

Temporal variation in density dependent body growth of a large herbivore

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

Temporal variation in performance of large herbivores is thought to arise mainly due to density- and climate dependent processes (Gaillard et al. 2000). Most ecologists regard competition for food as the main mechanism behind density dependence in ungulates (Fowler 1987, Bonenfant et al. 2009). Effects of climate on herbivore performance may be more variable, but, at least during summer, effects are often found to be mediated by effects on plant quality and availability (Weladji et al. 2002, Mysterud and Sæther 2011). Evidence of both density-dependence and climate effects has been reported in numerous life history traits (reviewed by Gaillard et al. 2000), including body mass (Stewart et al. 2005). Moreover, climate and density-dependent effects frequently interact. Unfavourable climatic conditions are often more important at high population densities. Convincing evidence of climate-density interactions comes from the winter season, when animals in poor condition due to high population density are more prone to die during harsh winter conditions than at low density (Portier et al. 1998, Coulson et al. 2001, Jacobson et al. 2004). However, much less is known regarding how density dependent body growth during the plant growing season may interact with climate variation.

Northern ungulates experience substantial annual variation in plant phenology during the short growing season (Mårell et al. 2006). Conditions during spring and summer are particularly crucial for juvenile growth, as well as for deposition of fat reserves necessary to survive and sustain a harsh winter climate. For example, early onset of vegetation growth (Pettorelli et al. 2005a) and a slow phenological development throughout the growing season affect juvenile autumn body mass positively (sheep *Ovis aries* Mysterud et al. 2001b, reindeer *Rangifer tarandus* Pettorelli et al. 2005b, moose *Alces alces* Herfindal et al. 2006). In years of poor vegetation development, we would predict increased competition for forage, and thus that the strength of density dependence varies among years. For moose, there was evidence for more marked effects of environmental variation on body mass in populations with small mean autumn body mass living at higher densities than in populations with large-sized individuals living at lower densities (Herfindal et al. 2006). These interesting results suggest indeed that poor summer forage conditions would have a stronger negative effect at high population density also during summer, but the correlative study compares populations from areas that differ largely in a range of environmental

factors. There is yet no quantification of how variation in climate affects the strength of density dependence after controlling for potential regional differences in environment.

Another largely unresolved issue is the matter over which temporal scale different mechanisms of density effects occur (Kuijper et al. 2008). Even in the short term, high animal densities increase forage competition and reduce body mass gain (reviewed by Bonenfant et al. 2009). As large herbivores are selective foragers with preference for high quality plants or plant parts, they respond to increased competition by including more low quality plant material in their diet (white-tailed deer *Odocoileus virginianus* Kie et al. 1980, feral donkeys *Equus asinus* Freeland and Choquenot 1990, Choquenot 1991, goats *Capra aegagrus* Mellado et al. 2003, sheep *Ovis aries* Kausrud et al. 2006, Mørbæk et al. 2012a). At longer time scales, grazing pressure and selective foraging may alter productivity and composition of alpine plant communities (Austrheim and Eriksson 2001, Bråthen et al. 2007). If density effects gradually modify properties of the foraging habitat, for example by decreasing spatial heterogeneity (Adler et al. 2001), homogenizing the abundance of palatable plant species (Adler et al. 2001, Bråthen et al. 2007), changing plant productivity (Harrison and Bardgett 2008) or nutritive quality (Mysterud et al. 2011), this may have important consequences for ungulate foraging strategies potentially affecting body mass gain over time (Simard et al. 2008). Predicting the direction of plant–herbivore interactions and how long-term grazing pressure may affect temporal variation in ungulate body mass is not straightforward. Effects of grazing on plant community development may in theory lead to both negative and positive effects in the long-term depending on the ecosystem. Indeed, grazing may lead to facilitation in nutrient rich ecosystems by increasing nutrient cycling and productivity and by favouring tolerant grass species over resistant woody species (McNaughton et al. 1997, Arsenault and Owen-Smith 2002). Yet, empirical evidence of how body mass growth evolves under different densities is scarce. For a browsing herbivore (white-tailed deer) in a forest ecosystem, a manipulation of density documented that long-term browsing reduced diet quality and subsequent body growth (Simard et al. 2008). However, it remains unclear whether the same result applies to grazers in grassland ecosystems often thought to favour tolerant species.

In this fully replicated landscape-scale experiment, we kept a large grazing herbivore (domestic sheep) at high and low density in alpine habitats over nine successive grazing seasons (2002–2010). Our aim was to identify the relative role of density dependent and density independent processes for lamb body mass gain during summer, and to explore whether density–climate interactions could explain temporal variation in lamb autumn body mass. The foraging conditions within the experimental area are affected both by large annual variation in plant growth due to climate (Evju et al. 2006), and density dependent responses to grazing in vegetation development (Austrheim et al. 2008) and soil properties (Martinsen et al. 2012). For example, high sheep density reduced biomass of vascular plants, and highly selected herbs declined, whereas vascular plants were largely unaffected by low sheep density

(Austrheim et al. 2008). Further, soil nitrogen decreased more at high sheep densities as compared to low densities although N removal is minor in relation to the total soil N pool (Martinsen et al. 2012). At low sheep density, grazing increased soil carbon storage over years (Martinsen et al. 2011). In line with these results, we tested the following predictions:

H1. *Density dependence.* Lamb autumn body mass is density dependent with lambs at high density having lower body mass than lambs at low density.

H2. *Annual variation.* We predicted body mass to vary irregularly between years (H2a). Competition for forage may be more severe in years with poor vegetation development; we therefore predicted annual variation in the strength of the density dependent response (H2b).

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

Material and methods

Study area

The study area is located in Hol municipality, Buskerud county in southern Norway (60°40'N, 7°55'E). The area is characterized by a sub-continental alpine climate with annual precipitation approximately 1000 mm (Evju et al. 2009). The bedrock consists of metaarkose (Sigmond 1998), and the soil is moderately base-rich. In year 2001, a large fenced experimental enclosure covering 2.7 km² was established, mainly in the lower alpine zone. The enclosure covers an altitudinal span from the forest line (1050 m a.s.l.) up to 1320 m a.s.l. Vegetation is dominated by dwarf shrub heathland with scattered lichen heaths, snow-beds and grass-dominated meadows (Rekdal 2001). A few birch *Betula pubescens* trees are found in the areas with lowest elevation (Speed et al. 2010). The vegetation types with highest grazing value for sheep, low- and tall herb meadows (Mørbæk et al. 2009), constitute 9% of the vegetation cover (Rekdal 2001).

Experimental design and data collection

The large enclosure was divided into nine sub-enclosures in order to facilitate a randomized replication within three blocks, the average size of the sub-enclosures being 30 ha or 0.3 km² (Austrheim et al. 2008). The division of the enclosure was performed in a manner that ensured that each of the sub-enclosures covered approximately the same altitudinal range and a comparable distribution of vegetation types. Lastly, each of the three sub-enclosures within a block was randomly assigned the treatments high density, low density or control (no sheep). A botanical survey estimating the distribution of different vegetation

types and their respective grazing value for domestic sheep provided the basis for calculation of sheep density levels. Consequently, 80 and 25 sheep per km² were chosen as high and low density treatments, respectively, numbers that correspond to actual densities of free ranging sheep grazing on Norwegian mountain pastures. Sheep grazing was initiated in 2002, and a total of 23 to 26 lactating ewes and 44 to 49 lambs were released into the experimental enclosure each grazing season (Mobæk et al. 2012b). As far as possible, ewes with singleton, twin and triplet lambs were distributed evenly between the sub-enclosures to ensure an equal representation of ewes with different reproduction status between the two density levels. The sheep were of the breed ‘Norsk Kvit Sau’, which is the largest and most common breed in Norway. Each grazing season lasted from late June to late August or early September, and the number of grazing days used in this experiment thus mirrors a typical grazing season in Norwegian alpine pastures. Individual sheep could switch treatments between years.

Ewes and their lambs were weighed at the days of release and recapture from the alpine pastures. Before release, all sheep were treated with anthelmintic parasite treatment (Ivermectin). Body mass was determined to the nearest 0.5 kg. This study comprises data from nine consecutive grazing seasons (2002–2010) (Supplementary material Appendix A1 Table A1 for details). During this period a total of 413 lambs and 217 ewes have been grazing in the enclosures. Note that as many of the ewes were used in the experiment more than one season and some of the lambs were lost due to predators and diseases, we use body mass from 394 lambs with 132 individual mothers in the statistical analyses (Table 1).

Statistical analyses

Body mass was ln-transformed prior to analyses to stabilize variance. We used GAM-plotting in the R library ‘mgcv’ to check for any possible non-linearity and to explore patterns in our data and establishing sound parameterizations of higher order terms. Then, we fitted generalized linear mixed effects models in the R library ‘lme4’ to analyse whether

lamb autumn body mass was affected by density, annual variation, sex, litter size (categorical; 1–3), spring body mass, mother spring body mass, ewe age and length of grazing season (grazing days), and to test whether the density effect interacted with annual variation and/or other variables (Supplementary material Appendix A1 Table A2). When testing the effect of annual variation, we tried both year as a categorical and a continuous (trend) variable, in addition to testing year as trend using smoothing splines in the library ‘splines’ (Supplementary material Appendix A1 Table A2).

As we have three replications of the density treatment and repeated samplings of body mass from individual lambs with the same mothers (i.e. some ewes had 2–3 lambs within a season and/or were used several grazing seasons), we always fitted ‘sub-enclosure’ and ‘mother-id’ as random variables in the mixed effect models. To facilitate model comparison and select the most parsimonious model we used AIC (Akaike information criterion). The model with the lowest AIC value was used to estimate parameters in order to test our predictions. Finally, we used Markov chain Monte Carlo simulations in the R library ‘coda’ to estimate highest probability density (HPD) intervals for the model parameters, as is recommended over normal confidence limits for GLMMs fitted with lmer (Pinheiro and Bates 2000). All statistical analyses were done using R ver. 2.12.0 (R Development Core Team).

Results

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

Temporal variation significantly affected autumn body mass of lambs. The most parsimonious model included year

Table 1. Parameter estimation from mixed effects model of (ln) lamb autumn body mass from the grazing seasons 2002–2010 in Hol, Norway (no. of lambs = 394, Mother ID = 132, Sub-enclosures = 6). Reference level for the density effect is ‘high’, for sex ‘female’ and for litter size ‘singleton lamb’.

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

as a trend and its interaction with density (Supplementary material Appendix A1 Table A2), thus supporting our prediction that the grazing effect (H3), rather than annual fluctuations (H2a), was the most important factor determining temporal variation in density dependent growth of lambs. A significant interaction between density and year indicates a divergence in body mass development over years for lambs grazing at high and low density, as predicted in H3. For lambs at high density, autumn body mass decreased the first 2–3 years before stabilizing for the rest of the nine years studied, whereas autumn weights for lambs at low density were slightly increasing (Table 1, Fig. 1).

In general, male lambs were heavier than female lambs (Table 1). Singleton lambs had higher body mass than twins and triplets (Table 1). Further, lambs with high spring body mass were heavier in autumn, and lamb body mass increased with length of the grazing season (Table 1). Ewes' body mass in spring influenced lamb autumn body mass positively, i.e. heavy ewes produced heavier lambs, while ewe age (linear or squared) did not enter the best model (Supplementary material Appendix A1 Table A2).

Discussion

Disentangling the contribution of density dependent and independent processes on ungulate performance is challenging, partly due to their often interactive effects. By keeping sheep numbers constant at two densities replicated three times over nine summer seasons, we showed experimentally for the first time in a large grazing herbivore that density dependent processes may interact with annual variation possibly caused by climate effects also during the summer season (Fig. 1). The only closely related study is

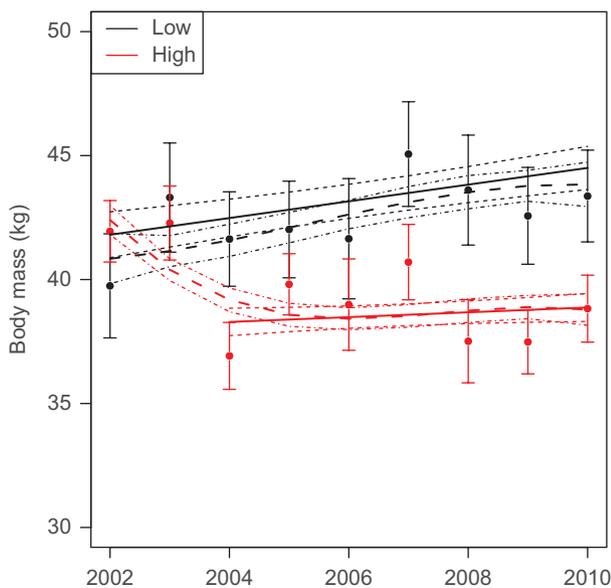


Figure 1. Predicted autumn body mass of lambs in Hol, Norway derived from models using year as trend using splines (thick, stippled lines), year as linear term (thick, solid line; starting year 2004 for high density), and year as categorical variable (points). The predicted values are estimations for male triplet lambs with average values for other factors.

that of Simard et al. (2008) for a browsing herbivore, the white-tailed deer, reporting a long-term negative effect of high density on body growth. Our study highlights the contrasting effect of keeping grazing herbivore numbers at low and high density, having a negative effect if kept at high density and a tendency towards a positive effect if kept at low density (Fig. 1).

Mechanisms in the short-term

Climate-induced temporal variation in body mass is well documented. At northern latitudes, the availability of high-quality forage in early spring and summer is regarded as particularly important (Klein 1965, Sæther and Heim 1993, Myrsetrud et al. 2001a, Pettorelli et al. 2005a). Body mass gain during summer season depend both on summer weather conditions affecting plant growth (Bø and Hjeljord 1991, Hjeljord and Histøl 1999), but also on previous winters snow depth operating through delaying plant phenological development (Myrsetrud et al. 2001b, Nielsen et al. 2012).

Density dependent variation in performance may arise from several mechanisms also operating in the short-term, such as competition for food or parasite load (Fowler 1987). Sheep in our experiment was treated for parasites before release. Though we cannot control for potential reinfection later in the season, the short-term effects of density most likely arise from competition for forage. Indeed, a count of parasite eggs in ewe and lamb faeces conducted during recapture of sheep (September 2009) found no difference in parasite load between sheep at high and low density (Ø. Holand unpubl.). In our experiment, density affected selection at both fine (diet) and coarse (habitat) spatial scale, which at least partly explain density dependent reductions in growth. Sheep at low density grazed more in high-quality vegetation types (low- and tall herb meadows) than sheep at high density (Mobæk et al. 2009). As a result, sheep at high density consumed an average diet of lower quality, including more graminoids and less herbs compared to sheep at low density (Kausrud et al. 2006, Mobæk et al. 2012a), but the density dependent pattern varied between years due to annual climatic variation in plant growth (Mobæk et al. 2012a).

In addition, ewes at high density spent more time active than ewes at low density, indicating increased searching time due to lower availability of preferred forage species at high density (Mobæk et al. 2012b). At the individual level, a 10% increase in activity of the ewes lead to 112 g higher growth of lambs, but increased activity at high density was not sufficient to counter the effect of lower quality diet. Already six to seven weeks old, lambs gain approximately the same energy uptake directly through grazing plant material as indirectly through milk (Nedkvitne et al. 1995). Higher competition for the most nutritious forage could reduce milk yield as shown for red deer *Cervus elaphus* (Landete-Castillejos et al. 2003), and this combined with lower forage availability and quality throughout the summer season may contribute to the reduced autumn body mass by lambs at high density.

Grazing by ungulates may both reduce and increase primary production (Hobbs 1996), and one potential

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

Long-term effects – delayed competition versus facilitation

Increased densities indicative of increased food competition on summer pastures has been reported to lower autumn body mass for a range of different ungulates (Bonenfant et al. 2009), but mainly on short timescales. There is an increasing interest in delayed effects of density on ungulate performance, as mechanisms of density dependence may change with time scale (Kuijper et al. 2008). Such delayed effects of high density might arise due to 'population momentum' operating through age structure changes or maternal effects (Koons et al. 2007, Ezard et al. 2010). For example, despite no vegetation deterioration (Virtanen et al. 2002), newborn red deer calves on Rum, Scotland continued to decrease in size after 30 years of stable population size most likely due to maternal effects (Coulson et al. 2004). In our case, such effects were controlled for, by entering ewe body mass as a covariate and by not having the same sheep at high and low density every grazing season. Possible cumulative effects of maternal condition can thus be ruled out. Keeping winter conditions constant (i.e. indoor feeding, providing the abundant food availability to all sheep) also possible buffered any 'carry-over-effects' from previous summer.

Increasing attention is now paid to how herbivore-induced changes in the nutritive value or abundance of forage over longer time spans may cause density-dependent feedback influencing ecosystem productivity (Mysterud 2006, Van der Wal 2006, Bråthen et al. 2007), potentially altering the carrying capacity of the foraging habitat. To be able to test predictions related to grazing effects, manipulating density is recommended. We found a significant interaction between density and year, and the relationship between lamb autumn body mass and annual variation was better explained by a temporal trend than by erratic between-year variation likely linked to climatic factors. There was an increasing trend in summer temperature in our study area over the last decades (Speed et al. 2012), though values for the period 2002–2010 were stable (correlation with year: June temp.: -0.06 ; July temp.: 0.04). This suggests that properties of the foraging habitat have been changed by sheep grazing, and that long-term grazing effects differ between the low and high density enclosures. The grazing effects are nevertheless likely affected by the higher temperatures in recent years. The whole vegetation community were shifted uphill during the study period in the controls not grazed by sheep, while the trend was reverse at high sheep density (Speed et al. 2012). Climate change may thus play a role for affecting the speed of grazing effects (see also Olofsson et al. 2009).

For white-tailed deer, high browsing intensity over years minimized the abundance of preferable and palatable tree and shrub species and reduced diet quality (Simard et al. 2008). Long-term grazing may also reduce species diversity and promote dominance of grazing tolerant graminoid species (Austrheim and Eriksson 2001, Hester et al. 2006). An important distinction between grazing and browsing effects however, is that while the grazing process generally accelerates nutrient (i.e. nitrogen) cycling (Augustine and Frank 2001), browsing returns less nitrogen to benefit plant production (Singer and Schoenecker 2003, Pastor et al. 2006). Thus, grazers are more capable of improving their foraging habitat than browsers, but confounding effects of ecosystem productivity in these comparisons make the role of feeding type uncertain. In our experimental area grazing had minor effects on N cycling in soils, but N in soil declined more at high density (Martinsen et al. 2011a, 2012). Our experiment clearly demonstrated that grazing effects may both promote and constrain performance, depending on density. The diverging trends in lamb body mass over years at low and high density may be due to long-term alterations of the most important forage plants for sheep, either in terms of availability, biomass, or nutritive value.

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

As low sheep density had minor effects on abundance of important forage species in the same study site as in this paper (Austrheim et al. 2008, Speed et al. 2012), the slight increase in lamb body mass over years at low density cannot alone be explained by changes in plant distribution and frequency. We found no clear evidence that low grazing intensity has altered soil properties in a direction that enhanced nutritive quality of the forage, or that high density reduced soil quality (Martinsen et al. 2011a). However, vascular plant biomass in meadows and snowbeds increased from 2002 to 2008 at low sheep densities, while biomass at high sheep densities decreased (Austrheim unpubl.). Indeed, sheep at low density tended to use meadows more over years than sheep at high density (2003–2006; Møbæk et al. 2009), and low grazing intensity in these vegetation types may have improved growing conditions for preferable plant species such as herbs. Increased body mass gain over years for lambs at low density are consistent with expectations from grazing facilitation, while long-term temporal

development in autumn body mass was that high sheep density has changed properties of the foraging habitat towards a state with reduced availability of high-quality forage.

Conclusion

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

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Supplementary material (available as Appendix O20888 at <www.oikosoffice.lu.se/appendix>). Appendix A1.