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Norwegian University of Life Sciences
NO–1432 Ås, Norway
Phone +47 64 96 50 00
www.umb.no, e-mail: postmottak@umb.no

Ragnhild Mobæk

Philosophiae Doctor (PhD) Thesis 2012:02

Norwegian University of Life Sciences • Universitetet for miljø- og biovitenskap
Department of Animal and Aquacultural Sciences
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Density dependent foraging ecology and performance of domestic sheep on alpine ranges

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PhD supervisors

Prof. Øystein Holand
Department of Animal- and Aquacultural Sciences
Norwegian University of Life Sciences
P.O. Box 5003
NO-1432 Ås, Norway

Prof. Atle Mysterud
Centre for Ecological and Evolutionary Synthesis (CEES)
Department of Biology
University of Oslo
P.O. Box 1066 Blindern
NO-0316 Oslo, Norway

PhD evaluation committee

Dr. Ivar Herfindal
Centre for Conservation Biology
Department of Biology Realfagbygget
Norwegian University of Science and Technology
NO-7491 Trondheim, Norway

Dr. René van der Wal
Aberdeen Centre for Environmental Sustainability (ACES)
University of Aberdeen
School of Biological Sciences
Auris, 23 St Machar Drive, AB24 3UU
Aberdeen - Scotland, UK

Dr. Åshild Randby
Department of Animal and Aquacultural Sciences
Norwegian University of Life Sciences
P.O. Box 5003
NO-1432 Ås, Norway

Contents

Papers I-IV

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Ås, November 2011 – Ragnhild Mobæk

Abstract

Populations of large herbivores are strongly influenced by density dependent and independent processes such as climatic variability, which have common effects on individual performance and demographic rates. However, little is known about proximate mechanisms involved in these processes, such as how foraging behavior vary as a function of population density. Whether density-climate interactions during summer may affect ungulate performance is also little explored. Domestic sheep is the most abundant large herbivore in alpine pastures during the Norwegian summer grazing season. Increasing numbers of sheep foraging in many alpine areas have been heavily debated. Despite this, knowledge about their foraging ecology and thus their impact on alpine ecosystems is scarce. In a landscape scale experiment, I collected long term data from sheep kept at two densities and tested whether density dependent foraging patterns, alone or in interaction with climate, could explain annual variation in autumn body mass by lambs. I predicted an inclusion of habitats and plant species with lower quality at high density. Sheep generally selected high productive meadow vegetation. The most selected plants were the grass *Avenella flexuosa*, herbs, and *Salix* spp. Both habitat selection and diet choice was density dependent. Ewes at high density selected less meadow vegetation than ewes at low density and consumed a diet of average lower quality. Further, activity patterns differed depending on density, and ewes at high density spent more time grazing. I documented a negative effect of high sheep density on individual performance. Contrasting foraging patterns at the two density levels signify that reduced abundance of high quality forage plants due to food competition is the main mechanism promoting density dependence in this system. Temporal variation also affected selection and performance patterns, and especially diet choice was strongly influenced by seasonal and annual variation in plant phenology. I found limited evidence of interactions between density and temporal variation, except that density dependent performance patterns varied between years, likely reflecting annual variation in diet composition. A long term temporal trend (nine years) in body mass development indicated that processes related to grazing effects, rather than annual climatic variation, was most important for sheep's performance pattern. Sheep at both densities likely altered their foraging habitat with long term opposite consequences for performance. This was most evident at high density, and the performance pattern suggests that lamb growth were restricted by delayed vegetation responses to high grazing pressure. At low density, lamb body mass tended to increase over years. This could be indicative of a grazing facilitation within the most selected meadow vegetation types. In conclusion, density dependent foraging patterns affecting performance as documented in this study may provide one behavioural mechanism explaining density dependent variation in vital rates.

Sammendrag

Populasjoner av store beitedyr påvirkes av både tetthetsavhengige- og uavhengige prosesser, slik som klimavariasjon. Disse prosessene har ofte sammenfallende effekter på individuell tilvekst og demografiske parametre i populasjonen. Vi vet imidlertid lite om proksimate mekanismer bak tetthetsavhengig tilvekst, slik som hvordan beiteatferden endrer seg med populasjonsstørrelsen. Hvordan interaksjoner mellom tetthet og klimavariasjon kan påvirke tilveksten gjennom sommersesongen er også lite kjent. Sau dominerer norske fjellbeiter målt i antall beitedyr. En økende sauetetthet i mange fjellområder har vært omstridt. På tross av dette har vi lite kunnskap om sauens beiteatferd, og med dette også hvordan sauebeiting kan påvirke fjelløkosystemet. Jeg brukte et storskala innhegnings-eksperiment i det sørnorske lavfjellet for å samle data fra sau som beitet ved to bestandstettheter, og undersøkte om tetthetsavhengig beitevalg, mellom- og innenårsvariasjon, og interaksjoner mellom disse prosessene kunne forklare årlig variasjon i lammenes tilvekst. Jeg forventet at sau ved høy tetthet ville beite mer i vegetasjonstyper med dårligere beiteverdi, og inkludere arter med lavere næringsverdi i dietten. Sauene beitet generelt mest i lågurt- og høystaudeeng. De mest selekterte beiteplantene var smyle (*Avenella flexuosa*), urter og vierarter (*Salix* spp.) Både valg av vegetasjonstyper og plantearter var tetthetsavhengig. Søyer ved høy tetthet beitet mer i mindre produktive vegetasjonstyper og valgte beiteplanter som til sammen ga en diett med lavere næringsverdi enn søyer ved lav tetthet. Også aktivitetsmønsteret endret seg med tetthet, og søyer ved høy tetthet brukte mer tid på beiting. Lammenes tilvekst var redusert ved høy tetthet. Det ulike beitemønsteret ved høy og lav tetthet sannsynliggjør at konkurranse om de beste beiteplantene er den viktigste mekanismen bak den tetthetsavhengige tilveksten. Sauenes beitemønster varierte både mellom år og gjennom beitesesongen. Mellom- og innenårsvariasjon var spesielt viktig for diettsammensetningen, noe som antakeligvis skyldes variasjon i klimatiske forhold som påvirker planteveksten. De tetthetsavhengige effektene på tilvekst varierte også mellom år, og på kort tidsskala kan dette ha sammenheng med den observerte mellomårsvariasjon i dietten. Over en lengre tidsskala (ni år) var imidlertid andre prosesser, som langtidseffekter av beiting, viktigere for lammenes tilvekst. Slike langtidseffekter skyldes antakelig at sauene endrer sine beiteområder, og utviklingen ser ut til å gå i ulik retning for de to tetthetene. Ved høy tetthet var lammenes tilvekst sannsynligvis begrenset av forsinkete tetthetsavhengige responser i vegetasjonen. Ved lav tetthet økte lammevektene svakt over år, noe som kan indikere en fasilitering av vegetasjonen i de mest brukte engsamfunnene. Dette studiet viser at tetthetsavhengig beiteatferd påvirker individuell tilvekst, noe som kan være en potensiell atferdsmessig forklaring på tetthetsavhengig variasjon i vitale rater hos store beitedyr.

List of original papers

This thesis is based on the following original papers referred to by author and their Roman numerals in the text:

I Mobæk, R., Mysterud, A., Loe, L.E., Holand, Ø. & Austrheim, G. (2009).
Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach. Oikos 118 (2): 209-218

II Mobæk, R., Mysterud, A., Holand, Ø. & Austrheim, G. (2011).
Age, density and temporal effects on diet composition of sheep on alpine ranges: 6 years of experimental data. Manuscript.

III Mobæk, R. Mysterud, A., Loe, L.E., Holand, Ø. & Austrheim, G. (2011).
Experimental evidence of density dependent activity pattern of a large herbivore in an alpine ecosystem. Submitted to Oikos.

IV Mobæk, R. Mysterud, A., Holand, Ø. & Austrheim, G. (2011).
Temporal variation in density dependent body growth of a large herbivore.
Manuscript.

Paper I is printed with permission from the publisher (Wiley – Blackwell).

Introduction

Density dependent and density independent processes have common effects on vital rates and dynamics of large herbivore populations (Gaillard et al. 2000). Density dependence (or regulation; Sinclair 1989) is described as a negative influence of population density on individual performance, whereas density independent limitation relates to the role of abiotic factors, particularly weather and large-scale climatic fluctuations in altering demographic rates (Stenseth et al. 2002, Mysterud et al. 2003). Estimating the contribution of either process in population dynamics is challenging due to complex interactions between density and climate (Bonenfant et al. 2009). For example, climate effects are often more important at high population densities (Milner et al. 1999, Coulson et al. 2001). Arguably, these interactions often arise since both stochastic weather events and population density influence large herbivores' food resources (Sæther 1997), and temporal variation in food availability and quality is an important component in population dynamics (Illius 2006).

Food competition is regarded the main factor promoting density dependence in large herbivores (Bonenfant et al. 2009). Effects of climate on herbivore performance may be more variable, but including also mechanisms working through plant quality and availability (Mysterud et al. 2001, Mårell et al. 2006). A basic knowledge of how foraging behaviour varies with population density and temporal variation in resource availability is thus imperative to understand the connection between individual behaviour and vital rates, which in turn determine population dynamics and ecosystem processes (Choquenot 1991, Jefferies et al. 1994, Hobbs 1996). The relationship between habitat quality, diet choice and individual growth and performance is well described in ecology at a basic level (White 1983, Moen et al. 1997, Parker et al. 1999, Pettorelli et al. 2002). However, there are few experimental studies of density dependence in foraging behaviour of large mammals. Not all behavioural changes with increased herbivore density are likely to influence performance. Habitat selection is regarded an important determinant of diet. In turn, there is an assumed tight relationship between diet quality, rumination time, and herbivore performance (White 1983). How habitat selection, diet and the activity pattern are affected by density therefore provide candidate behaviours for understanding density dependence in vital rates of ruminants.

Density, climate and their interactions are assumed most important during winter when animals are in poor physical condition (Gaillard et al. 2000, Coulson et al. 2001). In order to enhance our understanding of population regulation, more research is needed on density dependent- and independent processes at summer ranges. This thesis investigates density dependence and temporal variation in foraging patterns and performance of a large herbivore, using domestic sheep (*Ovis aries*) as a model species and lamb body growth as a measure of performance. Domestic sheep provide a suitable "model herbivore" for studying density-climate mechanisms operating within the growing season. Their habitat use and diet preferences are comparable to sympatric reindeer (*Rangifer tarandus*) and red deer (*Cervus elaphus*) populations (Mysterud 2000), and body mass gain by lambs over the summer responds similar to temporal variation in summer foraging conditions as reindeer calves (Weladji et al. 2003) and red deer (Mysterud et al. 2001). Sheep is also important in itself from an agricultural perspective.

Domestic sheep grazing in alpine habitats

Sheep farming is a cornerstone in many rural areas of Norway. About 2 million domestic sheep are released annually to forage freely in outlying pastures during the summer grazing season (Austrheim et al. 2008c). The majority of these sheep are located on alpine pastures (ca. 75 %; Austrheim et al. 2008b), and thus free-ranging sheep are the most dominating herbivores in Norwegian alpine areas during summer (Austrheim et al. 2011). Utilizing the "free" forage available in alpine pastures in 3 months during summer contributes both to economy and maintenance of cultural landscape qualities. Despite the long history of sheep grazing in Norway (i.e. since the Bronze age; Kvamme 1988), little is known about their distribution pattern and foraging ecology (Kausrud et al. 2006). Knowledge about sheep's foraging patterns at different densities and how individual foraging strategies affect growth of lambs may be key to determine critical factors for sheep production on outfield pastures (Armstrong et al. 1997a, Armstrong et al. 1997b). Further, information about density dependent foraging patterns is required in order to predict how alterations in sheep numbers may affect biodiversity and the cultural landscape (DeGabriel et al. 2011). Since 1920 and sheep numbers have increased substantially, reaching a maximum in 2005 (Austrheim et al. 2008c). Our knowledge about how these increasing densities impact alpine ecosystems is far from complete (Mysterud and Mysterud 1999). The few existing studies of sheep grazing effects on Norwegian alpine vegetation were conducted either by using small enclosures stocked with very high sheep numbers, not representative for actual sheep densities on alpine ranges, or by using grazing exclosures (comparing grazed vs. not grazed areas) with no specific control of the density level (Mysterud and Austrheim 2005).

A scientific debate reaching media during the late 1990'ies regarding whether sheep grazing represents a threat to alpine ecosystems by inducing plant defenses that might be detrimental to other species (i.e. trophic cascading effects; Högstedt and Seldal 1998) publicized the lack of empirical evidence of sheep grazing effects. This was the background for establishing a large-scale experimental research project in year 2001, which my thesis is part of. The experiment was design to determine short- and long term ecological effects of sheep grazing on a range of ecosystem components, including vegetation (plant traits, demography and abundance; Austrheim et al. 2008a, Evju et al. 2006, Evju et al. 2009, Evju et al. 2010, Evju et al. 2011, treeline dynamics; Speed et al. 2010, Speed et al. 2011, plant quality; Mysterud et al. 2011), fauna (invertebrates; Mysterud et al. 2005, Mysterud et al. 2010, rodents; Steen et al. 2005, birds; Loe et al. 2007), soil processes (Martinsen et al. 2011a, Martinsen et al. 2011b, Martinsen et al. 2011c) and habitat use by sheep (Kausrud et al. 2006, Mysterud et al. 2007).

Objectives

The main objective of this thesis was to provide long term experimental data on density dependent foraging strategies and performance of a large herbivore. By investigating sheep's foraging behaviour at several spatial (coarse/fine) and temporal (hour/season/annual/long term) scales at two population densities, this thesis aimed to increase our understanding of how density dependent- and independent processes (climate) and their interactions affect sheep's performance at mountain pastures. The following research questions were addressed:

- Does sheep habitat selection (i.e. selection of vegetation types) depend on density? And does this density dependence vary temporally, i.e., is there an interaction with seasonal and/or annual variation in climate (Paper I)?

- How is diet composition affected by sheep density, age, seasonal variation in plant development and annual fluctuations in climate, and do these factors interact (Paper II)?

- Do sheep adjust their activity patterns and movement distances when densities increase, and are activity budgets affected by density-climate interactions (Paper III)?

- What is the contribution of density dependence and annual climatic fluctuations in explaining variation in lamb autumn body mass (Paper IV)?

Material and methods

Study area

This thesis is part of a larger research project investigating ecological effects of sheep grazing in an alpine ecosystem, using a landscape scale experimental setup located in Hol municipality, Buskerud county in southern Norway (7º55´ - 8º00´ E, 60º40´ - 60º45´ N). In year 2001, a large experimental enclosure was established, covering an area of 2.7 km^2. The enclosure is mainly situated in the lower alpine zone, and covers an altitudinal span from the forest line (1050 m a.s.l.) up to middle alpine zone (1320 m a.s.l.). This is an alpine habitat with sub-continental alpine climate with mean annual temperature – 1.5 ºC and mean annual precipitation about 1000 mm (Evju et al. 2009). The area is characterized by high seasonal and annual variation in temperature and precipitation (Martinsen et al. 2011d), with large between-year variation in plant development as measured by plant height (Evju et al. 2006). The bedrock consists of metaarkose (Sigmond 1998) and the soil is moderately base-rich. Vegetation is dominated by dwarf shrub heaths interspersed with grass-dominated meadows, lichen heaths on ridge tops and snow-bed communities in leesides (Rekdal 2001) (Fig. 1 and Appendix 1). A few birch trees (*Betula sp.*) occur in the lower part of the enclosure. This vegetation pattern is representative for alpine pastures used for summer grazing by sheep in southern Norway. In 2001, a total of 104 vascular plant species was recorded in the enclosure (using 180 randomly distributed quadrats each of 0.25 km^2), and herbs dominated (constituting 53% of the vascular species recorded) (Austrheim et al. 2005). Low- and tall herb meadows, the vegetation types with highest grazing value for sheep, comprise 9 % of the vegetation cover (Rekdal 2001). A more detailed description of vegetation types in the experimental enclosure is given in Appendix 1.

Experimental design

The research project was designed as a fully experimental study with the purpose of investigating how various components of an alpine ecosystem respond to differing sheep density levels over time; no sheep, low sheep density and high sheep density. To facilitate a block-wise, randomised and replicated experimental design, the large enclosure was split into nine sub-enclosures. The whole experimental area was fenced using 17.3 km of standard sheep fencing (“Nasjonalgjerde”; 110 cm high). Each of the sub-enclosures was designed to include a comparable distribution of vegetation types and habitats used by sheep and to cover

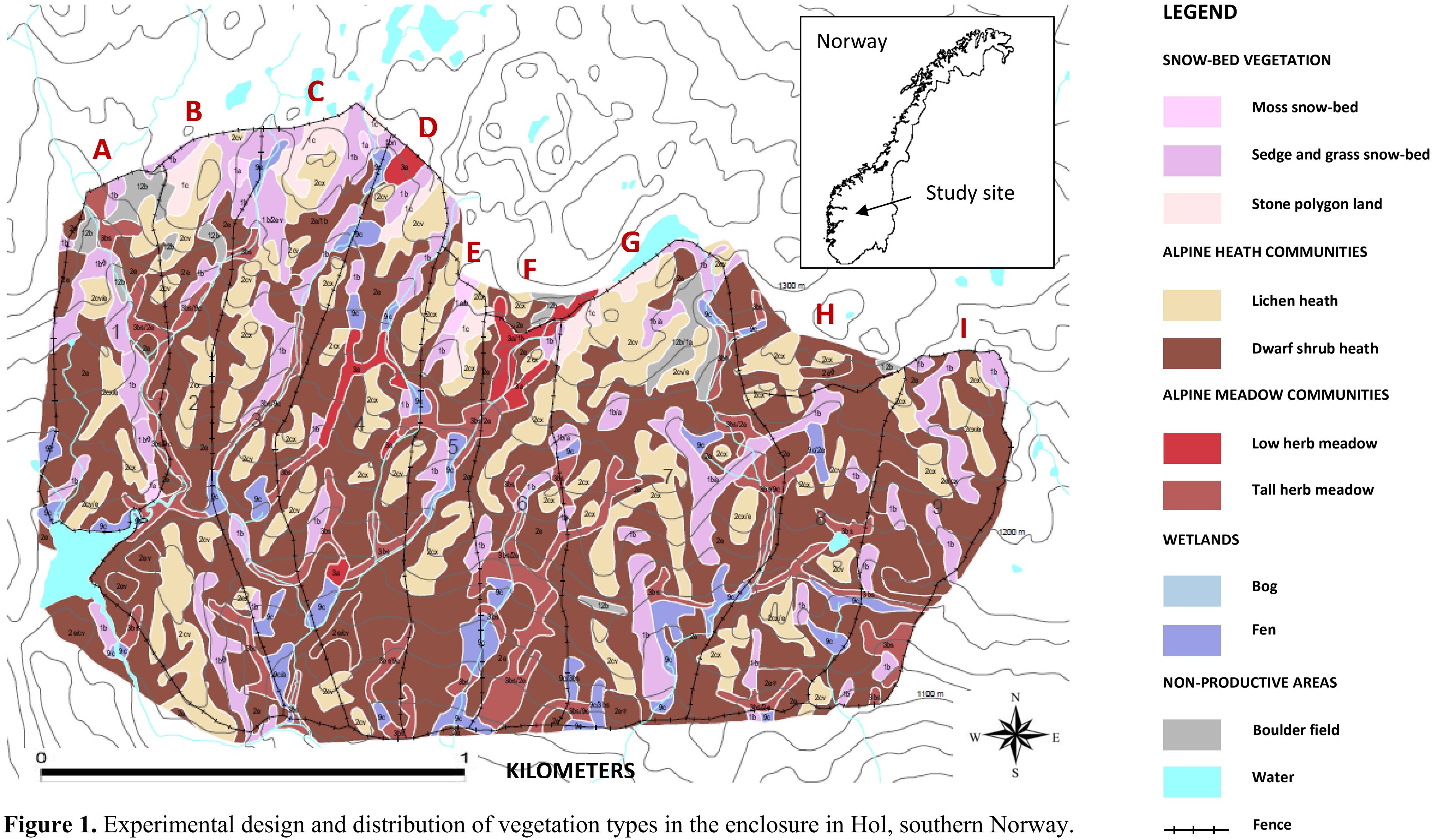

Figure 1. Experimental design and distribution of vegetation types in the enclosure in Hol, southern Norway. Each of the three grazing treatments were replicted three times; high sheep density (sub-enclosures B, F, H), low sheep density (C, D, I) and no sheep (i.e. control; A, E, G). The map is modified after Rekdal (2001).

approximately the same altitudinal range. The size of the sub-enclosures averaged 0.3 km^2, ranging from 0.22 to 0.38 km^2 due to problems with putting up fences over bare rock. Within each block (western, middle and eastern), one of three adjacent sub-enclosures were randomly assigned as control (no sheep), low sheep density and high sheep density sub-enclosure, providing three replications of each grazing treatment.

A botanical survey and assessment of the different vegetation types' grazing values for sheep was conducted in 2001 (Rekdal 2001) and used as a basis for calculating sheep density levels. After excluding habitats that offer no or very few forage plants for sheep (i.e. water bodies and habitats with high dominance of lichens, mosses, bogs and rocks), animal numbers corresponding to 80 sheep/km^2 grazeable area was used in the high density sub-enclosures (B, F and H), and 25 sheep/km^2 in the low density sub-enclosures (C, D and I). These densities are representative for current sheep density levels on Norwegian alpine pastures (Mysterud and Austrheim 2005). Prior to fencing, grazing pressure in this area was low (< 10 sheep/km^2), and sporadic visits by moose (*Alces alces*) and individual or small herds of reindeer (*Rangifer tarandus*) are assumed to have negligible grazing impact on the system (Mysterud and Austrheim 2005).

Sheep grazing treatment was initiated in 2002. Each summer 23 to 26 lactating ewes and 44 to 49 lambs belonging to the same sheep farmer were released into the experimental enclosure (Fig. 2; see Appendix 2 for details). Each of the ewes carried 1-3 lambs, and mothers with singleton, twins and triplets were distributed evenly between the different sub-enclosures to ensure that reproductive status was on average the same at both density levels. To facilitate individual recognition from a distance, both ewes and lambs were equipped with colour coded neck bands in addition to the individually numbered plastic ear tags (Fig. 2). The grazing seasons lasted from late June to late August/early September (Appendix 2), and the number of grazing days used in this experiment thus corresponds to a typical grazing season in Norwegian alpine pastures. All sheep were of the crossbreed “Norsk Kvit Sau”, which is a relatively large sheep and the most common breed among Norwegian sheep farmers (Drabløs 1997). Sheep were treated with anthelmintic parasite treatment (“Ivermectin”) before release on the alpine pasture. Ewes and lambs were weighed at the day of release and recapture from the enclosure. Body mass was determined to the nearest 0.5 kg (Fig. 2). The average live weight at release and recapture for ewes was 81 kg and 82 kg, respectively, and for lambs the mean live weight was 19 kg when released in spring and 40 kg when recaptured in autumn (Mobaek et al. 2011).

Data collection

Direct observations of ewes and their lambs provided data used in Paper I and III, and background information used in Paper II. As this breed has limited grouping behaviour and does not form large herds, the family group (i.e. a single ewe and her lambs) was considered the smallest stable social and independent unit, and thus defined as our sampling unit. Sheep were followed the entire grazing season and observed using two working cycles distributed randomly over the summer; one early from 09:00 – 17:00 and one late from 14:00 – 22:00. The observing schedule was a trade-off between full randomization and retaining field efficiency; each day the observer randomly selected which part of the large sub-enclosure to cover (eastern or western), then in which sub-enclosure to start observing and lastly whether to start observing from the top or bottom from that sub-enclosure. All ewes within this sub-enclosure were then recorded before moving to the next randomly selected sub-enclosure. Due to the lower number of ewes in the low density enclosures, these individuals were observed twice as often to avoid problems with unbalanced number of samples from the two density levels. Sheep were observed from a distance of 50-20 meter using binoculars. Whenever a ewe was located, individual, behaviour and time was recorded. Behaviour was assessed as active (grazing/walking) or inactive (lying/standing/resting) behaviour. Then the observer approached the exact point where each focal ewe was spotted and mapped its location using a handheld GPS. Finally, vegetation type was recorded.

A total of 3077 direct observations from the seasons 2003-2006 were used to analyse sheep habitat selection in Paper I, and 5580 direct observations from the seasons 2003-2009 were used to investigate sheep's activity budget in Paper III. Due to a different sampling technique (yielding not directly comparable data) in 2002 (Kausrud et al. 2006), data from this season was not included in Paper I and III. In year 2008 and 2009, ewes were equipped with GPS collars with activity sensors (Fig. 2), yielding on average 3313 fixes per collar. This enabled inclusion of data on behaviour during a 24 h period, thus extending the results derived from direct observations with more high-resolution analyses of activity- and movement patterns in Paper III.

Faeces samples were collected when obtaining direct observations of sheep. Defecating ewes and lambs were observed and identified using binoculars, and only faeces from known individuals were sampled. Microhistological analyses of a stratified assortment (441 samples from 236 individuals) of the total material collected during the seasons 2002-2007 provided data for examining sheep diet composition in Paper II.

Body mass by lambs and ewes at release and recapture was used to assess temporal variation in performance in Paper IV. This study comprised data from the seasons 2002-2010, analysing body mass from 394 lambs and 217 ewes.

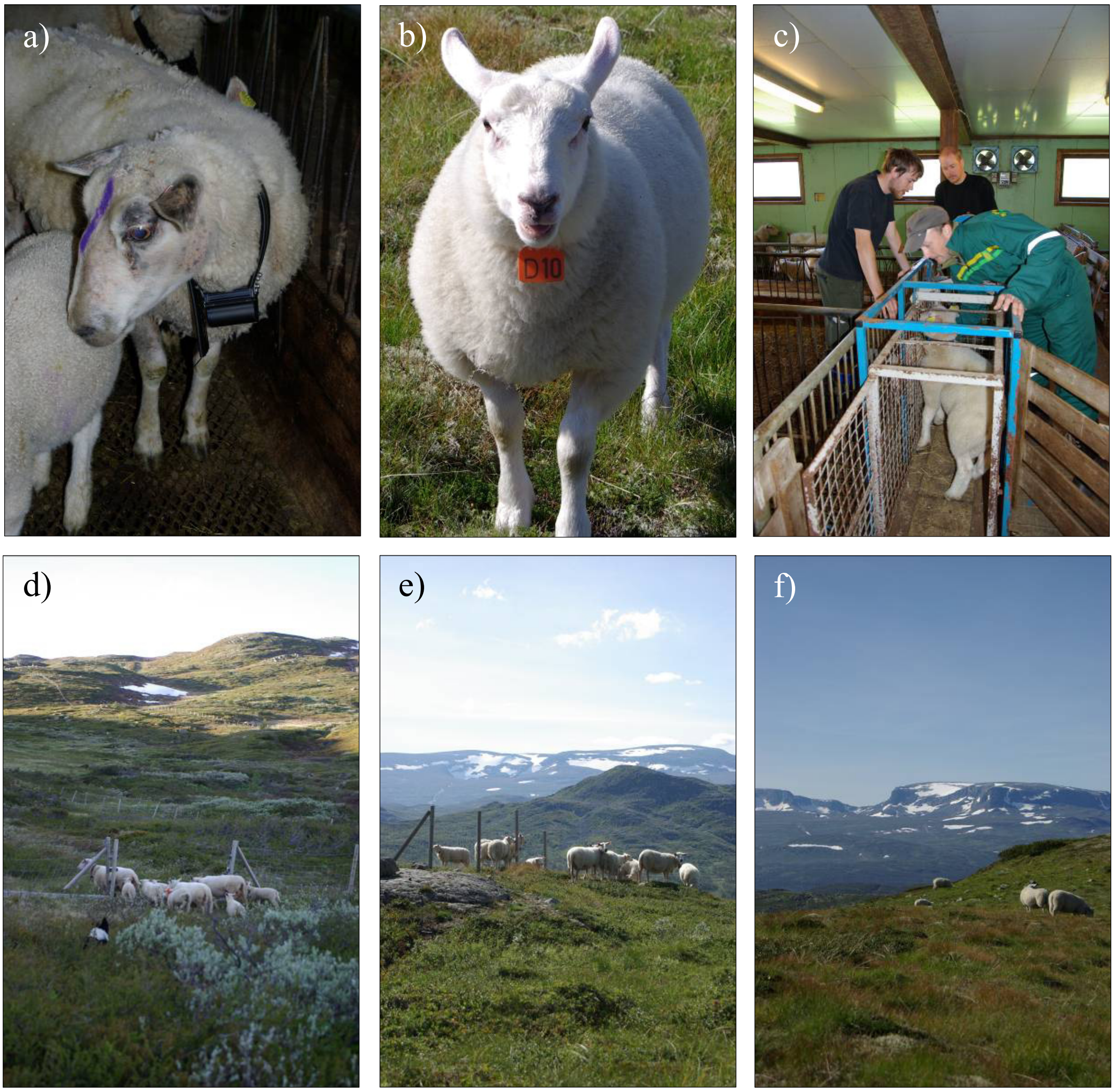

Figure 2. Study animals and experimental enclosure in Hol, Hallingdal, southern Norway. a) Ewe with GPS collar. b) Lamb with colour coded neck band. c) Weighing of lamb. d) Releasing sheep into the enclosure. e) Fence separating low and high density treatments. f) Sheep grazing in grass snowbed vegetation at high altitude. (Photos: R. Mobæk)

Statistical analyses

All statistical modelling was done in R (see Paper I-IV for specific versions) (http://cran.r-project.org/). Prior to modelling, data was plotted with General Additive Models (GAM) to search for potential non-linearity in the datasets (Woods 2006). As the randomised block design in the experimental setup facilitated implementation of both fixed and random factors, we fitted linear mixed-effects models using the function "lmer" in R library "lme4" (Paper I-IV). We always used "individual" (i.e. ewes; n = 23-26 per year) nested within "sub-enclosure" (n = 6) as random factors to account for temporal and spatial pseudoreplication due to sampling from the same individuals continuously throughout the season and individual variation within the replicated density treatments (3 sub-enclosures). Fixed factors were density, date, year and selected interactions between these variables (see Table 1), in addition to ewe age and litter size whenever these factors were expected to influence the particular biological process of interest. We used model selection with AIC (Akaike Information Criterion) to find the most parsimonious mixed model and mainly chose the model with the lowest AIC value (and corresponding AIC weight) for calculating parameter estimates. In addition to mixed models, we used the R package "adehabitat" to fit Resource Selection Functions (RSF) (Calenge 2006) in Paper I and for analysing GPS data in Paper III. When exploring diet composition in Paper II, we also ran ordination analyses using Canoco for Windows 4.5 (Ter Braak and Smilauer 2002).

Brief summary of papers I-IV

As all papers in this thesis investigate how different aspects of sheep behaviour and performance is affected by density and temporal variation, the specific hypotheses, predictions and model parameters in each paper are related. A simple overview of predictions tested in paper I-IV and their main results is given in Table 1. In the next section, each paper is described more in detail. Lastly, a summary figure illustrating how the results are interpreted in terms of short term mechanisms working at high and low density is presented (Fig. 3).

Table 1. Main results of predictions tested in Paper I-IV. Parameters applied in the linear mixed-effects models in brackets.

	Paper			
Predictions tested in paper I-IV	I. Habitat selection	II. Diet choice	III. Activity pattern	IV. Perfor-mance
Density dependence				
• At high density, competition for forage leads to selection of habitats and plants with lower quality, increased food searching activity and reduced performance (Density)	Yes	Yes	Yes	Yes
Seasonal variation				
• Sheep alter their foraging behavior in response to a seasonal decline in plant quality (Date)	Yes	Yes	Yes	-
• Increased density effect in late season as forage senesce (Date x Density)	No	No	No	-
Annual variation – climatic factors				
• Foraging behavior and performance vary between years in response to climate induced variation in plant growth (Year as category)	Weak support	Yes	Yes	Some support
• Stronger effect of density in "poor" years when there is less biomass (Year as category x Density)	No	Some support	No	No
Trends over years – grazing effects				
• Long term trend in foraging behavior and performance due to grazing effects altering sheep's foraging habitats (Year as trend)	Yes	No	No	Yes
• Temporal trends at high and low density diverge as vegetation is most affected by high grazing pressure (Year as trend x Density)	Weak support	No	No	Yes

Paper I – Habitat selection

Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach

By this study I aimed to explore temporal variation in habitat selection and examine density-climate interactions at the foraging scale. I pooled vegetation types into three productivity categories according to their grazing value for sheep (high, medium and low) and tested whether sheep's selection of these habitats was density dependent and whether density dependent selection patterns varied seasonally and annually (see predictions in Table 1).

Main results

Sheep's habitat selection depended on activity. When active they selected high productivity habitats and avoided low productivity habitats, and when resting they showed a weak selection for low productivity habitats (Fig. 2; Paper I). When foraging, habitat selection was density dependent. Sheep at low density selected more high productivity habitats (meadows) than sheep at high density (Fig. 2 and Table 2; Paper I). Habitat selection varied temporally. As the season progressed selection of meadow habitats declined (Fig. 3 and Table 2; Paper I), but there was no interaction between seasonal variation and density. Selection of meadows also differed between years. We found limited interactive effects between annual climatic variation and density. However, selection of meadows increased over years, and tended to increase more for sheep at low density than for sheep at high density (Figure 4 and Table 2; Paper I).

Main conclusions

Foraging sheep at low density had a higher selection of meadows, and this density dependent selection pattern was consistent over years. Although sheep varied their habitat selection temporally, we found no strong evidence of density-climate interactions. There was no support for a stronger effect of density in late grazing season, and no indication of more pronounced density dependence in years with poor vegetation development. Rather, we found weak support that grazing effects were more important than climatic fluctuations in explaining the annual variation in habitat selection, as selection of the most productive habitats increased over time. This may indicate grazing facilitation within meadows.

Paper II – Diet composition

Age, density and temporal effects on diet composition of sheep on alpine ranges:
6 years of experimental data.

The intention of this study was to examine how sheep vary their diet according to density, age (ewe/lamb) and temporal variation. Diet composition was estimated from plant fragments in faeces samples, and the most dominating plant taxa were analyzed in detail by aid of microhistological analysis. I predicted that sheep at high density would include more low-quality forage in their diet, and tested whether this density dependence interacted with seasonal and annual variation in plant development.

Main results

Diet composition varied with season, year, sheep age (ewe or lamb) and density. The most important forage plants were *Avenella flexuosa*, herbs and *Salix* spp. (Fig. 1; Paper II). Intake of herbs and *Salix* spp. declined over the season and was replaced by *A. flexuosa*. Annual variation in diet was high (Fig. 2; Paper II). Sheep grazing at high density consumed more of the low-quality grass *A. flexuosa* and less “other plants” than sheep at low density (Table 2; Paper II). We found a significant and marked interaction between density and annual variation only for *A. flexuosa* (Table 1; Paper II). The density effect on *A. flexuosa* varied in sign from negative to positive between years. When estimating the combined effect of density and annual variation also for herbs and “other plants”, we found a pronounced density dependence pattern that varied between years and among species (Fig. 2 and Table 2; Paper II). For herbs, the sign of the density effect did not change between years, although the strength of the density dependence varied somewhat between years. Lambs ate more high-quality plants than ewes, but the age effect did not interact with density or temporal variation.

Main conclusions

Effects of age, density and temporal variation on sheep’s diet choice were mainly additive, and interactions were few. Annual variation in plant development strongly influenced diet composition. At the seasonal scale, sheep included more grass in their diet when availability of high-quality plant material decreased towards autumn. Density dependent diet choice was found for the bulk food plant *A. flexuosa* and for the category “other plants” which comprises forage plants of minor importance. The density dependent selection for *A. flexuosa* showed no consistent pattern among years, as this depended on the response for herbs and “other plants”.

Paper III – Activity pattern

Experimental evidence of density dependent activity pattern of a large herbivore in an alpine ecosystem.

The objective of this study was to investigate whether activity budgets and movement distances by sheep varied depending on density. Using long term behaviour data, I tested whether forage availability or plant quality were the main activity constraint for sheep at high density. I also analyzed temporal variation in sheep’s activity in order to examine interactions between the density effect and seasonal and annual variation in climate.

Main results

Sheep at high density spent more time active (i.e. foraging) than sheep at low density. This density dependent activity pattern was consistent over years (Fig. 1 and Table 1; Paper III). Sheep were more active towards the end of the season, and activity varied between years. However, this temporal variation did not interact with the density effect (Appendix 1; Paper III). Sheep at low density moved longer distances than sheep at high density, and movement distances declined weakly over the season (Fig. 2 and Table 2; Paper III).

Main conclusions

Population density affected both activity budget and movement distances by sheep. The fact that sheep at high density spent more time active indicates that they responded to food competition by increasing searching time. Thus the main constraint at high density is likely availability of high-quality food rather than processing low-quality food. Longer movement distances by sheep at low density are probably due to their higher use of meadow habitats that are dispersed in the area.

Paper IV – Performance

Temporal variation in density dependent body growth of a large herbivore.

In this study I intended to explore temporal variation in performance, by indentifying how density and annual variation in climate, alone or combined, influenced autumn body mass by lambs. I predicted that lambs at high density would gain less weight over the season than lambs at low density. Further, if density independent processes were most important, I predicted body mass to vary irregularly between years. If grazing effects were important in altering the quality of the habitat, I expected to find a long term trend in body mass development.

Main results

Lambs at high density had lower autumn body mass than lambs at low density (Fig. 1; Paper IV). Body mass varied between years, and this temporal variation was better explained by a long term trend than by erratic annual variation likely linked to climatic fluctuations (i.e. year as trend was a better predictor than year as category; Table S2 in Paper IV). A significant interaction between density and year demonstrated that development in autumn body mass diverged over years for lambs grazing at different densities; declining at high density and slightly increasing at low density (Fig. 1 and Table 1; Paper IV).

Main conclusions

Lamb autumn body mass was density dependent, but the strength of density dependence varied temporally. A long term diverging trend in body mass at high and low density is coherent with the prediction that temporal development is mediated by grazing effects. Clearly, this opens for the inference that sheep alter their foraging habitats qualitatively different depending on density, and that this feedback on the sheep yielding contrasting long term density dependent effects. Increased food competition due to either plant community changes, lowered biomass production or quality is the most likely causes for changed lamb growth at high density over years, while grazing facilitation may possibly contribute to the increasing body mass gain over years by lambs at low density. At least, differing foraging patterns due to reduced availability of high quality plants at high density seem to be important short term mechanisms promoting the density dependent performance observed (Fig. 3).

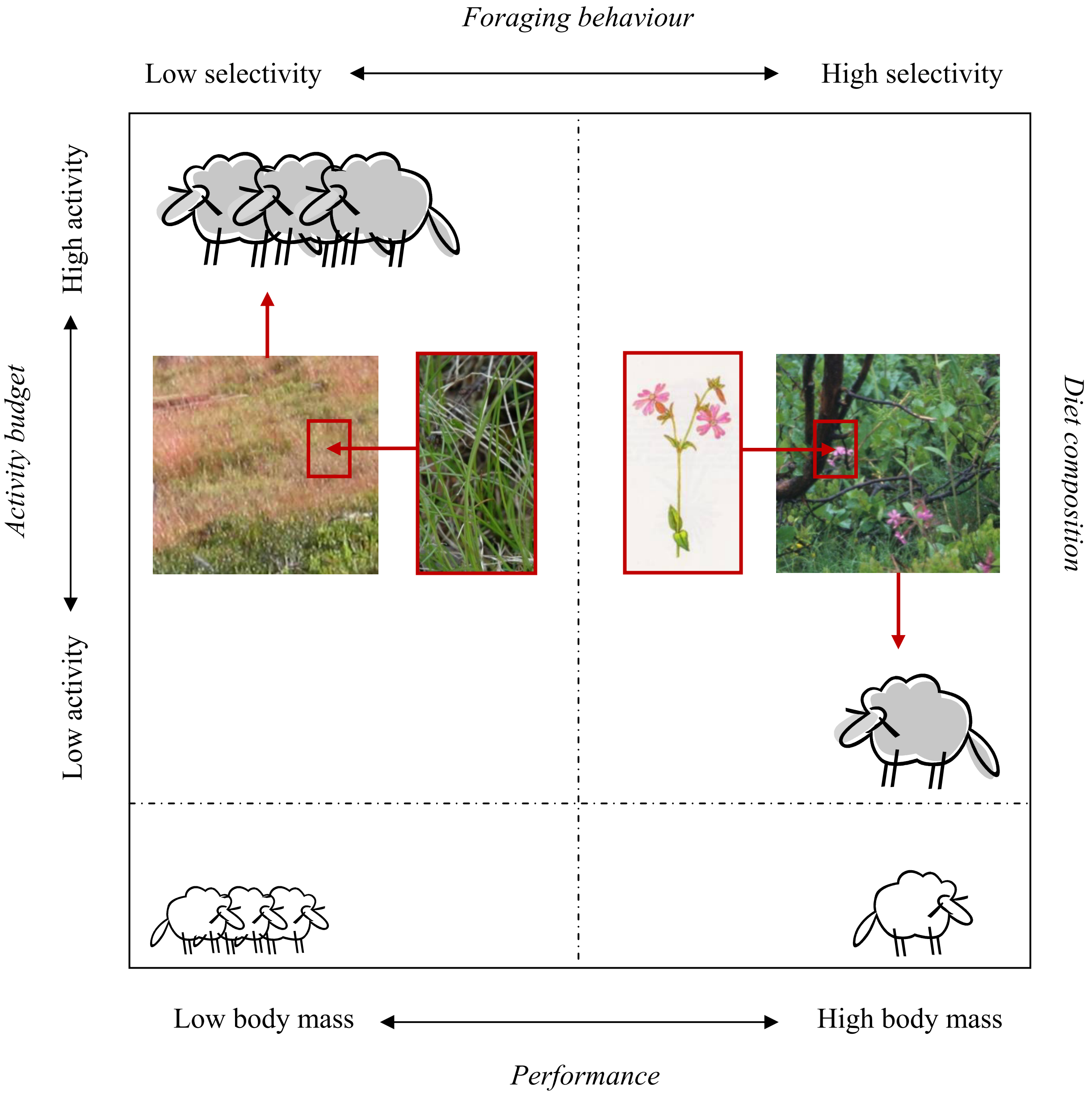

Figure 3. Short term mechanisms involved in density dependent foraging patterns and performance. Ewes at high density (left) are more active and less selective than ewes at low density (right). They have a more even use of vegetation types (illustrated by dwarf shrub heath with a pink cover of *A. flexuosa*; photo R. Mobæk) and ingest more grass (illustrated by *A. flexuosa*; photo A. Mysterud) compared to ewes at low density who select more high productivity foraging habitats (illustrated by tall herb meadow; photo A. Mysterud) containing more herb species (illustrated by *Silene dioica*; Gjærevoll and Jørgensen 1991). The reduced availability of high-quality forage due to food competition at high density results in reduced performance of lambs (lower panel), i.e. they have lower autumn body mass as compared to lambs at low density.

General discussion

Understanding mechanisms causing density dependent responses in vital rates are important to predict population dynamics and ecosystem responses when densities increase, and to recognize how these responses in turn may feedback and affect the grazing animal. This is the first experimental long term study on effects of density and temporal variation on sheep's foraging patterns and performance on alpine ranges. My study provides empirical evidence that increased density affected sheep's habitat selection, diet choice and activity pattern, as would be predicted if high density increased food competition. Selection and activity patterns varied temporally, but there were limited interactions between seasonal and annual climatic variation and density (Table 1). Over longer time scales, long term trends assumed to reflect grazing effects seemed more important for habitat selection and temporal variation in lamb body mass than annual variation in climate. Both sheep at high and low density apparently altered habitat qualities, with lasting effects on performance.

Density dependent foraging – short term effects

Habitat selection by large herbivores is an intricate process operating at multiple spatial scales from landscape, habitats and patches to diet choice (Senft et al. 1987, Wiens 1989). Herbivores are able to alter their foraging behaviour rapidly in response to variations in the foraging environment (Provenza and Balph 1990, Bryant et al. 1991), and since food resources are subject to seasonal and annual variation, herbivores also vary their habitat selection temporally (Moen et al. 2002). Selective foraging relates to the variety of nutritive classes of plant species and plant parts within a given habitat (Van Soest 1994). Sheep, as other ruminants, are indeed capable of selecting between food items on fine spatial scales as well as responding to aggregation of differing forage quality on larger scales (Edwards et al. 1994). At both spatial scales investigated sheep's foraging was non-random (Paper I and II). Sheep generally selected high productive meadow habitats with herb vegetation, in addition to a high selection of the grass *Avenella flexuosa* and *Salix* spp., species that occur in most high- and medium productive vegetation types (Appendix 1).

Alterations in population density may affect short term selection patterns if intraspecific competition reduces abundance of high quality food resources, forcing individuals to use more low quality habitats (white-tailed deer (*Odocoileus virginianus*); Kohlmann and Risenhoover 1997, sika deer (*Cervus nippon*); Borkowski 2000, grey kangaroo (*Macropus giganteus*); Ramp and Coulson 2002) and include less nutritive plant species in their diet (feral donkey (*Equus asinus*); Freeland and Choquenot 1990, *grey kangaroo*; Ramp and Coulson 2002, domestic sheep; Kausrud et al. 2006). Whether density dependent foraging patterns may vary temporally is still poorly investigated, and the few studies available are short term (1-2 seasons). In a study of grey kangaroos (Ramp and Coulson 2002), the effect of density on habitat selection varied within a year in response to seasonal variation in resource availability and quality.

At the habitat scale, I found density dependent foraging patterns as predicted from ideal free distribution theory (IFD; Fretwell and Lucas 1970). Ewes at high density used more of the medium productive vegetation types (i.e. dwarf shrub heath and snow bed vegetation), whereas ewes at low density had a higher selection of meadow vegetation. This density dependent selection pattern was consistent over years (i.e. 2003-2006; Paper I) According to Edwards et al. (1994), sheep are less selective at fine scale when less satiated. Indeed, diet composition was density dependent as sheep at low density tended to have a wider diet (Fig. 1; Paper II) and grazed more of the bulk food plant available in this alpine area (*A. flexuosa*; Paper II). Density also influenced how sheep distributed time to different activities. Ewes at high density were more active than ewes at low density, spending more time grazing (Paper III). They moved shorter distanced when foraging than ewes at low density, likely because they expanded their food search to include vegetation types of lower grazing value that have a uniform distribution within the experimental enclosure (i.e. dwarf shrub heaths). In contrast, sheep at low density had longer walking distances, as they moved between interspersed patches of meadow vegetation (see Fig. 1).

The fact that sheep at high density spent more time searching for food and were less selective than sheep at low density (Fig. 3), indicates that food competition and thereby reduced availability of high quality forage is the key constraint at high density. In fact, foraging patterns at high density resemble sheep’s general response to plant senescence and lower abundance of high quality plant material in late grazing season. When plants mature, protein content declines and cell-wall structure (carbohydrates and lignin) increases, thus gradually reducing nutritive quality and digestibility (Hebblewhite et al. 2008). Sheep responded to this seasonal decline in forage quality by increasing activity (i.e. searching time; Paper III), replacing meadow vegetation with medium productive habitats such as dwarf shrub heath and late thawing snow beds (Paper I) and including more grass (especially *A. flexuosa*) in their diet when herb vegetation deteriorated (Paper II). Movement distances also declined weakly over the season as sheep used more of the evenly distributed dwarf shrub heaths. My results imply that the adopted tactic by sheep when high quality food resources become scarce (either as a result of seasonal development or increased competition) is to alter their foraging behaviour from selective- more towards bulk feeding.

Temporal variation in density dependent foraging

I found both within- and between-year variation in foraging patterns, and annual variation in performance (Table 1). Some of this variation likely reflects climatic temporal variation in food abundance and quality, though this was not quantified directly. Alpine habitats experience high annual variation in plant biomass and quality, partly linked to large-scale climatic fluctuations (such as the NAO; Mysterud et al. 2001). While snow cover and temperature in spring determine the onset of vegetation growth (Langvatn et al. 1996), temperature and prevailing weather throughout the summer season influence plant development within the season (Lenart et al. 2002).

Plant development as measured by plant height differed considerably between years in our study area (Fig. 4; Paper I), and accordingly grazing pressure on selected herbs varied between years (Evju et al. 2006). The strong annual variation in sheep's diet composition clearly indicates that climatic conditions to a large extent influenced the overall abundance of forage quality or its temporal distribution within a season. In early summer, there is usually an abundance of forage, and it might be that the duration of period with access to high quality food resources during the grazing season is lower in "poor years". Apparently, between-year variation in plant biomass or quality also affected sheep's habitat selection and activity pattern. Climatic conditions were more important for annual variation in sheep's activity budgets than long term effects of density, but the interpretation was less clear for habitat selection. At this scale, a steady increase in selection of meadow habitats over years suggested that other processes than erratic climatic variation, such as grazing effects, could better explain the selection patterns observed. Climate-induced variation in plant development likely also influenced lamb body growth. Despite a more pronounced effect of long term grazing effects, the density dependent pattern varied between years (Fig.1; Paper IV). On short time scales, annual variation in herb growth affecting diet quality (i.e. nutritional intake) and activity (i.e. energy expenditure) probably contributed to this annual variation in performance.

Food competition could be predicted to increase when resources are limited by climatic factors operating within- and between seasons. Assuming that sheep at high density would be more negatively affected by climate-induced food scarcity, I predicted stronger density dependence in late grazing season when availability of high quality plant material declined, and more pronounced effect of density in years with poor vegetation development. For example, Kausrud et al. (2006) found interaction between density and season in the first year (2002) of this grazing experiment. Sheep at high density consumed more *A. flexuosa* in late grazing season, while intake of this grass remained stable throughout the season at low density (Kausrud et al. 2006). Similarly, intake of herbs declined at a slower rate at low density than at high density in preliminary analyses of diet composition comprising the grazing seasons 2002-2004 (Ehrlinger 2006). I failed to find any interactions between sheep density and seasonal temporal variation, as density dependent patterns were consistent within season (Table 1). These contrasting results may be due to specific short term effects only observable immediately after initiation of the sheep grazing treatment, and exemplify how results from short term studies may differ from studies conducted over longer time scales.

I found limited evidence of annual variation in density dependent responses, except for some attributes of diet choice, as density dependent selection pattern of *A. flexuosa* varied significantly between years. When estimating interactions between density and annual temporal variation for the most important forage plant species/groups in sheep's diet I found some support for stronger density dependence in "poor" years, but no consistent selection patterns for *A. flexuosa.* In years with density dependent diet choice, sheep at high density compensated a lower availability of herbs by either increasing their intake of *A. flexuosa* or intake of "other plants", such that the density dependent response of *A. flexuosa* in fact showed opposite patterns between years (Fig. 2; Paper II). Access to high quality forage benefits nutritional intake, body size and physical condition (Parker et al. 2009). The large annual variation in diet composition interacting with the density effect could be expected to induce similar variation in vital rates, and indeed annual- and density dependent body mass gain by lambs interacted (Fig. 1; Paper IV).

Density-climate interactions and performance

Body mass is one of the most important factors influencing ungulate life histories (Calder 1984). Birth weight and growth in early life is closely linked to survival and reproductive performance in large herbivores, and conditions experienced while *in utero* or in the juvenile stage may shape a variety of phenotypes within a population (Forchhammer et al. 2001). Combined effects of adverse weather and high densities are reported to act strongest upon vital rates of juveniles (Sæther 1997, Gaillard et al. 1998), and differing life histories may develop depending on whether individuals are born in “poor” or “good” years (Lindström 1999). In turn, fitness differences among cohorts may affect population dynamics (as seen in Soay sheep; Forchhammer et al. 2001). In many species of large herbivores, females are only able to reproduce after reaching a certain body mass threshold (roe deer (*Capreolus capreolus*); Gaillard et al. 1992, bighorn sheep (*Ovis canadensis*); Jorgenson et al. 1993, moose (*Alces alces*); Sand 1996, red deer; Bonenfant et al. 2002). For female red deer, Langvatn et al. (1996) found that reduced body growth due to harsh environmental conditions during the first year of life resulted in a 1 year delay in age at first reproduction. In the Soay sheep population, cohort-specific climatic and density dependent conditions affected individual lifetime reproduction. A mother that was born heavy herself produced heavier lambs that were born later and had more siblings than lighter-born mothers (Forchhammer et al. 2001). The importance of body mass for lifetime reproductive success is also established for Norwegian domestic sheep. Ewes with high initial body weight produced larger lambs throughout their lifespan than ewes with low initial body weight (Steinheim et al. 2002). Thus, the density dependent juvenile performance as documented in my study may have important repercussions for individual sheep’s life histories.

Density, climate and their interactions are considered particularly important during winter season, as the combination of food competition and harsh winter climate strongly affects over-winter survival (Gaillard et al. 2000, Coulson et al. 2001). Density-climate interactions on summer ranges are less described, although conditions during the growing season determine body mass gain and hence physical condition when entering the winter season (Klein 1965, Hjeljord and Histøl 1999, Stewart et al. 2005). Norwegian alpine habitats are characterized by a short growing season (about 130 days with temperatures above 5° C; Tveito et al. 2001) and biomass production is mainly limited by temperature more than precipitation in alpine ecosystems (Deinum 1984). Body mass gain by ungulates in alpine areas is strongly influenced by phenological plant development in spring and early summer (Pettorelli et al. 2005, Herfindal et al. 2006, Pettorelli et al. 2007), and weather conditions throughout the summer season affecting forage availability and quality (Bø and Hjeljord 1991, Ericsson et al. 2002, Lenart et al. 2002). For example, juvenile growth responds positively to a slow development in plant phenology, as this provides a prolonged period with access to high quality plant material (sheep; Mysterud et al. 2001, reindeer; Pettorelli et al. 2005). Local population density on summer ranges may also be important for juvenile body mass gain, and increased densities on summer pastures has been reported to reduce autumn body mass for reindeer- (Holand et al. 2010) and moose calves (Herfindal et al. 2006).

Although the best model for body mass included the density interaction with long term year trend, the estimated between-year variation in the density effect seemed also to be quite important. My results at least suggest also some density-climate interactions affecting juvenile performance during summer, most likely linked to annual climatic variation in plant growth. Since density-climate interactions were not detected at the habitat selection scale, and absent for sheep's activity pattern, this is likely a fine scale process operating via diet composition or any other qualitative change in the vegetation not measured in my study. In fact, NDF (i.e. neutral detergent fibre, related to content of cell-wall structure) in faeces was slightly higher at high than low density (data from 2008; R. Mobæk, unpublished), indicating increased roughage associated with a diet of lower quality (Van Soest 1994). I had no exact measure of plant biomass or forage quality to be able to distinguish between "poor" and "good" years from the herbivores' point of view. Density-climate interactions could potentially be more pronounced in years with more "extreme" summer weather or during periods with even higher animal densities and thus food competition than applied in this experiment. These perspectives warrant further scrutiny.

Besides food competition, higher parasitic loads and increased social interference is also reported to contribute to density dependence in large herbivore populations (Stanko et al. 2002). In this experiment, all animals were treated with anthelmic medicine before release into the enclosure to minimize parasite load. At least a count of parasite eggs in faeces conducted immediately after recapture revealed no different infection rate between the two density levels (data from 2009; Ø. Holand, unpublished). Further, among a total of 5580 observations of sheep behaviour we have no observations of interference activities. Thus, I conclude that resource limitation due to food competition is the main short term mechanism promoting density dependence in performance in our study system (Fig. 3).

Delayed density dependence – long term grazing effects

An important issue when studying foraging behavior is spatial and temporal scaling (Senft et al. 1987), while a similar framework to a limited extent have been applied to mechanisms of density dependence. Spatial variation in density dependent responses due to habitat quality has received quite much attention (Ray 1996, Donalson and Nisbet 1999). However, these mechanisms are likely also to change with time scale (Kuijper et al. 2008). In the longer term, large herbivores may strongly affect ecosystem processes (Jefferies et al. 1994, Hobbs 1996).

Their ability of modifying habitats is primarily mediated by grazing and browsing impacts on the structure and functioning of plant communities (Austrheim and Eriksson 2001). As selective foragers, they prefer plant species and plant parts with high nutrient content and low chemical and structural defense (Hanley 1997). These foraging decisions, in addition to trampling, urinating and defecating, may alter intra- and interspesific competition and nutrient availability for plants, thereby affecting plant productivity and plant species composition (Huntly 1991, Jefferies et al. 1994, Augustine and McNaughton 1998). Changes in plant quantity and quality may in turn affect the individual performance, life history strategies and hence the population dynamics (Jefferies et al. 1994, Simard et al. 2008). Short term studies miss the potential to discover mechanisms due to interactions between herbivores and their foraging habitats that operate over the time scale of years. Manipulating herbivore density and monitoring changes in habitat quality, foraging behavior and performance over time is a constructive approach in order to improve our understanding of mechanisms involved in density dependent regulation in the long term. A problem with most studies of large mammals is that single populations are followed over time. Several processes may be involved when performance change as density of a population increase over time. Typically, short term food competition is identified as the main mechanism. In other studies, the role of changes in age structure and maternal effects has been highlighted (Coulson et al. 2004). Indeed, large mammal population dynamics have a “history” (Koons et al. 2007, Ezard et al. 2010). In my study, such lagged effects are partly broken by indoor feeding during winter and because ewe age is controlled for.

Over years, vegetation development in my study area differed between the two density treatments, i.e. long term grazing effects were density dependent. At high density, vascular plant cover decreased already two years after sheep was introduced, and abundance of highly selected herbs species declined after four years. The reduction in vascular plants was accompanied by an increase in graminoids. At low density, however, vegetation changes were moderate and sheep grazing had minor effects on herbs and other important forage plants (Austrheim et al. 2008a). In general, it has been noted that density dependence may be difficult to detect because of lagged responses to changes in animal density (Bonenfant et al. 2009). These lags could be attributed to a parallel decline in habitat quality and individual performance when densities increase. As individual performance will not improve until habitat quality is restored, performance typically respond delayed to a decrease in population size (Caughley 1977). At high sheep density, body mass by lambs dropped during the first two-three years apparently analogous to the decline in availability of high quality herbs, and then more or less stabilized (Fig. 1; Paper IV). These results indicate that delayed density dependence restricted lamb growth at high density, and that increasing abundance of graminoids could not compensate the reduced cover of herb vegetation. Sheep grazing at high density possibly altered their foraging habitat towards a state with lower availability of high quality food resources, with long term consequences for dietary intake.

Lambs at low density showed the opposite performance pattern as compared to lambs at high density, as body mass tended to increase over years. According to the minor vegetation changes at low density (Austrheim et al. 2008a), this development was likely not related to alterations in overall abundance of preferred plant species. Rather, this could be due to below-ground processes altering soil nutrients availability for plants, or enhanced plant production within the most selected foraging habitats. Actually, soil carbon storage increased over years at low density, which could potentially benefit biomass production (Martinsen et al. 2011b). Indeed, biomass of vascular plants within meadows and snow beds increased during the period 2002-2008 at low density (G. Austrheim, unpublished). This is at least indicative of grazing facilitation. However, as my results only showed a weak increase in lamb body mass over years at low density, whether this long term trend represents a “true” grazing facilitation remains to be further studied.

Management issues

Management of rangelands grazed by domestic livestock may be challenging since livestock often are stocked at high population densities as compared to wild herbivores (Oesterheld et al. 1992). Overabundance of herbivores with selective feeding patterns, either wild (Côté et al. 2004), domestic or semi-domestic (Van der Wal 2006), may lead to overuse of some areas and avoidance of others (Launchbaugh and Howery 2005), causing shifts in vegetation composition towards dominance of unpalatable species (Husheer et al. 2003) or homogenization of palatable plants (Bråthen et al. 2007). Indeed, the concept of “overgrazing” is controversial and value-laden (Mysterud 2006). The central and demanding issue is to define and sustain sound levels of grazing pressures not detrimental to the ecosystems, including the herbivores’ foraging resources.

I document a negative feedback of population density on individual performance. Lambs at high density weighed on average 4 kg less than lambs at low density when recaptured in autumn (Paper IV). The decreasing body mass trend stabilizing at a lower level about three years after initiation of the grazing experiment could imply that sheep at high density quite rapidly reduced the grazing capacity of their foraging habitat. Herbivores may alter succession rates and ultimately switch habitats between alternate stable states not easily reversible when grazing or browsing pressure is reduced (Dublin et al. 1990, Côté et al. 2004, Briske et al. 2005). My performance data comprises only eight grazing seasons. Hence it is premature to forecast the direction of a grazing-induced succession. Recently, a study of red deer revealed that almost four decades after reducing deer densities to a minimum, palatable species were still suppressed, even at low density levels, and only able to reestablish within deer-exclosures (Tanentzap et al. 2009). Clearly, degraded foraging habitats may require long time to recover. This point should be highlighted in management.

How can sheep farmers or ecologists assess whether alpine pastures are at the risk of being overstocked or not? The most obvious answer is to monitor performance over time. However, additional management tools are required in order to recognize when population densities are close to the "tipping point", i.e. approaching density levels that may reduce grazing capacity. One possibility is to follow development within vegetation types of high grazing value, since sheep's selection of vegetation types evidently is density dependent (Paper I). Another proposal is to monitor plant species with particular forage value, as sheep's utilization of different species also depend on density (Paper II).

Selecting herb species and morphological traits as indicators of grazing pressure in our experimental area has proved difficult due to large annual climatic variation in plant height overriding grazing effects (Evju et al. 2006). Based on my analyses of sheep's diet composition, I may propose an alternative species for estimating grazing pressure. Sheep at high density in particular compensated a lower intake of herbs by consuming more of the grass *A. flexuosa* throughout the grazing season (Paper II). Although *A. flexuosa* is regarded medium quality forage (Rekdal 2001), this grass maintains a higher content of crude protein (Eknæs et al. 2011) throughout the season relative to other grass-, sedge- and woody species in alpine pastures, and could thus be a significant forage species for sheep at high density when the overall availability of high-quality plant species is reduced by food competition. This grass, constituting ~31 % of sheep's diet and thus the bulk food in our system (Paper II), might be important in sustaining body mass at the current high density level. Although grazing treatment did not affect abundance of *A. flexuosa* compared to controls without sheep in our system (Mysterud and Austrheim 2008), *A. flexuosa* is reportedly sensitive to grazing pressure (Pakeman 2004) and was found to be negatively affected by high sheep densities in nutrient-poor alpine areas (Austrheim et al. 2007), suggesting that its response to grazing is ecosystem-dependent (Austrheim et al. 2008a). Being a common grass on alpine pastures, perhaps monitoring changes in abundance of this species, for example by using grazing exclosures, could be a simple management tool in evaluating grazing pressure in addition to observing lamb body mass development over years.

Main conclusions and future perspectives

This thesis documents density dependent foraging behaviour and performance by sheep grazing at alpine ranges. Foraging behaviour varied temporally likely in response to seasonal and annual variation in abundance of high quality food plants. Annual variation in foraging patterns could be due to both increased food competition and climatic variation affecting plant development. I found that short term density-climate interactions may affect performance on summer ranges, and propose that such interactions might arise via diet composition effects. However, at longer time scales grazing pressure were more important for lamb body growth than annual climatic variation. Diverging lamb performance patterns suggest contradictory long term grazing effects at high and low density; delayed density dependence at high density and habitat preservation and perhaps facilitation at low density. My study investigating how density dependent foraging behaviour affects performance may hopefully contribute to increase our understanding of proximate mechanisms behind similar variation in vital rates. Nevertheless, results from nine grazing seasons are barely long term in an ecological context. More research is needed to nail the mechanisms behind density dependent temporal variation in sheep performance, especially now that the future climate is expected to change markedly. For example, continued research using the experimental infrastructure in Hol could increase our knowledge of long term consequences of sheep grazing in alpine habitats, advancing our understanding of density dependent modification of alpine vegetation and how this feedback on lamb body growth and sheep production. The following future research questions could be raised:

- Are meadows still increasingly used over years, and do the density dependent selection patterns for meadow vegetation continue to diverge? Are meadows over-exploited over time at high density while sheep at low density facilitate these habitats? Does sheep performance at high and low density respond to diverging development within the most selected vegetation types?

- Land-use changes and global warming are processes facilitating increased bush encroachment at low alpine sites. This is also observed in our study area, as birch trees recruits at a higher rate in the low density sub-enclosures. How does this vegetation succession affect the grazing value of foraging habitats at low sheep density? How may bush encroachment affect the levels of density dependent performance patterns?

Knowledge gained from this study system may have implications for sheep grazing management. These issues require further investigations:

- Could we expect the same density dependent responses in other alpine ecosystems, for example in more nutrient poor areas? Our sheep density levels were calculated based on an evaluation of the vegetation's grazing capacity. This approach, balancing animal density with site-specific plant resources, in addition to monitoring sheep's performance could be an important management tool in order define and sustain sound levels of grazing pressure. Is this method applicable at a scale relevant for management?

General knowledge from this experiment may also be useful in order to predict vegetation and animal responses to a changing climate. Important questions for future studies are:

- Grazing in a future climate – could we expect increased effects of density-climate interactions in summers with more extreme weather events such as drought? Late thawing snow beds with fresh plant material are important for sheep in late grazing season. Global warming predicts reduced snow cover and increased precipitation and temperatures (IPCC). The predicted effect on snow cover is rather dramatic, and an increased mean summer temperature in Scandinavian alpine areas is expected to reduce snow cover considerably. How may reduced access to snow bed vegetation affect the level of density dependence of sheep's performance?

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Appendix 1

Vegetation classification

I here provide a detailed account of the vegetation types in the area that was mapped in 2001 (Rekdal 2001):

Heaths: Dwarf shrub heaths constitute a major component of the enclosure vegetation and is dominated by *Betula nana*, mixed with *Avenella flexuosa*, *Vaccinium myrtillus* and *Empetrum nigrum* and bryophytes. The amount of herbs is generally low, except *Trientalis europaea, Melampýrum* spp. and *Solidago virgaurea* that are all quite common. *Lichen heaths* are typically found on ridges and other places with thin, unstable snow cover and considerable wind abrasion. The dominating feature are lichens, while *Betula nana*, *Empetrum nigrum*, *Loiseluria procumbens, Arctostaphylos uva-ursi, Vaccinium uliginosum, Vaccinium vitis-idaea*, *Arctostaphylos alpinus* and *Juncus trifidus* are frequent in patches or low-growth forms.

Meadows: The most abundant type is the *tall herb meadow*, which is the richest vegetation type in the area, occurring where nutrients and water are steadily available. A dense cover of bushes such as *Salix lapponum* and *Salix glauca* is common, with scattered individuals of *Salix lanata*. Common herbs are *Geranium sylvaticum* and *Aconitum septentrionale*. Graminoids like *Deschampsia caespitosa, A. flexuosa*, *Agrostis capillaris* and *Anthoxanthum odoratum* commonly achieve high coverage. A less common meadow type is the *low herb meadow*. This is a species-rich vegetation type somewhat intermediate between grass snowbed and tall herb meadow. A mixture of graminoids and low-growing herbs dominate. A nutrient poor version typically contains *Carex bigelowii*, *A. flexuosa*, *Viola biflora*, *Taraxacum* spp., *Veronica alpina*, *Ranunculus acris* and *Alchemilla* spp. in addition to snowbed species like *Salix herbacea, Sibbaldia procumbens*, *Bistorta vivipara*, *Alchemilla alpina* and *Oxýria digyna*. *Poa alpina, Anthoxanthum odoratum* and *Agrostis mertensii* are also common. More calcareous versions approach tall herb meadow, and contain more of *Salix reticulata, Thalictrum alpinum, Saxifraga aizoides, Parnassia palustris, Saussurea alpina* or low-growing *Geranium sylvaticum* and *Ranunculus acris*.

Snowbeds: The far most abundant snowbed type is the *grass snowbed*, which thaw out at the end of June or in early July. The soil is poor to moderate in nutrients, and water availability is highly variable over the growing season. The vegetation is dominated by graminoids, mainly *A. flexuosa*. However, *Anthoxanthum odoratum, Salix herbacea* and

Carex bigelowii may also have high coverage. Other common herbs include *Alchemilla alpina*, *Gnaphalium supinum*, *Bistorta vivipara*, *Rumex acetosa* and *Sibbaldia procumbens*. There are also small areas of *moss snowbed* in the study area, characterized by a dominant moss cover that is normally partly covered by snow until July/August. In addition, s*tone polygon land* exists at small patches in the upper reaches of the enclosures. Lichens and ericoids dominate this vegetation type together with *Salix herbacea*.

Marsh: The vegetation type *bog* is poor in species and nutrients and dominated by peat mosses (*Sphagnum* sp.). Among vascular plants there are non-demanding species such as *Calluna vulgaris*, *Empetrum nigrum*, *Betula nana*, *Vaccinium uliginosum*, *Rubus chamaemorus, Eriophorum vaginatum* and *Carex pauciflora*. Another marsh vegetation type is *fen,* dominated by *Carex* spp. and other graminoids and herbs depending on water level and nutrition availability.

Appendix 2. Release and recapture dates, number of grazing days and number of ewes and lambs released into the high- and low density sub-enclosures each season.

Year	Release dates	Recapture dates	Grazing days	High density		Low density		Total
				Nr. of ewes	Nr. of lambs	Nr. of ewes	Nr. of lambs	
2002	24., 29. & 30. June	2., 8., & 11. Sept.	64-79	17	34	7	11	69
2003	26., 27. & 28. June	29. Aug.	62-64	17	34	7	11	69
2004	22. June	1. & 4. Sept.	71 or 74	18	33	6	12	69
2005	28. & 29. June	5. Sept.	68-69	18	33	7	12	70
2006	24. & 25. June	1. Sept.	65-66	17	33	7	11	68
2007	25. June	31. Aug.	64	17	32	6	13	68
2008	25. June	12. Sept.	76	19	34	7	12	72
2009	23. June	3. Sept.	72	17	36	7	13	73
2010	22. June	2. Sept.	72	17	36	6	13	72
Total				157	305	60	108	630

Paper I

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Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach

Ragnhild Mobæk, Atle Mysterud, Leif Egil Loe,
Øystein Holand, Gunnar Austrheim

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Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach

Ragnhild Mobæk, Atle Mysterud, Leif Egil Loe, Øystein Holand and Gunnar Austrheim

R. Mobæk and Ø. Holand, Dept of Animal- and Aquacultural Sciences, Norwegian Univ. of Life Sciences, PO Box 5003, NO–1432 Ås, Norway. – A. Mysterud (atle.mysterud@bio.uio.no) and L. E. Loe, Centre for Ecological and Evolutionary Synthesis (CEES), Dept of Biology, Univ. of Oslo, PO Box 1066 Blindern, NO–0316 Oslo, Norway. – G. Austrheim, Museum of Natural History and Archaeology, Section of Natural History, Norwegian Univ. of Science and Technology, NO–7491 Trondheim, Norway.

Both density dependent and density independent processes such as climate affect population dynamics in large herbivores. Understanding herbivore foraging patterns is essential to identify the underlying mechanisms behind variation in vital rates. However, very little is known about how animals vary their selection of habitat temporally, alone or in interaction with density during summer. At the foraging scale, we tested using a fully replicated experiment whether domestic sheep *Ovis aries* stocked at high (80 per km^2) and low (25 per km^2) densities (spatial contrasts) varied their habitat selection temporally over a four year period. We predicted reduced selection of high productivity vegetation types with increasing density, and that seasonal and annual variation in climate would affect this density dependent selection pattern by increasing competition for high quality habitats in late grazing season and in years with poor vegetation development and over time related to vegetation responses to grazing. As predicted from the Ideal free distribution model, selection of high productivity habitat decreased at high density. There was also a marked temporal variation in habitat selection. Selection of the most productive vegetation types declined towards the end of each grazing season, but increased over years both at low and high sheep density. There was only weak evidence for interactions, as selection ratio of highly productive habitats tended to increase more over years at low density as compared to high density. Limited interactive effects of density and annual variation on habitat selection during summer may explain why similar interactions in vital rates have rarely been reported for summer seasons. Our results are consistent with the view that variation in habitat selection is a central mechanism for climate and density related variation in vital rates.

The dynamics of large herbivore populations are strongly affected by both density dependent and density independent processes such as climate (Gaillard et al. 2000). These factors typically interact, especially during the winter, as climate effects are often more important for dynamics at high population densities when individuals are in poor condition. Competition for food is considered as the main mechanism promoting density dependence (though clearly parasites also may play a role; Fowler 1987), and climate often operates indirectly by altering summer foraging conditions (Mysterud et al. 2001, Stewart et al. 2005). Northern ecosystems typically show considerable annual climatic variation (Loe et al. 2005), and such climate-induced changes in plant growth shape spatial and temporal variation in the distribution of high quality food available for herbivores (Mårell et al. 2006). Climatic conditions in spring, such as snow cover and temperature, determine the onset of plant growth (Langvatn et al. 1996, Pettorelli et al. 2005), whereas temperature, precipitation and cloud cover during summer influence plant phenology and biomass production throughout the growing season (Lenart et al. 2002). High temperatures and a long photosynthetic season are found to increase food quantity (Ericsson et al. 2002), whereas cold and wet summers are associated with high food quality (Bø and Hjeljord 1991, Langvatn et al. 1996). Increasing attention is given to the link between climate, plant phenology and ungulate performance (Mysterud et al. 2001, Pettorelli et al. 2005). There is, nevertheless, little information regarding how climate and density singly or combined affect foraging patterns such as habitat selection (but see Ramp and Coulson 2002), which is necessary to better understand the processes leading to climate and density induced variation in vital rates.

Habitat selection by large herbivores results from different processes operating at multiple spatial scales from landscape to diet choice. At coarse scales, habitat selection relates to dispersal processes, and large herbivores frequently violate the ideal-free-distribution (IFD) (Coulson et al. 1997, Pettorelli et al. 2003). At finer, daily movement scales, animals may select different habitats for purposes of foraging, drinking, resting and escaping from adverse weather conditions (Mysterud et al. 2007), predators

(Lima and Dill 1990) or insects (Mooring et al. 2003). There are studies reporting how habitat selection (Kohlmann and Risenhoover 1997) and diet choice (Choquenot 1991, Daigle et al. 2004, Kausrud et al. 2006, Nicholson et al. 2006) vary as a function of density. As noted by Ramp and Coulson (2002), very little is known about how animals vary their selection of habitat temporally, particularly at the foraging scale.

Using a landscape-scale experimental setup, we tested whether selection of low, medium, or high productivity vegetation types was density dependent and whether or not density-dependence interacted with temporal variation (see overview of hypotheses and predictions in Table 1).

Hypothesis 1. Breadth of habitat selection (H_1)

We predicted stronger selection for more productive habitats at low than at high population density, since at high density, there is expected to be competition for forage and thus also lower productivity habitats will be used, as predicted from the IFD (Fretwell and Lucas 1970).

Hypothesis 2. Seasonality (H_2)

There is gradual reduction in forage quality due to aging of plants towards the end of the grazing season (Hebblewhite et al. 2008). We predicted selectivity for the most productive habitat to decline over the grazing season (H_{2a}). Further, because diet choice in late grazing season was found to be density-dependent in our study system (Kausrud et al. 2006), we predicted that the selection for high productivity habitats towards the end of the grazing season should decline more at high density compared to low density of sheep (H_{2b}).

Hypothesis 3. Annual variation (H_3)

As inter-annual climatic variation influences plant productivity on alpine ranges, we expected to find between-year variation in habitat selection (H_{3a}). Specifically, we predicted that sheep at high density, being more food-limited, would be more affected by years of poor vegetation development than sheep at low density (H_{3b}).

Table 1. An overview of how the hypotheses and their predictions are interpreted in terms of parameters in the generalized linear mixed effects model.

Hypotheses and predictions	Rationale	Parameter of interest	Conclusion
H_1. Breadth of habitat selection	At high population density there is competition for forage leading to increased use of lower productivity vegetation types	Density × HabProd	Supported (Table 2)
H_2. Seasonality			
H_{2a} *Selection of the most productive habitat declines over the season*	Forage quality decreases over the season due to aging of plant material	Date × HabProd	Supported (Table 2, Fig. 3)
H_{2b} *Density dependent selection pattern is more pronounced in late grazing season*	Competition increases towards the end of the grazing season as availability of high-quality forage declines	Date × HabProd × Density	No support (did not enter the best model; Table 3)
H_3. Annual variation			
H_{3a} *Habitat selection varies between years*	Inter-annual variation in climate affects vegetation development and influences habitat selection	Year (as categorical) × HabProd	Weak support as selection differed among years, but monotonous increase indicate that other variables than weather play a role (Table 2, Fig. 4)
H_{3b} *Density dependent selection pattern is more pronounced in years of poor vegetation development*	Warm and dry summer climate affects forage quality negatively, thus increasing competition at high density	Year (as categorical) × HabProd × Density	No support (did not enter the best model; Table 3)
H_4. Longterm trend			
H_{4a} *Temporal trend in selection*	Grazing affects foraging habitats over the time-scale of years	Year (as trend) × HabProd	Supported since selection of meadows increased over years (although the two different models including year as trend and year as categorical have the same AICweights; Table 3, Fig. 4)
H_{4b} *The two densities diverge in their selection of the most productive habitat over years*	Vegetation is more affected by high grazing pressure	Year (as trend) × HabProd × Density	Weak tendency because the model containing this interaction has equivalent support to the simpler model that excludes this interaction term (in terms of AIC values; Table 3)

Hypothesis 4. Long-term trend (H_4)

Lastly, it is increasingly recognised that heavy grazing may affect the habitat over a time-scale of years (Crawley 1997, Mysterud 2006). In our study area, such changes include a gradual increase in graminoids and a decrease in tall herbs selected by sheep at high grazing vs controls (i.e. no grazing by sheep), while vegetation composition at low grazing plots were found to be relatively unaffected after four years (Austrheim et al. 2008). We therefore predicted a temporal trend in selection over years (H_{4a}), and further that this should be most marked at sheep grazing at high density (H_{4b}) if the temporal change was related to plant community composition.

Material and methods

Study area

This study was conducted in Hol municipality, Buskerud county in southern Norway (60°40′N, 7°55′E). The climate is alpine and sub-continental, and the annual precipitation range is 700–800 mm. The bedrock consists of metaarkose, and the soil is moderately base-rich. A large experimental enclosure covering 2.7 km^2 was established in 2001 and grazed by domestic sheep from 2002 onward (Kausrud et al. 2006). The enclosure is mainly situated in the lower alpine zone, with the lowest parts (1050 m a.s.l.) bordering the forest line, and extending upwards to the middle alpine zone (1300 m a.s.l.) (Mysterud et al. 2007). The vegetation is characterized by low shrubs interspersed with grass-dominated meadows, and only a few scattered birch *Betula* sp. trees occur in the lower parts (Rekdal 2001). This alpine environment and vegetation pattern is representative for summer pastures used for sheep grazing in southern Norway. Prior to fencing of the experimental enclosure, the area was subject to a relatively low grazing pressure (<10 sheep per km^2).

Experimental design

To allow block-wise randomised replication, the large enclosure was split into nine sub-enclosures. Average size of each sub-enclosure was 0.3 km^2 (ranging in size from 0.22 to 0.38 km^2 due to practical problems with putting up fences over bare rock; Fig. 1). They were designed to ensure that each of them contain approximately the same altitudinal range and the same distribution of main habitat types used by sheep. For each of three adjacent sub-enclosures, one was randomly assigned as control (no sheep), one as low-density and one as high-density stocking rate area. Based on recommendations provided by a botanical survey and assessment of the vegetation's grazing value for sheep (Rekdal 2001), 25 and 80 sheep per km^2 were used as low and high densities, respectively. These two sheep density levels are typical for Norwegian alpine summer pastures and yield low and moderate grazing pressure on the plants (Evju et al. 2006), and measurable lower growth rates of lambs at high compared to low density (Mysterud and Austrheim 2005). For further details on calculation of sheep densities for this particular experiment, see Kausrud et al. (2006). In total, 24 or 25 ewes and 44 or 45 lambs belonging to the same sheep farmer were released each grazing season. Each of the ewes carried 1–3 lambs. Ewes with singletons, twins and triplets were distributed evenly to the different sub-enclosures to assure that reproductive status of the ewes was on average the same for the two density levels over time. All sheep were of the breed 'Norsk Kvit Sau' (often referred to as the 'Dala' breed), which is the most common breed among Norwegian sheep farmers. This is a relatively large breed; ewes' live weight averaged 87 kg in spring and for lambs the live weight averaged 20 kg in spring and 40 kg in autumn (Mysterud et al. 2007).

Data collection

Direct observations (n = 3077) of the individually marked ewes and their lambs were done from a distance of 20–50 m

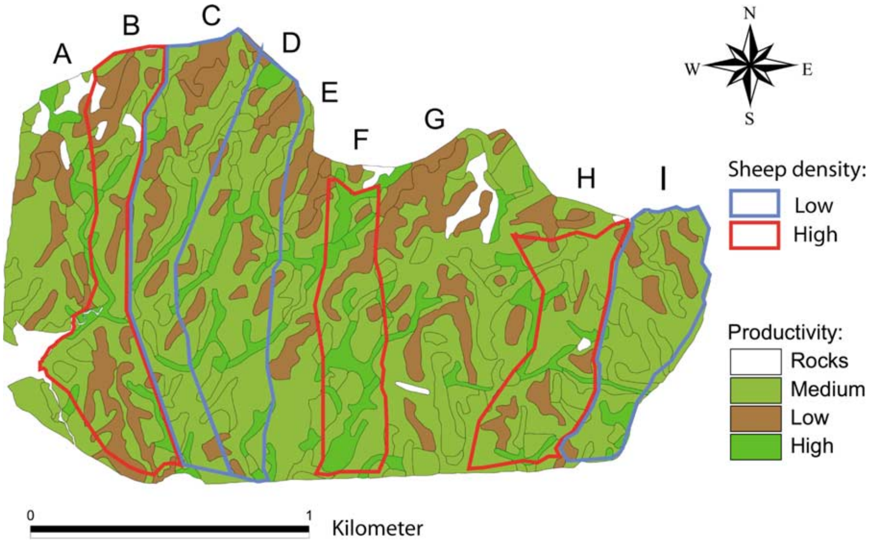

Figure 1. Map showing the distribution of vegetation of the three productivity levels (high, medium and low) as well as bare rocks (excluded from analyses) in all sub-enclosures (A–I) for the experiment in Hol, Norway.

using binoculars over the entire grazing season for four consecutive summers (2003–2006). In year 2003, sheep location and behaviour was recorded from 30 June to 24 August (798 observations from 24 ewe–lamb groups), in 2004 from 28 June to 30 August (718 observations), in 2005 from 5 July to 30 August (861 observations) and in 2006 from 25 June to 24 August (700 observations). For this breed with limited grouping behaviour, the family group (i.e. an individual ewe and her lambs), is considered to be the stable social unit and was thus defined as the sampling unit (Kausrud et al. 2006). To allow individual recognition from a distance, all animals were equipped with colour coded neck bands in addition to the individually numbered plastic ear tags. Observation of sheep behaviour was done using two working cycles distributed randomly throughout the season; one early from 9:00 to 17:00 and one late from 14:00 to 22:00. Each day the observer first randomly selected which part of the enclosure (eastern or western) to cover, then in which sub-enclosure to start observing and finally whether to start locating the animals from the bottom or the top of that particular sub-enclosure. All ewes within a sub-enclosure were observed before repeating this selection procedure and moving to the next sub-enclosure. As there were fewer ewes in the low density sub-enclosures, these individuals were recorded twice as frequent to avoid too unbalanced samples with respect to the number of observations within each density level. Sheep behaviour was assessed as inactive (resting/ruminating) or active (grazing) behaviour. As soon as the sheep's identity was confirmed and behaviour was recorded, the observer approached the point where each focal animal was spotted and mapped its exact location by using a handheld GPS. Lastly, the vegetation type was recorded (below).

Habitat productivity classification and plant development

The distribution of vegetation types in the experimental area was mapped in 2001 (Rekdal 2001). As we had clear predictions (Table 1) relating habitat to their productivity (rather than to habitat per se), and since the productivity of the vegetation types was known (Rekdal 2001), we classified the nine vegetation types into three classes (Fig. 1):

- high productivity: tall herb meadow, low herb meadow
- medium productivity*:* grass snowbed, dwarf shrub heath
- low productivity: moss snowbed, lichen heath, bog, fen, stone polygon land

Analysis of selection requires that all habitat types are available. This categorization avoids issues that arise when a particular vegetation type does not occur in all sub-enclosures, or when some vegetation types were recorded as used, but not available, because vegetation mapping was conducted on a coarser scale (raster, resolution of 2 ha; Rekdal 2001) than activity observations (points).

As an index of annual variation in plant development, we used data on plant height of three herb species measured at fixed plots within the study area (Evju et al. 2006, Austrheim unpubl.). We only used data from the controls, so that sheep grazing would not affect estimates.

Statistical analyses

Resource selection functions

The sub-enclosures represent the sheep's summer home range, and our habitat selection corresponds to a type III design (Thomas and Taylor 1990) with repeated observations of known individuals but where availability differs among individuals (they are in different sub-enclosures). To quantify the availability of each habitat we made a raster map (each pixel corresponding to 10 m^2) from the habitat productivity vector map. Pixels containing bare rock and pixels that had not been classified were discarded (one pond in one enclosure only). Availability was quantified by counting the number of pixels in each productivity class ($1 =$low, $2 =$medium and $3 =$high) per sub-enclosure and thereafter calculating the proportion of each class. Habitat use was recorded in the field and later grouped into the three productivity classes as described above. The function widesIII in the R package adehabitat was used to analyse habitat selection (Calenge 2006). We divided the used data into 16 subsets consisting of all combinations of year (2003–2006), activity (active/inactive) and sheep density (high/low). Availability was always the same for a specific individual, i.e. the proportion of each productivity class in the respective sub-enclosures. For each of the 16 subsets we fitted a resource selection function (RSF) providing the selection of each of the three habitat productivity classes with associated confidence limits (Manly et al. 2002). The process of fitting data to RSF's yielded Resource selection ratios (Fig. 2), which is the ratio of the proportion used habitats to the proportion available habitats. If use is proportional to availability (random use), the selection ratio is ~ 1. When use is greater than availability the ratio is >1 and implies selection; a ratio <1 implies avoidance (sensu Thomas and Taylor 1990).

Generalized linear mixed-effects models

Randomised block designs are suitable for a priori implementation of random effects (Experimental design) and generalized linear mixed-effects models (GLMM; Woods 2006) are highly suitable for multivariate analyses of habitat selection (Gillies et al. 2006, Godvik et al. 2009). GLMMs were fitted to address how habitat selection varies with habitat productivity, density, date and years (trend and categorical), with a focus on selected interactions such as habitat productivity interacting with the other factors (Table 1). In this second part of the analysis we only included data when sheep were actively feeding and discarded the data when sheep were inactive. Based on preliminary analyses, low and medium productivity habitat was grouped into a new 'low' group while retaining the high productivity class (i.e. reducing from three to two productivity classes to simplify the model). The binomially distributed response variable consists of use (given a value of 1) and availability (0) of map pixels. From the field observations we know which map pixels are used by sheep. Available map pixels are represented by a random selection of all map pixels within the relevant sub-enclosure (Manly et al. 2002). To increase precision in

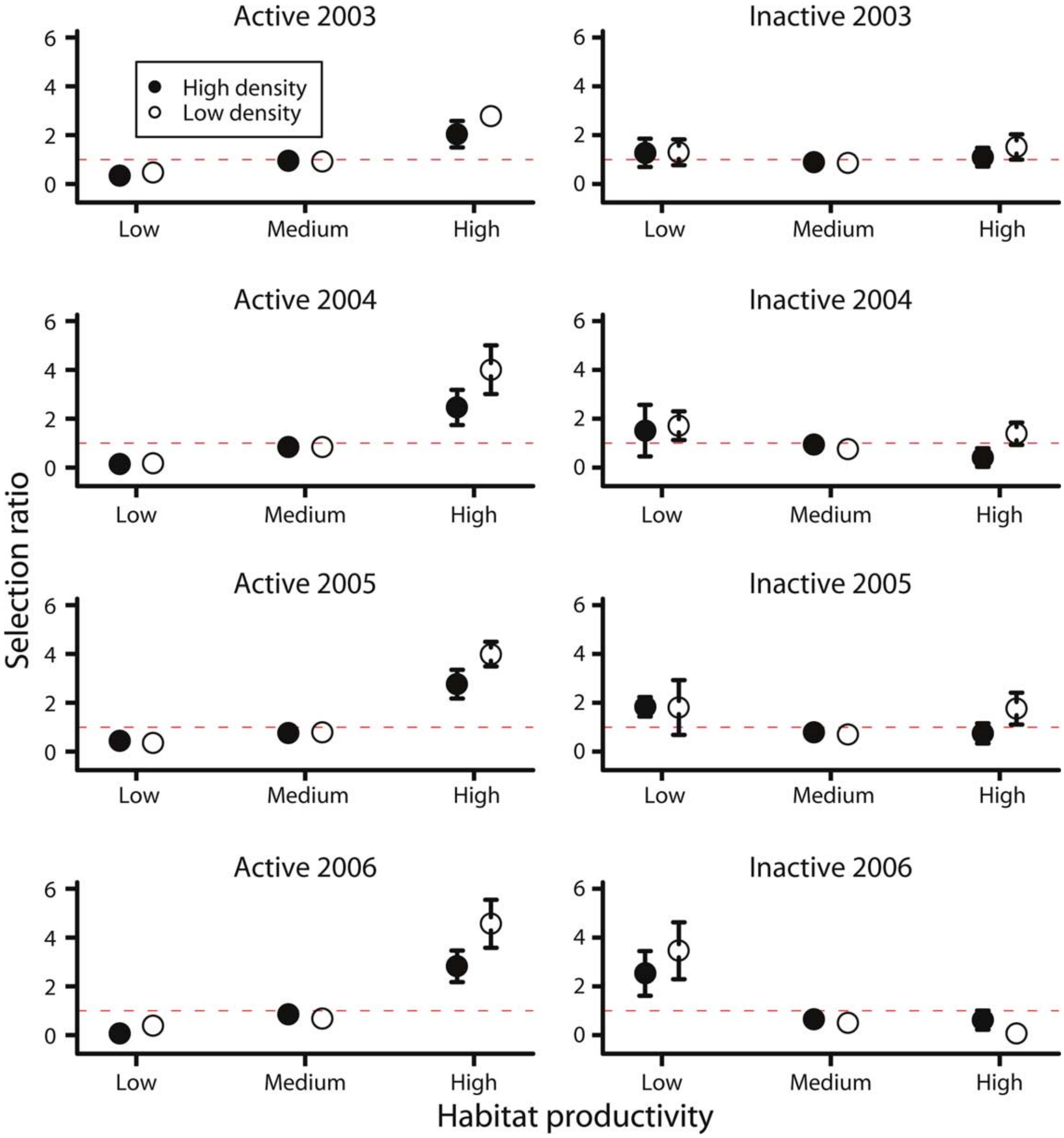

Figure 2. Selection of habitats varying in productivity over four summer grazing seasons by active and inactive sheep at high and low population density. Estimates above 1 indicate selection and estimates below 1 indicate avoidance. If the confidence interval does not overlap zero the relationship is significant.

estimates of habitat availability, we selected 20 times as many random locations as used locations for each individual and year. To account for variation in habitat use among enclosures and for repeated observations of individuals we fitted 'individual' nested within 'sub-enclosure' as random intercepts. All models were fitted using maximum likelihood (ML) estimation using the function lmer in the R library lme4. To estimate confidence limits of parameter estimates (Table 2), we computed Bayesian highest probability density (HPD) intervals using Markov chain Monte Carlo simulations in the R library coda as this is favoured over normal confidence limits for GLMMs (Bates 2006). We fitted a suite of models starting with the most complex but still biologically reasonable model as well as all simpler combinations of the full model. Thereafter their AIC values and calculated AICweights were compared (Table 3).

Selection and avoidance of habitat types are identified differently in GLMMs compared to the classical RSF approach (above). 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. Since it is not known which map pixels are truly unused (it is a random selection of available sites), the absolute values of log odds are meaningless (Keating and Cherry 2004). However, log odds ratios are sensible and the model output makes it easy to directly interpret odds ratios. For example, the odds ratio of using high productivity compared to low productivity habitat is 2.65 (exponent of 0.975; Table 2), i.e. use of high productivity habitat is 2.65 times as frequent as low

Table 2. A generalised linear mixed-effects model of sheep habitat use when actively grazing with three replicates of high and low density on alpine range over four years in Norway. The presented model is one of the three most parsimonious models with equivalent AIC values (Table 3). The response variable 'use' is a binomial variable (used = 1, available = 0). Density is fitted as a factor variable (high/low). The reference level for the density effect is 'high'. Year is fitted as a factor variable (years 2003–2006) with year '2003' as the reference level. Habitat productivity is fitted as a binomial variable (1 = high; 0 = low and medium productivity). Date is Julian date (standardized).

Fixed effects	Estimate	95% HPD-interval	z	p
Intercept	−3.22	−3.57, −2.88	−28.044	<0.001
Habitat productivity (high–low)	0.975	0.768, 1.20	8.747	<0.001
Year (2004 vs 2003)	−0.176	−0.334, −0.0190	−2.163	0.031
Year (2005 vs 2003)	−0.185	−0.343, −0.0333	−2.343	0.019
Year (2006 vs 2003)	−0.224	−0.396, −0.0700	−2.691	0.007
Density (low–high)	0.0533	−0.423, 0.547	0.352	0.725
Date	0.0488	−0.0122, 0.105	1.636	0.102
Hab. prod. × Year (2004 vs 2003)	0.552	0.280, 0.819	3.889	<0.001
Hab. prod. × Year (2005 vs 2003)	0.592	0.326, 0.864	4.223	<0.001
Hab. prod. × Year (2006 vs 2003)	0.632	0.357, 0.914	4.423	<0.001
Hab. prod. × Density (low–high)	0.274	0.0745, 0.492	2.589	0.010
Hab. prod. × Date	−0.133	−0.230, −0.0304	−2.653	0.008
Random effects				
Groups	Name	95% HPD-interval	SD	
ID:Sub-enclosure	Intercept	−20.1, −9.27	0.0000224	
Sub-enclosure	Intercept	−4.38, −1.10	0.170	

No. of observations: 40533, groups: ID: Sub-enclosure, 97; Sub-enclosure, 6.

productivity habitat in the reference categories (year 2003, at high density and at the mean date). If the estimate is positive and the interval does not overlap 0 there is positive selection. Conversely, a negative estimate not overlapping zero identifies avoidance. When illustrating log odds ratios (as in Fig. 3) a reference point is selected with value 0 and no variance (in Fig. 3 it is the first date category and low productivity habitat). Log odds ratios of all other combinations of predictor variables were calculated relative to log odds of use of this reference category. Interval estimates for fitted odds ratios were based on 10 000 mcmc samples from the posterior distribution of the parameters and random effects (Godvik et al. 2009).

Importing shape files (function readOGR), selection of random points (function csr) and matching of points (function join.asc) with the habitat productivity map were done by using the R packages rgdal, splancs and adehabitat, respectively.

Results

Sheep habitat selection differed depending on activity. When active, sheep selected the high productivity and avoided the low productivity habitats (Fig. 2, Table 2). When resting, they selected habitats close to what was expected based on availability, with a small selection for low productivity habitats (Fig. 2). This activity dependent selection was fairly consistent in all years (Fig. 2). The medium productivity habitats were neither selected nor avoided (Fig. 2).

When they were active, sheep at low density had a higher selectivity for the high productivity habitats compared to sheep at high density (Fig. 2; the interaction Hab. prod. × Density in Table 2; consistent in all years), as predicted from H_1. Further, selection of high productivity habitat decreased towards the end of each grazing seasons in accordance with H_{2a} (Fig. 3; the interaction Hab.

Table 3. A priori generalized linear mixed-effects models for habitat use in sheep. Only fixed effects are presented. Random effects were always individual nested within sub-enclosure (Material and methods). Models are ranked in descending order after AIC value (i.e. the most parsimonious models are presented first). Models with AIC weight <0.005 are not displayed. Date and year were standardized prior to analysis.

Model	AIC	ΔAIC	AICweight
Use ~ Hab. prod. + as.factor(Year) + Density + Date + Hab. prod. × as.factor(Year) + Hab. prod. × Density + Hab. prod. × Date	14924	0	0.202
Use ~ Hab. prod. + Year + Density + Date + Hab. prod. × Year + Hab. prod. × Density + Hab. prod. × Date	14924	0	0.202
Use ~ Hab. prod. + Year + Density + Date + Hab. prod. × Year + Hab. prod. × Density + Hab. prod. × Date + Year × Hab. prod. × Density	14924	0	0.202
Use ~ Hab. prod. + Year + Density + Date + Hab. prod. × Year + Hab. prod. × Density + Hab. prod. × Date + Date × Hab. prod. × Density	14925	1	0.123
Use ~ Hab. prod. + Year + Density + Date + Hab. prod. × Year + Hab. prod. × Density + Hab. prod. × Date + Hab. prod. × Year × Date + Hab. prod. × Year × Density	14926	2	0.074
Use ~ Hab. prod. + Year + Density + Date + Hab. prod. × Year + Hab. prod. × Density + Hab. prod. × Date + Hab. prod. × Year × Date	14926	2	0.074
Use ~ Hab. prod. + Year + Density + Date + Hab. prod. × Year + Hab. prod. × Density	14927	3	0.045
Use ~ Hab. prod. + Year + Density + Date + Hab. prod. × Year + Hab. prod. × Date	14928	4	0.027
Use ~ Hab. prod. + as.factor(Year) + Density + Date + Hab. prod. × as.factor(Year) + Hab. prod. × Density + Hab. prod. × Date + as.factor(Year) × Hab. prod. × Density	14928	4	0.027
Use ~ Hab. prod. × Year + Density	14929	5	0.017
Use ~ Hab. prod. + Year + Density + Date + Hab. prod. × Year	14931	7	0.006

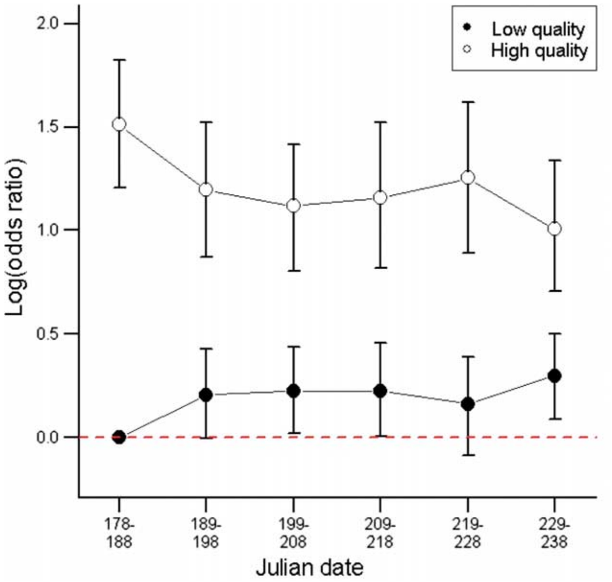

Figure 3. Seasonal changes in selection of habitats with high and low productivity by active sheep in Hol, Norway. The predicted log odds ratios are derived from the generalized mixed-effects model presented in Table 2, except that Julian date is binned in 10-day groups. All log odds ratios are compared to the start of the grazing season (Julian date 178–188) in low productivity habitat (see Material and methods for interpretation of log odds ratios).

prod. × Date; Table 2). However, in contrast to H_{2b}, the lower selectivity for high productivity habitat in late season was not affected by sheep density (the model including the 3-order interaction Hab. prod. × Date × Density is the 4th most parsimonious model with AICweights = 0.123; Table 3).

Selection for high productivity habitats differed significantly between years, with selection of high productivity habitat increasing monotonically but non-linearly over years (Fig. 4; the interactions Hab. prod. × Year in Table 2). This was mainly a difference between the first year (2003) and the other years (2004–2006). The monotonic trend does not provide strong support for H_{3a}, which predicted a more erratic variation among years. There was no close relationship between annual variation in selection of high productivity habitat and plant development (Fig. 4). Further, there was no interaction between sheep density and between-year variation in habitat selection, thus rejecting H_{3b} (the model including the 3-order interaction Hab. prod. × Year (as categorical) × Density is the 9th most parsimonious model with AICweights = 0.027; Table 3). There was, however, a tendency for an increasing difference in selection of high productivity habitat between the two densities over years, as expected in H_{4b} (Fig. 4; the model including the 3-order interaction Hab. prod. × Year (as trend) × Density is among the three best models with equivalent AIC values; Table 3). There was no effect of litter size on habitat selection, as the model including litter size and interaction with Hab. prod. was less parsimonious (ΔAIC = 4).

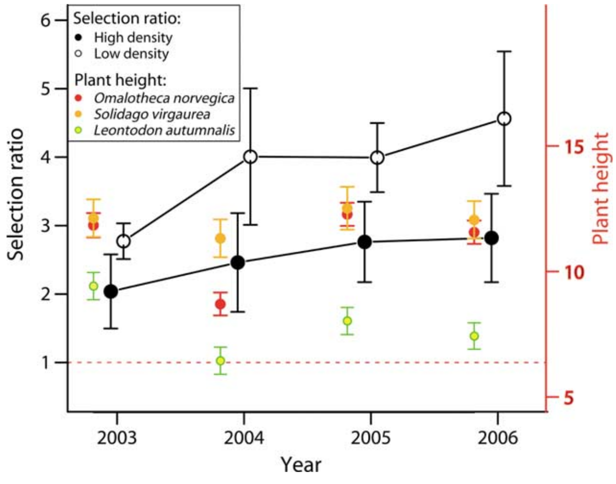

Figure 4. Selection of high productivity habitat in different years for active sheep at high and low density in alpine habitat in Hol, Norway. Selection ratio is defined as the ratio of the proportion used to the proportion available. Estimates above 1 indicate selection. Annual variation in plant development is indicated by plant height (in cm) of three herb species.

Discussion

Herbivores alter their foraging behaviour rapidly in response to variations in the foraging environment. Knowledge of how population density and temporal variation in the environment influences foraging behaviour of large herbivores is key to understanding variation in vital rates and population dynamics. We found that habitat selection in sheep was density dependent. Though habitat selection changed both within the grazing season and over years, there was only a weak indication that this interacted with the density effect.

Density dependent habitat selection

The ideal free distribution theory (Fretwell and Lucas 1970) predicts that animals should distribute themselves relative to the profitability of habitat patches, a process that results in a more even use of foraging habitats when population density increases (i.e. via the inclusion of habitats with lower quality). In support of this, we found that sheep had a more even use of habitat types at high density, while sheep at low density had a stronger selection for the most productive habitat types. At the smaller foraging scale, there are examples that ungulates increase their use of low quality habitats at higher population densities in accordance with the IFD (red deer *Cervus elaphus*; Clutton-Brock et al. 1987, grey kangaroo *Macropus giganteus*; Ramp and Coulson 2002). Our study is the first to document explicitly that this result depends on activity, as is implicit in the IFD (Fretwell and Lucas 1970). Although selection of foraging habitat varied temporally, the density dependent foraging pattern was maintained both over the seasons and the years. In contrast, when sheep were resting they showed higher selection of low productivity habitat (dry with short vegetation, suitable for resting) and lower between-year variation in selection of resting habitat.

Plant development and temporal variation in habitat selection

Climate, density and their interactive effects during winter are assumed to be critical in population limitation and regulation (reviewed by Gaillard et al. 2000). Therefore, for winter seasons, variation in habitat selection has been much studied related to severe climatic effects such as snow depth, low temperature and wind (Armleder et al. 1994, Mysterud et al. 1997). Much less is known about how annual and seasonal variation in summer weather affects habitat selection, apart from at the very coarse migration scale (Albon and Langvatn 1992). In temperate and alpine/arctic regions, conditions during spring and summer are important for body growth (Hjeljord and Histøl 1999, Stewart et al. 2005). Both seasonal variation due to plant senescence and annual variation due to prevailing weather conditions are likely to affect habitat selection if these factors do not operate at the same rate in the different habitat types. Consistent with such a view, we found that the overall selection of the most productive vegetation types decreased towards the end of each grazing season. As the plants grow old, carbohydrates and lignin increase and the protein concentration declines, thereby reducing digestibility and nutritive value (Hebblewhite et al. 2008). This is particularly applicable to grasses. Apparently, the less productive vegetation types, including late thawing grass snowbeds with fresh plants later in the season, became more important towards autumn as the meadow vegetation deteriorated.

Habitat selection can similarly be predicted to vary between years due to annual variation in climate affecting plant development (Bø and Hjeljord 1991, Bowyer et al. 1998, Lenart et al. 2002). Assuming that warm and dry summer weather would speed up plant phenology and thereby increase competition for high-quality forage earlier in the season, we expected the density dependent selection pattern to be more pronounced in years with a warm and dry summer climate than during a cold and wet summer. Although the main finding was that selection of high productivity habitat increased monotonically over years, the trend over time was not linear. While habitat selection did not show a clear relationship to annual variation in plant development (Fig. 4), we cannot fully exclude some role of between-year weather variation in forming the selection pattern observed.

Limited interaction of density and temporal variation

When testing the IFD, it is usually assumed that habitats are stable over time, while in reality vegetation structure, biomass and quality may also change in the long term due to grazing effects (Crawley 1997, Olofsson 2006) or other factors such as successional processes due to relaxation of other land uses common in outlying pastures in Norway. However, effects of time scale on density dependent habitat selection are poorly investigated (but see Ramp and Coulson 2002). We predicted interactions between density and the temporal variation assumed to reflect similar variation in vegetation development. This prediction derived from the observations that vegetation development was variable over the grazing season and between years (Evju et al. 2006), and that growth of lambs was density dependent indicating resource limitation at high density (Mysterud and Austrheim 2005). We nevertheless found that the pattern of density-dependent habitat selection was fairly consistent over the seasons and years.

At a seasonal level, intake of the bulk food (*D. flexuosa*) increased markedly in the last half of the season for sheep at high density, while it remained constant throughout the grazing season at low density (Kausrud et al. 2006). Moreover, the intake of high quality herbs declined at a faster rate in late season at high density than at low density (Mysterud and Austrheim 2005). Our result suggests that these dietary changes do not involve a similar shift in habitat selection between high and low density as the season progresses. Indeed, the medium quality *D. flexuosa* (Mysterud and Austrheim 2005) is a highly abundant grass, occurring in all the vegetation types within our medium and high productivity habitat categories (Rekdal 2001). The dietary shift in late season may instead reflect a decrease in biomass of highly selected herbs within vegetation types not involving a density dependent shift in vegetation type selection. Similarly, density did not affect inter-annual variation in habitat selection significantly, as we found limited support for our prediction that sheep at high density are more constrained by unfavourable climatic conditions in their selection of foraging habitat.

Typically, discussions of density dependent effects in large herbivore populations ignore or do not explicitly address the interactive effects of herbivores and habitat (but see Simard et al. 2008). By feeding selectively, herbivores affect plant species composition and regulate plant standing crops (Jefferies et al. 1994), which over time can change the quality of a given habitat. Increasing herbivore densities may impact primary production negatively or positively, depending on the plant's ability to resist herbivory or to replace lost tissue by compensatory growth (McNaughton 1983). The steady increase in use of the high productivity habitat (meadows) over the four years, as found in our study, is at least indicative of grazing facilitation (Arsenault and Owen-Smith 2002); i.e. increased quality and/or quantity of forage as an effect of grazing. Indeed, grazing is found to decrease carbon/nitrogen ratios in plants in productive habitats (Harrison and Bardgett 2008), and C:N ratios for herbs were found to be significantly lower at high densities as compared to controls with no grazing in our study (Austrheim unpubl.). In contrast, the increase of graminoids on behalf of highly selected herbs indicates a decrease in forage quality at high grazing which was not evident at low grazing as compared to controls (Austrheim et al. 2008). Moreover, the reduction in plant biomass (i.e. plant height) was significantly higher for several herbs at high densities of sheep as compared to low densities (Evju et al. 2006). Thus, several mechanisms for grazing facilitation are possible in our experimental system, but as argued above the resulting effects of these mechanisms could be density dependent. Coincidently, there was a (non-significant) tendency for a stronger increase in selection ratio of high productivity habitat over time at low density as compared to high density of sheep. However weak, this tendency might imply that the consistent density dependent selection pattern observed is not stable over time and may respond to changes in the foraging habitats.

Conclusion

Our study provides new insight into how population density affects herbivore habitat selection at summer ranges, and how foraging patterns vary temporally. Identifying how climatic variation and density in concert affect selection of foraging habitat can contribute to explaining the climate and density dependent variation in vital rates. We found limited support that it was the interactions between density and annual variation related to plant development that determined sheep's selection of vegetation types during summer. Our results are therefore consistent with the literature reporting effects of population density and annual variation on vital rates, but rarely interactions, during the summer season. We suggest that variation in habitat selection related to plant development during summer is a central mechanism for reported patterns of variation in vital rates in large herbivores.

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Paper II

Age, density and temporal effects on diet composition of sheep on alpine ranges: 6 years of experimental data

Ragnhild Mobæk, Atle Mysterud, Øystein Holand, Gunnar Austrheim

Manuscript

Age, density and temporal effects on diet composition of a large alpine ungulate: 6 years of experimental data

Ragnhild Mobæk[1], Atle Mysterud[2*], Øystein Holand[1] and Gunnar Austrheim[3]

[1]Department of Animal and Aquacultural Sciences, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway.

[2]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway.

[3]Museum of Natural History and Archaeology, Section of Natural History, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway.

[*] Corresponding author: Atle Mysterud (atle.mysterud@bio.uio.no)

Running headline: *Ungulate diet composition*

Summary

1. Understanding diet selection in large herbivores is important since diet determines energy intake and therefore growth of large herbivore populations. Yet very few studies have reported annual variation in diet. Density-dependent diet choice by large herbivores has been reported several times, but these studies are typically either short-term or with no replication of the density treatment.

2. In a landscape-scale experiment with 3 replicates of two densities (25 and 80 per km^2) of domestic sheep, we determined diet composition using microhistological analysis during 6 summer grazing seasons (2002-2007) in alpine habitats. We tested how age, density and temporal variation (within season, annually, and over years) affected summer diet.

3. There was marked evidence of additive effects of these factors on overall diet composition, but interactions were few. The interaction between density and annual variation was an important determinant of the proportion of the main dietary component; *A. flexuosa*, and there was some evidence for such interaction also for herbs and for "other" dietary plants. Surprisingly, the density effect on this intermediate quality forage (*A. flexuosa*) was not consistent among years (both positive, negative and no effects). This was due to the fact that the proportion of *A. flexuosa* depended on the density dependent response in the proportion of the other dietary plants that also varied between years.

4. The overall pattern of strong effect of density and annual variation in diet composition is consistent with predictions from variation observed in body growth of lambs. We discuss how foraging ecology supplement the insight from life history theory in explaining variation in vital rates.

Key-words: climate effects, density dependence, foraging, life history, large mammals, seasonality, ungulates

Introduction

Life history theory and the incorporation of interactions between age, density and climate in vital rates has successfully enabled prediction of population dynamics of large herbivores (Coulson et al. 2001). Some of this variation clearly results from how mothers allocate resources to self maintenance rather than to offspring survival (Gaillard & Yoccoz 2003; Martin & Festa-Bianchet 2010). Less attention has been paid to understand foraging behaviour as one potential proximate mechanism behind density and climate generated variations in demography and population dynamics (but see Simard *et al.* 2008 for a notable exception). Diet choice is particularly important with its direct link to energy intake and therefore individual growth (White 1983). It likely may explain some of the large individual variation seen in ungulate populations (Hamel *et al.* 2009). However, obtaining data at the scale of herbivore diet choice is considered particularly challenging. Though numerous methods are available such as rumen or microhistological analysis of faeces (Holechek, Vavra & Pieper 1982), they are often costly to apply. Compared to the vast literature on habitat selection at coarser scales using either VHF or GPS collar technology (e.g. Hebblewhite & Haydon 2010), the knowledge of variation in diet selection at the plant species or group level is typically from very short-term studies. Therefore, very few studies have addressed possible variation in diet due to age, climate, population density and their interactions despite that this is a core team in population ecology (Gaillard et al. 2000).

Spatial and temporal scaling play a key role in foraging studies (Senft et al. 1987; Wiens 1989). Empirical studies can be organized from landscape (coarse scale) to habitat and patch selection (intermediate scale) and diet selection (fine scale) (Johnson 1980), and similarly from short-term (hours to daily), intermediate (annual) or long-term scale (trends over years). Density-dependent diet choice has been reported for several large herbivore species; in grey kangaroo *Macropus giganteus* (Ramp & Coulson 2002), feral donkey *Equus* *asinus* (Freeland & Choquenot 1990), white-tailed deer *Odocoileus virginianus* (Daigle et al. 2004), mule deer *Odocoileus hemionus* (Nicholson, Bowyer & Kie 2006), and domestic sheep *Ovis aries* (Kausrud et al. 2006). Either these studies have no replication of the density treatment (Freeland & Choquenot 1990; Daigle et al. 2004) or they are short-term (1 year; Kausrud et al. 2006), and they do not consider that the density effect may interact with climatic conditions. Climate induced annual variation in plant growth and phenology is a common phenomenon in northern ecosystems (Loe et al. 2005), and we therefore expect large annual variation in diet possibly interacting with the density effect.

In this landscape-scale experiment, we analysed diet of domestic sheep (ewes and lambs) kept at two densities (replicated 3 times) in alpine habitats during 6 consecutive grazing seasons (2002-2007). In this experiment, body growth of lambs was markedly density dependent, and the strength of the density effect varied annually (Mysterud & Austrheim 2005). We tested the following predictions regarding how age, climate and density, additively or interactively, affect summer diet:

H1. Diet breadth and composition.

Due to the intraspecific competition for forage and observed lower body growth rate at high density, we predicted that sheep at high density would have a broader diet composition with less herbs (i.e. high-quality forage) and more graminoid and woody species (i.e. lower quality forage) than sheep at low density.

H2. Seasonal variation.

As high-quality herbs are the most preferred forage by sheep (Bowns & Bagley 1986) and due to the gradual deterioration of high-quality plant material within season (Fryxell, Greever & Sinclair 1988; Hebblewhite, Merrill & McDermid 2008), we predicted herbs to be replaced by graminoids towards the end of the grazing seasons (H_{2a}). We further expected that the density-dependent diet choice would be stronger towards the end of grazing season, expressed by a lower intake of herbs and higher intake of graminoids in late season by sheep at high density when compared to low density (date x density interaction) (H_{2b}).

H3. Annual variation.

Since between-year variation in climate affects primary production in alpine habitats (Mårell, Hofgaard & Danell 2006) and the observed annual variation in body growth rate, we expected sheep diet to vary among years (H_{3a}). We also predicted a stronger density-dependence in years with poor vegetation development and the observed variation in strength of density dependence between years; we expected that sheep at high density would consume less herbs and more graminoids than sheep at low density (year x density interaction) (H_{3b}) in some years. We also tested for trends over years.

H4. Age.

As nutritional requirements vary as a function of metabolic body mass in ruminants, we predicted that lambs, with their smaller body size and hence higher nutritional requirements (Demment & Van Soest 1985), would have a diet of higher quality, i.e. including more herbs and less graminoids than ewes. We also explore interactions between the above factors.

Materials and methods

Study area

This study was conducted in Hol municipality, Buskerud county in southern Norway (60º40´N, 7 º55´E). The study area has alpine and sub-continental climate, and the annual precipitation ranges from 7-800 mm (Førland 1993). The bedrock consists of metaarkose (Sigmond 1998), and the soil is moderately base-rich. In 2001, a large experimental enclosure covering 2.7 km^2 was established and grazed by domestic sheep from 2002 (Kausrud et al.

2006). The enclosure is mainly situated in the lower alpine zone, with the lowest parts (1050 m a.s.l.) adjoining the forest line, and continuing upwards to the middle alpine zone (1300 m a.s.l.) (Mysterud, Iversen & Austrheim 2007). The vegetation is mostly composed of low shrubs interspersed with grass-dominated meadows, and only a few birch (*Betula sp.*) trees are found in the lower parts of the enclosure though birch recruit at higher altitudes when fenced (Speed et al. 2010). This alpine terrain and vegetation pattern is typical for summer pastures grazed by sheep in southern Norway.

Dwarf shrub heath is the dominating vegetation type, covering 51 % of the enclosure (Rekdal 2001). In terms of biomass, woody species, such as *Betula nana, Empetrum nigrum* and *Vaccinium myrtillus* constitute 85 % of this plant community, while graminoids add up to 6 % and bryophytes and lichens to 8 %. The amount of herbs is generally low (1 %). Tall herb meadow and low herb meadow, the vegetation types with the highest grazing values for sheep (Mobæk et al. 2009), comprise 9 % of the total vegetation cover. Graminoids dominate the meadow vegetation (47 % of the biomass), with *Carex bigelowii*, *Avenella flexuosa* and *Deschampsia caespitosa* as the most common species. Dense cover of bushes like *Salix lapponum* and *Salix glauca* are frequent in the tall herb meadows, while low herb meadows are characterized by a mixture of graminoids and low-growing herbs (Rekdal 2001). Woody and herb species make up 31 % and 12 % of the biomass in meadow vegetation, respectively, while bryophytes and lichens amount to 9 %. In general vascular plant richness is high in the study area, with herbs constituting 53 % of all vascular plant species (Austrheim, Evju & Mysterud, 2005). Before fencing of the experimental enclosure, there was a relatively low grazing pressure by domestic sheep in the area (< 10 sheep per km^2), and only sporadic visits by moose (*Alces alces*) and individual or small herds of wild reindeer (*Rangifer tarandus*).

Experimental design

The large experimental enclosure was split into nine sub-enclosures to allow a block-wise randomised replication with 3 replicates (Austrheim et al. 2008). Each of the sub-enclosures averaged 0.3 km^2 (the actual sizes are ranging from 0.22 to 0.38 km^2 due to practical problems when putting up fences over bare rock), and they were designed to ensure that each of them enclose roughly the same altitudinal span and the same distribution of main vegetation types used by sheep. For each of three neighbouring sub-enclosures, one was randomly assigned as control (no sheep), one as low-density and one as high-density sub-enclosure. A botanical examination and estimation of the vegetation types' grazing value for sheep was conducted in 2001 (Rekdal 2001), and based on recommendations provided here, 25 sheep per km^2 and 80 sheep per km^2 were chosen as low and high densities, respectively. These sheep density levels are typical for alpine summer pastures in southern Norway, and correspond to low and moderate grazing pressure as measured by grazing frequency of the most important forage plants in our study area (Evju et al. 2006).

Each grazing season, 24 or 25 lactating ewes and 44 or 45 lambs belonging to the same sheep farmer were released into the enclosure. The actual number of sheep in each sub-enclosure ranged from 2-3 ewes with lambs (low density) to 5-6 ewes with lambs (high density). Ewes with one, two or three lambs were distributed evenly between the high and low density treatment sub-enclosures. To allow individual recognition, both ewes and lambs were marked with colour coded neck bands in addition to the individually numbered plastic ear tags. All sheep were of the breed "Norsk Kvit Sau" (also known as the "Dala" breed), which is a heavy and the most common breed among Norwegian sheep farmers (Drabløs 1997). Ewes weighed on average 81 kg when they were released into the sub-enclosures, and lambs weighed on average 20 kg when released and 42 kg when recaptured in autumn (Mysterud & Austrheim 2005). A grazing season typically lasted from late June to late August (see Table

A1 in the online supporting information for details), which is the representative length of summer grazing seasons for sheep on alpine pastures in southern Norway.

Data collection

Individual sheep were followed during the entire summer grazing seasons from 2002 to 2007. Direct observations of defecating ewes and lambs were obtained from a distance of 20-50 m using binoculars (see Mobæk et al. 2009 for details on sampling times). Faeces samples were collected from known individuals only, and a careful sampling procedure ensured equal representation of densities (high vs. low), ages (ewe vs. lamb) (Table A1 in the electronic appendix) and 3 time periods (early, middle and late grazing season). All faeces samples were put in plastic bags and frozen, and later a stratified assortment (consisting of 441 samples from 236 individual sheep) of the total sampled material was selected for analyses of diet. Microhistological analyses (Stewart & Stewart 1970; Cortés *et al.* 2003; Takatsuki 2003) were performed following a standard procedure (boiling 1 ml of faeces in 4 mm of nitric acid). Each faeces sample was split into two parallel sub-samples that were processed independently. The mean number of faeces samples analyzed per individual sheep was 1.88 (±1.35 SD). Plant fragments were identified to species whenever possible, otherwise family names were determined. Most herb species (except *Geranium silvaticum*, *Viola biflora* and *Liliaceae,* all constituting a minor component of diet) were particularly difficult to identify and hence they were only recognized at plant group level.

Statistical analyses

Multivariate gradient analyses

Diet composition was estimated as proportions (%) of the individual plant taxa within a particular faeces sample. Proportions were arcsine[sqrt(proportion/100)]-transformed to avoid heteroscedasticity (Crawley 2003). We used ordination methods to investigate how sheep's total diet composition (selection of the different plant taxa) varied as a function of sheep density, age, date and years. Ordination analyses are particularly useful when large numbers of species are involved (Ter Braak & Smilauer 2002). In this case, a total of 33 plant taxa were identified in the faeces samples and employed as response variables. To choose which ordination methods to apply, the total beta diversity or "gradient length" (a measure of change in species along environmental gradients) was calculated using a detrended correspondence analysis (DCA). Unimodal ordination methods are appropriate when the length of the first DCA ordination axis is ≥ 4 SD (SD; unit of species turnover on ordination axis), whereas a linear ordination method should be applied if the gradient length is ≤ 2 SD (Ter Braak & Smilauer 2002). For intermediate lengths both methods would be useful, however Ter Braak and Prentice (1988) advice unimodal models when the gradient length exceeds 3 SD and linear models below this value. A DCA showed that the gradient length for our species data/response variables was 2.062 SD, suggesting that our species responses might be close to linear (Jongman, Braak & van Tongeren 1995). Consequently we proceeded with principal component analysis (PCA) and redundancy analysis (RDA) both ordination methods assuming a linear response. In RDA the axes are constrained to be linear combinations of the explanatory variables (i.e. a constrained PCA), a method that is suitable when gradients are short (≈ 2 SD) (Ter Braak & Smilauer 2002). We entered each of the explanatory variables in the RDA model by manual forward selection and tested them for significance using Monte Carlo Permutations (number of unrestricted permutations = 499). DCA, PCA and RDA ordination analyses were performed with Canoco for Windows 4.5.

Generalized linear mixed-effects models

Based on the PCA of the total diet composition, the most dominant plant taxa in sheep's diet; *Avenella flexuosa,* herbs, *Salix* spp. (see Fig. 1), and "other dietary plants" were selected for more detailed statistical analyses with a focus on determining interactions. First, we used plotting with General Additive models (GAMs) to search for possible non-linearity in our data (Wood 2006). Then, we fitted generalized linear mixed-effects models (GLMM's in library "lme4" in R) to determine how sheep's selection of each of these four plant taxa varied with selected interactions between the main factors (see Introduction).

Mixed-effects models are useful when temporal and spatial pseudoreplication is involved (Crawley 2003), which is the case for our data with repeated samplings and an experimental set-up with 3 replications of each density treatment. Thus, we fitted "individual" and "sub-enclosure" as random variables. We used model selection with AIC (Akaike Information Criterion) to find the most parsimonious model. The model with the lowest AIC value (and highest AIC weight) was applied to estimate the parameters for testing our predictions. All modelling was done in R vs. 2.8.0 (R Development Core Team 2008). To estimate confidence limits for the model parameters we constructed highest probability density (HPD) intervals by using Markov chain Monte Carlo simulations in the R library "coda", which is recommended over normal confidence limits for GLMMs fitted with lmer (Pinheiro & Bates 2000). Because of difficulties with obtaining SE from the mixed models, we used predicted values from linear models (LM) to construct figures.

Results

A PCA of the total diet composition indicated that sheep's diet varied within a season and between years, and that both sheep age and density affected the quantity of different plant taxa in the diet (Fig. 1). Both PCA (Table A2) and RDA (Table A3) ranked date as the most important factor determining sheep's diet, followed by year, age and density, respectively. The most frequently eaten plants by sheep (given as a mean for all samples all years) were the grass *Avenella flexuosa* (31.4 % ± 14.5 SD), herbs (24.3 % ± 13.5 SD) and *Salix* spp. (12.3 % ± 9.8 SD). In addition to these 3 most important taxa, we pooled "other plants" (though not necessarily forming a coherent functional group) in further analyses focussing on potential interactions.

A strong positive correlation between the proportion of herbs in the diet and low sheep density and positive correlations between *A. flexuosa* and *Salix* spp. and high sheep density (Fig. 1), supported our prediction regarding a lower quality diet by sheep at high density ($H_{1)}$. However, when analysing these forage species separately, there was no main effect of density for either herbs or *Salix* spp*.,* but sheep at high density consumed more *A. flexuosa* and less "other plants" than sheep at low density (Table 2). Thus, H_1 was only partly supported.

As predicted in H_{2a}, sheep's intake of high-quality herbs and *Salix* spp. declined toward the end of the grazing seasons and was replaced by a higher intake of *A. flexuosa* (Table 2) . The selection of "other plants" remained constant throughout the season (Table 2). Since the interaction between density and date was not included in any of the best models for either *A. flexuosa*, herbs, *Salix* spp. or "other plants" (Table 1), we found no support for our prediction H_{2b} that density dependent selection was stronger in late grazing season.

Diet varied between years, in accordance with H_{3a} (Fig. 1). Sheep's intake of *A. flexuosa*, herbs, *Salix* spp. and "other plants" showed marked annual variation (Table 2). The interaction between year and density entered the best mixed model only for *A. flexuosa* (Table 1), while it was in the 2nd best model for both herbs and "other plants". When using linear models, this interaction entered the best model. We therefore included this term to estimate the effect, which was quite marked (Table 2, Fig. 2). There was thus clearly some support for our prediction that the effect of density depend on year (H_{3b}). When estimating the combined effect of annual variation and density on diet composition, we found that density dependence varied between years and among species (Table 2, Fig. 2). For *Salix* spp., there was no clear effect of density, and the density and year interaction did not enter any of the better models. When estimated for *Salix* spp., the density effect was indeed weak (and not significant) and fairly consistent among years (Fig. 2C). For intake of herbs, the pattern was consistent in all years, with either no or negative effect of high density on intake of herbs (Table 2, Fig. 2B). The response was, however, not consistent for *A. flexuosa*, as sheep at high density consumed both more and less of this grass than sheep at low density in a specific year with density-dependent diet choice (Fig. 2A).

Age affected sheep's diet composition with lambs eating more high-quality plant material than ewes, in accordance with H_4. The mixed models confirmed also the pattern found in the PCA analysis, with lambs consuming less *A. flexuosa*, but more herbs and *Salix* spp. than ewes (Fig. 1, Table 2). However, the age effect did not interact with either density, seasonal, annual variation or the trend over years (Table 1).

Discussion

Evidence for density dependence (reviews in Fowler 1987; Bonenfant et al. 2009) and climate induced annual variation in demographic rates are persuasive (reviews in Gaillard et al. 2000; Weladji et al. 2002; Mysterud et al. 2003). The mechanisms behind these patterns are to a large extent expected to operate through diet quality or quantity (Simard *et al.* 2008). The results from this first fully replicated experimental, long-term study of large herbivore diet highlight how the combination of age, density and temporal variation determine diet composition (Fig. 1). There was marked evidence that age, density and temporal variation additively affected diet, but less strong evidence of interactions, apart from the density and year interaction (Fig. 2). The strong annual variation that interacts with the density effect might indeed be expected to give raise to similar variation in vital rates, and indeed, annual and density dependent body growth of lambs interacted (Mysterud & Austrheim 2005).

From the demographic and life history viewpoint, the annual scale and density dependence are arguably the most interesting. In the ordination of the overall diet composition, there was evidence for both density dependence and annual variation (Fig. 1, Table A2 and A3). The strong annual variation in diet suggest changes in species specific biomass or quality. We have earlier reported evidence for marked variation in herb growth among years (Mobæk et al. 2009), which likely have consequences for herbivore body mass gain during summer. Reduced growth by lambs at high density (Mysterud & Austrheim 2005) is likely to arise partly due to differences in diet composition at the two density levels. We expected less herbs to be eaten in years with little forage biomass, and similarly, high density of sheep to increase competition for forage reducing intake of high quality forage. Further, we predicted inter-annual climatic variation to interact with the density effect such that a stronger density dependent selection would occur in years with poor vegetation development. The interaction term between annual variation and density entered the best model for *A. flexuosa* only, but was in the 2nd best models for both herbs and "other dietary plants" and clearly significant when estimated (Table 2, Fig. 2). Estimating the interaction term for all components proved necessary to understand the overall interactive effect (Fig. 2). For herbs, assumed to be of high quality (Bowns & Bagley 1986), there was either no variation between high and low density (years 2003-2004) or a higher proportion (years 2002, 2005-07) in the low density treatment. In contrast, for "other plants", not forming a coherent functional group, but many species can be assumed to be of fairly low nutritional value due to low intake rates, there was usually an increase in the proportion at high density (Fig. 2). For the intermediate quality forage, the graminoid *A. flexuosa*, the effect of density between years therefore was not consistent – depending on the response for both the high quality herbs and the lower quality "other plants". Therefore, intermediate quality forage may show opposite density dependence between years as their proportion in the diet is affected by the development of more than one other dietary component. There was annual variation also in proportion of *Salix* spp., but no effect of density alone or in interaction with annual variation.

Climatic conditions influence plant phenology (Mårell et al. 2006), and thereby affect habitat selection and in turn herbivore performance (Pettorelli et al. 2005). In alpine ecosystems, high spring/summer temperatures and little snow typically benefit rapid plant growth and early maturation, while cold weather reduce plant growth and also slow down snow melt prolonging access to newly emergent high-quality forage (Hebblewhite et al. 2008). There was clear evidence that seasonal progression in plant development was important for diet composition. The intake of herbs and *Salix* spp. gradually declined and was replaced by grasses such as *A. flexuosa* towards the end of the grazing seasons. Although we expected the density dependent selection to be stronger in late grazing season when both forage availability and plant quality is reduced, we found no strong interaction between date and density for any of our focal forage plants, suggesting this was a short term effect found only in the first year of our study (2002; Kausrud et al. 2006). At longer time scales (over years), intense selective feeding may affect the availability of important forage species (Jefferies, Klein & Shaver 1994; Augustine & McNaughton 1998) with repercussion for the life history (Simard et al. 2008). However, such effects are fairly moderate within the time frame of our study (Austrheim et al. 2008; Evju *et al.* 2009, and this may explain no clear trends in diet over years (Table 1). In large herbivores, juveniles are more sensitive to both environmental fluctuations and density dependence than adults (Gaillard, Festa-Bianchet & Yoccoz 1998). During periods with resource shortage, ungulate females may favour their own mass gain rather than the growth of their offspring (Gaillard & Yoccoz 2003; Martin & Festa-Bianchet 2010). For example, lactating bighorn sheep (*Ovis canadensis*) provided less maternal care and produced lighter lambs in years with high population density and poor resource availability than during years with low population density and hence less food competition (Festa-Bianchet & Jorgenson 1998; Martin & Festa-Bianchet 2010). In accordance with energy-body size allometric theory (Demment & Van Soest 1985), we found that diet composition of the most important forage species differed markedly between lambs and ewes, and that lambs selected more high-quality herbs and less grass. Our data supported only a main effect of age, and we failed to find any interactions between age and density or temporal variation on diet.

Our study quantifying age, density and temporal effects in diet of a large herbivore increase our understanding of mechanism determining vital rates. We document the expectation that density effects and annual variation in diet is present, forming one potential mechanism of similar patterns found in lamb body growth. Reduced body growth during the first year of life typically delay age at first reproduction with a year (Langvatn *et al.* 2004). Our results for *A. flexuosa* and partly for herbs and "other plants" suggest that interactions can arise due to diet composition effects. We suggest that more studies on proximate mechanisms can further advance our understanding of factors limiting ungulate populations.

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Table 1. Results for model selection of sheep diet in alpine habitats in Norway using generalized linear mixed effects models. Explanation of hypotheses in header row is given in the Introduction. Random effects were always “Individual” and “Sub-enclosure”. Main effects were included in all models due to results from the PCA (Fig. 1). The models are ordered according to descending AIC values. AIC = Akaike Information Criterion. ΔAIC = difference in AIC value between the AIC for the model given in that row and the most parsimonious model (lowest AIC). AICw = AIC weight. Year (cat) = year entered as a categorical variable; Year (trend) = year entered as a continuous variable.

	H_1	H_{2a}	H_{3a}		H_{2b}	H_{3b}		H_4						
Parameter	Density	Date	Year (cat)	Year (trend)	Date x Density	Year (cat) x Density	Year (trend) x Density	Age	Age x Density	Age x Date	Age x Year (cat)	AIC	ΔAIC	AICw
A. *A. flexuosa*														
	x	x	x			x		x				-1075	0	0.76
	x	x	x		x	x		x				-1072	3	0.17
	x	x	x					x				-1069	6	0.04
	x	x	x			x		x	x			-1069	6	0.04
	x	x	x			x		x		x		-1060	15	0.00
	x	x	x			x		x			x	-1052	23	0.00
	x	x		x				x				-1051	24	0.00
	x	x		x			x	x				-1043	32	0.00
B. Herbs														
	x	x	x					x				-1231	0	0.56
	x	x	x			x		x				-1229	2	0.21
	x	x	x					x		x		-1229	2	0.21
	x	x	x					x	x			-1225	6	0.03
	x	x	x		x			x				-1219	12	0.00
	x	x	x					x			x	-1209	22	0.00
	x	x		x			x	x				-1132	99	0.00
	x	x		x				x				-1124	107	0.00
C. *Salix* spp.														
	x	x	x					x				-1211	0	0.72
	x	x	x					x	x			-1209	2	0.26
	x	x		x				x				-1203	8	0.01
	x	x	x		x			x				-1201	10	0.00
	x	x	x					x		x		-1198	13	0.00
	x	x		x			x	x				-1193	18	0.00
	x	x	x			x		x				-1192	19	0.00
	x	x	x					x			x	-1187	24	0.00
D. Other														
	x	x	x					x				-1342	0	0.86
	x	x	x			x		x				-1338	4	0.12

Table 1 cont.

	H_1	H_{2a}	H_{3a}		H_{2b}	H_{3b}		H_4						
Parameter	Density	Date	Year (cat)	Year (trend)	Date x Density	Year (cat) x Density	Year (trend) x Density	Age	Age x Density	Age x Date	Age x Year (cat)	AIC	ΔAIC	AICw
	x	x	x					x		x		-1327	15	0.00
	x	x	x					x			x	-1322	20	0.00
	x	x		x				x				-1315	27	0.00
	x	x		x			x	x				-1311	31	0.00

Table 2. Generalized linear mixed effects model for the proportion of A. *A. flexuosa*, B. herbs, C. *Salix* spp. and D. “other plants” in the diet of sheep at low and high density treatment for the summer grazing seasons 2002-2007 in Hol, Norway. The parameter estimates are based on the best models for *A. flexuosa* and Salix spp. However, we used the 2nd best model for herbs and “other plants” due to the inclusion of the biologically interesting interaction term between “density” and “year” that was in the best model of *A. flexuosa* (Table 1). The 95% HPD intervals for fixed effects not including 0 are bolded. (Number of samples = 784, Sheep ID = 236, Sub-enclosure = 6).

	A. *A. flexuosa*			B. Herbs			C. *Salix* spp.			D. Other plants		
Fixed effects	Estimate	Lower 95%	Upper 95%	Estimate	Lower 95%	Upper 95%	Estimate	Lower 95%	Upper 95%	Estimate	Lower 95%	Upper 95%
Intercept	-0.054	-0.168	0.064	**0.994**	**0.885**	**1.107**	**0.633**	**0.524**	**0.743**	**0.601**	**0.500**	**0.701**
Density (Low vs. high)	**-0.101**	**-0.192**	**-0.018**	-0.001	-0.103	0.089	0.046	-0.034	0.137	**0.071**	**0.000**	**0.151**
Date	**0.004**	**0.003**	**0.004**	**-0.003**	**-0.003**	**-0.002**	**-0.002**	**-0.002**	**-0.001**	0.000	-0.001	0.000
Year (2003 vs. 2002)	**-0.057**	**-0.102**	**-0.009**	**0.129**	**0.085**	**0.172**	**-0.054**	**-0.090**	**-0.019**	-0.026	-0.066	0.015
Year (2004 vs. 2002)	-0.002	-0.050	0.042	**-0.099**	**-0.142**	**-0.054**	0.035	-0.001	0.069	**0.057**	**0.015**	**0.097**
Year (2005 vs. 2002)	**-0.091**	**-0.136**	**-0.044**	**0.049**	**0.004**	**0.090**	-0.021	-0.056	0.012	**0.070**	**0.030**	**0.109**
Year (2006 vs. 2002)	**-0.089**	**-0.133**	**-0.044**	-0.026	-0.068	0.018	**-0.113**	**-0.146**	**-0.078**	**0.175**	**0.136**	**0.214**
Year (2007 vs. 2002)	0.003	-0.048	0.051	**-0.060**	**-0.105**	**-0.012**	**-0.051**	**-0.089**	**-0.016**	**0.078**	**0.034**	**0.120**
Age (Lamb vs. ewe)	**-0.090**	**-0.112**	**-0.070**	**0.065**	**0.045**	**0.086**	**0.075**	**0.054**	**0.096**	**-0.024**	**-0.043**	**-0.006**
Year (2003 vs. 2002) * Density (Low vs. high)	**0.126**	**0.054**	**0.197**	**-0.082**	**-0.151**	**-0.015**				-0.061	-0.125	0.001
Year (2004 vs. 2002) * Density (Low vs. high)	**0.176**	**0.105**	**0.244**	-0.029	-0.095	0.036				**-0.131**	**-0.191**	**-0.066**
Year (2005 vs. 2002) * Density (Low vs. high)	**0.162**	**0.094**	**0.230**	0.032	-0.034	0.095				**-0.178**	**-0.237**	**-0.119**
Year (2006 vs. 2002) * Density (Low vs. high)	**0.107**	**0.039**	**0.173**	**0.103**	**0.037**	**0.165**				**-0.188**	**-0.246**	**-0.128**
Year (2007 vs. 2002) *	-0.034	-0.110	0.036	**0.134**	**0.065**	**0.204**				**-0.082**	**-0.146**	**-0.019**

Table 2 cont.

Density (Low vs. high) Random effects	SD	Lower 95%	Upper 95%	SD	Lower 95%	Upper 95%	SD	Lower 95%	Upper 95%	SD	Lower 95%	Upper 95%
Sheep ID	0.098	0.043	0.059	0.100	0.045	0.060	0.116	0.047	0.063	0.098	0.039	0.053
Sub-enclosure	0.050	0.021	0.094	0.062	0.023	0.096	0.046	0.018	0.093	0.056	0.020	0.083

Figure captions

Fig. 1. Species-environment biplot diagram from PCA of plant species composition in sheep's diet (n=441 feces samples) in relation to sheep density (high or low), sheep age (ewe or lamb), date and grazing season (2002-2007). Eigenvalues of PCA axes 1 (horizontally), 2 (vertically) and 3 (not displayed) are 0.493, 0.222 and 0.112 respectively. The axes in this biplot explain 71.5 % of the total variation in diet composition, and are not constrained by the explanatory variables (i.e. they are passive variables). To ease interpretation of the diagram, all plant species are classified into four different plant groups which are illustrated by colours: blue arrows and species names = woody species, lilac = graminoids, green = herbs and yellow = cryptogams. Abbreviations: Agr spp, *Agrostis spp;* Ant odor, *Anthoxanthum odoratum;* Bet spp, *Betula* spp.*;* Cal vulg, *Calluna vulgaris;* Car spp, *Carex* spp.*;* Cyp, *Cyperaceae;* Des caes, *Deschampsia caespitosa;* A flex, *Avenella flexuosa;* Emp herm, *Empetrum hermaphroditum*; Equ spp, *Equisetum* spp.*;* Fes ovin, *Festuca ovina;* Fes rubr, *Festuca rubra;* Fes spp, *Festuca* spp.*;* Ger silv, *Geranium silvaticum;* Jun comm, *Juniperus communis;* Lyc, *Lycopoduim;* Mil effu, *Millium effusum;* Mol caer, *Molinia caerula;* Nar stric, *Nardus stricta;* Phl spp, *Phleum spp;* Pin sylv, *Pinus sylvestris;* Sal glau, *Salix glauca;* Sal herb, *Salix herbacea;* Sal spp, *Salix* spp.*;* Vac myrt, *Vaccinium myrtillus;* Vac olig, *Vaccinium oligonosum;* Vio bifl, *Viola biflora*. Nomenclature follows Lid and Lid (2005).

Fig. 2. Proportion of A. *Avenella flexuosa*, B. herbs, C. *Salix* spp. and D. “other plants” in diet of sheep at low (black) and high (red) density treatment for the summer grazing seasons 2002-2007 in Hol, Norway. The predicted values are from linear models. To facilitate comparison, we included the interaction term “year” and “density” in all models, though this was included in the best model only for *A. flexuosa*, in the 2nd best model for herbs and “other plants”, while not among the top models for *Salix* spp. (Table 1).

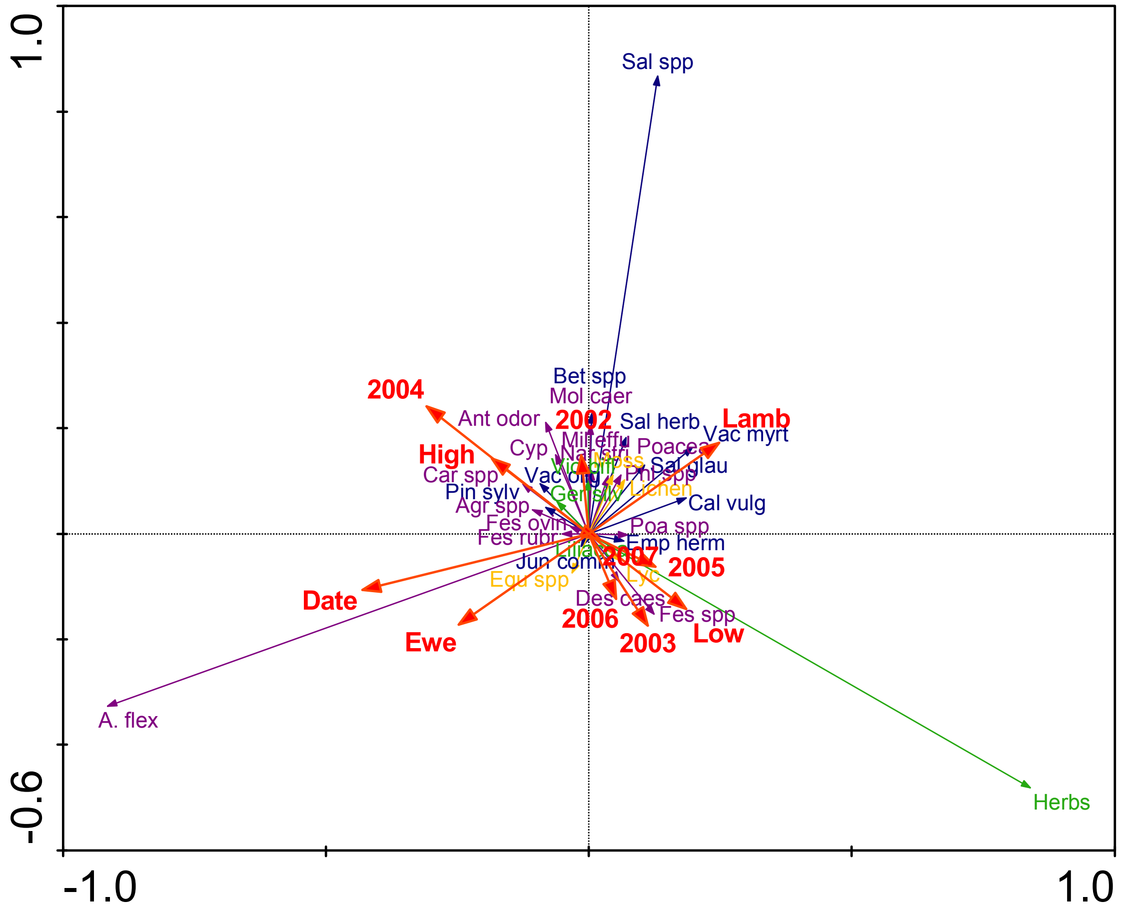
1.0
-0.6
-1.0
1.0
Sal spp
Bet spp
Mol caer
2004
Ant odor
2002
Sal herb
Lamb
Vac myrt
High
Cyp
Mil effu
Nar stri
Poacea
Moss
Vio biff
Sal glau
Car spp
Vac olig
Phl spp
Pin sylv
Ger silv
Lichen
Agr spp
Cal vulg
Fes ovin
Poa spp
Fes rubr
Emp herm
Liliaceae
2007
Jun comm
2005
Equ spp
Lyc
Date
Des caes
Fes spp
2006
Low
Ewe
2003
A. flex
Herbs

Fig. 1

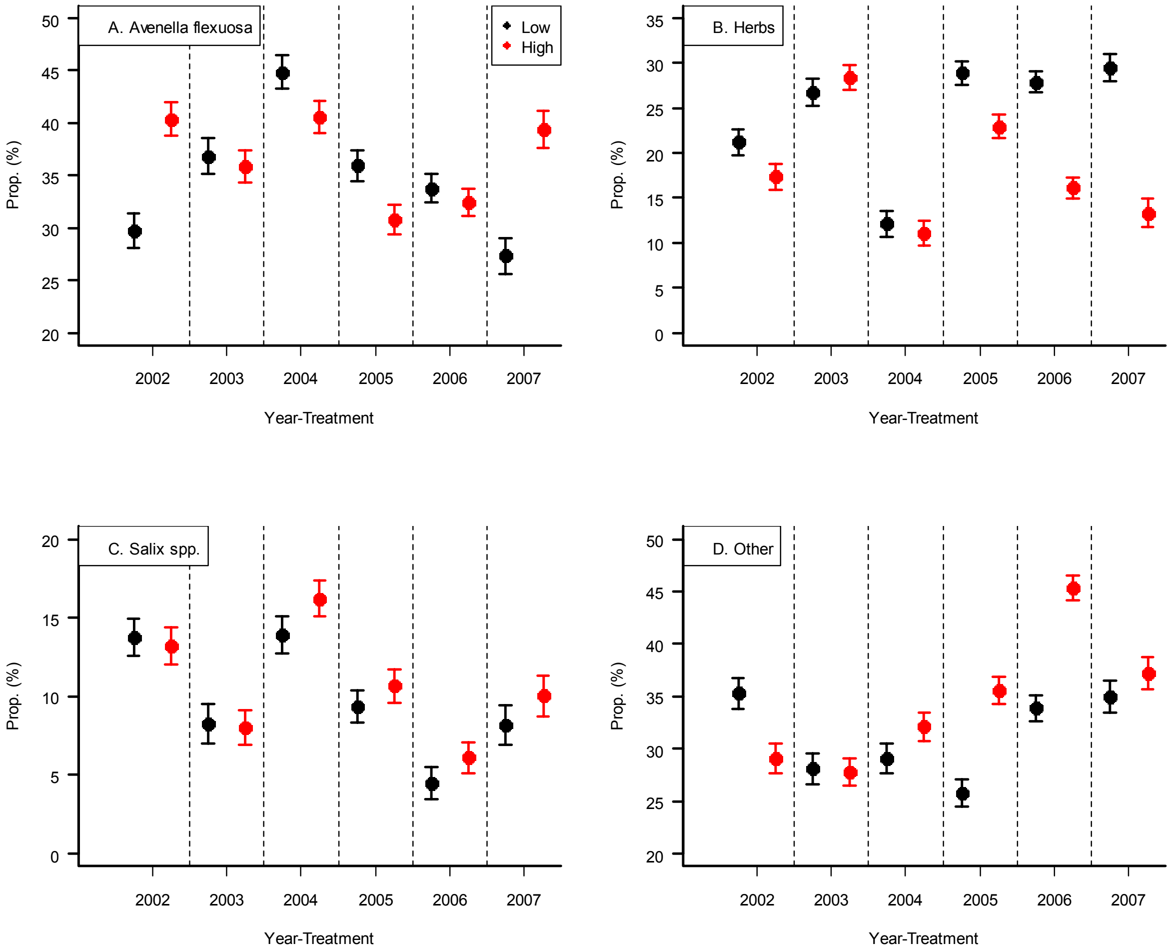
A. Avenella flexuosa
Low
High
B. Herbs
C. Salix spp.
D. Other
Prop. (%)
Year-Treatment
2002
2003
2004
2005
2006
2007
50
45
40
35
30
25
20
15
10
5
0

Fig. 2

Online supporting information

Table A1. The length of each grazing season and the total number and distribution (with respect to density and age) of faeces samples analysed each year.

Year	Length of grazing season	High density	Low density	Ewe	Lamb	Total
2002	28. June – 29. August	29	29	28	30	58
2003	30. June – 24. August	33	27	34	26	60
2004	28. June – 30. August	33	30	27	36	63
2005	5. July – 30. August	38	39	33	44	77
2006	25. June – 24. August	42	43	44	41	85
2007	28. June – 28. August	47	51	54	44	98
Total		222	219	220	221	441

Table A2. Fraction of variance explained by PCA axes in the species-environment biplot (Fig. 1) and t-values of regression coefficients when using the explanatory variables as passive variables in PCA of plant species composition in sheep's diet (number of samples = 441). t-values > 2.1 indicate that the variable is important for the species data.

	Axis 1	Axis 2	Axis 3	Axis 4
Variation explained	0.6490	0.1426	0.0684	0.0330
		t value		
Explanatory variable				
Date	-14.2469	-5.0988	1.3348	4.1389
Age	-9.9220	-5.0995	5.0916	-1.2170
Year 2004	-7.0913	4.4067	-3.2069	3.2003
Density	-4.6049	5.0685	4.3458	-6.6216
Year 2002	-1.4672	2.6894	-3.2070	8.0820
Year 2005	1.4207	-1.2278	-2.2683	3.2412
Year 2003	0.8087	-3.7259	-3.0065	6.5041
Year 2006	-0.0615	-2.0870	4.0995	1.0150
Year 2007	-	-	-	-

Table A3. Results from RDA using the explanatory variables in a constrained ordination of plant species composition in sheep's diet (number of samples = 441). All explanatory variables are tested for significance by Monte Carlo Permutations (number of unrestricted permutations = 499).

Explanatory variable	Variation explained	F-ratio	P-value
Date	0.10	85.22	0.002
Year 2004	0.06	54.48	0.002
Age	0.05	53.88	0.002
Year 2002	0.02	23.14	0.002
Density	0.02	19.86	0.002
Year 2003	0.02	15.49	0.002
Year 2005	0.01	9.99	0.002
Year 2006	0.00	5.45	0.004
Year 2007	-	-	-

Paper III

Experimental evidence of density dependent activity pattern of a large herbivore in an alpine ecosystem

Ragnhild Mobæk, Atle Mysterud, Leif Egil Loe,
Øystein Holand, Gunnar Austrheim

Submitted to Oikos

Experimental evidence of density dependent activity pattern of a large herbivore in an alpine ecosystem

Ragnhild Mobæk[1], Atle Mysterud[2*], Leif Egil Loe[3], Øystein Holand[1] and Gunnar Austrheim[4]

[1]Department of Animal and Aquacultural Sciences, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway.

[2]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway.

[3] Norwegian University of Life Science, Department of Ecology and Natural Resource Management, P.O. Box 5003, NO-1432 Aas, Norway

[4]Museum of Natural History and Archaeology, Section of Natural History, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway.

[*]Corresponding author

e-mail: atle.mysterud@bio.uio.no

Tel: +47 22 85 40 45, Fax: +47 22 85 47 26

Summary

Density dependent processes affecting foraging strategies may in turn influence vital rates and population regulation in large herbivores. Increased competition may lower both forage availability and quality, but whether the main activity constraint at high density is increased searching time or increased digestion time is poorly investigated. In a fully replicated landscape-scale experiment, we used long-term data (2003-2009) from domestic sheep grazing at high and low density (80 and 25 sheep pr km^2, respectively) on alpine summer ranges to test density dependence in allocation of time to feeding (moving) versus digestion (resting) activities. Sheep at high density spent more time actively feeding than sheep at low density, but sheep moved shorter distances while foraging at high density. Increased activity levels at high density suggest that the main activity constraint at high density was availability of high-quality food increasing searching time possibly reducing intake rates. Increased movement distances at low density is consistent with a higher selection for more productive vegetation types since high-quality patches are dispersed in the landscape. The alternative hypothesis, that food processing time increased at high density was not supported as it would have reduced overall activity levels. Our experiment clearly documents changes in activity budgets and movement distances of a large herbivore at high population density, providing one potential behavioural mechanism of density dependent responses observed in vital rates.

Keywords: density dependence, activity budget, ungulates, foraging, GPS

Introduction

Density dependent responses in vital rates are well documented and a key to understand population regulation of large herbivores (Bonenfant et al. 2009, Fowler 1987). Vital rates at a population level arise as a result of individual life history choices, which in turn are affected by the level of resource competition determining the amount of energy available for resource allocation. At high density when competition is increased, herbivores are forced to utilize marginal habitats (Mobæk et al. 2009, Ramp and Coulson 2002) lower in forage quality and/or quantity (Choquenot 1991, Kausrud et al. 2006) leading to less energy for reproduction and survival. How population density affects activity budgets in large herbivores is however little explored.

Large ruminants display distinct activity bouts attributed to feeding and resting, the latter category including processing of food (rumination). Whether the main constraint to activity budgets and forage intake is digestion time, searching time or short-term intake rate is debated (Bergman et al. 2001). A high quality diet is easily digested and does not require very long retention time, allowing more time to forage (Demment and Van Soest 1985). A decline in forage quality (i.e. higher fiber content) necessitates increased rumination time (Pérez-Barbería and Gordon 1998), which may reduce time available for feeding. Two studies available report decreased activity at high density levels (sika deer (*Cervus nippon*); Borkowski 2000, white-tailed deer (*Odocoileus virgianius*); Coulombe et al. 2008), interpreted as a result of intraspecific competition possibly increasing rumination time. However, another study report increased activity at high density (domestic sheep; Animut et al. 2005). These studies were either not experimental (density was not controlled; Borkowski 2000), or short term (Animut et al. 2005, Coulombe et al. 2008), underlying the need for further longer-term experimental studies.

We here analyze long-term data (2003-2009) on foraging activity of a large herbivore, domestic sheep (*Ovis aries*) in a landscape-scale experiment in an alpine ecosystem. Sheep were stocked at high and low density and each treatment was replicated 3 times. We tested the following predictions: Sheep at high density are more active than sheep at low density due to more time spent searching for food (i.e. biomass and/or availability of high-quality food is the main constraint; H_1), or alternatively sheep at high density are less active due to increased rumination time (i.e. processing poor-quality food is the main constraint; H_2). We also test for density dependence in movement distances, and we explore whether the density effect is constant within season and between years, i.e., whether or not there is an interaction between density and climate on activity pattern.

Materials and methods

Study area and experimental design

The study area is located in Hol municipality, Buskerud county in southern Norway (60º40´N, 7º55´E). The area has a sub-continental alpine climate with annual precipitation approximately 1000 mm (Evju et al. 2009). Vegetation is mainly composed of low shrubs with scattered grass-dominated meadows, and birch (*Betula pubescens*) trees are found in the areas with lowest elevation (Speed et al. 2010). In 2001, a fenced experimental enclosure covering 2.7 km^2 was established and split into nine sub-enclosures in order to facilitate a randomized replication within three blocks (Austrheim et al. 2008). The division of the enclosure was performed such that each of the sub-enclosures covered approximately the same altitudinal range (i.e. within 1050 m and 1320 m a.s.l.) and a comparable distribution of vegetation types. Each of the three sub-enclosures within a block was then randomly assigned as high density, low density or control (no sheep) sub-enclosure. Sheep density levels were calculated based on a botanical survey and estimation of the different vegetation types' grazing value for sheep, and 80 and 25 sheep per km^2 were chosen as high and low density treatment, respectively. Since year 2002, a total of 24 to 27 lactating ewes and 44 to 46 lambs belonging to the same sheep farmer were released into the experimental enclosure each summer. Each grazing season lasted from late June to late August or early September. The sheep were of the breed "Norsk Kvit Sau", which is the most common breed in Norway.

Direct observations of activity

A total of 5580 direct observations (i.e., focal watches) of ewes from seven consecutive grazing seasons (late June to late August or early September 2003-2009) were used in this study (see Mobæk et al. 2009 for details). Individually marked ewes and their lambs were followed the entire seasons, and observations were done using two working cycles distributed randomly throughout the season; either "early" from 9:00 to 17:00 or "late" from 14:00 to 22:00. This sheep breed does not form stable large herds, and we therefore used ewe as the unit of within sub-enclosure replication. Ewe's behaviour was recorded from a distance of 20-50 m using binoculars. Prior to analyses behaviour was categorized as active (grazing, n = 3346; walking, n = 183) or inactive (lying, n = 1549; standing, n = 500) behaviour. A total of 21 observations of ewes doing "other" activity were discarded.

GPS-data on movement distances

In 2008 and 2009, ewes were marked with GPS-collars from Televilt programmed to take a position every 30 min. We retrieved data from 18 ewes in 2008 and 22 ewes in 2009. We removed all data points from outside the given subenclosure for each ewe, which remove most GPS errors. We also removed data from the dates of release and capture. This yielded on average 3410 fixes out of 3744 possible (91.1%; between 2176 and 3698) and 3216 fixes out of 3360 possible (95.7%; between 2978-3341) per collar in 2008 and 2009, respectively. Fix success rates were high for most collars. Three collars stopped during the field season; on 13. August 2008 (2176 fixes), 17. July 2009 (835 fixes) and 26. August 2009 (2832 fixes), but data from these collars are still included as the fix success rates were high up to the point of failure. Most of the reduction in fixes came from our strict rule of only allowing fixes inside fences, as many fixes were just a few m outside.

Statistical analyses

All statistical analyses were done in R vs. 2.9.2 and 2.12.0 (R Development Core Team 2008). First, we explored the dataset for any possible non-linearity using GAM-plots. Then, we fitted generalized linear mixed models (LME) using the function lmer in the R library lme4. We tested whether our binomially distributed response variable active (given a value of 1) and inactive (0) behaviour was affected by the fixed effects sheep density (high vs. low), date (Julian date; continuous), year (continuous or categorical) and interactions between these variables. To account for pseudoreplication due to repeated observations of the same ewe and a block-wise experimental design with three replicates of sheep density, we always fitted "individual" and "sub-enclosure" as random variables. We used AIC values (and AIC weights) to find the most parsimonious model. Finally, we tested the most parsimonious model's goodness of fit using the function lrm in the R library Design. When constructing figures, we used parameter estimates from linear models (LM), since it is difficult to predict SE values from mixed models.

For GPS-data, we used the library "Adehabitat" (Calenge 2006). We focused on the distance between successive locations using the Ltraj function. We restricted analysis to those with exactly 30 min. interval between locations. Distances between locations (+1 m) were log-transformed before analysis. Fixed effects were sheep density (high vs. low), date (Julian date; continuous) and time of day (continuous as a proportion between 0 and 1), while "individual" and "sub-enclosure" were fitted as random variables. Exploratory modeling with GAM showed a marked non-linear relationship between distance travelled and time of day, and was subsequently modeled with a 2nd order term. We defined stationary periods (indicative of resting) as those with successive movements <10 m per 30 min (after initial screening of using 5, 10, 20, 30 and 40 m). The movement analyses excluded stationary periods.

Results

Sheep spent 63.9 % (± 3.0, SD) of their time being active and 36.1 % inactive (± 3.0) as determined from direct observations during the period from 09:00 to 22:00. The most parsimonious model of sheep activity included the main effects of density, date and year (Table 1; Appendix 1). Density significantly affected activity pattern (Table 1), and sheep at high density spent more of their time active (mean ± SD; 66.2 ± 4.6) than sheep at low density (60.8 ± 3.2), supporting H_1 (Fig. 1). This density dependent activity pattern was consistent over years (Fig. 1). Activity increased over the season and varied between years (Table 1). There was no interaction between the seasonal or annual variation effect and sheep density (Appendix 1).

The GPS-data showed a similar pattern for activity and density when considering the whole 24 hr period, with activity (defined as steps <10 m) being 68.5% at high density and 66.5% at low density (raw data). The analysis of movement distances (>10 m) revealed that sheep moved longer distances at low density compared to high density (Fig. 2), while there was no difference in movement distances between 2008 and 2009 (Table 2). Sheep reduced movement distances as the season progressed, but very weakly (28 cm for a 2 weeks period), and movement distances peaked during daytime.

Discussion

While patterns of density dependent responses in vital rates are well described, we know comparatively little regarding density dependent changes in behaviour. Our results comprising data from seven grazing seasons provide robust experimental evidence that population density affects activity patterns and movement distances by a large herbivore. Sheep at high density spent considerably more time active (i.e. grazing and walking) than sheep at low density (Fig. 1). This supports our prediction that food availability and searching time (H_1), rather than processing time of lower quality forage (H_2), is the main constraint to sheep at high density. Increased food competition may reduce the availability of preferred forage species and thus lower average diet quality (Jefferies et al. 1994, Olofsson 2006). Indeed, sheep at high density had a higher intake of plant species with low nutritive value (Kausrud et al. 2006) and showed a lower (but still positive) selection of productive habitats when foraging (Mobæk et al. 2009) compared to sheep at low density in our experimental system. This suggests that the increased food competition with lower access to high-quality forage, forces sheep to switch their foraging strategy from selective more towards bulk feeding.

Further evidence for such an interpretation comes from the seasonal and annual pattern of activity. In northern, alpine ecosystems, forage quality typically peaks in spring and summer, and decreases towards autumn as plant material mature and senesce (Hebblewhite et al. 2008). Large-scale climatic fluctuations also contribute to between-year variation in plant phenology in alpine areas (Pettorelli et al. 2005). In line with this, we found increased activity towards the end of the grazing season and annual variation in sheep's activity pattern, likely reflecting temporal variation in biomass and plant quality (Mysterud et al. 2011). This seasonal and between-year variation did not interact with the density effect. The increase in activity in late grazing season further corroborates our prediction that the adopted strategy for sheep is to compensate reduced availability of high-quality forage by increasing foraging time. However, this increased foraging time did not result in increased movement distances, as sheep at low density moved more than those at high density (Fig. 2). This is likely due to that sheep at high density have a more even use of vegetation types, while sheep at low density select more productive vegetation types that are dispersed in the area (Mobæk et al. 2009). A study in elephants (*Loxodonta africana*) found also decreased daily movements with increased density, while the pattern seemed to reverse at the very highest densities (Young and Van Aarde 2010).

The fact that sheep at high density spent less time resting than sheep at low density did not support that processing poor-quality food is the main constraint to sheep at high density (H_2). We had no observation of interference among sheep, so we find it unlikely to affect the patterns observed. However, as we have no measurements of time spent ruminating when resting, we cannot exclude the possibility that also rumination patterns for sheep at high and low density differ. Ruminants may partly compensate low quality plant material by increasing mastication (Pérez-Barbería and Gordon 1998), which in turn decreases particle size and by this speed up digestion (Bjorndal et al. 1990). For example, Blanchard (2005) showed that lactating bighorn ewes (*Ovis canadensis*) had a higher chewing rate when ruminating than yeld ewes with lower energetic requirements. Our study reports consistently increased activity thus suggesting increased searching time at high density, and thus yields new insight to density dependent foraging patterns by large ruminants.

Acknowledgements

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Table 1. Parameter estimates from linear mixed effects model analyzing sheep activity during the period 9:00 and 22:00 at high and low population density over the grazing seasons 2003-2009 in Hol, Norway. The response variable activity is a binomial variable (active = 1, inactive = 0). Density and year were fitted as factor variables with “high” and “2003” as reference levels, respectively. Date is Julian date (standardized). Number of observations = 5580, number of individual sheep = 123, number of sub-enclosures = 6. SE = standard error. CL = confidence limit. The 95% CLs for fixed effects not including 0 are bolded.

Fixed effects	Estimate	SE	95% lower CL	95 % upper CL
Intercept	-1.42	0.324	**-2.068**	**-0.772**
Density (low-high)	-0.231	0.100	**-0.431**	**-0.031**
Date	0.011	0.002	**0.008**	**0.014**
Year (2004 vs. 2003)	-0.159	0.123	-0.405	0.087
Year (2005 vs. 2003)	-0.408	0.118	**-0.644**	**-0.172**
Year (2006 vs. 2003)	-0.100	0.125	-0.350	0.150
Year (2007 vs. 2003)	-0.332	0.120	**-0.572**	**-0.092**
Year (2008 vs. 2003)	-0.353	0.116	**-0.585**	**-0.121**
Year (2009 vs. 2003)	-0.328	0.120	**-0.568**	**-0.088**
Random effects				
Groups	Name	Variance	SD	
Sheep ID	Intercept	0.037697	0.19416	
Sub-enclosure	Intercept	0.00866	0.09306	

Table 2. Parameter estimates from linear mixed effects model analyzing (ln+1) distance above 10 m between 30 min. locations of sheep at high and low population density over the grazing season 2008 and 2009 in Hol, Norway. Density and year were fitted as factor variables with "high" and "2008" as reference levels, respectively. Date is Julian date (standardized). Number of observations = 84092, number of individual sheep = 33, number of sub-enclosures = 6. SE = standard error. CL = confidence limit. The 95% CLs for fixed effects not including 0 are bolded.

Fixed effects	Estimate	SE	95% lower CL	95% upper CL
Intercept	3.417	0.052	**3.312**	**3.522**
Density (low-high)	0.185	0.072	**0.042**	**0.328**
Date	-0.009	0.004	**-0.017**	**-0.001**
Time of day	2.606	0.051	**2.505**	**2.707**
(Time of day)^2	-2.718	0.049	**-2.816**	**-2.619**
Year (2009 vs. 2008)	0.025	0.025	-0.024	0.074
Density:year	-0.022	0.043	-0.109	0.065
Random effects				
Groups	Name	Variance	SD	
Sheep ID	Intercept	0.0085567	0.092502	
Sub-enclosure	Intercept	0.0064097	0.080061	

Figure captions

Figure 1. Proportion of active behaviour by sheep (n = 5580) at high and low density for the summer grazing seasons 2003-2009 in alpine habitat in Hol, Norway. The predicted values (closed circles) are derived from the linear mixed effect model in Table 1, including the variables density, date and year, with “year 2003” and “high density” as reference levels. Open circles are raw data values.

Figure 2. Distance moved by sheep ewes measured over a 30 min. period with the aid of GPS-collars at low and high density for the summer grazing seasons 2008-2009 in alpine habitat in Hol, Norway. The circles are predicted values derived from the linear mixed effect model in Table 2. Non-active locations (< 10 m) are removed before analysis.

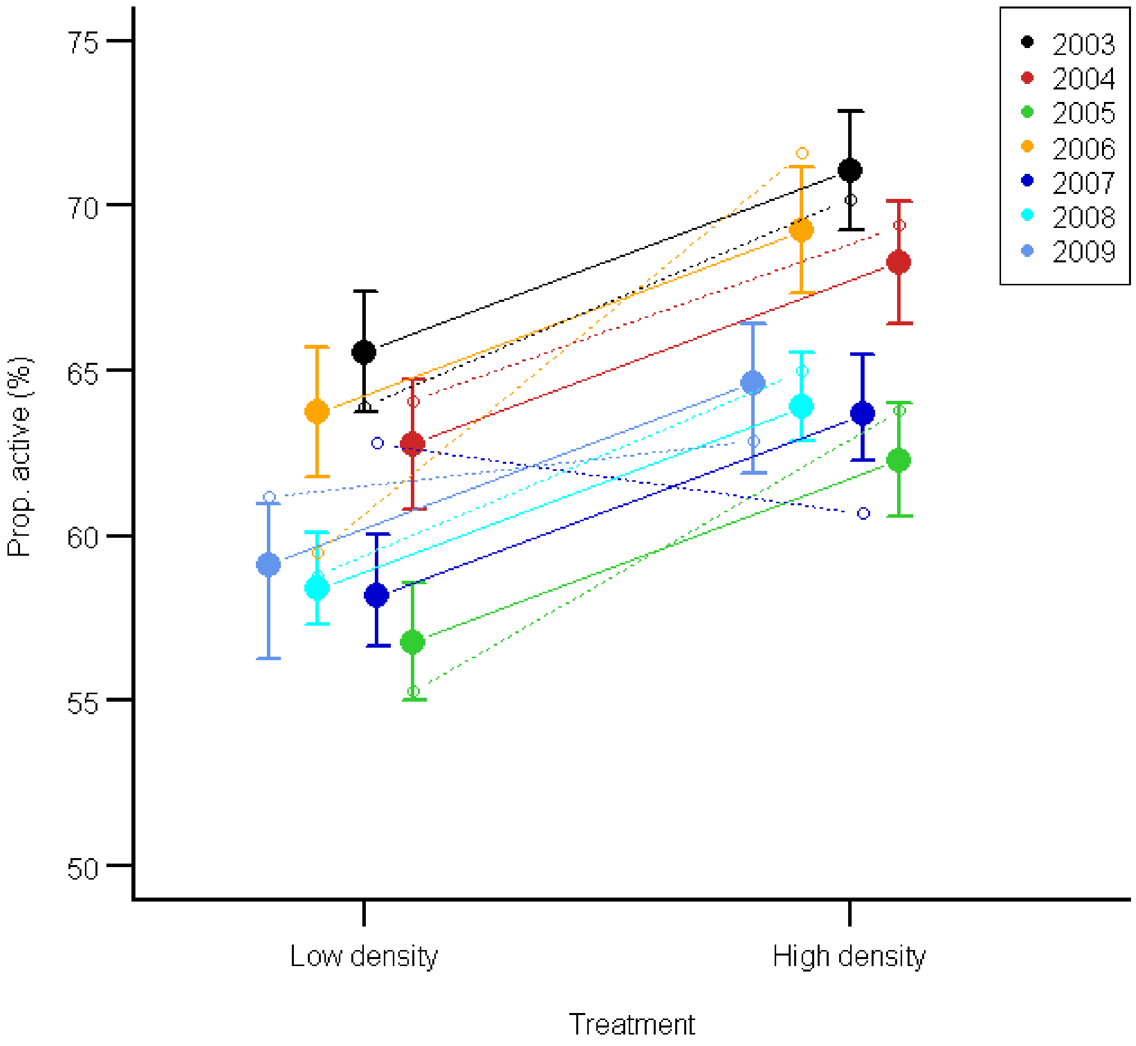
Prop. active (%)
75
70
65
60
55
50
Low density
High density
Treatment
2003
2004
2005
2006
2007
2008
2009

Figure 1.

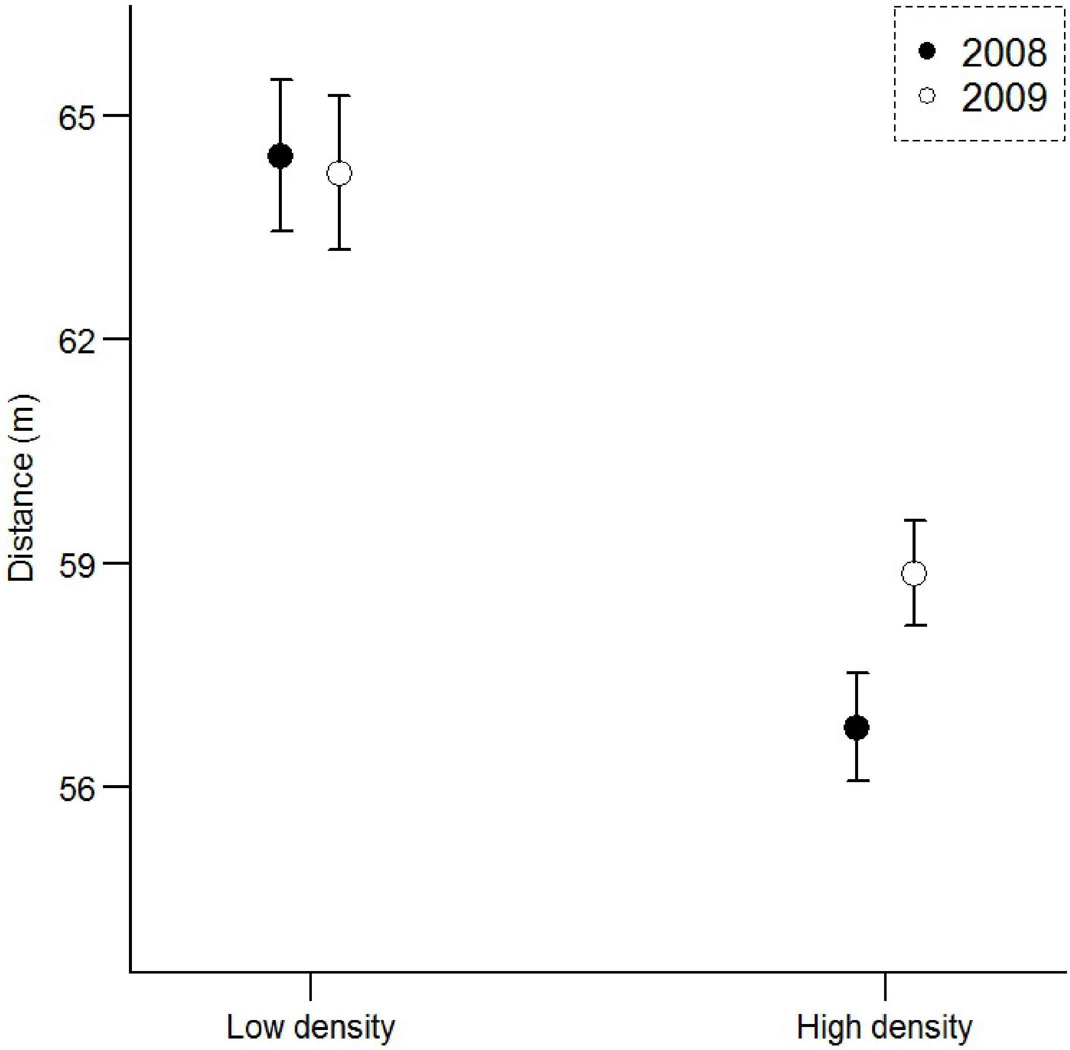

Figure 2.

Electronic supplementary material

Appendix 1. Results of model selection of sheep activity in Hol, Norway, using linear mixed effects models. The response variable is the binominal variable active (1) or inactive (0) behavior. Main effects were included due to predictions specified in Introduction. Random effects were always “individual” and “sub-enclosure”. The models are ordered according to descending AIC values. ΔAIC = difference in AIC value between the AIC for a given model and the most parsimonious model (lowest AIC). AIC w = AIC weight. Date is Julian date (standardized). Year was entered both as a categorical (cat) and a continuous (trend) variable.

Variables:							**AIC**	**ΔAIC**	**AIC w**
Density	Date	Year (cat)	Year (trend)	Density x Date	Density x Year (cat)	Density x Year (trend)			
x	x	x					7232.0	0.0	0.365
x	x	x			x		7233.0	1.0	0.221
x	x		x				7234.0	2.0	0.134
x	x	x		x			7234.0	2.0	0.134
x	x		x			x	7234.0	2.0	0.134
x	x						7239.0	7.0	0.011
x		x					7285.0	53.0	0.000
x			x				7285.0	53.0	0.000
x							7288.0	56.0	0.000

Paper IV

Temporal variation in density dependent body growth of a large herbivore

Ragnhild Mobæk, Atle Mysterud, Øystein Holand, Gunnar Austrheim

Manuscript

Temporal variation in density dependent body growth of a large herbivore

Ragnhild Mobæk[1], Atle Mysterud[2*], Øystein Holand[1] and Gunnar Austrheim[3]

[1]Department of Animal and Aquacultural Sciences, Norwegian University of Life Sciences,
P.O. Box 5003, NO-1432 Ås, Norway.

[2]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology,
University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway.

[3]Museum of Natural History and Archaeology, Section of Natural History, Norwegian
University of Science and Technology, NO-7491 Trondheim, Norway.

[*]Corresponding author

email: atle.mysterud@bio.uio.no

Tel: +47 22 85 40 45, Fax: +47 22 85 47 26

Running headline: *Density dependent body growth*

Abstract

Temporal variation both due to density dependent and density independent processes affect performance and vital rates in large herbivores. Annual fluctuations in climate affect foraging conditions and thus body growth of large herbivores during the short growing season in alpine habitats. Also, high animal densities on summer ranges may increase competition for food and reduce body mass gain. Yet, little is known about interactive effects of density and climate on alpine summer ranges, and the time scales these processes operate on. In this fully replicated landscape-scale experiment, we kept domestic sheep at high and low densities over nine grazing seasons in an alpine habitat, and tested the relative role of density and annual variation in climate for lamb body mass gain during summer and whether effects of density and annual variation interacted. We found that lambs at high density gained less mass over the summer season than lambs at low density. At short time scales the density effect interacted with annual fluctuations. We documented a longterm temporal trend in body mass development likely due to grazing effects operating differentially at high and low density. At high density lamb autumn body mass declined during the first three grazing seasons and then stabilized, whereas body mass slightly increased over years at low density. This longterm trend suggests accumulative density dependent effects from either biomass or quality reduction and hence delayed food competition at high density and possibly facilitation at low density. Our experiment provides new insight into how density dependent effects on performance of a large herbivore depend on temporal scale of observation.

Introduction

Temporal variation in performance of large herbivores are thought to arise mainly due to density- and climate dependent processes (Gaillard et al. 2000). Most ecologists regard competition for food as the main mechanism behind density dependence in ungulates (Bonenfant et al. 2009). Effects of climate on herbivore performance may be more variable, but at least during summer often found to be mediated by effects on plant quality and availability (Weladji et al. 2002, Mysterud and Sæther 2011). Evidence of both density-dependence and climate effects has been reported in numerous life history traits (Fowler 1987, Sæther 1997, Gaillard et al. 2000), including body mass (Hjeljord and Histøl 1999, Stewart et al. 2005). Moreover, climate and density-dependent effects frequently interact. Unfavourable climatic conditions are often more important at high population densities (Gaillard et al. 1997, Milner et al. 1999, Coulson et al. 2001). Convincing evidence of climate-density interactions comes from the winter season, when animals in poor condition due to high population density are more prone to die during harsh winter conditions than at low density (Portier et al. 1998, Coulson et al. 2001). However, much less is known regarding how density dependent body growth during the plant growing season may interact with climate variation.

Northern ungulates experience substantial annual variation in plant phenology during the short growing season (Mårell et al. 2006). Conditions during spring and summer are particularly crucial for juvenile growth, as well as for deposition of fat reserves necessary to survive and sustain a harsh winter climate. For example, early onset of vegetation growth (Pettorelli et al. 2005, Herfindal et al. 2006) and a slow phenological development throughout the growing season (Mysterud et al. 2001, Herfindal et al. 2006, Pettorelli et al. 2007) affect juvenile autumn body mass positively (sheep *Ovis aries*; Mysterud et al. 2001, reindeer *Rangifer tarandus*; Pettorelli et al. 2005, moose *Alces alces*; Herfindal et al. 2006). In years of poor vegetation development, we would predict increased competition for forage, and thus that the strength of density dependence varies among years. For moose, there was evidence for more marked effects of environmental variation on body mass in populations with small mean autumn body mass living at higher densities than in populations with large-sized individuals living at lower densities (Herfindal et al. 2006). These interesting results suggest indeed that there may be interaction between climate and density effects also during summer, but the correlative study compares populations from areas that differ largely in a range of environmental factors. There is yet no quantification of how variation in climate affects the strength of density dependence after controlling for potential regional differences in environment.

Another largely unresolved issue is the matter over which temporal scale different mechanisms of density effects occur (Kuijper et al. 2008). Even in the short term, high animal densities increase forage competition and reduce body mass gain (review in Bonenfant et al. 2009). As large herbivores are selective foragers with preference for high quality plants or plant parts, they respond to increased competition by including more low quality plant material in their diet (white-tailed deer *Odocoileus virginianus texanus*; Kie et al. 1980, Freeland and Choquenot 1990, feral donkeys *Equus asinus*; Choquenot 1991, goats *Capra aegagrus hircus*; Mellado et al. 2003). At longer time scales, grazing pressure and selective foraging may alter productivity and composition of alpine plant communities (Austrheim and Eriksson 2001, Bråthen et al. 2007). If density effects gradually modify properties of the foraging habitat, for example by decreasing spatial heterogeneity (Adler et al. 2001), homogenizing the abundance of palatable plant species (Adler et al. 2001, Bråthen et al. 2007), changing plant productivity (Harrison and Bardgett 2008) or nutritive quality (Mysterud et al. 2011), this may have important consequences for ungulate foraging strategies potentially affecting body mass gain negatively over time (Simard et al. 2008). Predicting the direction of plant-herbivore interactions and how longterm grazing pressure may affect temporal variation in ungulate body mass is not straightforward. Effects of grazing on plant community development may in theory lead to both negative and positive effects in the longterm depending on the ecosystem. Indeed, grazing may lead to facilitation in nutrient rich ecosystems by increasing nutrient cycling and productivity and by favouring tolerant grass species over resistant woody species (McNaughton et al. 1997, Arsenault and Owen-Smith 2002). Yet, empirical evidence of how body mass growth evolves under different densities is scarce. For a browsing herbivore (white-tailed deer) in a forest ecosystem, a manipulation of density documented that longterm browsing reduced diet quality and subsequent body growth (Simard et al. 2008). However, it remains unclear whether the same result applies to grazers in grassland ecosystems often thought to favour tolerant species.

In this fully replicated landscape-scale experiment, we kept a large grazing herbivore (domestic sheep) at high and low density in alpine habitats over 9 successive grazing seasons (2002-2010). Our aim was to identify the relative role of density dependent and density independent (climate) processes for lamb body mass gain during summer, and to explore whether density-climate interactions could explain temporal variation in lamb autumn body mass. The foraging conditions within the experimental area are affected both by large annual variation in plant growth due to climate (Evju et al. 2006), and density dependent responses to grazing in vegetation development and soil properties. For example, high sheep density reduced biomass of vascular plants, and highly selected herbs declined, whereas vascular plants were largely unaffected by low sheep density (Austrheim et al. 2008a). Further, soil nitrogen decreased more at high sheep densities as compared to low densities although N removal is minor in relation to the total soil N pool (Martinsen et al. 2011a). At low sheep density, grazing increased soil carbon storage over years (Martinsen et al. 2011b). In line with these results, we tested the following predictions:

H1. Density dependence. Lamb autumn body mass is density dependent and lambs at high density have lower body mass than lambs at low density.

H2. Annual variation. If climate (working through plant phenology, quality or biomass) contributes most to a between-year variation in lamb autumn body mass, we predicted body mass to vary irregularly between years (H2a). Competition for forage may be more severe in years with poor vegetation development, we therefore predicted annual variation in the strength of the density dependent response (H2b).

H3. Year trend. Since sheep grazing may affect the foraging habitat over the time-scale of years (Austrheim et al. 2008a), we predicted a longterm density dependent trend in body mass development. The trend might be both positive if grazing enhanced habitat productivity, or negative if grazing removes the best quality forage. Thus, we predicted a negative longterm trend for lambs at high density and positive trend for lambs at low density. We also tested whether the difference in autumn body mass for lambs at high and low density increased over years (i.e. an interaction between density and year), if grazing at high and low levels differentially affect the habitat.

Material and methods

Study area

The study area is located in Hol municipality, Buskerud county in southern Norway (60º40´N, 7 º55´E). The area is characterized by a sub-continental alpine climate with annual precipitation approximately 1000 mm (Evju et al. 2009). The bedrock consists of metaarkose (Sigmond 1998), and the soil is moderately base-rich. In year 2001, a large fenced experimental enclosure covering 2.7 km^2 was established, mainly in the lower alpine zone. The enclosure covers an altitudinal span from the forest line (1050 m a.s.l.) up to 1320 m a.s.l. Vegetation is dominated by dwarf shrub heathland with scattered lichen heaths, snow-beds and grass-dominated meadows (Rekdal 2001). A few birch (*Betula pubescens*) trees are found in the areas with lowest elevation (Speed et al. 2010). The vegetation types with highest grazing value for sheep, low- and tall herb meadows (Mobæk et al. 2009), constitute 9 % of the vegetation cover (Rekdal 2001).

Experimental design and data collection

The large enclosure was divided into nine sub-enclosures in order to facilitate a randomized replication within three blocks, the average size of the sub-enclosures being 0.3 km^2 (Austrheim et al. 2008a). The division of the enclosure was performed in a manner that ensured that each of the sub-enclosures covered approximately the same altitudinal range and a comparable distribution of vegetation types. Lastly, each of the three sub-enclosures within a block was randomly assigned the treatments high density, low density or control (no sheep). A botanical survey estimating the distribution of different vegetation types and their respective grazing value for domestic sheep provided the basis for calculation of sheep density levels. Consequently, 80 and 25 sheep per km^2 were chosen as high and low density treatments, respectively, numbers that correspond to actual densities of free ranging sheep grazing on Norwegian mountain pastures. Sheep grazing was initiated in 2002, and a total of 23 to 26 lactating ewes and 44 to 49 lambs belonging to the same sheep farmer were released into the experimental enclosure each grazing season. As far as possible, ewes with singleton, twin and triplet lambs were distributed evenly between the sub-enclosures to ensure an equal representation of ewes with different reproduction status between the two density levels. The sheep were of the breed “Norsk Kvit Sau”, which is the largest and most common breed in Norway (Drabløs 1997). Each grazing season lasted from late June to late August or early September, and the number of grazing days used in this experiment thus mirrors a typical grazing season in Norwegian alpine pastures.

Ewes and their lambs were weighed at the days of release and recapture from the alpine pastures. Before release, all sheep were treated with anthelmintic parasite treatment ("Ivermectin"). Body mass was determined to the nearest 0.5 kg. This study comprises data from nine consecutive grazing seasons (2002-2010) (see Table S1 in the electronic appendix for details). During this period a total of 413 lambs and 217 ewes have been grazing in the enclosures. Note that as many of the ewes were used in the experiment more than one season and some of the lambs were lost due to predators and diseases, we use body mass from 394 lambs with 132 individual mothers in the statistical analyses (Table 1).

Statistical analyses

Body mass was ln-transformed prior to analyses to stabilize variance. We used GAM-plotting in the R library "mgcv" to check for any possible non-linearity and to explore patterns in our data and establishing sound parameterizations of higher order terms. Then, we fitted generalized linear mixed effects models in the R library "lme4" to analyze whether lamb autumn body mass was affected by density, annual variation, sex, litter size (categorical; 1-3), spring body mass, mother spring body mass, ewe age and length of grazing season (grazing days), and to test whether the density effect interacted with annual variation and/or other variables (see Table S2 in the electronic appendix). When testing the effect of annual variation, we tried both year as a categorical and a continuous (trend) variable (see Introduction), in addition to testing year as trend using smoothing splines in the library "splines" (Table S2).

As we have three replications of the density treatment and repeated samplings of body mass from individual lambs with the same mothers (i.e. some ewes were used several grazing season), we always fitted "sub-enclosure" and "mother-id" as random variables in the mixed effect models. To facilitate model comparison and select the most parsimonious model we used AIC (Akaike Information Criterion). The model with the lowest AIC value was used to estimate parameters in order to test our predictions. Finally, we used Markov chain Monte Carlo simulations in the R library “coda” to estimate highest probability density (HPD) intervals for the model parameters, since this is recommended over normal confidence limits for GLMMs fitted with lmer (Pinheiro and Bates 2000). All statistical analyses were done using R vs. 2.12.0 (R Development Core Team 2008).

Results

Lamb body mass averaged 19.3 kg (± 5.0 SD) when released into the experimental enclosure in spring, and 40.2 kg (± 7.7 SD) when recaptured in autumn. Ewes weighed on average 80.5 kg (± 11.1 SD) in spring and 81.8 kg (± 10.9 SD) in autumn. Lamb autumn body mass was density dependent (Table 1). Lambs grazing at high density had lower body mass than lambs at low density (mean 39.1 ± 7.3 SD at high density vs. 43.1 ± 7.9 SD at low density), supporting H1.

Temporal variation significantly affected autumn body mass of lambs. The most parsimonious model included year as a trend and its interaction with density (Table S2), thus supporting our prediction that the grazing effect (H3), rather than climatic fluctuations (H2a), was the most important factor determining temporal variation in density dependent growth of lambs. A significant interaction between density and year indicates a divergence in body mass development over years for lambs grazing at high and low density, as predicted in H3. For lambs at high density, autumn body mass decreased over the nine years studied, whereas autumn weights for lambs at low density were slightly increasing (Table 1, Figure 1).

In general, male lambs were heavier than female lambs (Table 1). Singleton lambs had higher body mass than twins and triplets (Table 1). Further, lambs with high spring body mass were heavier in autumn, and lamb body mass increased with length of the grazing season

(Table 1). Ewes' body mass in spring influenced lamb autumn body mass positively, i.e. heavy ewes produced heavier lambs, while ewe age (linear or squared) did not enter the best model (Table S2).

Discussion

Disentangling the contribution of density dependent and independent processes on ungulate performance is challenging, partly due to their often interactive effects. By keeping sheep numbers constant at two densities replicated 3 times over 9 summer seasons, we showed experimentally for the first time in a large grazing herbivore that density dependent processes may interact with annual variation likely caused by climate effects also during the summer season (Figure 1). The only closely related study is that of Simard et al. (2008) for a browsing herbivore, the white-tailed deer, reporting a longterm negative effect of high density on body growth. Our study highlights the contrasting effect of keeping grazing herbivore numbers at low and high density, having a negative effect if kept at high density and a tendency towards a positive effect if kept at low density (Figure 1).

Mechanisms in the shortterm

Climate-induced temporal variation in body mass is well documented. At northern latitudes, the availability of high-quality forage in early spring and summer is regarded particularly important (Klein 1965, Sæther and Heim 1993, Mysterud et al. 2001, Pettorelli et al. 2005). Body mass gain during summer season depend both on summer weather conditions affecting plant growth (Bø and Hjeljord 1991, Hjeljord and Histøl 1999), but also on previous winters snow depth operating through delaying plant phenological development (Mysterud et al. 2001).

Density dependent variation in performance may arise from several mechanisms also operating in the shortterm, such as competition for food or parasite load (Fowler 1987). Sheep in our experiment was treated for parasites before release. Though we cannot control for potential reinfection later in the season, the shortterm effects of density most likely arise from competition for forage. Indeed, a count of parasite eggs in ewe and lamb faeces conducted during recapture of sheep (September 2009) found no difference in parasite load between sheep at high and low density (Ø. Holand, unpubl.). In our experiment, density affected selection at both fine (diet) and course (habitat) spatial scale, which at least partly explain density dependent reductions in growth. Sheep at low density grazed more in high-quality vegetation types (low- and tall herb meadows) than sheep at high density (Mobæk et al. 2009). As a result, sheep at high density consumed an average diet of lower quality, including more graminoids and less herbs compared to sheep at low density (Kausrud et al. 2006, Mobæk et al. 2011b), but the density dependent pattern varied between years due to annual climatic variation in plant growth (Mobæk et al. 2011b).

In addition, ewes at high density spent more time active than ewes at low density, indicating increased searching time due to lower availability of preferred forage species at high density (Mobæk et al. 2011a). Food search is energy demanding, and if this activity additively constrains ewe's total forage intake, growth rates by their lambs could potentially be affected either by a similar activity pattern or indirectly by lactation. Already six to seven weeks old, lambs gain approximately the same energy uptake directly through grazing plant material as indirectly through milk (Nedkvitne et al. 1995). Higher competition for the most nutritious forage could reduce milk yield in the first place as shown for red deer (Landete-Castillejos et al. 2003), and this combined with lower forage availability and quality throughout the summer season may contribute to the reduced autumn body mass by lambs at high density.

Grazing by ungulates may both reduce and increase primary production (Hobbs 1996), and one potential short-term facilitation mechanism arise when grazing stimulates grass regrowth (Arsenault and Owen-Smith 2002), thus extending the period of fresh plant material during the summer season. We found indeed a higher N content later in the season in grasses from high sheep density enclosures likely due to grazing keeping grasses in young phenological stages (Mysterud et al. 2011). Apparently, this effect was not strong enough to counter the likely effect of food competition at high density.

Longterm effects – delayed competition vs. facilitation

Increased densities indicative of increased food competition on summer pastures has been reported to lower autumn body mass for a range of different ungulates (Bonenfant et al. 2009), but mainly on short timescales. There is an increasing interest in delayed effects of density on ungulate performance, as mechanisms of density dependence may change with time scale (Kuijper et al. 2008). Such delayed effects of high density might arise due to "population momentum" operating through age structure changes or maternal effects (Koons et al. 2007, Ezard et al. 2010). For example, despite no vegetation deterioration (Virtanen et al. 2002), newborn red deer calves on Rhum, Scotland continue to decrease in size after 30 years of stable population size most likely due to maternal effects (Coulson et al. 2004). In our case, such effects were controlled for, by entering ewe body mass as a covariate and by not having the same sheep at high and low density every grazing season. Keeping winter conditions constant (i.e. indoor feeding, providing the abundant food availability to all sheep) also possible buffered any "carry-over-effects" from previous summer. Increasing attention is now paid to how herbivore-induced changes in the nutritive value or abundance of forage over longer time spans may cause density-dependent feedback influencing ecosystem productivity (Mysterud 2006, Van der Wal 2006, Bråthen et al. 2007), potentially altering the carrying capacity of the foraging habitat. To be able to test predictions related to grazing effects, manipulating with density is recommended. We found a significant interaction between density and year, and the relationship between lamb autumn body mass and annual variation was better explained by a temporal trend than by erratic between-year climatic variation. This signifies that properties of the foraging habitat have been changed by sheep grazing, and that grazing effects differ between the low and high density enclosures.

For white-tailed deer, high browsing intensity over years minimized the abundance of preferable and palatable tree and shrub species and reduced diet quality (Simard et al. 2008). Longterm grazing may also reduce species diversity and promote dominance of grazing tolerant graminoid species (Austrheim and Eriksson 2001, Hester et al. 2006). An important distinction between grazing and browsing effects however, is that while the grazing process generally accelerates nutrient (i.e. nitrogen) cycling (Augustine and Frank 2001), browsing returns less nitrogen to benefit plant production (Singer and Schoenecker 2003, Pastor et al. 2006). Thus, grazers are more capable of improving their foraging habitat than browsers, but confounding effects of ecosystem productivity in these comparisons make the role of feeding type uncertain. In our experimental area grazing had minor effects on N cycling in soils, but N in soil declined more at high density (Martinsen et al. 2011a, Martinsen et al. 2011c). Our experiment clearly demonstrated that grazing effects may both promote and constrain performance, depending on density. The diverging trends in lamb body mass over years at low and high density may be due to longterm alterations of the most important forage plants for sheep, either in terms of availability, biomass, or nutritive value.

Herbs are considered highly preferable plant species for sheep and other alpine ungulates such as reindeer, and typically decline when grazing pressure increases in alpine ecosystems (Bowns and Bagley 1986, Moen and Oksanen 1998, Austrheim and Eriksson 2001, Bråthen et al. 2007). In our study area, highly selected herb species decreased at high density after four years but were not much affected by low sheep density as compared to controls without sheep (Austrheim et al. 2008a). The decline in herbs was accompanied by an increase in graminoids. Vascular plant cover was reduced at high density vs. low density already after two years since initiation of the experiment. Apparently, lambs at high sheep density responded quickly to a reduced plant biomass, as body mass dropped during the first two-three years and then more or less stabilized (Figure 1). When high grazing pressure over a few years suppressed herbs, the shift towards graminoids likely restricted growth rates and body mass gain.

As low sheep density had minor effects on abundance of important forage species (Austrheim et al. 2008a), the slight increase in lamb body mass over years at low density cannot be explained by changes in plant distribution and frequency. Rather, we propose that low grazing intensity may have altered soil properties in a direction that enhanced nutritive quality of the forage, or perhaps increased biomass within the most productive meadow vegetation. At least, low grazing pressure increased soil carbon storage over years (Martinsen et al. 2011b), which may improve biomass production and thus body mass. Further, vascular plant biomass in meadows and snowbeds increased from 2002 to 2008 at low sheep densities, while biomass at high sheep densities decreased (G. Austrheim, unpubl.). Indeed, sheep at low density tended to use meadows more over years than sheep at high density (2003-2006; Mobæk et al. 2009), and low grazing intensity in these vegetation types may have improved growing conditions for preferable plant species such as herbs. As our results show only a tendency towards increased body mass gain over years for lambs at low density, evidence of grazing facilitation was weak. Thus, the main finding on longterm temporal development in autumn body mass was that high sheep density has changed properties of the foraging habitat towards a state with reduced availability of high-quality forage, resulting in lower performance by lambs.

Conclusion

Our experiment provides new knowledge of how density and temporal variation in interaction determine ungulate performance during summer. On short time scales both annual variation related to climate and density affected lamb body growth, but over years longterm grazing pressure had a stronger effect on body mass gain than annual variation in climate. We found contrasting longterm density dependent effects for lamb growth at high and low density, suggesting that delayed food competition reduced carrying capacity at high density but that the foraging habitat was preserved and maybe even improved by low densities of sheep. Our study contributes to an increased understanding of how longterm plant-herbivore interactions and density dependent foraging strategies may affect juvenile performance, with important implications for temporal variation in vital rates and demography in large herbivores.

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Table 1. Parameter estimation from mixed effects model of (ln) lamb autumn body mass from the grazing seasons 2002-2010 in Hol, Norway (Number of lambs = 394, Mother ID = 132, Sub-enclosures = 6). Reference level for the density effect is “high”, for sex “female” and for litter size “singleton lamb”. When confidence intervals for an estimate do not overlap 0, the variable is significant at 0.05 p-level.

Fixed effects	Estimate	Std. Error	Lower 95% HPD-interval	Upper 95% HPD-interval
Intercept	16.370	4.581	8.421	24.461
Density (low-high)	-36.670	7.884	-51.184	-21.551
Year	-0.008	0.002	-0.012	-0.004
Sex (male vs. female)	0.053	0.008	0.037	0.071
Litter size (triplet vs. singleton)	-0.068	0.015	-0.093	-0.037
Litter size (twin vs. singleton)	-0.042	0.013	-0.060	-0.010
Ln (spring bodymass)	0.595	0.020	0.556	0.633
Ln (ewe spring bodymass)	0.122	0.034	0.045	0.171
Grazingdays	0.010	0.001	0.009	0.012
Density x year	0.018	0.004	0.011	0.026
Random effects			Lower 95%	Upper 95%
Groups	Variance	SD	HPD-interval	HPD-interval
Mother ID	0.002	0.042	0.000	0.025
Enclosure	0.000	0.015	0.000	0.050

Figure captions

Figure 1. Predicted autumn body mass by lambs in Hol, Norway derived from linear models using year as trend[1] (lines) and year as categorical[2] variable (points). The reference level for density is “high”. The predicted values are estimations for female singleton lambs.

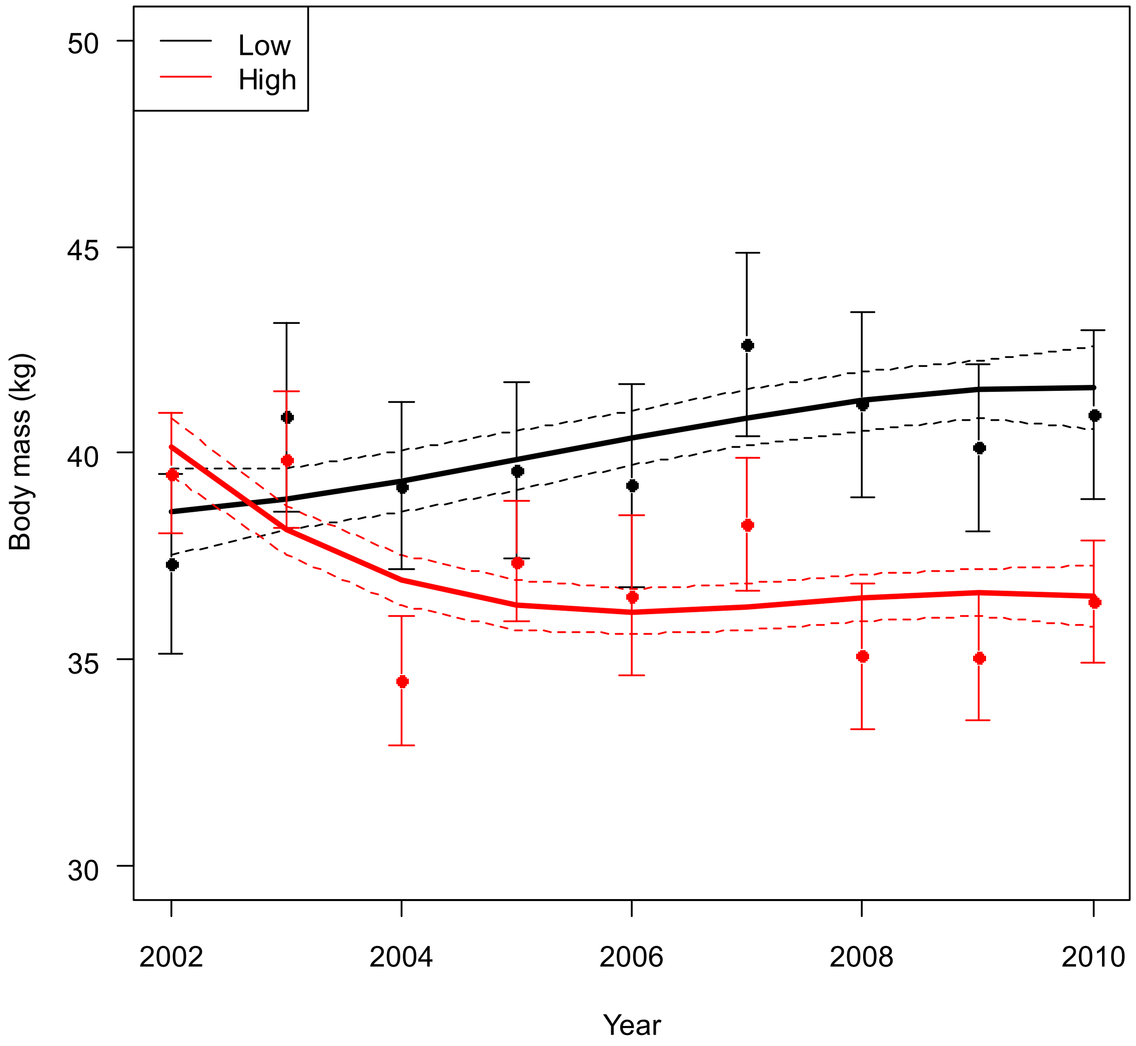
Low
High
50
45
40
35
30
Body mass (kg)
2002
2004
2006
2008
2010
Year

Figure 1

Appendix/Supplementary online material

Table S1. Release and recapture dates, number of grazing days and number of lambs released into the high- and low density sub-enclosures each season.

Year	Release dates	Recapture dates	Grazing days	High density	Low density	Total
2002	24., 29. & 30. June	2., 8., & 11. Sept.	64-79	34	11	45
2003	26., 27. & 28. June	29. Aug.	62-64	34	11	45
2004	22. June	1. & 4. Sept.	71 or 74	33	12	45
2005	28. & 29. June	5. Sept.	68-69	33	12	45
2006	24. & 25. June	1. Sept.	65-66	33	11	44
2007	25. June	31. Aug.	64	32	13	45
2008	25. June	12. Sept.	76	34	12	46
2009	23. June	3. Sept.	72	36	13	49
2010	22. June	2. Sept.	72	36	13	49
Total				305	108	413

Table S2. Results of model selection of (ln) lamb autumn bodymass

density	yearcat	yearcat2	year	sex	as.factor(littersize)	ln_springbodymass	ln_ewespringbodymass	eweage	eweage2	grazingdays	density:yearcat	density:year	density:sex	density:as.factor(littersize)	density:ln_springbodymass	density:ln_ewespringbodymass	yearcat:sex	year:sex	yearcat:as.factor(littersize)	year:as.factor(littersize)	year:ln_springbodymass	yearcat:ln_ewespringbodymass	sex:as.factor(littersize)	sex:ln_springbodymass	sex:ln_ewespringbodymass	AIC	ΔAIC	AIC w
x			x	x	x	x	x			x		x														-756.4	0.0	0.4174
x			bs*	x	x	x	x			x		bs*														-755.5	0.9	0.2661
x			x	x	x	x				x		x														-753.7	2.7	0.1082
x			x	x	x	x	x			x		x				x										-752.8	3.6	0.0690
x			x	x	x	x	x			x		x										x				-752.3	4.1	0.0537
x			x	x	x	x	x			x		x	x													-750.6	5.8	0.0230
x			x	x	x	x	x			x		x													x	-750.5	5.9	0.0218
x			x	x	x	x	x			x		x			x											-749.8	6.6	0.0154
x			x	x	x	x	x			x		x												x		-749.4	7.0	0.0126
x			x	x	x	x	x			x		x						x								-747.4	9.0	0.0046
x			x	x	x	x	x			x																-746.6	9.8	0.0031
x			x	x	x	x	x			x		x									x					-746.2	10.2	0.0025
x			x	x	x	x	x	x		x		x														-745.4	11.0	0.0017
x			x	x	x	x	x			x		x		x												-741.9	14.5	0.0003
x			x	x	x	x	x		x	x		x														-741.6	14.8	0.0003
x			x	x	x	x	x			x		x											x			-740.9	15.5	0.0002
x			x	x	x	x	x			x		x		x											x	-736.0	20.4	0.0000
x			x	x	x	x	x			x		x								x						-735.4	21.0	0.0000
x			x	x	x	x	x	x	x	x		x														-735.2	21.2	0.0000
x			x	x	x	x	x	x	x	x		x												x		-728.3	28.1	0.0000
x			x	x	x	x	x	x	x	x		x		x												-720.5	35.9	0.0000
x	x			x	x	x	x			x	x															-697.2	59.2	0.0000
x	x			x	x	x	x	x	x	x																-694.3	62.1	0.0000

Table 2 cont.

density	yearcat	yearcat2	year	sex	as.factor(littersize)	ln_springbodymass	ln_ewespringbodymass	eweage	eweage2	grazingdays	density:yearcat	density:year	density:sex	density:as.factor(littersize)	density:ln_springbodymass	density:ln_ewespringbodymass	yearcat:sex	year:sex	yearcat:as.factor(littersize)	year:as.factor(littersize)	year:ln_springbodymass	yearcat:ln_ewespringbodymass	sex:as.factor(littersize)	sex:ln_springbodymass	sex:ln_ewespringbodymass	**AIC**	**ΔAIC**	**AIC w**
x	x			x	x	x	x	x	x																	-682.8	73.6	0.0000
x	x			x	x	x	x	x	x				x													-675.7	80.7	0.0000
x	x			x	x	x	x	x	x	x	x															-675.4	81.0	0.0000
x	x			x	x	x	x	x	x					x												-669.7	86.7	0.0000
x	x			x	x	x	x	x	x		x															-662.8	93.6	0.0000
x		x		x	x	x	x	x	x																	-643.0	113.4	0.0000
x			x	x	x	x	x	x	x																	-641.0	115.4	0.0000
x	x			x	x	x	x		x	x	x		x	x			x		x							-525.1	231.3	0.0000

* bs denote use of spline in the variable year (i.e. bs(year,k=3) in the model)