



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

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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 km²) and low (25 per km²) 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 (H₁)

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 (H₂)

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 (H₃)

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} <i>Selection of the most productive habitat declines over the season</i>	Forage quality decreases over the season due to aging of plant material	Date × HabProd	Supported (Table 2, Fig. 3)
H _{2b} <i>Density dependent selection pattern is more pronounced in late grazing season</i>	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} <i>Habitat selection varies between years</i>	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} <i>Density dependent selection pattern is more pronounced in years of poor vegetation development</i>	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} <i>Temporal trend in selection</i>	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} <i>The two densities diverge in their selection of the most productive habitat over years</i>	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 (H₄)

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 km² 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 km²).

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 km² (ranging in size from 0.22 to 0.38 km² 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 km² 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

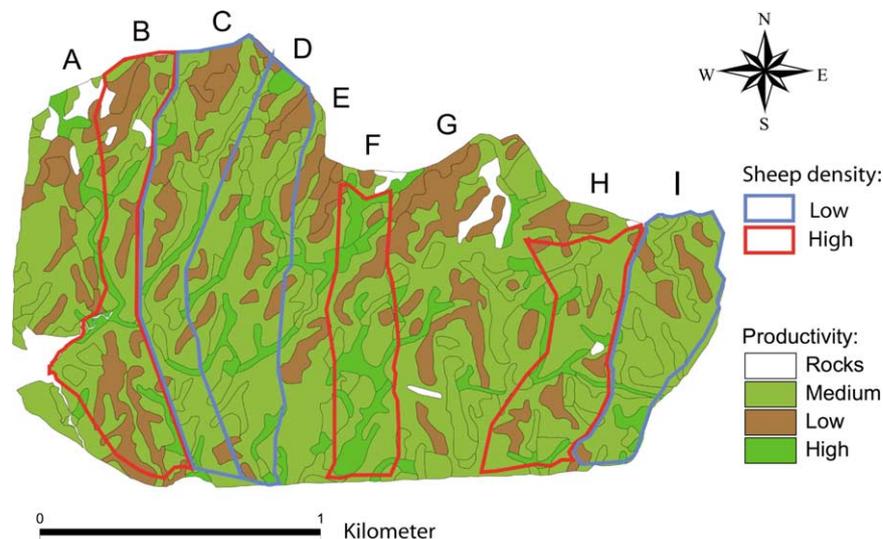


Figure 1. Map showing the distribution of vegetation of the three productivity levels (high, medium and low) as well as bare rocks (excluded from analyses) in all sub-enclosures (A–I) for the experiment in Hol, Norway.

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 m²) 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

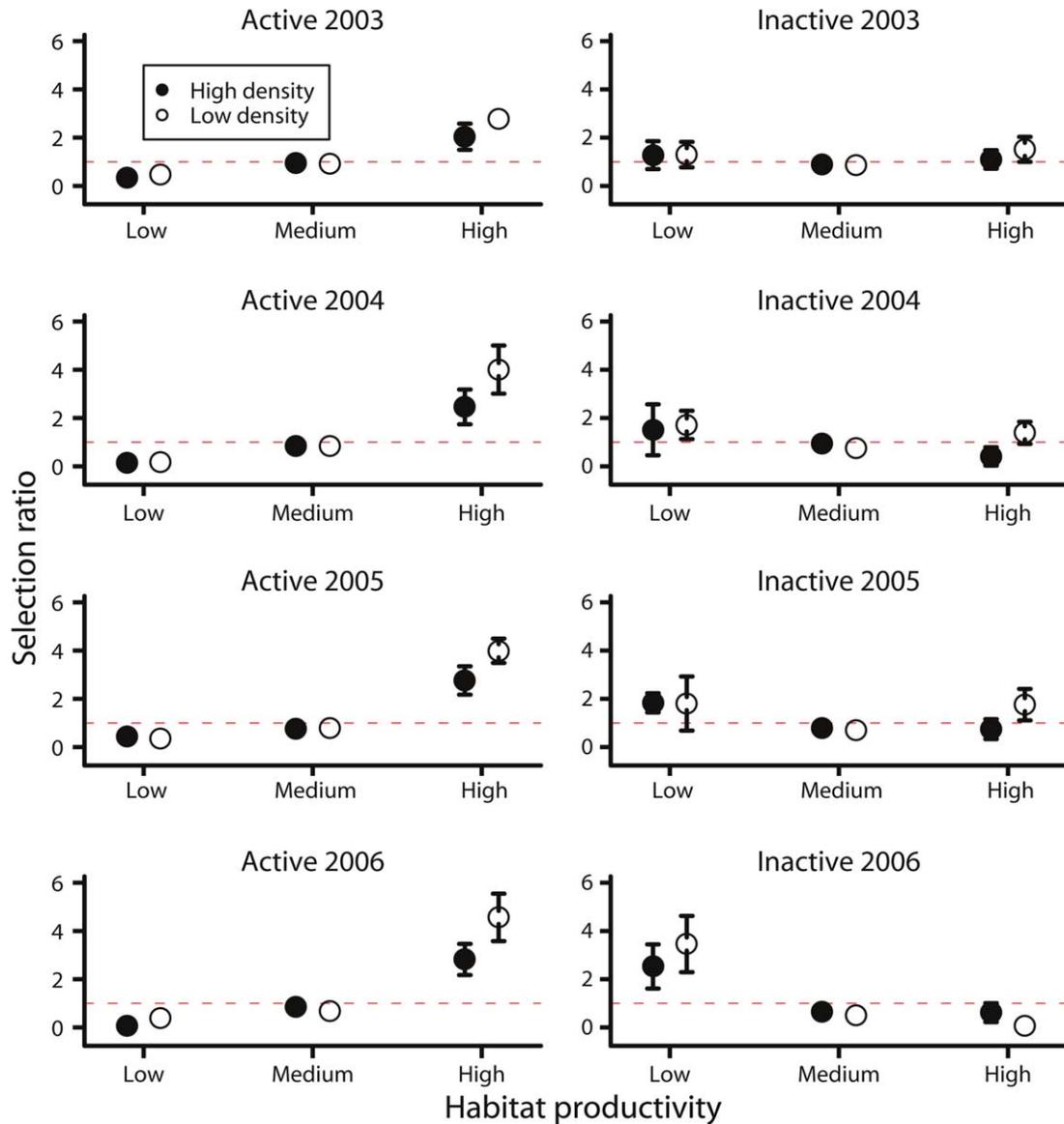


Figure 2. Selection of habitats varying in productivity over four summer grazing seasons by active and inactive sheep at high and low population density. Estimates above 1 indicate selection and estimates below 1 indicate avoidance. If the confidence interval does not overlap zero the relationship is 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 H₁. 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

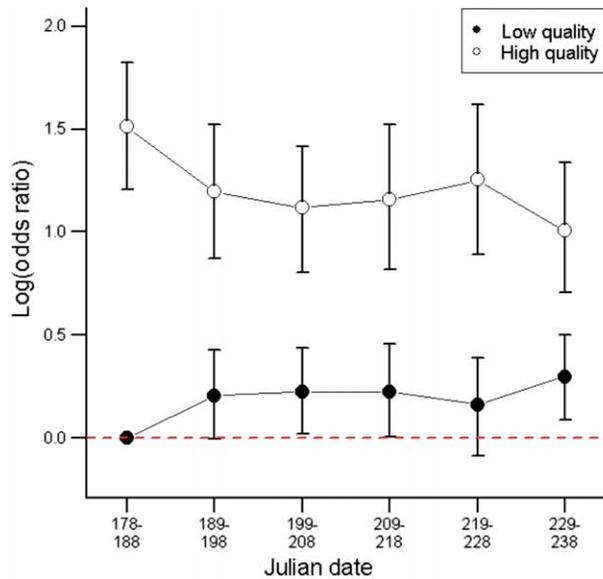


Figure 3. Seasonal changes in selection of habitats with high and low productivity by active sheep in Hol, Norway. The predicted log odds ratios are derived from the generalized mixed-effects model presented in Table 2, except that Julian date is binned in 10-day groups. All log odds ratios are compared 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. \times 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. \times Date \times 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

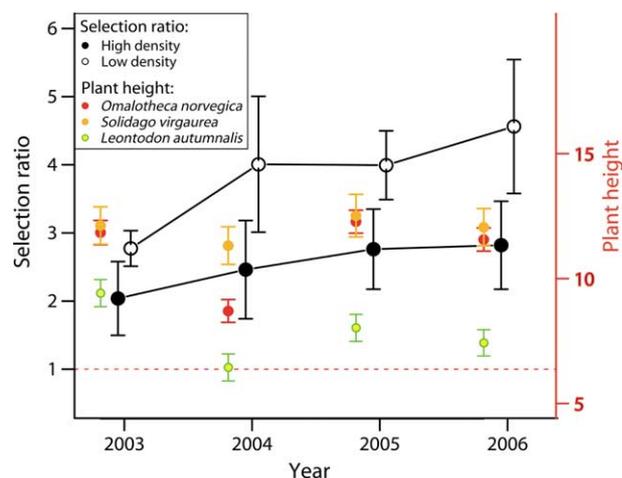


Figure 4. Selection of high productivity habitat in different years for active sheep at high and low density in alpine habitat in Hol, Norway. Selection ratio is defined as the ratio of the proportion used to the proportion available. Estimates above 1 indicate selection. Annual variation in plant development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

(Fig. 4; the interactions Hab. prod. \times 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. \times Year (as categorical) \times 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. \times Year (as trend) \times 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 (Δ AIC = 4).

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, Myrsetrud 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 (Myrsetrud 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 (Myrsetrud 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* (Myrsetrud 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. Coincidentally, 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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