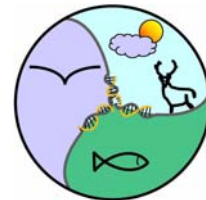**Master of Science thesis**

Annual and density-dependent variation in foraging and growth rates of sheep on alpine pastures

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Preface

This study was conducted at the University of Oslo, Norway and is a part of a bigger project called "Sustainable use of outlying fields in animal husbandry: Ecological effects of sheep on high mountain pastures". This project is a collaboration between the University of Oslo (UiO), the University of Trondheim (NTNU) and the Norwegian University of Life Sciences (UMB). Supervisors of the project were Prof. Atle Mysterud (UiO) and researcher Dr. Gunnar Austrheim (NTNU). Throughout my two years of working I found this to be a very interesting project of great usefulness, as it represents general ecological insights and important results for eventual use in management applications. I liked the crossover of botany and zoology and this made me expand my interest from botany to zoological behaviour biology.

Professor Atle Mysterud from the University of Oslo supervised statistical analyses and succeeding work on this study. I would like to thank Atle Mysterud for his exceptional and time-consuming supervision. Thanks for the help you initiated, when I hurt my knee in the field. You always had some spare minutes to answer my questions and no question was ever too silly. Thank you for being so straight forward, refreshingly honest and always positive minded.

I want to thank all the helpful people who contributed to this work in one or another kind. First of all I want to thank my fiancé Kjell Henrik Jacobsen for always being there for me. I admire his patience with my temper and appreciate him keeping my spirits up. Many others have helped me by commenting, discussing and correcting former versions of this thesis: Irja Ida Ratikainen, Line Gustavsen, Bjørg-Solveig Ingum Lindanger, Hege Line Magnussen Løwer and Rebecca Chance.

I would like to give my honest and greatest gratitude to Camilla Iversen. You were a big help when my knee refused its services in the middle of the grazing season. I also want to thank the Sveingaard family for their enormous hospitality, I always felt welcome and it was a pleasure to visit you after days of loneliness. Thanks to everybody who came to see me, way up in the mountains, I really appreciated the company.

Special thanks go to my friends from the CEES master students reading room. You all helped me when my limited knowledge failed on zoological subjects, and I hope I was able to add some botanical interest to your otherwise zoology orientated weekdays.

Kristina,

Blindern, June 9th 2006

Abstract

A lot of studies have been performed on demographic changes in ungulate population due to density dependence, but little is done on density dependent changes in foraging behaviour which can be a mechanism of such demographic changes. This study presents results of density dependency and annual variation (linked to weather) on sheep grazing behaviour over three years and is the first study to experimentally test for density effects on lamb body mass. In a fully replicated, landscape-scale experiment on mountain pastures in southern Norway sheep were grazing at two density levels. Results of the analyses showed annual variation and density-dependence, but the latter always occurred in interaction with other variables.

The use of the altitudinal gradient by sheep depended on density and year as well as prevailing weather. A clear sky and high temperatures made the animals to seek to higher elevations especially when resting. This might be an adaptation to avoid insect harassment or to keep an optimal body temperature. There was no effect of density on the selection of vegetation types. Sheep selected meadow first both in 2003 and 2004, while ranking of other vegetation types differed between years. The comparison between low quality (*Deschampsia flexuosa*) and high quality (herbs) forage showed effects of density, year and age. The use of *D. flexuosa* varied slightly between years and due to density, while there was a marked effect of age. Ewes ate more grass than lambs did and sheep at high density increased their intake of low quality forage over the season likely due to higher competition. Lambs ate more herbs than ewes in 2003 and 2004 than in 2002 and sheep at low density were able to utilize herbs for a longer time throughout the season. One main result was that lamb body mass showed increased density-dependence from 2002 to 2004. Further, the difference in mass between triplet lambs and singleton lambs was more pronounced at high than at low density. Since triplet lambs growth rates are more sensitive to population density, this suggests monitoring their mass can be used for managing sheep densities on mountain pastures in Norway.

Contents

Introduction

There are many studies of demographic changes in ungulate populations due to density and climate (Gaillard *et al.*, 2000; Sæther, 1997), but fewer studies address the behavioural mechanisms behind such variation. Changes in population density may alter diet and habitat selection being responsible for changes in population vital rates (Borkowski, 2000; Choquenot, 1991; Freeland & Choquenot, 1990). When population densities rise, the increased number of animals can force animals to choose low quality food to supplement to the preferred high quality plants (Borkowski, 2000). Intake of less nutritious food increases rumination time and as a consequence can result in reduced body mass (Choquenot, 1991; White, 1983). Several studies have tried to disclose if cervids respond in their distribution patterns to the predictions made by the Ideal Free Distribution theory (IFD) by Fretwell and Lucas (1969), but the results are very ambiguous. At a small scale, Kohlmann and Risenhoover (1997) found that white-tailed deer (*Odocoileus virginianus*) foraging in a setting with two artificial patches largely confirmed predictions of the IFD. On the other hand, studies on roe deer (*Capreolus capreolus*) at broader scales showed strong spatial structuring in high and low quality habitats and did not obey the IFD (Pettorelli *et al.*, 2001; Pettorelli *et al.*, 2002). In two earlier studies (Iversen, 2004; Kausrud *et al.*, 2006) on domestic sheep (*Ovis aries*) no signs of distributional patterns according to the IFD were shown.

Due to recent climatic changes, increased attention has been paid to the influence of large scale weather phenomena like the North Atlantic Oscillation (NAO) which can affect demography and in turn population dynamics (Stenseth *et al.*, 2002). However, few studies have reported how annual variation in weather conditions on local scales influence grazing behaviour, which may be candidate mechanisms to understand the changes in demographic rates. Additionally, most studies on ungulates are done in winter, because winter survival is crucial for population demography and density, but also because animals are easier to track in the snow (Mysterud, 1999; Mysterud, Bjørnsen & Østbye, 1997; Mysterud, Lian & Hjermann, 1999; Ratikainen, 2005). Many studies therefore show an effect of snow depth on diet selection (Mysterud *et al.*, 1997). Generally, we know much less about how variation in summer weather may affect dietary choices of large herbivores. The selection of altitude may depend on weather criteria like temperature and precipitation decisive for plant development. New emerging plants are of high nutritious quality and are easy digestible (Albon & Langvatn, 1992), and red deer (*Cervus elaphus*) left their winter range later, in years with late

plant phenological development with subsequent reduced summer growth (Pettorelli *et al.*, 2005a). Variation in diet is not the only mechanism that can vary with climate or density. For example reindeer (*Rangifer tarandus*) are harassed by oestrid flies (*Oestridae*) and other parasitic insects on warm and sunny days. The animals select cooler and windier patches to escape harassment (Hagemoen & Reimers, 2002), which leads to less grazing time with subsequent reduced summer growth rates (Colman *et al.*, 2003; Weladji, Holand & Almøy, 2003a).

Large herbivores may have a considerable impact on the environment, and knowing density dependent effects on foraging behaviour is also important to predict ecosystem effects (Kausrud *et al.*, 2006). Free roaming domestic sheep (*Ovis aries*) on mountain pastures are the most abundant large mammal during summer in Norway (Mysterud & Austrheim, 2005). Apart from the fact that sheep foraging is interesting to study from a management perspective; sheep are also ideally suited for studying herbivore summer grazing behaviour in general due to the possibility of experimental manipulation of population densities.

Kausrud *et al.* (2006) showed that density dependence in grazing behaviour in domestic sheep was scale-dependent. Diet selection was density dependent, as sheep at high density selected more low quality forage than sheep at low density, but no density dependence was evident at larger scales (vegetation type selection or altitudinal selection). Similarly, Iversen (2004) at a coarse scale (altitude gradient) found no density-dependence, while there was significant effects of weather variables such as temperature and cloud cover. So far, there has been no attempt to link annual and density dependent variation in diet and habitat selection to body growth, as I here attempt.

As part of a fully replicated, experimental study at a landscape scale with two levels of sheep density on alpine summer range (Mysterud *et al.*, 2005), and based on data from the years 2002, 2003 and 2004, I tested the hypotheses below regarding effects of density and weather on diet and habitat selection and lamb body growth. Sheep habitat selection on a coarse scale is in this study restricted by fences, and focus is therefore on within home range scales (Johnson, 1980) Three spatial scales are examined: from distribution along an (1) altitudinal gradient (Iversen, 2004) to selection of (2) vegetation types and (3) to diet on the finest scale (Kausrud *et al.* 2006). Additionally I examined the effect of density and litter size on (4) lambs' body growth. I expected a higher proportion of low quality habitat and diet at high density and in years with poor vegetation development, with subsequent reduced growth of lambs. Lambs at low densities and small litter size are expected to be heavier than lambs

from high density and those with bigger litter size. I expected that lambs from larger litters were the first to show density-dependent decrease in body mass.

Materials and methods

Study area

The study area is a 2.7 km^2 enclosure located in Hol municipality in the county of Buskerud in Southern Norway. Weather conditions are dominated by a subcontinental alpine climate with moderate to low annual precipitation around 700-800 mm (Førland, 1993). The area spreads from 7°55' - 8°00' and 60°40' - 60°45' (UTM) and lies from 1050-1300 m above sea level with the lowest parts touching the tree line with scattered birches (*Betula pubescens*). It represents a typical Norwegian summer pasture in a fairly rich alpine environment, mainly with low shrubs interspersed with grass meadows. The bedrock is of metaarkose (Sigmond, 1998) and the soil is base-rich. Before the start of the project the area was exposed to very low grazing pressure (<10 sheep per km^2) by domestic sheep. The area is occasionally visited by reindeer (*Rangifer tarandus*) in winter and by moose (*Alces alces*) and roe deer (*Capreolus capreolus*) at night during summer, but this is likely to have negligible effects on the system (Mysterud *et al.*, 2005).
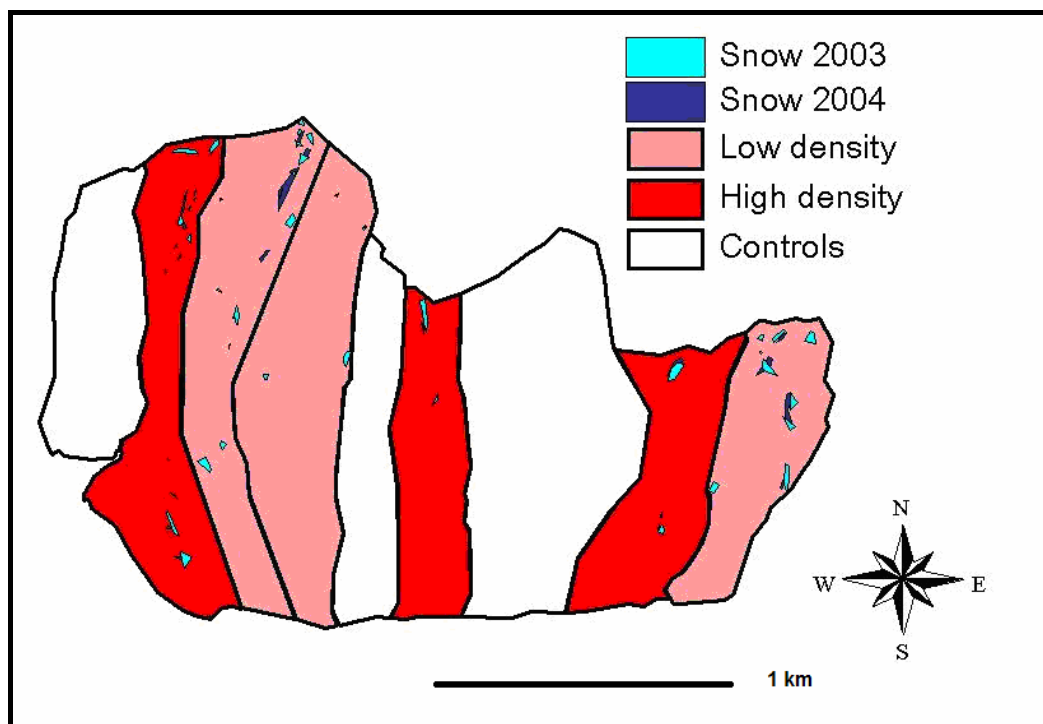

Figure 1: Map over the study area. Experimental set up with 9 sub-enclosures showing controls, high and low and density sub-enclosures. Snow-patches are measured every year at July 1st .

Experimental design

The enclosure established in 2001 contained 9 sub-enclosures of about 0.3 km^2. There was some variation in size due to practical problems when putting up the fences (Mysterud & Austrheim, 2003). A block-wise randomised design with three replicates was used with the treatments: control, low density and high density of sheep. Low density enclosures contained 25 sheep per km^2 and high density enclosures contained 80 sheep per km^2, while control areas did not contain any sheep. These densities are representative for similar areas in southern Norway (Mysterud *et al.*, 2003; Mysterud *et al.*, 2002b; Rekdal, 2001). Altitude is a main determinant for the vegetation in mountain areas because of the temperature changes with increasing elevation, so each sub-enclosure spanned the entire altitude and thereby temperature range. All sub-enclosures contained similar amounts of valuable habitats for sheep grazing (Rekdal, 2001). Every year a total of 69 sheep were released, 24 ewe and 45 lambs. All animals were of the "norsk kvit sau" breed, the most common breed in Norway and from the same sheep farmer. The grazing season in 2002 lasted from June 24th to September 11th, in 2003 from June 26th to August 29th and in 2004 from June 22nd to September 1st. In 2003 the sheep were captured earlier due to loss of two lambs to predators, likely to golden eagle (*Aquila chrysaetos*) and wolverine (*Gulo gulo*) (Mysterud *et al.*, 2005).

Data collection

Sheep location data

All sheep were individually marked by number and colour coded collars. In the years 2003 and 2004 sheep were followed in the enclosures and the use of vegetation types and altitude was recorded. This was also done in 2002 (Kausrud *et al.*, 2006), but following a different sampling scheme and data were thus not directly comparable. The ewe was chosen as the sample unit because the family group with lambs staying close to their mother, was the stable social unit (Kausrud *et al.*, 2006). Each sheep was identified through binoculars and the exact spot and altitude being recorded with GPS. The following variables were noted: date, time of the day, activity, group size and vegetation type. The vegetation types were divided into the categories moss snowbed, grass snowbed, stone polygon land, lichen heath, dwarf shrub heath, low herb meadow, tall herb meadow, bog, fen and boulder field (Mysterud *et al.*, 2005). Also the abiotic variables wind speed, temperature and cloud cover were measured and classified to wind or no wind, clear, changing or cloudy cloud cover (Iversen, 2004). A

stratified randomisation was used to decide which enclosure to pick first and it was randomly decided whether to start high or low in terrain. To cover the sheep activity throughout the whole day, two field observation cycles, early (9:00 to 17:00) and late (14:00 to 22:00) alternated randomly through the grazing season. All sheep of one sub-enclosure were registered before starting on a new sub-enclosure.

Diet

Faeces were collected when sheep location data were retrieved. The individual sheep was identified through binoculars when defecating and faeces were sampled from both lamb and ewe. The sample was packed in plastic bags, frozen and later analysed. About 60 samples were taken during each of the years 2002, 2003 and 2004. The microhistological analysis (Henley, Smith & Raats, 2001; Holechek, Vavra & Pieper, 1982; Mofareh, Bech & Schneberger, 1997; Takatsuki, 2003) was performed by Barbro Dahlberg at the Norwegian University of Life Sciences (Kausrud *et al.*, 2006).

Lamb body mass

Ewe and lambs were weighed before release and after capture in all years 2002, 2003 and 2004. In addition, data on age of ewe were retrieved from the sheep farmer.

Statistical analyses

Analyses were performed mainly by using model selection with linear models (LM). Model selection is used to identify the model that is best supported by the data. Models can be ranked and weighted by the Akaike Information Criterion (AIC). The most parsimonious model is chosen by the smallest AIC value, because it represents the compromise between most variance explained by the model and the smallest number of variables (Burnham & Anderson, 2004; Crawley, 2003; Johnson & Omland, 2004). The best model is then tested with linear mixed effects models (LME). This allows for nesting sub-enclosure and sheep-id numbers as random effects to account for repeated sampling of the same individuals and for the density effects, since the sub-enclosure is the correct replication unit (Crawley, 2003).

Aebischer's Compositional Analysis was used for estimating vegetation type ranking. (Aebischer, Robertson & Kenward, 1993)

All analyses were performed in S-Plus version 6.2 (Crawley, 2003) and the significance level was set to 0.05.

Sheep use of the altitudinal gradient

Sheep activity patterns can be divided into active (grazing) and passive (ruminating or resting) behaviour. The statistical analysis showed the most stable results by dividing the two activity patterns (Iversen, 2004; Kausrud *et al.*, 2006). Location data in the altitudinal gradient was analysed using linear models (LM) and then tested with linear mixed effects models (LME). Second and third order polynomials were included based on biological reasons. The model selection is based on data sampling from the years 2003 and 2004; due to a different sampling technique data from 2002 could not be included. The detailed procedures for model selection are given in tables in the appendix.

Selection of vegetation types

To assess the selection of vegetation types by sheep I compared proportions of utilization to availability of vegetation types. This was done using the compositional analysis method described in Aebischer, Robertson & Kenward (1993). With this method I determined whether or not the sheep used vegetation types at random. In case of non-random use, vegetation types are ranked from most to least selected. The most common vegetation type (dwarf shrub heath) was used as the denominator in the log-ratios. Vegetation types were pooled into five main categories to avoid problems with missing values (Iversen, 2004). The five categories are meadow (low herb meadow and tall herb meadow), lichen heath, snowbed (moss and grass snowbed), dwarf shrub heath and bog (bog and fen). Vegetation types stone polygon land and boulder field are taken out of the analysis, because of very low registrations in 2003 and none in 2004. A replacement value for the remaining numbers of null proportions was calculated. With n independent locations, the proportional use of vegetation type *i* was estimated by [(no. locations in *i*) + 0.5/ no. vegetation types]/(n+0.5), because the recorded use or absence of use is dependent on the sample size (Aebischer *et al.*, 1993). Multivariate ANOVA (MANOVA) was used to test for effects of population density, year and the interaction. The analysis is based on data samples from the years 2003 and 2004, due to a different sampling technique data from 2002 could not be included. I concentrated on the

vegetation selection when sheep were active and did not study effects of season, as these issues are dealt with in earlier studies (Iversen, 2004; Kausrud *et al.*, 2006).

Diet

Most dietary components were too rare for detailed statistical analysis. I therefore only analysed proportional use of the two dominant plant species/groups (herbs and *Deschampsia flexuosa*) with linear models (Colman *et al.*, 2001). As for altitude, I used the AIC to choose the best model subsequently used in parameter estimation with LME with the nested variables sheep-id and sub-enclosure as random effects. To avoid heteroscedasticity ,the data on percentage of herbs and the grass *Deschampsia flexuosa* were transformed with arcsin [sqrt(herbs/100)] (for herbs). Data from all three years 2002, 2003 and 2004 were included.

Lamb body mass

I analysed variation in (ln) autumn weight of lambs using linear models and used model selection with the AIC to find the most parsimonious model. Weight measures in kilograms were ln-transformed to stabilise the variance. The best model was used for parameter estimation with linear mixed effects models (LME), where I used sheep-id nested within sub-enclosure as a random effect. Data from all three years 2002, 2003 and 2004 were included.

Results

Sheep use of the altitudinal gradient

The most parsimonious model analysing variation in altitude at locations where the sheep was actively foraging explained 23.3% of the variation, and included the variables Julian date, density, cloud cover, wind, year and temperature. The interaction terms included in the model were between Julian date and temperature, Julian date and wind, density and cloud cover, density and year, cloud cover and temperature, wind and temperature, wind and year and temperature and year (table 1). All altitudes in the enclosures were used by the sheep in the grazing period, but the particular use of the altitude gradient varied throughout the season and between the two years. There was a tendency for a main effect of density, and density had significant interactions with both cloud cover and year. Sheep from low density enclosure grazed higher up the altitudinal gradient than sheep from high density when there was clear weather (fig. 2). Annual variation was only marked in cloudy weather where sheep grazed higher in 2004 than in 2003, but sheep at low density had lower positions. Generally, the sheep started the grazing season low in the enclosure, elevated their positions through summer and returned to lower areas towards autumn. They kept the low positions in autumn even when temperature rose or wind was blowing (i.e., interaction Julian date and temperature and date and wind). In warm weather sheep picked higher grazing spots, but sheep lowered their position by combination of cloudy sky and high temperature. They also chose lower grazing spots in wind at high temperature. The effect of wind and temperature showed some annual variation so sheep grazed lower under windy conditions in 2004. The same happened at high temperatures in 2004 compared to no wind and low temperatures in 2003.
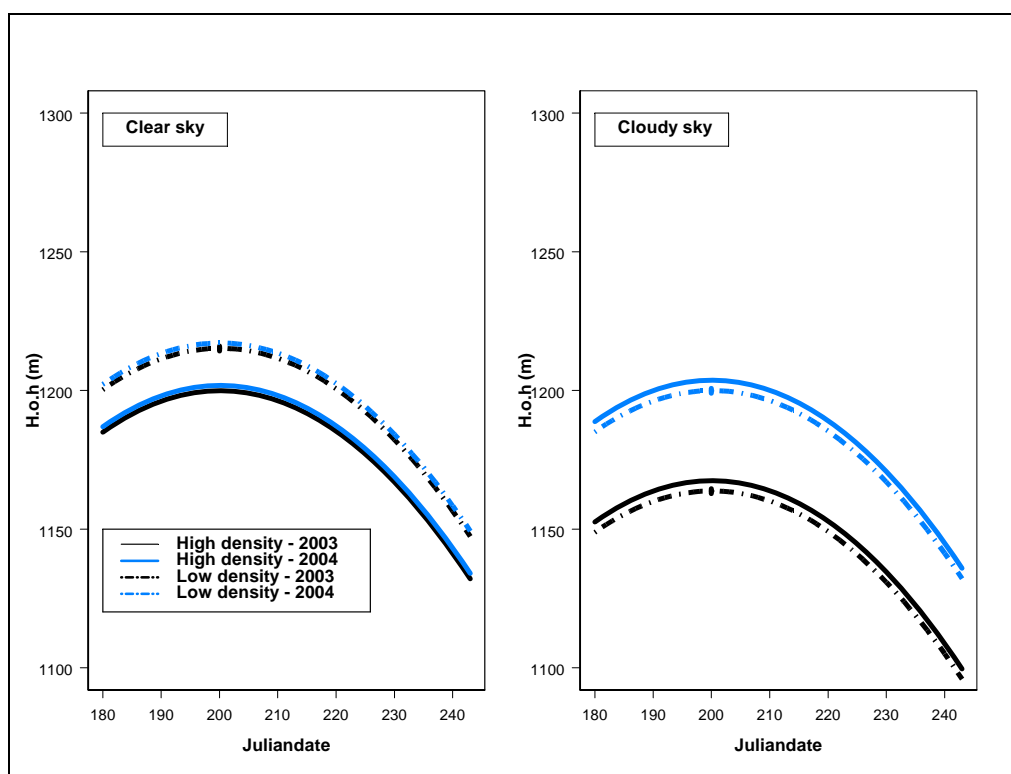
Figure 2: Sheep's grazing in the altitudinal gradient during clear and cloudy weather at different densities and in the years 2003 and 2004. The figure is based on the parameter estimates from table 1.

Table 1: Parameter estimation using linear models with altitude at sheep locations when foraging as a response. Estimations are based on the model with the lowest AIC value (AIC= 11078.16, appendix 1). P-values in **bold** are significant at the P= 0.05 level. LM= linear models, LME= linear mixed effects models.

Parameters	Estimate	Std. Error	LM T	P	LME P
Intercept	-945.650	349.305	-2.707	**0.007**	**0.001**
Julian date	16.725	3.219	5.195	**0.000**	**<.0001**
(Julian date)^2	-0.037	0.008	-4.921	**0.000**	**<.0001**
Density (low vs. high)	51.441	5.724	8.987	**0.000**	0.061
Cloud cover (cloudy vs. clear)	132.333	19.909	6.647	**0.000**	**<.0001**
Wind (wind vs. no wind)	-37.695	54.111	-0.697	0.486	0.739
Year (2004 vs. 2003)	88.929	16.531	5.380	**0.000**	**<.0001**
Temperature	45.994	6.683	6.882	**0.000**	**<.0001**
(Temperature)^2	-0.402	0.076	-5.286	**0.000**	**<.0001**
Julian date * temperature	-0.123	0.027	-4.639	**0.000**	**<.0001**
Julian date * wind (wind vs. no wind)	0.543	0.235	2.313	**0.021**	**0.032**
Density (low vs. high) * cloud cover (cloudy vs. clear)	-19.004	7.043	-2.699	**0.007**	**0.024**
Density (low vs. high) * year (2004 vs. 2003)	-34.301	7.012	-4.892	**0.000**	**<.0001**
Cloud cover (cloudy vs. clear) * temperature	-8.037	1.241	-6.475	**0.000**	**<.0001**
Wind (wind vs. no wind) * temperature	-2.279	0.804	-2.833	**0.005**	**0.000**
Wind (wind vs. no wind) * year (2004 vs. 2003)	-37.298	8.707	-4.284	**0.000**	**<.0001**
Temperature * year (2004 vs. 2003)	-3.295	0.890	-3.704	**0.000**	**0.000**

The best model for analysing variation in altitude at locations where the sheep were passive (resting or ruminating) explained 22.1% of the variation, and included the variables Julian date, density, wind, year, cloud cover, temperature and the interactions between Julian date and cloud cover, Julian date and wind, density and year, cloud cover and wind, cloud cover and temperature and wind and year (table 2). During model selection several competitive models turned up, but none of them explained more of the data or changed the significance of the estimates. Neither density nor year was a significant factor. Sheep rested at different altitudes during the grazing season, and they started early in summer with low resting places and increased height of resting to the middle of the summer. Weather variables temperature and cloud cover were of great influence and gave marked differences in resting at high temperature. Sheep rested higher when there was clear sky and high temperature, than when cloudy weather was combined with high temperatures.
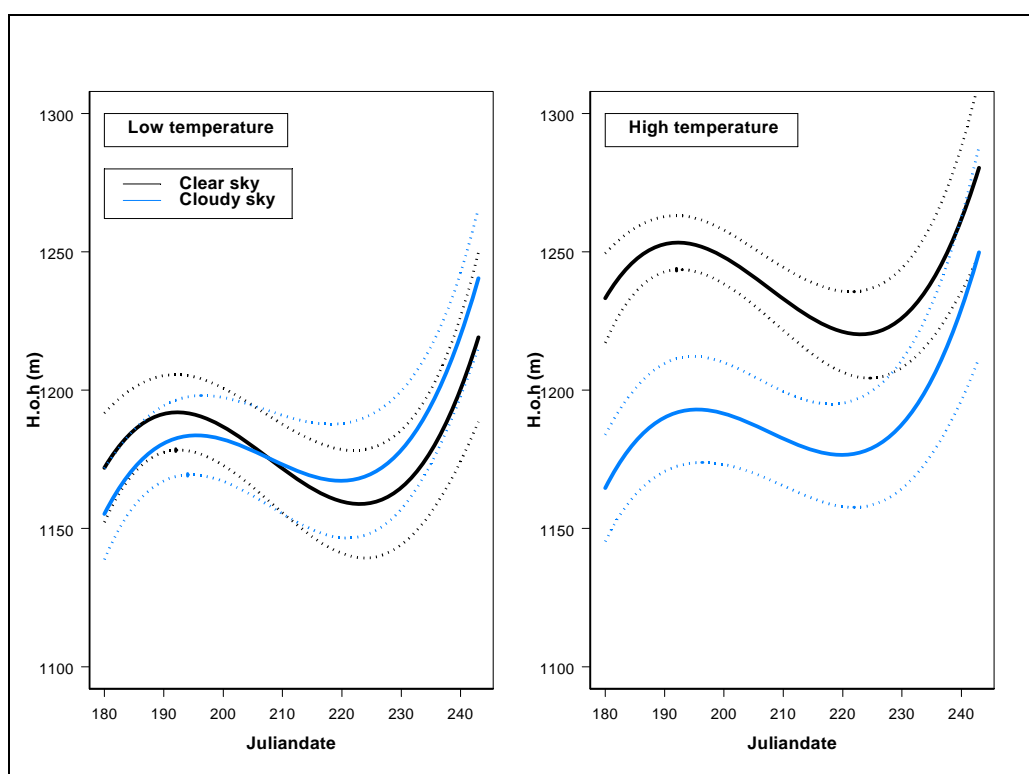
Figure 3: Sheep's resting positions in the altitudinal gradient in clear and cloudy weather at different temperatures throughout the season. The figure is based on the parameter estimates from table 2. Stiplet

Table 2: Parameter estimation using linear models with altitude at sheep locations when resting as a response. Estimations are based on the model with the lowest AIC value (AIC= 5417.042, appendix 2). P-values in **bold** are significant at the P= 0.05 level. LM= linear models, LME= linear mixed effects models

Parameters	Estimate	Std. Error	LM T	P	LME P
Intercept	-18988.741	7067.857	-2.687	**0.008**	**0.019**
Julian date	293.567	102.234	2.872	**0.004**	**0.011**
(Julian date)^2	-1.422	0.492	-2.891	**0.004**	**0.010**
(Julian date)^3	0.002	0.001	2.903	**0.004**	**0.010**
Density (low vs. high)	31.674	7.231	4.381	**0.000**	0.247
Wind (wind vs. no wind)	125.770	84.507	1.488	0.137	0.308
Year (2004 vs. 2003)	25.056	14.976	1.673	0.095	0.162
Cloud cover (cloudy vs. clear)	-94.280	74.073	-1.273	0.204	0.152
Temperature	4.090	0.785	5.210	**0.000**	**<.0001**
Julian date * cloud cover (cloudy vs. clear)	0.604	0.328	1.845	0.066	**0.039**
Julian date * wind (wind vs. no wind)	-0.527	0.428	-1.232	0.219	0.390
Density (low vs. high) * year (2004 vs. 2003)	-18.201	10.594	-1.718	0.086	**0.028**
Cloud cover (cloudy vs. clear) * wind (wind vs. no wind)	21.639	12.634	1.713	0.087	**0.030**
Cloud cover (cloudy vs. clear) * temperature	-3.467	1.703	-2.036	**0.042**	**0.015**
Wind (wind vs. no wind) * year (2004 vs. 2003)	-32.049	15.365	-2.086	**0.038**	0.062

Selection of vegetation types

The vegetation type selection was not density dependent (Pillai-Trace= 0.0929; df= 4, 41, P= 0.394), but animals used vegetation types differently in the year 2003 and 2004 (Pillai-Trace= 0.256; df= 4, 41, P= 0.016). There was no significant interaction between density and year (Pillai-Trace= 0.069; df= 4, 41, P= 0.560). The ranking of the vegetation types in order of selection is given in table 3. Meadow was in both years the most selected vegetation type, but was selected stronger in 2004 than in 2003 at the expense of snowbed and lichen heath (table 3). In 2003 snowbed was the second selected vegetation type while dwarf shrub heath, bog and lichen heath were less selected. In 2004 dwarf shrub heath was the vegetation type ranked after meadow followed by snowbed and bog. Meadow and bog were selected to an extended degree while dwarf shrub heath was selected almost equally both years. Lichen heath was the least selected vegetation type in 2004.

Table 3: An overview of the availability and utilization of vegetation types by sheep in Hol, Buskerud for the years 2003 and 2004. Vegetation types are ranked after their selection level. (Selection = Utilization/Availability)

Vegetation type	Rank 2003	2004	Utilization 2003	2004	Availability	Selection 2003	2004
Meadow	1	1	30.0	41.2	9.6	3.12	4.29
Snowbed	2	3	16.1	8.8	12.9	1.24	0.68
Dwarf shrub heath	3	2	45.5	44.3	54.1	0.84	0.82
Lichen heath	4	5	7.7	3.7	18.1	0.43	0.21
Bog	5	4	0.7	2.0	5.3	0.14	0.38

Diet

Quantitatively, the most important components of sheep diet were herbs (high quality), which represent 22.3% of the sheep's diet and the common grass *Deschampsia flexuosa* (low quality)*,* which represents 33.8% of the sheep's diet. The most parsimonious model explained 48.14% of the variation in the proportion of *Deschampsia flexuosa* in the diet. The model contains the parameters year, age, density, Julian date and the interactions between year and density, year and Julian date, age and density and density and Julian date (table 4). There was no main effect of density on diet selection, but the effect of density interacted with age, year and Julian date. The intake of *D. flexuosa*, considered as low quality food, was lower at low than high density, especially in year 2002, while this was less marked in year 2003 and 2004, and this was less consistent in lambs (fig. 4). The utilization of the grass *D. flexuosa* increased as the season progressed and ewes had more of the grass in their faeces than did lambs.
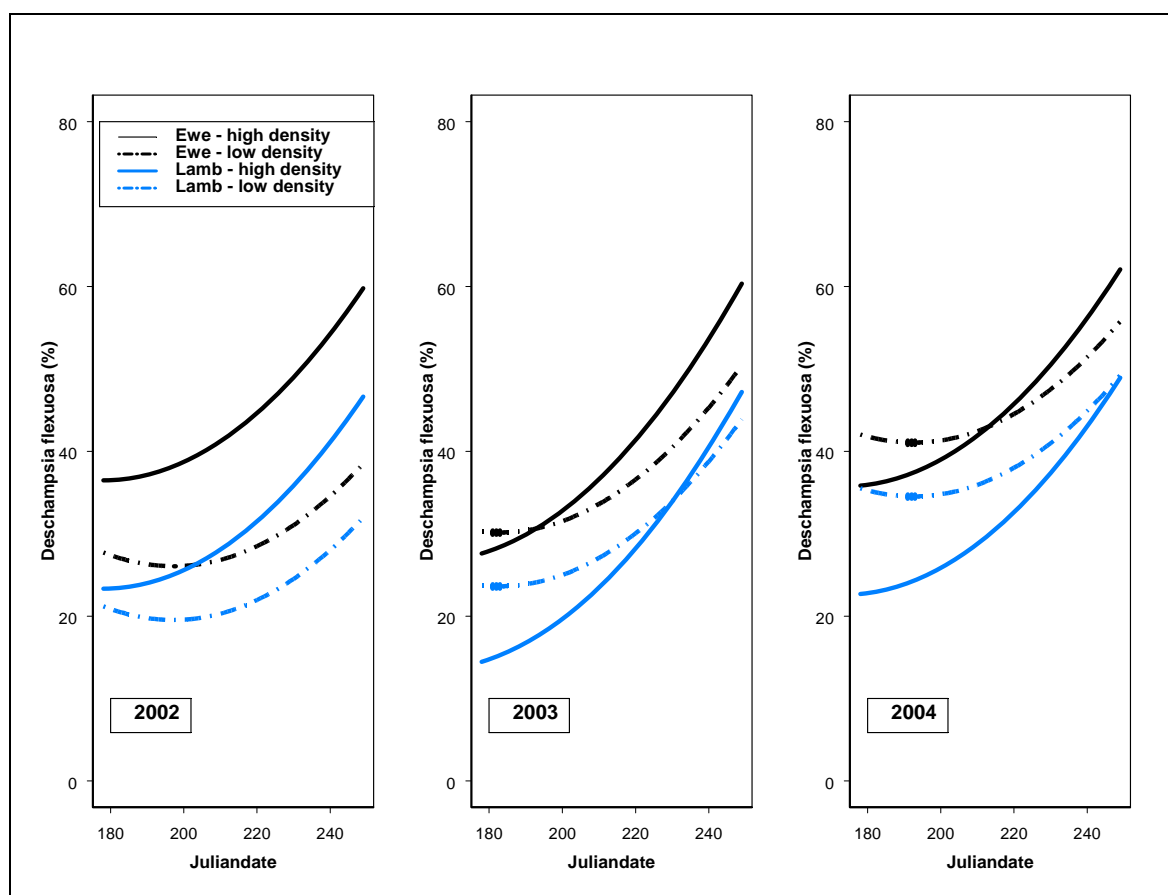
Figure 4: The average proportion of the grass *Deschampsia flexuosa* in the diet of ewe and lamb in the years 2002, 2003 and 2004 as estimated based on microhistological analysis of faeces. The figure is based on the parameter estimates from table 4.

Table 4: Parameter estimation using linear models for results from faeces probes of the grass *Deschampsia flexuosa*. Estimations are based on the model with the lowest AIC value (AIC= -537.543, appendix 3). P-values in **bold** are significant at the P= 0.05 level. LM= linear models, LME= linear mixed effects models

			LM		LME
Parameters	Estimate	Std. Error	T	P	P
Intercept	2.158	0.862	2.502	**0.013**	**0.014**
Year (2003 vs. 2002)	-0.381	0.167	-2.283	**0.023**	**0.038**
Year (2004 vs. 2002)	-0.072	0.147	-0.488	0.626	0.557
Age (lamb vs. ewe)	-0.145	0.017	-8.673	**0.000**	**<.0001**
Density (high vs. low)	0.246	0.128	1.920	0.056	0.153
Julian date	-0.017	0.008	-2.103	**0.036**	**0.040**
(Julian date)^2	0.000	0.000	2.532	**0.012**	**0.013**
Year (2003 vs. 2002) * density (high vs. low)	0.134	0.031	4.297	**0.000**	**<.0001**
Year(2004 vs. 2002) * density (high vs. low)	0.163	0.029	5.578	**0.000**	**<.0001**
Year (2003 vs. 2002) * Julian date	0.002	0.001	1.957	**0.051**	0.082
Year (2004 vs. 2002) * Julian date	0.000	0.001	0.553	0.580	0.519
Age (lamb vs. ewe) * density (high vs. low)	0.071	0.024	2.922	**0.004**	**0.004**
Julian date * density (high vs. low)	-0.002	0.001	-3.176	**0.002**	**0.003**

The best model for the analysis of the proportion of herbs in the diet explained 51.25% of the variation in the available data. It contained the variables year, age, density, Julian date and the interactions between year and age, year and density, year and Julian date, age and density, age and Julian date as well as Julian date and density (table 5). There was no main effect of density, but there was interaction with year and Julian date. The use of herbs showed definitely annual variation as the utilization differed between the years, and in 2003 and 2004 lambs ate more herbs than ewes did (fig. 5). Herbs are continuously used throughout the season with use tending to decline towards the end, but in 2004 the grazing on herbs declined earlier towards autumn than in 2002. Sheep from low density sub-enclosures used herbs to a higher extend throughout the season than sheep from high density did, especially in lambs.
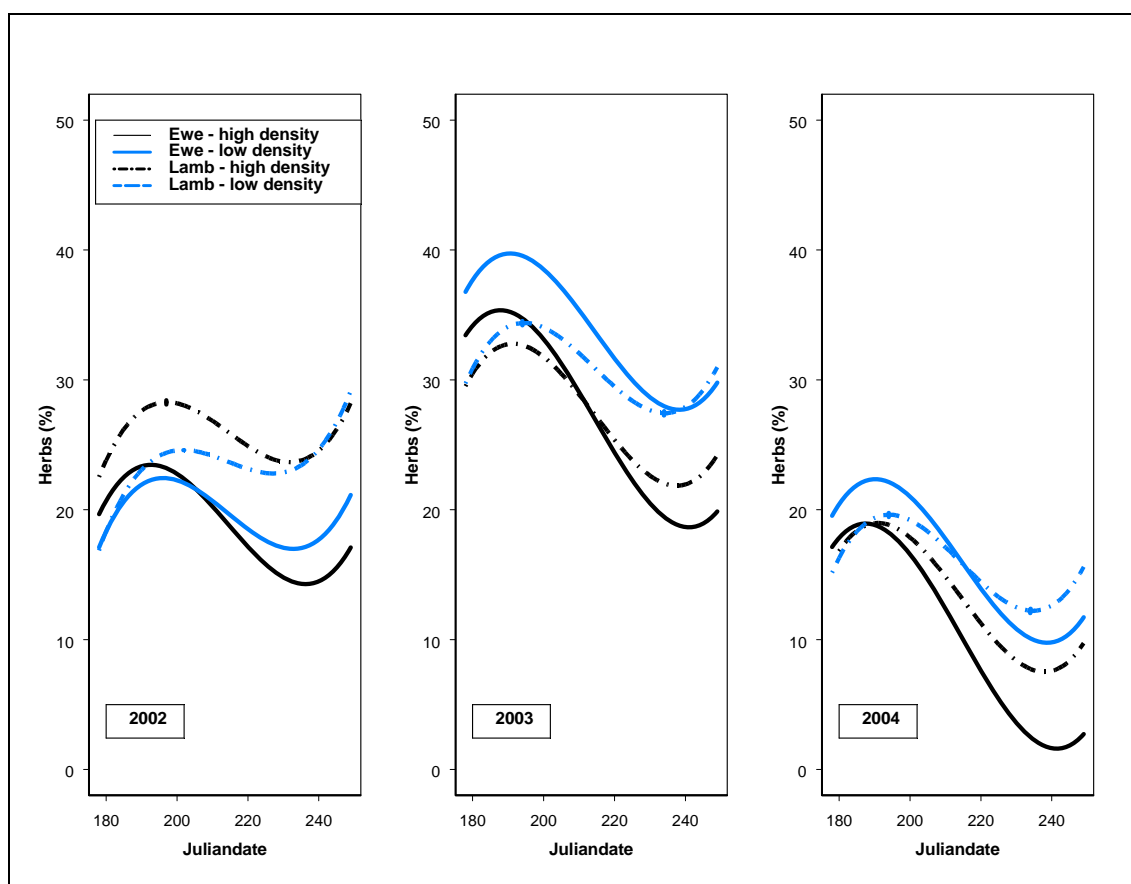
Figure 5: This figure is a prediction from the best model for the results from faeces probes. It shows the average intake of herbs for ewe and lamb in the years 2002, 2003 and 2004.

Table 5: Parameter estimation using linear models estimating proportion of herbs in the diet based on analyis of faeces . Estimations are based on the model with the lowest AIC value (AIC= -555.393, appendix 4). P-values in **bold** are significant at the P= 0.05 level. LM= linear models, LME= linear mixed effects models

Parameters	Estimate	Std. Error	LM		LME
			T	P	P
Intercept	-26.602	11.014	-2.415	**0.016**	0.062
Year (2003 vs. 2002)	0.417	0.172	2.424	**0.016**	**0.018**
Year (2004 vs. 2002)	0.435	0.153	2.839	**0.005**	**0.010**
Age (lamb vs. ewe)	-0.257	0.127	-2.026	**0.044**	**0.026**
Density (low vs. high)	-0.229	0.125	-1.826	0.069	0.123
Julian date	0.387	0.159	2.436	**0.015**	0.061
(Julian date)^2	-0.002	0.001	-2.403	**0.017**	0.068
(Julian date)^3	0.000	0.000	2.358	**0.019**	0.078
Year (2003 vs. 2002) * age (lamb vs. ewe)	0.075	0.029	2.550	**0.011**	**0.009**
Year (2004 vs. 2002) * age (lamb vs. ewe)	0.072	0.029	2.455	**0.015**	**0.010**
Year (2003 vs. 2002) * density (low vs. high)	-0.074	0.030	-2.436	**0.015**	**0.006**
Year (2004 vs. 2002) * density (low vs. high)	-0.040	0.029	-1.393	0.164	0.278
Year (2003 vs. 2002) * Julian date	-0.002	0.001	-1.855	0.064	0.085
Year (2004 vs. 2002) * Julian date	-0.003	0.001	-3.655	**0.000**	**0.001**
Age (lamb vs. ewe) * density (low vs. high)	-0.037	0.024	-1.574	0.116	0.116
Age (lamb vs. ewe) * Julian date	0.001	0.001	2.082	**0.038**	**0.024**
Julian date * density (low vs. high)	0.002	0.001	2.468	**0.014**	**0.006**

Lamb body mass

The most parsimonious model (table 6) explained 87.5% of the variation in (ln) autumn body mass of lambs and included the factors (ln) spring body mass, density, year, litter size and sex. The model also included the interactions between density and year, density and litter size and sex and spring body mass. There was no main effect of density on body mass (table 6). However, density gave marked results in interaction with year and litter size. Litter size was almost significant (LM: p= 0.061; LME: p= 0.060) and triplet lambs were of less body mass than singletons, especially at high density. Lamb body mass were lighter in 2004 at high density, but not at low density. In 2002 single female lambs in low density weighed on average 40.1 kg while single lambs in high density enclosures had a weight of about 41.2 kg. The body mass of triplet lambs in low density was around 39.6 kg while lambs in high density enclosures were 39.2 kg in weight. In the year 2004 single lambs from low density sub-enclosures weighed on average 41.1 kg and single lambs of high density had an average weight of 37.5 kg. Here triplets showed a difference with density, as lambs at low density weighed 40.6 kg and at high density had a body mass of 35.6 kg (fig.6).

Further, male lambs were heavier than female lambs. The (ln) spring body mass had positive influence on the weight of the lambs in autumn, and more so in male lambs (i.e. an interaction between sex and spring body mass). The mother spring weight showed a positive effect on the autumn body weight of her lambs. Body mass of the lambs also increased with increased length of the grazing season.
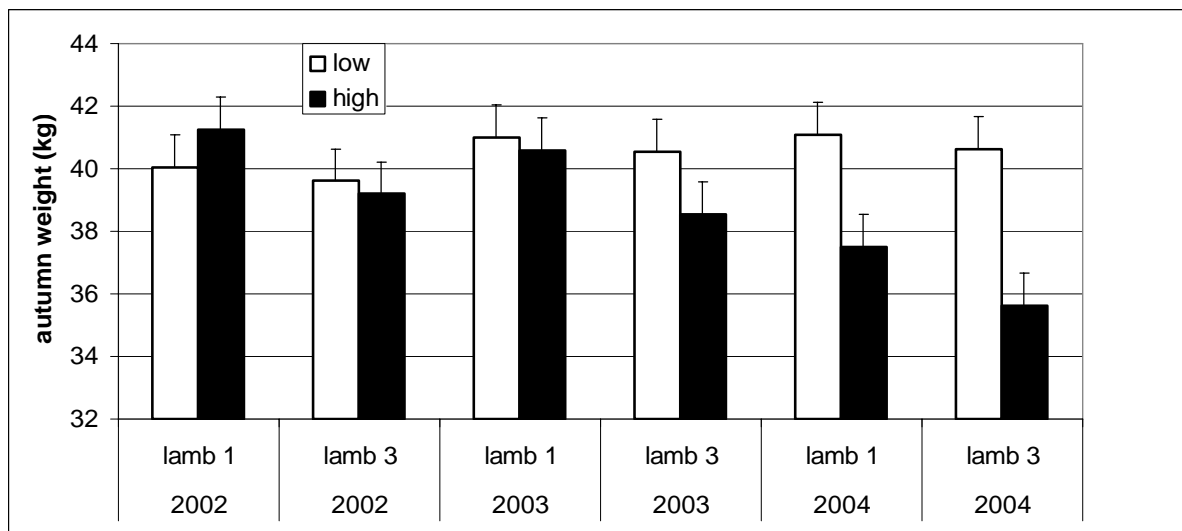
Figure 6: Predicted average (+Std. Error) autumn body mass for female lambs of different litter size (1 vs. 3) at high and low density in the years 2002, 2003 and 2004. Predicted values are based on the estimates from table 6.

Table 6: Parameter estimation using linear models for (ln) autumn body mass of lambs, based on the model with the lowest AIC value (AIC= -285.0513, appendix 5). P-values in **bold** are significant at the P= 0.05 level. LM= linear model; LME= linear mixed effects models

Parameters	Estimate	Std. Error	LM T	P	LME P
Intercept	0.100	0.323	0.309	0.758	0.766
Ln (spring body mass)	0.698	0.046	15.196	**0.000**	**<.0001**
Sex (male vs. female)	0.426	0.165	2.583	**0.011**	**0.014**
Year (2003 vs. 2002)	-0.016	0.024	-0.663	0.509	0.567
Year (2004 vs. 2002)	-0.095	0.021	-4.591	**0.000**	**<.0001**
Ln (mother spring body mass)	0.199	0.057	3.495	**0.001**	**0.001**
Litter size (2 vs. 1)	-0.016	0.025	-0.639	0.524	0.573
Litter size (3 vs. 1)	-0.051	0.027	-1.891	0.061	0.060
Density (low vs. high)	-0.029	0.040	-0.735	0.464	0.507
Julian date	0.010	0.002	4.919	**0.000**	**<.0001**
Year (2003 vs. 2002) * density (low vs. high)	0.040	0.040	1.003	0.318	0.301
Year (2004 vs. 2002) * density (low vs. high)	0.121	0.042	2.877	**0.005**	**0.004**
Sex (male vs. female) * ln (spring body mass)	-0.116	0.056	-2.084	**0.039**	**0.048**
Litter size (2 vs. 1) * density (low vs. high)	-0.040	0.043	-0.939	0.350	0.316
Litter size (3 vs. 1) * density (low vs. high)	0.040	0.044	0.908	0.366	0.349

Discussion

This is the first experimental study on the effect of density on both sheep foraging behaviour and lamb body mass. As sheep foraging behaviour has been studied in detail before (Iversen, 2004; Kausrud *et al.*, 2006) the main focus in this study is on effects of density and annual variation and lamb body mass performance. Generally the results show no main effect of density, but there often was an interaction between density and other factors, such as annual variation or climate. Density and annual variation influenced grazing behaviour, diet choice and lambs' growth rates. The selection for vegetation types was density-independent but affected by annual variation, while resting behaviour neither was density-dependent or influenced by the variation between years.

The use of the altitudinal gradient was density-independent when sheep were resting and only influenced by weather parameters and differences among years. Sheep went higher in high temperatures and lower when high temperature was combined with cloudy sky. The same applied for grazing behaviour but this was also density-dependent, as sheep at low density exploited the higher part of the sub-enclosures further. As found earlier (Kausrud *et al.*, 2006), meadow is the major selected vegetation type and its use is density-independent. However, there was annual variation in selection of vegetation types, as the ranking of other available vegetation types varied between the years 2003 and 2004. Diet selection, the intake of *Deschampsia flexuosa* was influenced by annual variation and density, but mainly by the length of the season and age. The sheep increased the intake of the grass towards the autumn and ewes ate more grass than lambs did. There was no main effect of density although density interacted with age and annual variation. The utilization of herbs showed no main effect of density either, but an effect of annual variation. Herbs were continuously used for forage over the grazing season and lambs ate more herbs than ewes did. An interesting result was that the effect of density on lamb body mass interacted with both annual variation and litter size. While mass was stable over time at low density, mass decreased from 2002 to 2004 at high density. Singleton and twins were larger than lambs from triplets, and this difference was more pronounced at high density.

Density dependence and annual variation in foraging and growth

Body mass is a major factor of individual fitness in ungulates. Body mass is generally density dependent and growth rates depend much on habitat and diet selection (Choquenot, 1991; Mysterud *et al.*, 2002a; Pettorelli *et al.*, 2001; Pettorelli *et al.*, 2002; Robertson *et al.*, 1992).

For example, red deer (*Cervus elaphus*) weighed less at high density than deer from low density along the west coast of Norway (Mysterud *et al.*, 2001b). In feral donkeys (*Equus asinus*) high densities led to intraspecific competition for forage, resulting in increased intake of low quality food (Choquenot, 1991). Borkowski (2000), for example, found that sika deer (*Cervus nippon*) at high densities had a different use of habitat resulting in a greater intake of low quality food. Sheep, like other ungulates, compete for high quality food, which become limited at high density. The Ideal Free Distribution (IFD) theory by Fretwell and Lucas (1969) predicts an even fitness among all individuals of a population, because the advantage of a richer habitat gets adjusted by higher density in richer habitats. With increasing density, one would expect a higher use of low quality habitats and altitude range. The previous results from this project (Iversen, 2004; Kausrud *et al.*, 2006) have failed to find distribution patterns according to such a prediction from the IFD theory. Vegetation type selection showed no differences between the two densities. Meadow is the vegetation type with the highest quality for grazing on alpine pastures (Rekdal, 2001) and it is used much more than expected based on its availability (Iversen, 2004; Kausrud, 2004). I show that this result is consistent over years. Neither results in this study from two years of observation on the use of the altitudinal gradient showed signs of density-dependence as it is expected in the IFD theory. The only clue which points towards a changed distribution due to density–dependence is that sheep at high density use lower parts of the sub-enclosures more often and they started earlier in season to eat low quality food (fig. 4). When eating low quality food the animals have to compensate by quantity and the lower parts of the enclosure contain more biomass (Iversen, 2004).

Annual variation in performance can reflect weather-density interactions (Portier *et al.*, 1998). In bighorn sheep (*Ovis canadensis*), the winter-survival of lambs was density-dependent as lamb body mass decreased with increasing density. Spring precipitation affected neonatal survival positively by increasing forage availability and this happened independent of density (Portier *et al.*, 1998). Adult body mass in roe deer was strongly affected by additive effects of cohort and habitat type and the variation in adult body mass was a delayed density-dependent process in reaction to population density at birth (Pettorelli *et al.*, 2002). In Scotland, Soay sheep (*Ovis aries*) cohorts born after warm, windy and wet winters (high NAO index) were lighter in birth body mass, born earlier and less likely to have a twin. Cold and dry winters (low NAO index) and high densities before birth showed a negative effect on lamb birth mass (Forchhammer *et al.*, 2001).

Climatic variation leads to annual variation in plant phenology, which is known to influence performance of northern herbivores (Pettorelli *et al.*, 2005a; Pettorelli *et al.*, 2005b). In years of poor vegetation development, we may expect increased effect of density, i.e., there may be an interaction between the two processes. High snow levels through winter may give an extended period of snowmelt in spring and a prolonged period of new emerging high quality forage (Mysterud *et al.*, 2001a; Pettorelli *et al.*, 2005a). In my study, while selection of meadow was similar between years (table 3), the snowbed vegetation type is a time-restricted high quality habitat that is likely to vary in quality between years depending on previous winter snow conditions. Snowbed (mainly grass snowbed) selection was ranked at second place in 2003 and third in 2004. On average the summer of 2003 was warmer but wetter compared with 2004 which was a dry and cooler summer (Evju *et al.*, 2006). Sheep selected dwarf shrub heath more than snowbed in 2004 probably because of dry conditions when snowbeds melted away faster. Size of snowfields in the study area on July 1st was smaller in 2004 than in 2003 (fig. 1). New emerging plants along the snowbeds are of high nutritional foraging value (Albon *et al.*, 1992) and in 2004 snowbeds may have dried out earlier in the season than usual and the sheep had to replace snowbed with other habitat types for foraging. In 2004 sheep were generally at a higher altitude than in 2003. This may again be due to a drier summer in 2004, where the animals had to roam more to find good forage.

Sheep diet on alpine pastures

Sheep can distinguish between rather small items and pick the highest quality, but hunger can make them less selective (Edwards *et al.*, 1994). Microhistological analyses revealed 28 different plants and their components in the diet of the sheep. One consideration to have in mind is that microhistological analyses generally under-represent easy digestible parts of the diet and over-represent plants that need long digestive period (Henley *et al.*, 2001; Mofareh *et al.*, 1997; Takatsuki, 2003). Herbs can not be distinguished into single species as they do not leave recognisable parts for species detection in the faeces probes after digestion.

From the microhistological analysis two important forage categories were picked to represent high and low quality food available for the sheep to select. *Deschampsia flexuosa* is regarded as a low quality food, is broadly available and quite evenly distributed on the pasture. As previously reported (Kausrud *et al.*, 2006), foraging for *D. flexuosa* shows no main effect of density, but density was highly interactive with year, age and Julian date (table 4). The intake of *D. flexuosa* varied significantly between years as sheep of low density sub-

enclosures increased the intake from 2002 to 2004, but ate less of it later in the season relative to high density. Herbs are both nutritious and easily digestible but are less abundant on the pasture. This may be the reason why season length is so important. When high quality food (herbs) declines at the end of the season, the sheep must change to eating quantity instead of quality at high density, where grazing pressure is higher. My results show no significant density-dependence, but the grazing on *D. flexuosa* is continuous throughout the season, while the intake of herbs declines towards autumn (fig. 5). Also the age of the animal has an impact on the amount of the grass in the faeces (Iversen, 2004). Ewes' uptake of herbs declines towards autumn which might indicate that after the lactation period ewes just maintain body mass, eating quantity instead of quality and do not have to gain mass at the same speed as lambs do. The difference in diet selection between ewes and lambs can either be due to difference in intake or in digestion.

The general intake of herbs in the diet shows no effect of season but is affected more by the age of the animal. Lambs eat more herbs and less grass than ewes do, because herbs are easier to digest and nutritious and smaller in mouth size, lambs might be able to distinguish better between single plants. The lambs start eating easily digestible food after weaning and when getting older increase their intake of heavier digestible, solid food (Iversen, 2004; Nedkvitne, Garmo & Staaland, 1995). Lambs select for the most herbs throughout the whole season to optimize protein uptake in order to gain body mass. Ewes might not be able to distinguish single plants and might not either be so dependent on the selection for high quality food for body growth, as lambs are. The results on diet selection of herbs are found to be density-dependent, but only in interaction with Julian date and year. Sheep at low density had an increased intake of herbs in 2002, but this density-dependent effect dropped over the following two years.

The annual variation in diet selection is most likely due to weather variation, because weather is limiting for plant development (Evju *et al.*, 2006). When herb abundance is low sheep compensate with low quality plants like *Deschampsia flexuosa*. Sheep use more low quality forage when food availability is scarce (Armstrong *et al.*, 1997). *D. flexuosa* as a low quality plant is increasingly selected when high quality plants such as herbs are declining at the end of the summer. Herbs had a significantly lower stature in 2004 than in 2003 due to weather conditions (Evju *et al.*, 2006). The increasing uptake of the grass over the years may indicate a change in vegetation composition over time. All sub-enclosures are treated with the same densities each year. This might reinforce density-dependent effects over time as plant communities gradually change with increasing number of years. Similar results to mine are

found in a study on grazing cattle where 4 stocking rates revealed no effect on utilization of two grass species or the spatial gazing distribution (Burboa-Cabrera, Schacht & Anderson, 2003).

Sheep use of the altitudinal gradient

The experimental design with its physical limitations to movement will certainly limit summer migration patterns in sheep. The physical restrictions (fences) might influence the results in use of the altitudinal gradient, because sheep are known to roam for long distances in a short period at the beginning of the outdoor grazing season, before they settle down in a home-range area (Warren, 1996; Warren & Mysterud, 1993). However, it is likely to give good predictions of possible principles within the range of altitudes observed. Sheep started the season low in the terrain and used, on average, more elevated areas towards the middle of the summer, followed by a return to lower elevation when autumn approached. Towards the end of the season I found that sheep were higher in the area when resting, and salt-stones can be one major reason for this behaviour (fig.3). As the season progresses plants become less nutritious, the sheep's need for minerals increases and they seek the saltlicks (Iversen, 2004). Salt-stones are placed in the middle of each sub-enclosure often on a ridge top (Mysterud *et al.*, 2005). Habitat selection on the altitudinal gradient and on selection of vegetation types depended on the sheep's activity and sheep showed a different use when ruminating or grazing. Sheep showed a preference for places with lichen heath for resting, but lichen heath is of no nutritional value (Rekdal, 2001). Those places are often of elevated position on ridge tops, which at the same time gives the animal the possibility to observe the surroundings i.e. for predators (Nedkvitne *et al.*, 1995).

Migration to higher elevations in large herbivores during summer is regarded as a strategy to increase energy intake (Mysterud *et al.*, 2001a). Animals benefit due to prolonged access to newly emerged forage, which is highly nutritious, as they elevate their positions (Mysterud *et al.*, 2001a). When grazing it should be of interest for the sheep to optimize its uptake of high quality plants, this might be a reason in my study for the strong influence of date on the use of the altitudinal gradient. Late in the season the high quality forage becomes scarcer and animals must vary their use of altitude in their search for the best food. In lower areas biomass of plants is higher and sheep can compensate for poor quality with increased quantity.

When passive, weather conditions might be of greater influence in the selection for altitude, because the need for food is outweighed by the importance for the animal to keep its body temperature at an optimum and to avoid insect harassment (Colman *et al.*, 2001, 2003; Hagemoen *et al.*, 2002; Weladji *et al.*, 2003a). Reindeer (*Rangifer tarandus*) for example are negatively affected by insect harassment and demonstrate a decrease in feeding and resting time and an increase in walking, running and standing (Hagemoen *et al.*, 2002). High temperature and solar radiation are good predictors for oestrid fly activity (Hagemoen *et al.*, 2002). The animals show a trade-off between optimal feeding and parasitic fly avoidance (Colman *et al.*, 2001). A study on bighorn sheep (*Ovis canadensis mexicana*) proved that insect attacks increased with rising temperatures, but insect abundance decreased with increasing wind speed. Bighorn sheep preferred high, open areas with lower temperatures and better wind conditions for resting (Mooring *et al.*, 2003). In reindeer (*Rangifer tarandus*) changed behaviour due to insect harassment had a negative effect on autumn body mass and adult females and calves weighed less after a summer with high insect abundance (Colman *et al.*, 2003). Weladji, Holand and Almøy (2003a) suggest that the expected temperature increase in the course of global warming may increase the insect-relate stress on reindeer. This may also be the case for sheep. Sheep at Minnestølen are higher in the terrain at high temperatures and clear sky than at high temperatures and cloudy sky or at high temperatures combined with wind. In Colman *et al.* (2003), insect harassment was positively correlated with increasing temperature and negatively correlated with increasing cloud cover. A further study should reveal if insect harassment is a reason for the patterns in sheep's use of the altitudinal gradient and the annual variations in this experiment.

Lamb growth on alpine pastures

Slight changes in plant quality can affect body mass of ungulates strongly, because with higher quality food the animal gains more protein and spends less time ruminating (White, 1983). Body mass is the major determinant of winter survival in ungulates (Loison, Langvatn & Solberg, 1999) and on reproductive effort (Mysterud *et al.*, 2001a). At high density, lambs birth body mass was less, litter size smaller and sheep had a delay in age at first reproduction in a study on Soay sheep (*Ovis aries*) (Forchhammer *et al.*, 2001). Robertson *et al.* (1992) found growth rates of lambs to be positively related to an increase in biomass of grass and herbs between spring and summer, but body mass declined with increasing density. In my study I found that lambs' autumn body mass was influenced by their spring body mass and

the spring body mass of their mother, as well as their sex, as male lambs are heavier than female lambs (table 6). The spring body mass of the ewe is a criterion for growth, because a healthy ewe invests more in its offspring. Iteroparous animals do not jeopardize their own life for one single season of offspring production, so populations facing harsh conditions, like high densities or changes in climate, females will favour their own survival rather than current reproduction (Gaillard & Yoccoz, 2003). Because the lactation period is the most energy demanding part of reproduction it is important to synchronize this time of the year with high quality forage availability (Clutton-Brock, Albon & Guinness, 1989).

In years with poor conditions for plant development or high competition for high quality plants due to high densities ungulates may neglect their offspring and focus on self maintenance because of resource shortage (Gaillard *et al.*, 2003). Bighorn sheep reduced maternal care when resources were scarce and favoured their own mass gain over development of their lambs (Festa-Bianchet & Jorgenson, 1998). So density-dependent effects will start to act on offspring levels and when increasing in severity also show impact on performance of adult individuals. High weight at birth also gives a head start for the rest of the life. Ewes with an initial low body mass produced smaller offspring throughout their lifespan (Steinheim *et al.*, 2002). Large mothers produce large offspring (Weladji *et al.*, 2003b) and birth size is less correlated with fitness in female than in male calves. This might be why heavier mothers tend to produce more male offspring (Trivers & Willard, 1973). In my study, spring body mass was more important for growth during summer in male than in female lambs, possibly suggesting that the ewe invests more in male offspring.

The interaction between density and litter size is an important feature in this study. Triplet lambs are lighter in terms of body mass than singleton lambs, in particular high density (fig.6). An interaction between year and density showed annual variation in the density-dependent influence on the autumn body mass, which can be an indirect effect of climate. At high densities high quality forage abundance declines fastest in dry summers and sheep consume more low quality food (Armstrong *et al.*, 1997). The decreasing body mass as an effect of litter size at high density shows the ewes lack of increased investment during unfavourable conditions. In 2004, a very dry year, lamb growth rates in triplet were at the lowest. I expect this effect to become even more significant with further years of observation and analyses, as negative density effects of grazing on plant development should increase.

Another factor influencing growth rate is parasite infection, which amount is indirectly an effect of climate and density. Sheep from this study were in 2004 infected by nematodes as I observed when picking the faeces probes for diet analysis. Nahed-Toral *et al.* (2003) found

that fluctuations in parasite infections in Mexican sheep were correlated to changes in climate. Periods with little food forced the sheep to graze near the ground which reinforced re-infestation and the effect increased with high density. In Sweden lambs treated for nematode infection had a much higher autumn body mass than lambs without treatment (Waller *et al.*, 2004). Ewes get infected each spring on summer pastures by larvae which survived winter and lambs get infected by their mothers faeces when beginning to eat solid food (Waller *et al.*, 2004). Warm winters with deep snow levels are favourable for parasite larvae survival and climate may have an indirect impact on lambs' autumn body mass through the levels of parasite infection. A study on the influence of parasitic infestation by nematodes could reveal the dimensions of impact on lamb body mass on Norwegian mountain pastures.

Management implications

Over 2 million sheep graze each year on Norwegian mountain pastures. This summer grazing of sheep can have tremendous effects on the mountain vegetations and can have negative impact on forage availability for wild ungulates in winter (Iversen, 2004; Mysterud, 2000). Norwegian scientists have expressed the need for conservation management in accordance to density restrictions. With this study I might contribute with a method for analyzing density-dependent overgrazing on summer pastures. Norwegian sheep farmers report each year the weights of sheep being slaughtered to a national database "Sauekontrollen". With the information in this database one can compare body mass of sheep over different densities and several years. In my study I found the most severe impact of density on triplet lambs. My suggestion is to trace triplet lambs' body mass and when body masses are decreasing, management should decide whether sheep densities on the summer pastures should be reduced. A management goal could be to introduce density thresholds according to changes in lamb growth rates. This method would also be an advantage to the farmer as his income rises when optimizing lambs growth rates over time. In western Norway we see the heaviest grazing densities in the country. An interesting case is the example of farmers from "Jæren smalelag" (Jæren sheep farmers union) who do not to let ewes with triplet lambs onto summer pastures (Atle Mysterud, pers. comm., 2006). This is likely a cultural adaptation to the impact of high density on growth rate as triplet lambs do not gain enough body mass to be profitable.

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Appendix

Appendix 1 – Model selection on altitude for active activity patterns

Results from model selection performed on altitude for the active activity pattern subset of the data. The most parsimonious model (**bolded**) explained 23.3% of the variation in altitude and was used for parameter estimation in table 1.

Julian date	(Julian date)²	(Julian date)³	Density	Cloud cover	Wind	Year	Temperature	(Temperature)²	(Temperature)³	Julian date*density	Julian date*cloud cover	Julian date*wind	Julian date*year	Julian date*temperature	Density*cloud cover	Density*wind	Density*year	Density*temperature	Cloud cover*wind	Cloud cover*temperature	Wind*temperature	Wind*year	Temperature*year	AIC	diff AIC
x			x	x	x	x	x																	11233.9	140.33
x	x		x	x	x	x	x																	11235.6	142.08
x	x	x	x	x	x	x	x																	11212.5	118.94
x	x	x	x	x	x	x	x	x																11214.5	120.94
x	x	x	x	x	x	x	x	x	x															11190.9	97.37
x	x		x	x	x	x	x	x																11235.8	142.31
x			x	x	x	x	x	x																11234.5	141.01
x			x	x	x	x	x	x			x													11202.3	108.77
x	x	x	x	x	x	x	x	x	x	x														11192.6	99.09
x	x	x	x	x	x	x	x	x	x		x													11185.2	91.68
x	x	x	x	x	x	x	x	x	x		x	x												11185.9	107.76
x	x	x	x	x	x	x	x	x	x		x		x											11187.2	109.04
x	x	x	x	x	x	x	x	x	x		x				x									11175.5	97.29
x	x	x	x	x	x	x	x	x	x		x				x	x								11171.3	93.15
x	x	x	x	x	x	x	x	x	x		x				x	x	x							11171.3	93.16
x	x	x	x	x	x	x	x	x	x		x				x	x		x						11145.2	67.05
x	x	x	x	x	x	x	x	x	x		x				x	x		x	x					11147.2	69.02
x	x	x	x	x	x	x	x	x	x		x				x	x		x		x				11137.3	59.12
x	x	x	x	x	x	x	x	x	x		x				x	x		x			x			11111.9	33.76
x	x	x	x	x	x	x	x	x	x		x				x	x		x			x	x		11109.1	30.91
x	x	x	x	x	x	x	x	x	x		x				x	x		x			x	x	x	11099.3	21.18
x	x		x	x	x	x	x				x				x	x		x			x	x	x	11122.1	43.90
x			x	x	x	x	x				x				x	x		x			x	x	x	11138.2	60.02
x	x		x	x	x	x	x	x			x				x	x		x			x	x	x	11096.6	18.48
x	x		x	x	x	x	x				x	x			x	x		x			x	x	x	11093.5	15.36
x	x		x	x	x	x	x				x	x			x	x	x	x			x	x	x	11094.8	16.65
x	x		x	x	x	x	x				x	x			x	x		x			x			11130.4	52.24
x	x		x	x	x	x	x				x				x	x		x			x	x	x	11085.2	7.00
x	x		x	x	x	x	x				x				x	x		x			x	x	x	11081.7	3.51
x	x		x	x	x	x	x				x	x			x	x	x	x			x	x	x	11110.1	31.95
x	x		x	x	x	x	x							x	x	x		x			x	x	x	11080.0	1.88
x	x		x	x	x	x	x							x	x	x		x			x	x	x	11083.2	5.00
x	x		x	x	x	x	x						x					x			x	x	x	11099.7	21.58
x	x		x	x	x	x	x						x	x				x			x	x	x	11085.5	7.31
x	x		x	x	x	x	x						x	x	x						x	x	x	11102.1	23.96
x	**x**		**x**	**x**	**x**	**x**	**x**				**x**		**x**	**x**				**x**			**x**	**x**	**x**	**11078.2**	**0.00**
x	x		x	x	x	x	x						x	x				x				x	x	11117.9	39.77
x	x		x	x	x	x	x						x	x				x		x		x	x	11084.3	6.13
x	x		x	x	x	x	x						x	x				x		x	x		x	11094.7	16.49
x	x		x	x	x	x	x						x	x				x		x	x	x		11090.0	11.86
x			x	x	x	x	x						x	x				x		x	x	x	x	11128.3	50.14

Appendix 2 – Model selection on altitude for passive activity patterns

Results from model selection performed on altitude for the passive activity pattern subset of the data. The most parsimonious model (**bolded**) explained 22.1% of the variation in altitude and was used for parameter estimation in table 2.

Julian date	(Julian date)²	(Julian date)³	Density	Cloud cover	Wind	Year	Temperature	(Temperature)²	(Temperature)³	Julian date*density	Julian date*cloud cover	Julian date*wind	Julian date*year	Julian date*temperature	Density*cloud cover	Density*wind	Density*year	Density*temperature	Cloud cover*wind	Cloud cover*temperature	Wind*temperature	Wind*year	Temperature*year	AIC	AICdiff
x			x	x	x	x	x																	5463.570	46.52
x	x		x	x	x	x	x																	5461.680	44.63
x	x	x	x	x	x	x	x																	5434.532	17.49
x	x	x	x	x	x	x	x	x																5436.237	19.19
x	x	x	x	x	x	x	x	x	x															5435.501	18.45
x	x	x	x	x	x	x	x				x													5436.516	19.47
x	x	x	x	x	x	x	x					x												5431.905	14.86
x	x	x	x	x	x	x	x					x	x											5424.297	7.25
x	x	x	x	x	x	x	x					x	x	x										5424.764	7.72
x	x	x	x	x	x	x	x					x	x		x									5426.063	9.02
x	x	x	x	x	x	x	x						x		x									5425.411	8.36
x	x	x	x	x	x	x	x					x	x	x	x									5426.176	9.13
x	x	x	x	x	x	x	x				x		x		x									5427.363	10.32
x	x	x	x	x	x	x	x					x	x			x								5425.747	8.70
x	x	x	x	x	x	x	x					x	x					x						5426.290	9.24
x	x	x	x	x	x	x	x					x	x				x							5423.860	6.81
x	x	x	x	x	x	x	x					x	x				x	x						5423.945	6.90
x	x	x	x	x	x	x	x					x	x				x		x					5422.519	5.47
x	x	x	x	x	x	x	x					x	x				x		x	x				5419.509	2.46
x	x	x	x	x	x	x	x					x	x				x		x	x	x			5421.383	4.34
x	**x**	**x**	**x**	**x**	**x**	**x**	**x**					**x**	**x**				**x**		**x**	**x**			**x**	**5417.042**	**0.00**
x	x	x	x	x	x	x	x					x	x				x		x	x		x	x	5417.565	0.52
x	x	x	x	x	x	x	x					x	x	x			x		x	x			x	5418.513	1.47
x	x	x	x	x	x	x	x					x	x						x	x			x	5418.077	1.03
x	x	x	x	x	x	x	x					x	x				x		x	x	x	x		5419.041	1.99
x	x	x		x	x	x	x					x	x						x	x	x	x		5435.712	18.67
x			x	x	x	x	x					x	x				x		x	x			x	5421.890	4.84
x	x	x	x	x	x	x	x					x	x	x			x		x	x		x	x	5423.756	6.71
x	x	x	x	x	x	x	x					x	x						x	x	x	x		5422.439	5.39

Appendix 3 - Model selection on proportion of *Deschampsia flexuosa* in faeces samples.

Results from model selection performed on proportion of *Deschampsia flexuosa* in faeces samples. The most parsimonious model (**bolded**) explained 48.14% of the variation and was used for parameter estimation in table 4.

Year	Age	Density	Julian date	(Julian date)²	(Julian date)³	Year*age	Year*density	Year*Julian date	Age*density	Age*Julian date	Julian date*density	AIC	AIC diff
x	x	x	x									-489.542	48.00
x	x	x	x	x								-492.267	45.27
x	x	x	x	x	x							-491.220	46.32
x	x	x	x	x		x						-489.712	47.83
x	x	x	x	x			x					-518.331	19.21
x	x	x	x	x			x	x				-523.148	14.39
x	x	x	x	x			x	x	x			-529.231	8.31
x	x	x	x	x			x	x	x	x		-527.237	10.30
x	x	x	x	x		x	x	x	x		x	-535.245	2.29
x	x	x	x	x			x	x	x	x	x	-535.552	1.99
x	x	x	x	x		x	x	x	x	x	x	-533.245	4.29
	x	x	x	x					x	x	x	-471.142	66.40
x		x	x	x			x	x			x	-455.795	81.74
x	x	x	x				x	x	x		x	-532.952	4.59
x	x	x					x			x		-437.827	99.71
x	**x**	**x**	**x**	**x**			**x**	**x**	**x**		**x**	**-537.543**	**0.00**

Appendix 4 - Model selection on proportion of herbs in faeces samples.

Results from model selection performed on proportion of herbs in faeces samples. The most parsimonious model (**bolded**) explained 51.25% of the variation and was used for parameter estimation in table 5.

Year	Age	Density	Julian date	(Julian date)^2	(Julian date)^3	Year*age	Year*density	Year*Julian date	Age*density	Age*Julian date	Julian date*density	AIC	AIC diff
x	x	x	x									-522.991	32.40
x	x	x	x	x								-522.513	32.88
x	x	x	x	x	x							-530.559	24.83
x	x	x	x	x	x	x						-535.747	19.64
x	x	x	x	x	x	x	x					-538.037	17.35
x	x	x	x	x	x	x	x	x				-547.352	8.04
x	x	x	x	x	x	x	x	x	x			-548.499	6.89
x	x	x	x	x	x	x	x	x	x	x		-551.060	4.33
x	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**-555.393**	**0.00**
x	x	x	x	x	x		x	x	x	x	x	-550.690	4.70
x	x	x	x	x	x	x		x	x	x	x	-553.138	2.25
x	x	x	x	x	x	x	x		x	x	x	-545.638	9.75
	x	x	x	x	x				x	x	x	-392.869	162.52
x	x	x	x	x	x	x	x	x		x	x	-554.801	0.59
x	x	x	x	x	x	x	x	x	x		x	-552.872	2.52
x		x	x	x	x		x	x			x	-541.463	13.93
x	x		x	x	x	x		x		x		-546.080	9.31
x	x	x		x	x	x	x		x			-476.669	78.72

Appendix 5 – Model selection on lamb autumn body mass

Results from model selection performed on ln (lamb autumn body mass). The most parsimonious model (**bolded**) was used for parameter estimation (table 6).

Ln (spring body mass)	Ewe age	(Ewe age)²	Sex	Year	Ln (ewe spring body mass)	Ln (ewe spring body mass)²	Litter size	Density	Julian date	Density*ln (spring body mass)	Density*ewe age	Density*sex	Density*year	Density*ln (ewe spring body mass)	Density*ln (ewe spring body mass)²	Density*litter size	Year*ln spring body mass	Year*ewe age	Year*sex	Year*ln (ewe spring body mass)	Year*litter size	Sex*ln (spring body mass)	Sex*ewe body mass	Sex*ln (ewe spring body mass)	Sex*litter size	AIC	AIC diff
x	x		x	x	x		x	x	x																	-271.003	14.04
x	x	x	x	x	x		x	x	x																	-270.770	14.28
x	x		x	x	x	x	x	x	x																	-275.459	9.59
x	x		x	x	x	x	x	x	x	x																-273.871	11.18
x	x		x	x	x	x	x	x	x			x														-275.920	9.13
x	x		x	x	x	x	x	x	x			x	x													-273.922	11.13
x	x		x	x	x	x	x	x	x			x		x												-282.377	2.67
x	x		x	x	x	x	x	x	x			x	x	x												-280.505	4.54
x	x		x	x	x	x	x	x	x			x		x	x											-280.491	4.56
x	x		x	x	x	x	x	x	x			x		x		x										-280.110	4.94
x	x		x	x	x	x	x	x	x			x		x			x									-281.221	3.83
x	x		x	x	x	x	x	x	x			x		x				x								-279.140	5.91
x	x		x	x	x	x	x	x	x			x		x					x							-281.503	3.55
x	x		x	x	x	x	x	x	x			x		x						x						-279.472	5.58
x	x		x	x	x	x	x	x	x			x		x							x					-280.448	4.60
x	x		x	x	x	x	x	x	x			x		x								x				-283.392	1.66
x	x		x	x	x	x	x	x	x			x		x								x	x			-282.421	2.63
x	x		x	x	x	x	x	x	x			x		x								x		x		-281.401	3.65
x	x		x	x	x	x	x	x	x			x		x								x			x	-282.070	2.98
x	x		x	x	x	x	x	x	x					x								x				-282.678	2.37
x			x	x	x	x	x	x	x					x								x				-284.593	0.46
x			x	x	x	x	x	x	x					x												-283.151	1.90
x			x	x	x	x	x	x	x													x				-279.758	5.29
x			x	x	x		x	x	x					x								x				-284.244	0.81
x			x	x	x	x	x	x	x					x	x							x				-284.452	0.60
x			**x**	**x**	**x**		**x**	**x**	**x**					**x**	**x**							**x**				**-285.051**	**0.00**