

Do different sheep breeds show equal responses to climate fluctuations?

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Abstract

Large herbivores can be directly affected by climate through effects on thermoregulation, but the strongest effects are expected to operate indirectly through plant quality and biomass. The extents to which different herbivores are affected by climate conditions in contrasting ways are poorly understood. We used an extensive dataset containing information on 38,587 lambs from the years 1992–2007. The lambs represented two breeds differing largely in digestive anatomy, diet composition and possibly other traits. The yearly average body mass values of the two breeds were strongly correlated, however, responses to climate variables nevertheless differed in strength. There were positive relationships between lamb autumn body mass and snow depth the previous winter, spring temperature and temperature and precipitation in August in both breeds. In the Norwegian white sheep (NWS) breed, there was a negative relationship between lamb autumn body mass and spring precipitation. The Spæl breed exhibited similar (although weaker) relationships with climate variables. Our results show that the NWS breed might, on a short time scale, benefit most from climate warming. However, the Spæl breed were less variable in body mass among years suggesting that this breed might be the better choice if the aim is to reduce uncertainty in meat production. We discuss the likely mechanisms behind the contrasting responses of the two different breeds relative to morphological, physiological and behavioural differences.

Zusammenfassung

Große Pflanzenfresser können durch Auswirkungen auf ihre Thermoregulation direkt durch das Klima beeinflusst werden. Man nimmt aber an, dass die stärksten Effekte indirekt durch Pflanzenqualität und -biomasse wirken. Wie stark unterschiedliche Herbivoren durch die Klimabedingungen beeinflusst werden, ist kaum bekannt. Wir nutzten einen umfangreichen Datensatz mit Informationen zu 38587 Lämmern aus den Jahren 1992–2007. Die Lämmer gehörten zu zwei Rassen, die sich deutlich hinsichtlich der Anatomie des Verdauungstraktes, der Nahrungszusammensetzung und möglicherweise weiterer Merkmale unterscheiden. Die jährlichen Durchschnittsgewichte der beiden Rassen waren stark miteinander korreliert, aber nichtsdestotrotz waren die Reaktionen auf Klimavariablen unterschiedlich stark. Bei beiden Rassen gab es positive Beziehungen zwischen dem Herbstgewicht der Lämmer und der Schneedicke im vorherigen Winter, der Frühjahrestemperatur sowie der Temperatur und Niederschlagsmenge im August. Beim norwegischen weißen Schaf (NWS) gab es eine negative Beziehung zwischen dem Herbstgewicht der Lämmer und den Frühjahrsniederschlägen. Die Spæl-Rasse zeigte ähnliche, wenn auch schwächere Beziehungen zu den Klimavariablen. Unsere Ergebnisse zeigen, dass die NWS-Rasse kurzfristig am meisten von der

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Klimaerwärmung profitieren könnte. Indessen variierte das Körpergewicht der Spæl-Rasse weniger stark von Jahr zu Jahr, was nahelegt, dass diese Rasse die bessere Wahl sein könnte, wenn es darum geht, Unsicherheiten in der Fleischproduktion zu reduzieren. Wir diskutieren die vermutlichen Mechanismen hinter den unterschiedlichen Reaktionen der beiden Rassen in Bezug auf morphologische, physiologische und Verhaltensunterschiede.

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Introduction

Large herbivores, such as sheep, can be directly affected by climate through effects on thermoregulation (Parker & Robbins 1985), but the strongest effects are expected to operate indirectly through plant quality and biomass (Mysterud, Stenseth, Yoccoz, Langvatn, & Steinheim 2001; Mysterud, Yoccoz, Langvatn, Pettoirelli, & Stenseth 2008). There is, however, large annual variation in diet and habitat selection in sheep (Mobæk, Mysterud, Loe, Holand, & Austrheim 2009). Alpine plant communities are affected by recent climate change through both increased temperature and precipitation effects (Engler et al. 2011). In alpine ecosystems, temperature during early summer as well as snow accumulation the previous winter affect the start of the vegetation season and are regarded key factors determining plant phenology and in turn quality for alpine grazers (Nielsen et al. 2012; Pettoirelli, Mysterud, Yoccoz, Langvatn, & Stenseth 2005a).

The extents to which different herbivores are affected by climate conditions in contrasting ways are poorly understood. The empirical evidence for a link between plant phenology and quality is stronger for grasses, but less so for browse (Mysterud et al. 2011). Ruminant diets vary with respect to the proportions of grasses and browse they included (Hofmann 1989) and are related to body size (Demment & Van Soest 1985). In particular, plant quality is more important for smaller herbivores, while larger herbivores can tolerate diets of lower quality (Bell 1971; Demment & Van Soest 1985). These issues are highly relevant also for agriculture/animal husbandry, as different livestock breeds have different ecology. In addition, future climate change is expected to favour more woody plant species (browse) at the expense of grasses (Gordon & Prins 2008). It may thus be useful to identify breeds of livestock that are more robust to future climate, or at least produce better under new environmental conditions, i.e. feed efficiently on novel plant communities.

Plant phenology can be estimated with the aid of the satellite-derived Normalized Difference Vegetation Index (NDVI) (Tucker & Sellers 1986) and different measures of NDVI have previously been shown to correlate with the performance of animals (Pettoirelli et al. 2005a, 2011). We have also shown that lamb autumn body mass is positively related to spring NDVI in our focal area (Nielsen et al. 2012). Hamel, Garell, Festa-Bianchet, Gaillard, and Côté (2009) found a negative correlation between the Integrated

NDVI (INDVI) in June (i.e. the sum of the two NDVI periods in early and late June) and faecal crude protein content of alpine ungulates, suggesting that high biomass years contained vegetation of lower quality.

As a model system we used domestic sheep roaming freely on alpine ranges during summer. In Norway, the long-tailed Norwegian white sheep (NWS) and the Nordic short-tailed Spel sheep (Spel) are the most common breeds, constituting 80 and 15% of the sheep population, respectively (Steinheim, Ødegård, Ådnøy, & Klemetsdal 2008). The two breeds differ in body size, digestive tract anatomy and diet composition (Steinheim, Nordheim, Weladji, Holand, & Ådnøy 2003). As the breeds feed on the same ranges this system is ideal for testing hypotheses related to whether responses to climate variability and vegetation phenology are similar in the two breeds. The NWS is known to show larger annual variation in lamb body mass than Spel (Steinheim et al. 2008), but whether this is related to specific climate variables has not been tested. In particular, we tested the “good year for all plants” hypothesis, which predicts synchronous body mass variation in the Spel and NWS breeds, against the alternative that their yearly average body mass is varying randomly with respect to each other. We used a hierarchical Bayesian statistical model framework to assess whether different climate variables affected the two breeds in similar or contrasting ways.

Materials and methods

Study area

The study area is the alpine range of Forollhogna at the border of the Hedmark and Sør-Trøndelag counties (N62°38', E10°47'). Its climate spans from semi-oceanic in the west to more continental in the east. The grazing areas considered in this study are situated within the municipalities Os, Tolga, Tynset, Midtre Gauldal, Rennebu, and Holtålen, covering approximately 960 km² at altitudes ranging from 500 m to 1300 m asl (mean = 981) m asl. Forollhogna is characterized by rich mountain vegetation with intense grazing by sheep and reindeer. It is considered an area of high conservation value due to its native flora and fauna as well as its long history of grazing from domestic animals (Fylkesmannen i Sør-Trøndelag 1995). The area has been protected as a national park since 2001.

Sheep data

Sheep grazing in Norwegian mountain ranges is organized in grazing areas. These grazing areas are defined geographical entities where the farmers have historical rights to release their animals over summer. The areas are not fenced, but the animals tend to stay within the particular area. In Norway most sheep are kept indoors during winter due to adverse climate conditions. The lambs are born in spring (May) and slaughtered in autumn (September/October). They are released to the mountains as soon as the vegetation allows for grazing (June) and are taken down to the farm in early autumn (late August). We used an extensive data set on autumn body mass of 38,587 lambs (Spel [$n=9871$] and NWS [$n=28,716$]), obtained from the Norwegian Sheep Recording System, covering the period 1992–2007. We selected the area of Forollhogna as it had a relatively stable number of lambs of the two breeds throughout the study period, though the number of lambs of the Spel breed was lower in any year (mean number of individuals in a year = 617 for Spel and 1796 for NWS). The two breeds were represented in all five grazing areas included in the study. Our response variable was lamb autumn body mass. We did not include birth weight as a covariate, as this variable was missing from a significant proportion of the animals (80.6% for NWS and 66.4% for Spel, respectively). We found however, that the correlation between autumn body mass and growth through the summer (autumn body mass – spring body mass) was identical in the two breeds ($r=0.83$, $p \ll 0.001$ for both breeds). This suggests that winter conditions for the mothers ultimately affecting the spring conditions of the lambs had no systematically different effect in the two breeds. For each individual, we had access to several individual-based covariates previously shown to affect lamb autumn body mass (Myrsterud, Steinheim, Yoccoz, Holand, & Stenseth 2002; Nielsen et al. 2012). We included in our models litter size (single, twin or triplet as categories), sex, lamb age (110–160 days) and maternal age (1–9 years) as a 2nd order term. In addition we included the particular grazing area ($n=5$) the lamb was grazing in as random factor and the stocking rate in that particular area (13.9–88.7 sheep per km² grazable area) as a covariate. The focal area is outside the core areas for large carnivores and the summer mortality rates for lambs were low (5.4% for the period 2004–2008); direct and indirect effects of predation are thus unlikely to have affected lamb body growth.

Local climate, the NAO and vegetation (NDVI) data

To quantify the among-year variation in climate conditions we obtained data on snow depth and precipitation from the weather station Blanktjernmoen (N62°43', E10°42', 690 m asl) and temperature data from the weather station Fokstugu (N62°11', E9°29', 973 m asl), located ~33 and ~100 km

from the centre of the study area, respectively. These stations were the ones situated closest to the area and with registered data for the full study period. All climate data are freely downloadable from The Norwegian Meteorological Institute (www.eklima.no).

To quantify large scale climatic fluctuations among years, we used the North Atlantic Oscillation (NAO) as predictor variable in our model (Hurrell, Kushnir, Ottersen, & Visbeck 2003). NAO has previously been shown to represent large scale weather patterns across Europe, ultimately affecting ecosystems (Stenseth et al. 2003). We used the PC (Principal Component) based winter NAO (December–March) provided by the Climate Analysis Section, NCAR, Boulder, USA as a measure for winter conditions. The rationale for using the NAO from this period is based on previous studies in this and nearby areas showing that the winter NAO is related to snow depth and can be a better variable for describing winter conditions in a particular location, than a snow depth measure taken several kilometres away (Myrsterud, Yoccoz, Stenseth, & Langvatn 2000; Nielsen et al. 2012).

To measure the among-year variation in vegetation phenology and biomass we used the Normalized Difference Vegetation Index (NDVI). This index is derived from the red – near infrared reflectance ratio ($NDVI = (NIR - RED)/(NIR + RED)$), where RED is red reflectance and NIR is near infrared reflectance from the vegetation (Myneni, Hall, Sellers, & Marshak 1995). NDVI is presented as a value between –1 and +1 where higher values indicate greener vegetation and negative values indicate lack of vegetation. We use the GIMMS data set obtained with the Advanced Very High Resolution Radiometer (AVHRR) instruments on-board the National Oceanic and Atmospheric Administration (NOAA) satellites (Tucker et al. 2005), as it covers the full study period. Despite its coarse spatial scale (8 km × 8 km pixels) it has proven to be a very useful measure of inter-annual variation in vegetation phenology (Tucker et al. 2005). It has also been used earlier in the area (Nielsen et al. 2012). We calculated NDVI as the mean NDVI value for all pixels falling within the focal area for each year. To estimate spring phenology we used the NDVI value for late May, as this period has been identified as a good indicator of spring onset in the area (Nielsen et al. 2012). To quantify the summer vegetation we used the integrated NDVI viz. the sum of the six NDVI values for June, July and August (INDVI) (Pettorelli et al., 2005b), as this is when the sheep roam freely in the mountains. We have previously shown that climate conditions in August are important for lamb autumn body mass in the focal area (Nielsen et al. 2012). Therefore, we also tested whether August climate conditions affected INDVI.

Statistical analyses

We analysed whether lamb autumn body mass in the two breeds fluctuated in synchrony, by use of a standard

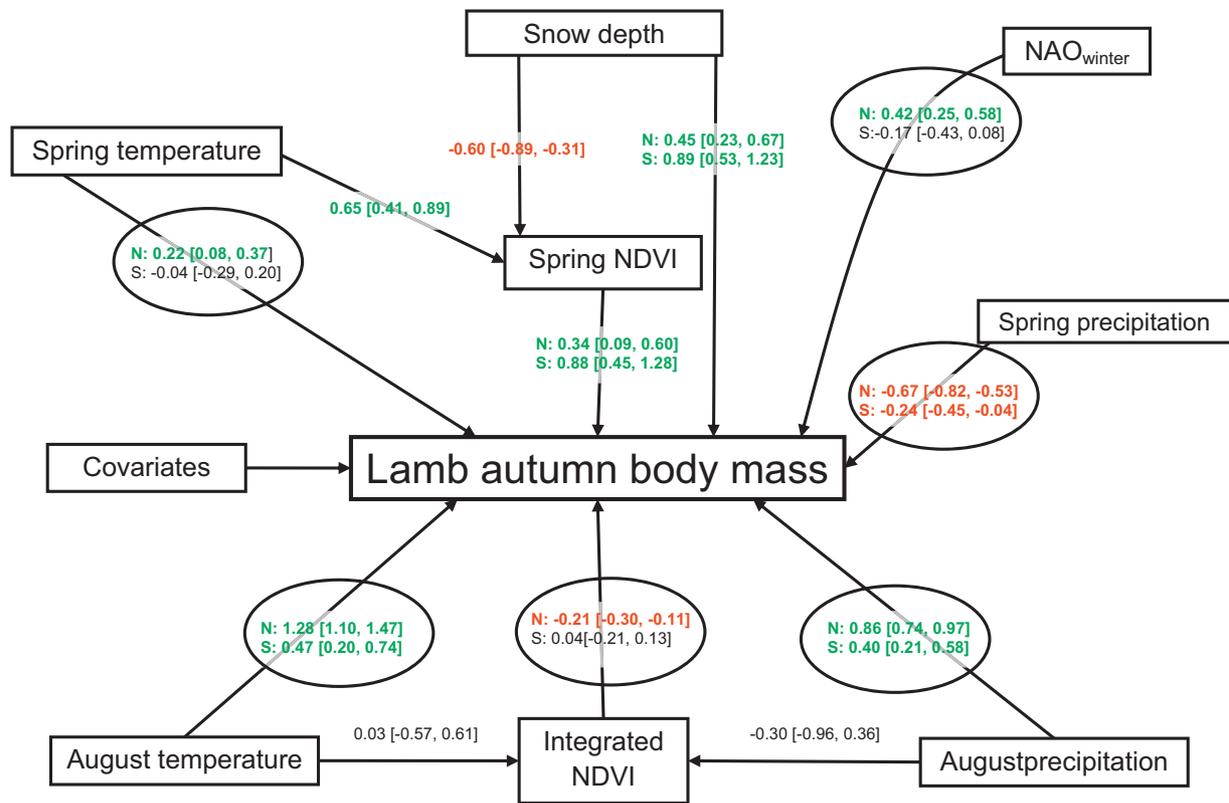


Figure 1. Nielsen *et al.*

Fig. 1. Illustrations of the hierarchical path model used to explain variations in lamb autumn body mass by means of environmental variables (climate and NDVI) in the Norwegian white sheep (N:) and Spel (S:) breeds. Mean effect sizes and 95% credibility intervals are based on three chains of 10,000 MCMC permutations the first 5000 of which were discharged as burn in. To avoid temporal autocorrelation among the permutations only every fifth permutation was included in the calculation of the model output. Statistically significant relationships are indicated in bold, negative effects in red and positive in green. Relationships being statistically different in strength in the two breeds, or where the effect is differing from zero in only one of the breeds, are circled. For parameter estimates and credibility intervals for the demographic covariates see Table 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

correlation test of the yearly average lamb body mass. We used linear mixed effects models (Pinheiro, Bates, DebRoy, Sarkar, & R Development Core Team 2011) to assess whether the demographic covariates (litter size, sex, lamb age [in days] and mother age [in years]) interacted with breed (Table 1). To assess whether the two breeds responded similarly to among-year variation in climate conditions we used a hierarchical path model as it allows the simultaneous estimation of direct and indirect effects of climate. The structure of the model (Fig. 1) was based on a previous study of variations in lamb autumn body mass in the focal area (Nielsen *et al.* 2012). In particular, we included a direct effect of winter NAO on lamb autumn body mass, as this has previously been shown to be of significance (Nielsen *et al.* 2012). All continuous covariates included in the model were centred and standardized (mean set to zero and standard deviation to 1 for each area) to ease the interpretation of effect sizes when comparing explanatory variables and to reach faster convergence when

fitting models. Climate variables (temperature, snow depth and precipitation) were centred on 30-year mean values (1981–2010) and standardized on the standard deviation of the same 30 years of data, to ease the calculations of the

Table 1. Model selection table for deciding on whether to include in the hierarchical path model interaction between breed and the demographic covariates. We decided to include none of the interactions since ΔAIC towards the model containing no interactions was small (<2).

Sex	Litter size	Age	Mother age	AIC	ΔAIC
				249178.6	0.4
×	×	×	×	249191.4	13.2
×	×	×		249188.4	10.2
×	×			249179.5	1.3
×				249179.8	1.6
	×			249178.2	0

total effects of a certain change in climate conditions (see below). We used a varying-intercept, varying-slope model enabling us to assess whether the effect of environmental variables varied between the two breeds. For each climate variable, NDVI and stocking rate, the model estimated a separate slope (regressor) for each of the two breeds. We also included separate slopes for the continuous variable “year”, as selective breeding for increased autumn body mass of lambs is expected to be stronger in the NWS breed (http://www.saueavl.nsg.no/ringanalyse.dmu.utvikling_list.cfm). Each breed was also assigned a separate intercept in the model. We included grazing area as a random factor with separate intercept but with the same relationships among lamb autumn body mass and the explanatory variables.

We used a Bayesian approach to fit our model and specified relationships among the environmental variables (local climate and NDVI) and between lamb body mass and local climate, NDVI, INDVI and additional covariates. To estimate the posterior distribution of the model parameters we used Markov Chain Monte Carlo algorithms in OpenBUGS (Lunn, Spiegelhalter, Thomas, & Best 2009) through the R package R2WinBUGS (Sturtz, Ligges, & Gelman 2005). We used non-informative normal prior distributions for regression intercepts and slopes, with a mean of 0 and variance of 10^6 . For the inverse of residual variance we used a Gamma distribution with shape and scale parameters of 0.5. The inverse variance distributions were narrowed (from the standard non-informative shape and scale parameters of 10^{-3}) to make the models converge within reasonable time while still keeping a prior wide enough to allow for all probable outcomes. We based our parameter estimates and credibility intervals on 3 chains of 10,000 MCMC permutations, with the first 5000 permutations in each chain discarded as burn-in. To avoid autocorrelation among the permutations only every 5th permutation was used, resulting in a total of 3000 sampled permutations in the analysis.

To calculate the total effect of climate variability on lamb body mass the results from the sampled permutations of our hierarchical path analyses was used. To assess the total effect of climate variables (directly on the lamb autumn body mass and indirectly through spring NDVI and INDVI) we included the results from all iterations using the following equation:

$$D = \beta_1(\Delta) + \beta_2 * \gamma(\Delta)$$

Here D is the expected change in average lamb body mass under a certain change in the focal climatic variable. β_1 is the mean effect size of the focal climate variable on the lamb body mass. β_2 is the mean effect size of spring NDVI or INDVI on lamb body mass and γ is the mean effect size of the focal climate variable on spring NDVI or INDVI. Δ is the climate variability used in the analyses (i.e. 1 °C increase in average monthly temperature, 10 mm increase in monthly precipitation and 10 cm increase in maximum snow depth). Since we, in our analyses, standardized our climate variables on 30 years of data we back-transformed our Δ by dividing

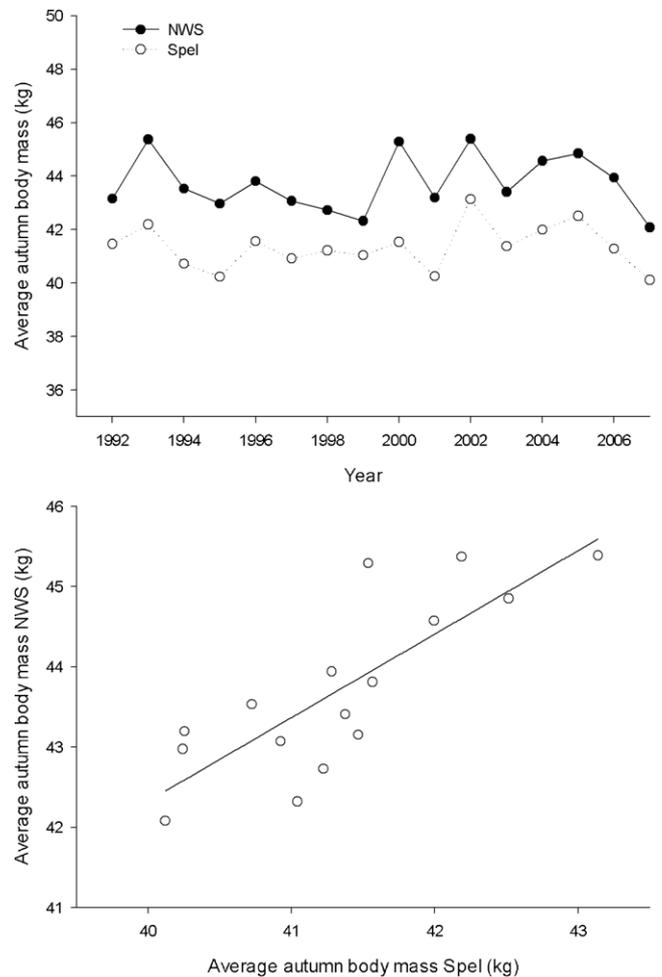


Fig. 2. Correlation in body mass between the two breeds of sheep included in the study (Spel and Norwegian white sheep [NWS]). Top panel: yearly average body mass for the two breeds over the study period. Bottom panel: correlation plot between the average autumn lamb body mass of the two breeds ($t=5.11$, $r^2=0.62$, $p<0.001$, $df=14$).

it on the 30-year standard deviation. All statistical analyses were performed in R version 2.13.1 (R Development Core Team 2010).

Results

The among-years variation in average lamb body mass was highly correlated between the two breeds ($r=0.81$, $t=5.11$, $p<0.001$, $df=14$) (Fig. 2). The among-year variation in average lamb body mass was, however, lower in the Spel breed than in the NWS ($sd=0.83$ (Spel) and $sd=1.08$ (NWS), $n=16$ years of data), indicating a stronger response to variations in environmental conditions in the larger, grass-eating NWS breed. Model selection using linear mixed models suggested no strong interaction between the demographic covariates and breed (Table 1), only the interaction between breed and litter size gave a marginally lower AIC value but

Table 2. The effect of the different individual and grazing area based covariates included in the hierarchical path model. Mean effect sizes and 95% credibility intervals based on three chains of 10,000 MCMC permutations where the first 5000 were discarded as burn in. To avoid temporal autocorrelation among the permutations only every fifth permutation was included in the calculation of the model output.

Covariate	Mean	2.5%	97.5%
Year	0.745	0.661	0.834
Lamb age (days)	1.793	1.725	1.86
Mother age (years)	2.074	2.002	2.145
Mother age ²	-1.316	-1.370	-1.265
Twins	-4.649	-4.825	-4.469
Triplets	-9.315	-9.545	-9.083
Sex (males = 1)	-4.24	-4.358	-4.12
Breed (NWS = 1)	-2.412	-2.606	-2.218
Stocking rate – NWS	-1.813	-2.181	-1.422
Stocking rate – Spel	-1.700	-2.097	-1.291

within 2 AIC units. Thus it was not significantly better than the simpler model without any interaction.

Our path model revealed relationships between lamb autumn body mass and demographic covariates corresponding to what has been shown earlier (Table 2). Males were on average heavier than females, single lambs were heavier than twins which were again heavier than triplets, older lambs were heavier and intermediate aged mothers had the heaviest lambs, as compared to young and old mothers. There was also a similar, positive effect of year (as continuous variable) in both breeds.

NDVI

There was a positive effect of spring temperature and a negative effect of snow depth on spring NDVI. There was no effect of summer climate (August temperature and precipitation) on NDVI (Fig. 1). There was a positive effect of spring NDVI on lamb autumn body mass in both breeds however the effect was stronger for Spel. NDVI had a negative effect on NWS, but no effect on Spel.

Climate

The NAO had a positive effect on lamb autumn body mass in the NWS breed but no effect on the Spel. When assessing only the direct effects of climate variables, snow depth, spring temperature, August temperature and August precipitation had a positive effect while spring precipitation had a negative effect on lamb autumn body mass in the NWS breed (Fig. 2). In the Spel breed we found the same effects for all climate variables but spring temperature, where there was no effect. However, when incorporating also the indirect effect of climate, through NDVI, there was a positive effect of spring temperature also in Spel (Fig. 3). The effects were

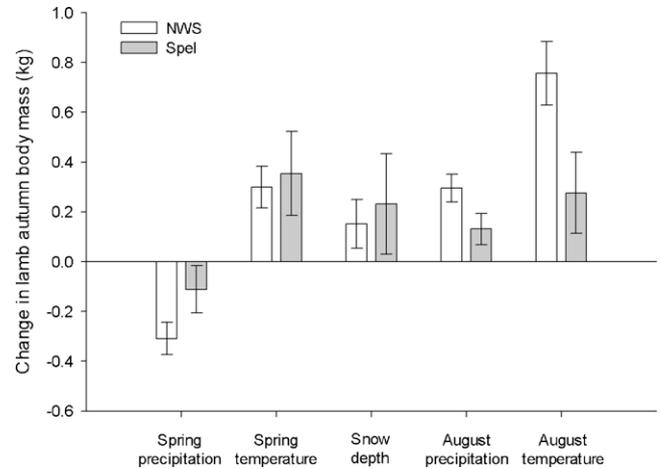


Fig. 3. The expected change in average lamb body mass (in kg) as a result of a given change in local climate conditions displayed for the two breeds of sheep (Spel and Norwegian white sheep [NWS]). The estimated effects are based on a 10 cm increase in maximum snow depth, a 10 mm increase in monthly precipitation and an increase in average monthly temperature of 1 °C. 95% credibility intervals not overlapping each other indicate statistically significant difference in effect between the two breeds.

significantly stronger for spring precipitation, August precipitation and August temperature on the NWS breed (Fig. 3).

Discussion

We found a high correlation in the annual variation in mean lamb body mass in autumn between the two breeds, but that responses to climate variables nevertheless differed in strength. Little attention has been paid to how climate changes may affect various members of the herbivore community. The summer growth of domestic sheep in Norway has shown to be correlated in annual body mass with moose (Sæther 1985), red deer (Myrsterud et al. 2001) and semi-domestic reindeer (Weladji et al. 2003). In wild ungulates, however, the issue of synchronous variation in body mass has been complicated by the potential problem of seasonal variation in diet composition (Mobæk, Myrsterud, Holand, & Austrheim 2012) and resource limitation (Owen-Smith 2008). Therefore, the use of domestic animals only feeding whilst free-ranging during summer can enhance inference regarding the specific role of summer foraging conditions.

Our study comparing two contrasting sheep breeds provides support to the hypothesis that a good year is a good year for herbivores differing in morphology, physiology and behaviour. Since we are only comparing two breeds, we cannot separate whether different responses to climate variability arise due to digestive, energetic or behavioural differences. The Spel breed is only slightly smaller than the NWS (Fig. 2), so overall size is unlikely to play a major role. Behavioural effects of livestock to climate variation might include different responses to heat stress (Nardone, Ronchi,

Lacetera, Ranieri, & Bernabucci 2010), but this is unlikely to be important in our cold, alpine ecosystem. The two breeds differ, however, markedly in digestive tract anatomy (Steinheim et al. 2003), and such morphological and physiological differences in ruminants are well known to yield different preferences for grasses versus browse (Hofmann 1989). Indeed, a previous study found that the Spel breed eats up to 30–50% browse whilst the NWS mainly rely on grass, eating around 10% browse when compared on sympatric ranges (Steinheim et al. 2005). This might influence their spacing and foraging behaviour (Jørgensen, Andersen, Holand, & Bøe 2011). Though we do not possess data on dietary composition of the two breeds for our area, we regard it likely that such large contrast in dietary composition may be an important mechanism behind the differing strength of responses to climate variables observed. Further work would be required to disentangle how much of such variation can be linked to either annual variation in quality of grasses versus browse, how much is due to annual variation in relative intake of grasses versus browse, and how much is due to other differences between the two breeds.

Though the specific mechanism cannot be inferred, the NWS breed was more sensitive to both spring and late summer weather, growing particularly large when conditions were dry/warm in early spring and warm/wet in late summer, conditions favouring continued grass growth. The Spel breed was more strongly affected by spring NDVI, suggesting that plant quantity is more important for this breed, at least in spring. There was a negative effect of integrated NDVI in NWS and no effect of this variable in Spel. This suggests that the positive effect of high plant biomass summers (high INDVI) might be outweighed by an earlier peak in vegetation quality (Hamel et al. 2009), affecting mainly the NWS breed. Both summer temperature and precipitation had a stronger effect in the NWS than in the Spel breed. Though the NWS breed seems to be more strongly affected by climate, the Spel breed was also affected by climate condition throughout the season. The negative effect of spring precipitation and temperature was stronger in NWS while the effect of snow depth was stronger in Spel. This can be viewed as an argument for the importance of spring conditions for the growth of the NWS breed in particular. The effect of spring NDVI was positive in both breeds, and more strongly so in Spel.

The NDVI are representations of the greenness of whole vegetation communities, and cannot be used to pinpoint responses of browse versus grass. The differences in strength of responses to climate variation between the two breeds however, suggest that plant functional groups might respond differently, at least in strength, to similar climate conditions. This might have implications for the development of the plant communities under future climate conditions. The ability of plant functional traits to determine responses to disturbances such as herbivory, is well developed (Díaz et al. 2007a, 2007b; Lavorel, McIntyre, Landsberg, & Forbes 1997), but how plant species located at different positions along the browse-grass continuum respond to annual climate variation remains

less clear. For meadows in the Great Yellowstone ecosystem, forbs and woody species responded differently to drought events, and their performance could be predicted based upon functional groups' responses to water availability (Debinski, Wickham, Kindscher, Caruthers, & Germino 2010). Also, other studies point to a key role of soil resource availability in interplay with competitive balance among plants (De Valpine & Harte 2001). In turn, herbaceous and woody plants differ in their use of water resources (Dodd, Lauenroth, & Welker 1998). The root system is hence identified as a crucial plant trait for predicting annual variation among functional plant groups (Yang et al. 2011). In other studies, species' responses to warming in terms of biomass production were reported from different functional groups, including sedges *Carex quatilis stans*, *C. membranacea*, and *Eriophorum angustifolium*, as well as the dwarf shrub *Salix arctica* and the forb *Polygonum viviparum* (Hill & Henry 2011). However, there is reason to believe that increased temperatures will favour browse, at the expense of grasses in alpine ecosystems (Gordon & Prins 2008), but how this change in the plant community structure will affect plant quality is more of an open question. We thus need more systematic synthesis of annual variation in biomass and quality for different plant functional groups to better understand differences in responses to annual climate variation in browsers and grazers.

Conclusion

We have documented that two breeds of sheep show contrasting responses to climate variations. With only two breeds studied, we cannot document whether this is related to their different position along the grazer-browser continuum reported in earlier studies, but at least it gives a starting point for further work on these issues. In the short term, increased temperatures will favour grazers more than browsers, as grasses show faster responses to environmental change. In a longer term, however, climate change may favour browsers, as the plant community composition in alpine ecosystems is expected to change in favour of browse species (Gordon & Prins 2008). For sheep this suggests that the Spel breed, in addition to being less sensitive to climate variations in general, may experience more favourable forage conditions and consequently perform better under future climate conditions. We believe our findings to be relevant also for wild ungulates in alpine habitats in the sense that browsing species might get an advantage over grazers as increasing temperatures alter the plant community.

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