod x Year (factor) x Dens H3b	Hab. prod x Year (trend) H4a	Hab. prod x Year (trend) x Density H4b	AIC	Δ AIC
x	x	x	x		x		x		x	x		x		x	x				38072	25
x	x	x		x		x		x	x	x	x	x		x			x	x	38130	83
x	x	x	x		x		x		x			x	x	x	x				38121	74
x	x	x	x		x		x		x	x		x	x		x	x			38071	24
x	x	x	x		x		x		x	x		x	x	x	x				38066	19
x	x	x	x		x		x		x			x	x	x	x				38114	67
x	x	x	x		x		x		x	x		x	x		x				38065	18
x	x	x	x		x		x		x	x		x	x	x					38146	99
x	x	x	x		x		x		x			x	x		x				38112	65
x	x	x	x		x		x		x	x		x			x				38065	18
x	x	x	x		x		x		x	x			x		x				38115	68
x	x	x	x		x		x			x	x		x		x				38063	16
x	x	x	x				x		x	x		x	x		x				38049	2
x	x	x	x		x				x			x							38207	160
x	x	x	x				x		x			x	x		x				38097	50
x	x	x	x						x			x							38191	144
x	x	x	x				x		x	x			x		x				38147	100
x	x	x	x				x			x		x	x		x				38047	0
x	x	x	x				x					x	x		x				38095	48
x	x	x	x									x							38189	142
x	x	x	x				x			x			x		x				38099	52

Table 3. A generalized linear mixed-effects model of sheep habitat use when actively grazing with three replicates of low and high density in an alpine environment over 9 years in southern Norway. The model is the most parsimonious model (Table 2). The response variable 'use' is binomial (used = 1, available = 0). Habitat productivity (Hab. prod) is fitted as a factor variable (low/high) with high as reference level. Density is fitted as a factor variable (low/high), with low as reference level. Date is standardized Julian date. Year is fitted as a factor variable (years 2003-2011), with year 2003 as reference level. SE = standard error. Random effects are individuals (n=216) nested within sub-enclosure (n=6), number of data points are 102077 (ratio use/random = 1/20).

Fixed effect	Estimate	SE	95% confidence limits	
			lower	higher
Intercept	-3.202	0.094	-3.391	-3.013
Habitat productivity (high-low)	1.340	0.116	1.108	1.572
Density (low-high)	0.021	0.081	-0.142	0.184
Date	0.126	0.078	-0.031	0.283
Year (2004 vs 2003)	-0.174	0.083	-0.341	-0.007
Year (2005 vs 2003)	-0.167	0.072	-0.311	-0.023
Year (2006 vs 2003)	-0.227	0.069	-0.365	-0.089
Year (2007 vs 2003)	-0.005	0.078	-0.162	0.152
Year (2008 vs 2003)	0.087	0.072	-0.056	0.230
Year (2009 vs 2003)	-0.153	0.073	-0.300	-0.006
Year (2010 vs 2003)	0.042	0.113	-0.185	0.269
Year (2011 vs 2003)	-0.009	0.056	-0.122	0.104
Year (2004 vs 2003) x Date	-0.103	0.081	-0.264	0.058
Year (2005 vs 2003) x Date	-0.261	0.085	-0.430	-0.092
Year (2006 vs 2003) x Date	0.075	0.090	-0.104	0.254
Year (2007 vs 2003) x Date	-0.085	0.073	-0.232	0.062
Year (2008 vs 2003) x Date	-0.139	0.073	-0.285	0.007
Year (2009 vs 2003) x Date	-0.080	0.080	-0.240	0.080
Year (2010 vs 2003) x Date	-0.001	0.074	-0.149	0.147
Year (2011 vs 2003) x Date	-0.001	0.075	-0.151	0.149
Hab. Prod x Density	-0.509	0.069	-0.647	-0.371
Hab. Prod x Date	-0.473	0.116	-0.704	-0.242
Hab. Prod x Year (2004 vs 2003)	0.558	0.148	0.262	0.854
Hab. Prod x Year (2005 vs 2003)	0.561	0.148	0.265	0.857
Hab. Prod x Year (2006 vs 2003)	0.600	0.152	0.296	0.904
Hab. Prod x Year (2007 vs 2003)	0.063	0.144	-0.224	0.350
Hab. Prod x Year (2008 vs 2003)	-0.308	0.147	-0.603	-0.013
Hab. Prod x Year (2009 vs 2003)	0.433	0.146	0.141	0.725
Hab. Prod x Year (2010 vs 2003)	-0.188	0.152	-0.491	0.115
Hab. Prod x Year (2011 vs 2003)	0.019	0.148	-0.277	0.315
Hab. Prod x Year (2004 vs 2003) x Date	0.447	0.147	0.153	0.741
Hab. Prod x Year (2005 vs 2003) x Date	0.809	0.155	0.499	1.119
Hab. Prod x Year (2006 vs 2003) x Date	-0.013	0.163	-0.339	0.313
Hab. Prod x Year (2007 vs 2003) x Date	0.316	0.146	0.023	0.609
Hab. Prod x Year (2008 vs 2003) x Date	0.545	0.155	0.236	0.854
Hab. Prod x Year (2009 vs 2003) x Date	0.402	0.150	0.102	0.702
Hab. Prod x Year (2010 vs 2003) x Date	-0.030	0.154	-0.338	0.278
Hab. Prod x Year (2011 vs 2003) x Date	0.098	0.149	-0.200	0.396

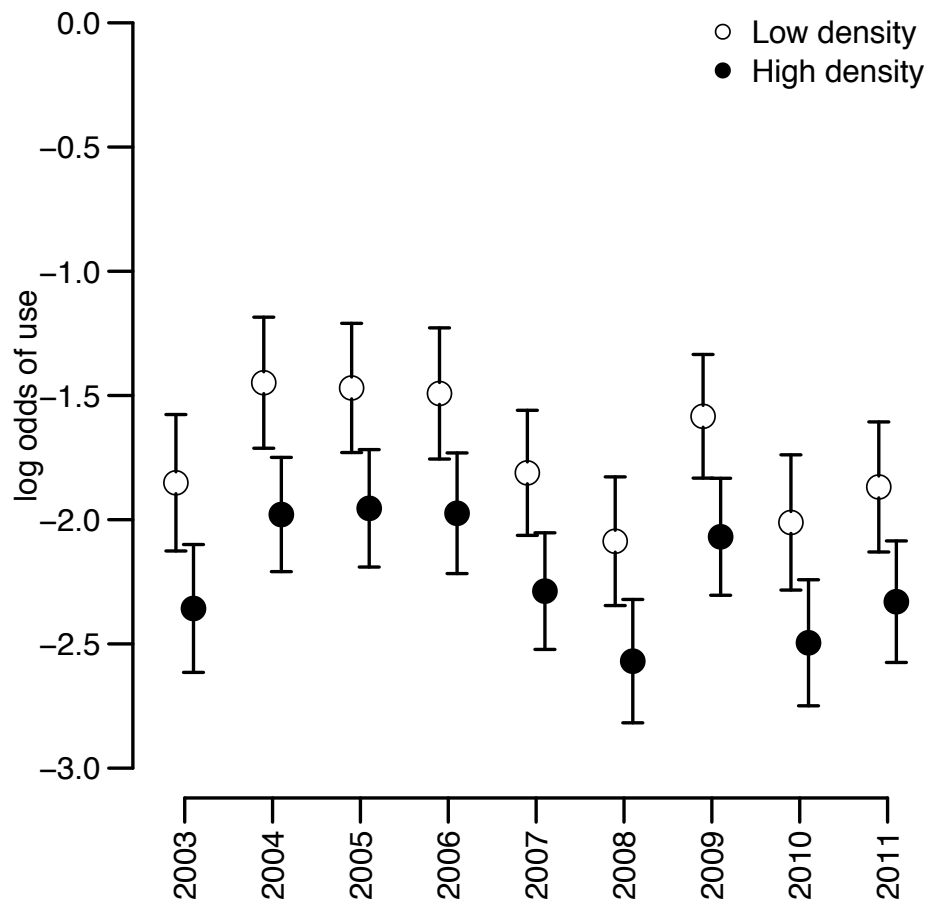


Figure 3. Selection of high productivity habitat for actively grazing sheep at low and high density in an alpine environment over 9 years in southern Norway. The ratio of use between high and low density (log odds ratio) varies between 1.6 and 1.7 every year, i.e. the probability for low density sheep to use high productivity vegetation is 1.6 to 1.7 times higher compared to high density sheep.

There was a high variation in selection within a given vegetation type, as AIC of the most parsimonious model in Table 2 (marked in grey) decreased when patchID was entered as random intercept (from AIC = 38047 to 36506 units, i.e. $\Delta\text{AIC} = 1541$). To investigate hypothesis 4 (see Material and Methods), the most parsimonious model was fitted with year as trend (H4a, AIC = 38124), with year as trend and patchID as random intercept (H4c, AIC = 36573) and with year as trend and Year (trend) as random slope and patchID as random intercept (H4d, AIC = 36533), where AIC-value decrease with increasing model complexity.

Biomass

The most parsimonious models explaining variation in biomass included only sheep density as an explanatory variable, while entering altitude or the interaction between altitude and density resulted in an increase in AIC. Results from the most parsimonious models are presented in Table 4 and Figure 3. Density had a significant effect on graminoids and herbs at high sheep density. There was no significant effect on woody and total biomass, and estimates of these models are not presented further. The biomass of graminoids increased with increasing density of sheep, where estimate at control level is 52.5 g/m^2 (95 % confidence interval (CI) = 38.17 to 72.24 g/m^2), and estimate at high density is 91.6 g/m^2 (95 % CI = 57.8 to 142.5 g/m^2). Graminoids at low density was in between control and high density, with an estimate of 75.3 g/m^2 . The biomass of herbs decreased with increasing density of sheep, from an estimate of 34.4 g/m^2 (95 % CI = 22.5 to 51.9 g/m^2) at control level to 14.5 g/m^2 (95 % CI = 8.0 to 26.31 g/m^2) at high density. Herbs at low density had an estimate of 30.2 g/m^2 . Variation within grazing levels is high, as seen from Fig. 4. A total of 71 species was found over all spots, but only the grass *Avenella flexuosa* was present in all plots. This grass showed a non-significant trend ($p=0.06$) of an increase in biomass with increasing grazing density, similar to the general significant trend for graminoids.

Table 4. Results of generalized linear mixed effect models of dry biomass weight (log(g)) from 54 sample points in sub-enclosures with three different grazing regimes; control without grazing (baseline), low grazing pressure (Density low) and high grazing pressure (Density high) in an alpine environment in Southern Norway. Random effect is enclosure. SE= standard error.

Parameter	Estimate	SE	95 % confidence limits	
			lower	higher
Total biomass				
Intercept	5.975	0.095	5.784	6.166
Density (low vs. control)	-0.049	0.135	-0.319	0.221
Density (high vs. control)	-0.125	0.135	-0.394	0.145
Graminoids biomass				
Intercept	3.961	0.160	3.642	4.280
Density low	0.361	0.226	-0.091	0.812
Density high	0.547	0.226	0.096	0.998
Herbs biomass				
Intercept	3.539	0.210	3.113	3.951
Density low	-0.131	0.296	-0.723	0.462
Density high	-0.862	0.296	-1.454	-0.269
Woody biomass				
Intercept	5.106	0.298	4.510	5.702
Density low	-0.186	0.422	-1.029	0.657
Density high	-0.340	0.422	-1.183	0.503

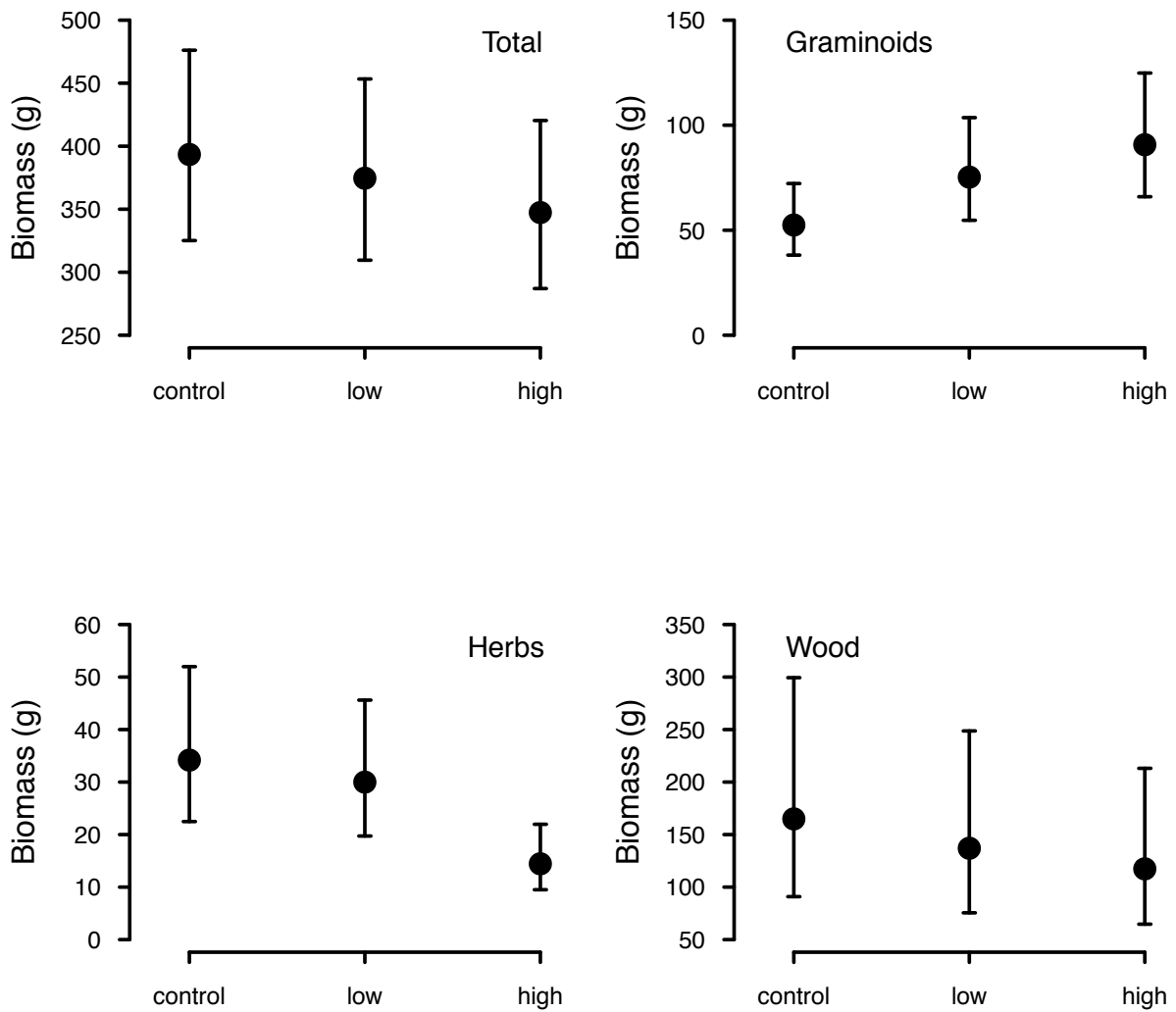


Figure 4. Generalized linear mixed effect model of weight of dried biomass (g/m^2), in total and for functional groups from 54 sample points in sub-enclosures with three different sheep grazing regimes: control (no grazing), low grazing pressure and high grazing pressure in an alpine environment in Southern Norway. Note different limits of y-axes.

DISCUSSION

The structure and functioning of terrestrial ecosystems are shaped by large grazing herbivores (Gordon et al. 2004), and understanding how herbivores select their habitat is a key to understand the mechanism that form these ecosystems. Analyzing sheep habitat selection at low and high density in an alpine environment in Southern Norway, I found that habitat selection was density dependent (H1). The selection for high productivity habitat declined during the season (H2a), and there was a variation in habitat selection between years (H3a). There was a high variation in selection within a given vegetation type, and there was a temporal trend in this selection, some habitat patches were used more over time by sheep and others were used less.

Sheep do select their grazing habitat relative to a number of factors. When the density is higher, most likely due to a higher competition, sheep select more medium and low productive habitat compared to when density is low. During the season, as plant material grows older and has a lower nutritional value, sheep utilize more medium and low productive habitat. Annual variation also influences sheep habitat selection; a climatic “good” or “bad” year leads to differences in habitat use. The habitat selection does not only happen at the scale of vegetation type. Within high productivity vegetation, sheep habitat selection was strongly variable. Use of some patches increased over time, suggesting that sheep by grazing improve their own habitat. These findings increase the general comprehension of habitat selection and how this affects biomass production, and helps us understand the interactive effects of herbivores and their habitat.

Density dependence

At low density, the sheep in this study had a higher selection for high productivity habitat (Fig. 3). This is consistent with the ideal free distribution (IFD) (Fretwell & Lucas 1970), and with the findings of Mobæk et al. (2009) from the same study area. As predicted by the IFD,

sheep at high density had a more even use of foraging habitats. The IFD model assumes that, when density declines, animals in poor patches should return to higher quality patches. According to the IFD, individuals will distribute themselves to gain the same overall fitness. In this study, the sheep can distribute themselves freely within their own sub-enclosure, but the distribution will not be completely free due to fences between treatments. Lamb weights in this experimental setting has been shown to be density dependent (Myrsetrud & Austrheim 2005, Mobæk et al. 2012a), indicating that the sheep are not able to achieve equal fitness by selecting habitat differently at different density, i.e. there is a resource limitation at high density. In a study of Soay sheep (Jones et al. 2006), the sheep distribution was positively correlated with habitat quality, but the distribution was not following the predictions of the IFD. The sheep did not use different habitat types as predicted when density increased in this naturally fluctuating population. At increasing sheep densities, the use of the most productive grasslands increased, whereas use of less productive habitats decreased. This observation was in contrast to the predictions from the IFD. The authors argue that this observation is due to the dynamic nature of the resource, where different functional groups respond differently to different grazing pressures, and the productivity of the most productive habitats increased with increasing grazing density. Others have found distributions in accordance with the IFD: Walhström & Kjellander (1995) found that female roe deer (*Capreolus capreolus*) had no significant difference in reproductive parameters, in a density dependent distribution between habitats of different quality. Eastern grey kangaroo (*Macropus giganteus*) was found to increase their use of low quality habitat with increasing density, although individual fitness was not addressed (Ramp & Coulson 2002).

In accordance with Mobæk et al. (2009), I found that sheep selection for the most productive habitat was higher at the beginning of the grazing season than later (Table 3), and that annual variation affects sheep habitat selection (Fig. 3). The descending selection for the most productive habitat during the season is consistent with plant physiology; that the nutritional value decreases as the plants grow older and accumulate more fibers (Hebblewhite

et al. 2008). Annual variation in climate affects vascular growth (Walker et al. 1994), which is a reasonable explanation of the annual variation in habitat selection.

Time scale is an important factor when analyzing feedback processes in grazing ecosystems (Kuijper et al. 2008; Ramp & Coulson 2002). An earlier analysis of data from the same experimental field, but with a shorter time scale, found a density dependent monotonically non-linear increase in selection of high productivity habitat (Mobæk et al. 2009). When increasing the time scale to 9 instead of 4 years, it is clear that the density dependent selection of high productivity habitat does not increase (Fig. 3). This study shows the importance of long timescale series. By increasing the timescale, a more correct picture of the actual effects can be obtained.

Herbivores affect their habitat, and the level of competition at a given density is thus not expected to be static (Bayliss & Choquenot 2002; Noy-Meir 1975). Density did not influence the seasonal habitat selection as predicted by H2b, nor did density influence the annual habitat selection (H3b). These predictions were based on the finding that growth of lambs are density dependent, indicating resource limitation at high density (Mysterud & Austrheim 2005), and the assumptions from the IFD: At high density animals will be less selective due to higher competition, and this competition in interaction with either seasonal or annual variation will lead to a higher decline in habitat selection at high sheep density. In this study, the probability for low density sheep to use high productivity vegetation is constantly between 1.6 and 1.7 times higher compared to high density sheep (Fig. 3), indicating that the density dependent habitat use may be static. Lamb weights suggest a difference in level of competition between the two sheep densities.

An important assumption of the IFD is that habitats are stable over time. Vegetation structure, biomass and quality may be effected by grazing or other processes, and change in the long term (Augustine & Frank 2001; Frank 1998; Olofsson 2006). This is not considered in the original version of the IFD. Grazing facilitation is the increased quality and/or quantity of forage as an effect of grazing (Arsenault & Owen-Smith 2002). Grazing on plants with a

tolerance response can lead to an investment in protein-rich regrowth that increases the quality and digestibility for the herbivore (McNaughton 1984; Van der Graaf et al. 2005). When grazers feed selectively, they affect plant species composition, and regulate plant standing crops (Jefferies et al. 1994). This can over time change the quality of a given habitat.

My data show that habitat selection is density dependent. The habitat selection is influenced by seasonal and annual variation, but the density dependence is maintained over years. There is an intraspecific effect of sheep grazing at different densities in an alpine landscape, and there is a density dependent change in biomass production. These findings direct the attention to the less studied interactive effects between herbivore and habitat.

Grazing Optimization

The grazing optimization hypothesis (GOH) predicts that primary production may under some circumstances be stimulated by intermediate grazing levels (Dyer 1975; Hilbert et al. 1981; McNaughton 1976; McNaughton 1979; Pearson 1965). Increasing grazing levels will lead to increased aboveground biomass production up to a certain point, where overgrazing leads to degradation of the habitat quality. How biomass production is affected by grazing is important per se, and it will also affect processes such as facilitation and competition among herbivores. At the study site in Hol, body growth of sheep at low density seems to increase slightly over time (Mobæk et al. 2012a). In the search for mechanisms explaining this, the authors touch upon grazing optimization and delayed competition among others. Grazing optimization is an animal-plant mechanism, which can lead to grazing facilitation, a mechanism between animals or from animal via plants to other animals (Arsenault & Owen-Smith 2002).

My data on biomass weight at different sheep densities does not show a peak at intermediate density (Fig. 4), as expected from the grazing optimization hypothesis. It could be that the densities used in this experiment are not at the levels that yield different grazing pressures on the vegetation. This is unlikely the case, as these grazing levels are shown to yield low and moderate grazing pressure on the plants (Evju et al. 2006). These densities have also

been shown to give measurable lower growth rates of lambs at high compared to low densities (Mysterud & Austrheim 2005).

The ecological significance and generality of the grazing optimization hypothesis has been questioned (Belsky 1986; Belsky 1987; Belsky et al. 1993). A global 236-site data set review concluded that most of the effects of grazing was negative on aboveground net primary production, but the amount of variability in the statistical models leads to the suggestion that there might be many exceptions (Milchunas & Lauenroth 1993). This is just another reminder of the need for understanding at which conditions the GOH operates. Modeling studies has shown that nutrient cycling and availability in the growth response to grazing is important (de Mazancourt et al. 1999; Holland et al. 1992; Leriche et al. 2001). A clipping study at the Lamto grasslands in Africa (Leriche et al. 2003) showed that the GOH was fulfilled when the treatment was both moderate clipping and fertilization, but not only at moderate clipping.

A study of nitrogen availability from the experimental enclosure in Hol found clear effects of grazing on nitrogen availability (PRSTM-adsorbed N, a measure of surplus N) and potential N mineralization (Martinsen et al. 2012), and concludes that grazing may significantly stimulate N-cycling, although the system is not released from a strong N deficiency. It has been shown that nitrogen returned to the soil from animal excreta has a higher effect on plant biomass and nitrogen flow to grazers than other sources of nitrogen (Ruess & McNaughton 1984; Ruess & McNaughton 1987).

Even if the overgrazing levels predicted by the GOH are not achieved in this study, the increase in biomass can be an indication of grazing optimization in the form of grazing facilitation, where sheep at high density increase the biomass productivity potential in high productivity habitat.

Plant responses

Different functional groups respond differently to grazing, and it is mainly grasses that are predicted to follow predictions from the grazing optimization hypothesis. The responses to grazing can be called a tolerance response or a resistance response (Karban & Baldwin 1997; Strauss & Agrawal 1999). Tolerant plants are characterized by having features that allow them to respond to grazing by regrowth, such as low apical meristem, high relative growth rate, high photosynthetic rate, high branching rate, high leaf production or short leaf lifespan (McIntyre et al. 1999; Strauss & Agrawal 1999). Resistant plants aim to avoid grazing by physical or chemical defense such as spines or secondary compounds or through low digestibility (Coley et al. 1985; Strauss & Agrawal 1999). Compensation refers to the degree of tolerance exhibited by plants (Strauss & Agrawal 1999). According to Belsky (1986), over-compensation occurs when the cumulative total dry weight increases after grazing or clipping, i.e. a response to injury with increased growth, exact compensation occurs when cumulative dry weight does not change, and under-compensation occurs when the dry weight of grazed or clipped plants decrease. When interpreting my results, it is important to remember that the grazing optimization hypothesis mainly predicts the effects on graminoids. The only species recorded in all biomass cages, the grass *Avenella flexuosa*, showed the same trend as the functional group graminoids; an increase with increasing grazing density.

It is common to use growth form as functional groups in grazing studies (Bråthen et al. 2007; Olofsson 2006), but these groups can not be generalized in their response to grazing (Austrheim et al. 2008; Grellmann 2002). In my study, herbs show a decline in biomass with increased sheep density, i.e. under-compensation for both levels of grazing. Herbs are a diverse functional group, with no special strategy against grazing. Evju et al. (2009) found that, in the same experimental setting as this thesis, tall herbs with a high shoot/root ratio declined with increasing grazing intensity, whereas small herbs with a high root/shoot ratio increased. Tall herbs will contribute more to aboveground biomass, and this shift in species composition can thus explain the decrease in herb biomass with increasing sheep density. Graminoid biomass increased with increasing sheep density. Graminoids in general have a tolerance

strategy towards grazing, with low basal meristem, but responses to grazing differ also in this group (Austrheim et al. 2008). The overall increase in graminoids with increasing sheep density can be explained by a tolerance strategy, with overcompensating biomass production able to tolerate the high grazing pressure in high sheep density enclosures. The temporal increase in lamb weight at low densities (Mobæk et al. 2012a), together with my results of increasing graminoid biomass at increasing sheep densities indicates that a shift in plant community composition induced by grazing can sustain a higher grazing pressure, but that other effects than increased plant biomass inhibits lamb growth at high sheep densities.

Within patch use

A neglected field in habitat selection studies is whether there is variation in use within a particular habitat or vegetation type, and what may explain such variation. Use of a given patch may increase over time if former grazing has improved the grazing quality of the patch. (Augustine & Frank 2001; Frank 1998), but this hypothesis has seldom been tested. Most studies of habitat selection often rely on habitat maps derived for other purposes (e.g. Godvik et al. 2009), and resource levels are not measured or they are averaged at the level of habitat or patch types. The scale of observation may also change from study to study. This leads to an uncertainty regarding the habitat/patch types reflecting the actual resource level, and how much resources a given habitat type have between different locations for a specific map. In this study, the variation of dry biomass weight within the different grazing treatments shows the high variation of vegetation within a particular vegetation type. In the high-density grazing treatment, the mean of graminoid biomass was 105.7 g, and the variance 4520.8 g², reflecting the major differences between biomass cages in the same grazing treatment.

It is time consuming and expensive to conduct a thorough habitat analysis. When examining large areas, modified aerial photos as in for example Ryan et al. (2006) can be effective, but often leads to very general habitat maps. Another solution is to find squares of habitat types of interest, and examine e.g. abundance of skylarks (*Alauda arvensis*) in the pre-selected patches (Chamberlain et al. 1999), avoiding a large-scale continuous habitat analysis. Also

common is to use smoothing algorithms on broad habitat maps, to minimize pixel size as done by McLoughlin et al. (2002). Depending on type of study and scale of interest, these methods may yield useful habitat maps, but the process of compiling these maps is complicated, and errors may be introduced at many points (Foody 2002; Veran et al. 2012).

Before grazing started in this experimental field in 2002, a thorough field-based vegetation type mapping was done at the resolution scale of 20 da (0.02 km²) (Rekdal 2001b). Also, vegetation type was recorded when sheep was observed in the field (see Material and Methods). Actual “use” points are thus correctly placed within high productivity habitat. A “patch” in this study is an exact map polygon defined by its border GPS-coordinates. Because of the increase in graminoid biomass with increasing sheep density, it is biological reasonable to expect a temporal trend in use of patches. Therefore, modeling of this was done, even if the annual variation in year (year as factor) explained the data better than year as trend. Modeling showed that year added as random slope and patch (patchID) as random intercept reduced AIC-value significantly. There is a temporal trend in variation in use of specific patches within a given vegetation type, but the analysis does not allow separating if this is specific to high productivity habitat. Also, modeling with year as factor and patch as random intercept causes a high reduction in AIC-value. This confirms the high variation in within habitat use between patches of vegetation types with the same classification in the map. That the term year enters as a random slope suggests that grazing changes the use of some patches over time. The increase in graminoid biomass, a functional group with a tolerance strategy, and decrease in herb biomass, a group highly preferred by sheep but without clear strategies against grazing indicates that grazing alters plant community composition. This change in biomass, and the change of use of patches over time, could indicate a certain level of grazing facilitation. A decrease of herb biomass could be an indication of a lower forage quality, but the increase of graminoid biomass and thus an increase in overall plant community productivity could counteract this. Sheep grazing leads to a change in plant community composition, which in turn leads to a change in use of specific habitat patches over time.

CONCLUSION

Are sheep grazing in alpine habitats affecting long-term use and productivity? Habitat selection is a dynamic process. I found that sheep habitat selection was density dependent, and influenced by seasonal and annual variation. In this study, the use of GLMMs gave the opportunity to investigate temporal trends in variation in within use of high productivity habitat. Annual variation explained overall habitat use better than a temporal trend over years. Still, when modeling temporal trends with year as random slope, a trend in change of within-use of patches over time appeared.

Sheep grazing in alpine habitats do affect plant biomass productivity, and lead to an increase in graminoid biomass with increasing sheep density in this study system. There was a trend in change in long-term within-patch use, but sheep habitat selection was more affected by seasonal and annual climatic variations. The finding that use of some patches increased over time suggests that sheep by grazing can improve their own habitat.

This study is one of few that address interactive effects of herbivores and habitat, and further studies are necessary in this field to understand the complicated dynamics that shapes the structure, diversity and functioning of terrestrial ecosystems. An interesting aspect would be to measure the effect of thawing snow beds on availability of forage and this effect upon density dependent habitat selection by sheep. This would, together with similar studies in other ecosystems, increase the understanding of grazing optimization and grazing facilitation as dynamic processes in large herbivore-dominated ecosystems.

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