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Climatic variability and effects on ungulate body weight: the case of domestic sheep

Geir Steinheim[1]*, Robert B. Weladji[1], Tåle Skogan[1], Tormod Ådnøy[1], Arne O. Skjelvåg[2] & Øystein Holand[1]

[1)] *Department of Animal and Aquacultural Sciences, Agricultural University of Norway, P.O. Box 5003, N-1432 Ås, Norway (*e-mail: geir.steinheim@iha.nlh.no)*
[2)] *Department of Plant and Environmental Sciences, Agricultural University of Norway, P.O. Box 5003, N-1432 Ås, Norway*

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Annual climatic variation is reported to affect life history traits such as body mass and reproductive parameters of several northern ungulates. Effects of spring and summer weather conditions on body weights of domestic sheep were studied, using data on 56 584 free-ranging lambs from six coastal and inland grazing areas along a 1200 km latitudinal gradient. Nineteen weather indices, most chosen from a study of relevant literature, were used in the analyses. Linear mixed models, with a variance structure designed to take within-flock and -year dependency into account, were applied. A correlation analysis indicated that the between-years lamb weight patterns of most of the areas, even ones far apart from each other, were related to each other. All weather indices had significant effects on the lamb weights in two or more areas (on average 4.6 areas). The directions of the effects (parameter estimates) were inconsistent among the areas, and possible explanations for the area-specific effects are discussed. Suggestions on future research on climate-ungulate body weight studies are given.

Introduction

Wild and domestic ungulate populations often have substantial between-year variation in adult and juvenile body weights (e.g. Clutton-Brock & Albon 1983, Sæther 1985, Albon *et al*. 1987, Hjeljord & Histøl 1999, Mysterud *et al*. 2001, Weladji *et al*. 2003a). Annual climatic variation is reported to affect life history traits such as body mass and reproductive parameters in the northern ungulates, thereby influencing population dynamic (*see* reviews by Putman *et al*. 1996, Post & Stenseth 1999, Weladji *et al*. 2002, Mysterud *et al*. 2003). Several local weather parameters, including temperature, precipitation and snow depth (e.g. Nedkvitne 1982, Langvatn *et al*. 1996, Loison & Langvatn 1998, Post & Stenseth 1999, Mysterud *et al*. 2001, Weladji *et al*. 2003a, 2003b) have been used to assess effects of climatic variability on northern ungulates' life history parameters.

Weather conditions may act directly on the animals through costs of thermoregulation (Christopherson & Young 1986, Hocquette *et al*. 1992, Parker & Robin 1985) and movement (Fancy & White 1985, Johnson *et al*.

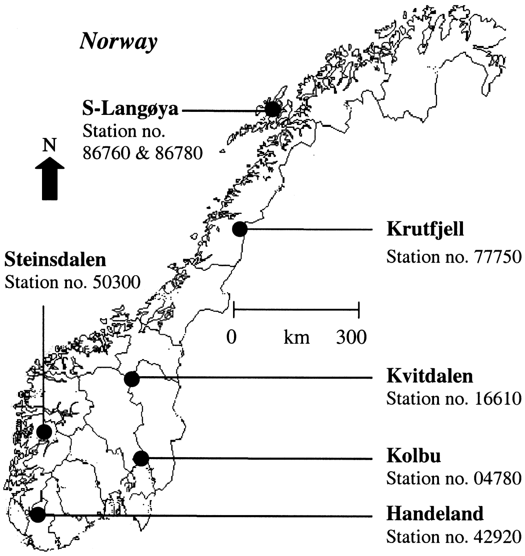

Fig. 1. The six grazing areas, and station number of the Norwegian Meteorological Institute's weather stations where the climatic data were recorded.

2001), or by affecting behaviour (Rouda *et al.* 1990, Warren & Mysterud 1991, Champion *et al.* 1994). Climatic stochasticity may also act indirectly on free-ranging herbivores' body growth through effects on temporal and spatial variation in quantity and quality of forage plants (review in Weladji *et al.* 2002).

There are many studies of the relationships between climatic conditions during summer and growth in northern ungulates (e.g., Clutton-Brock & Albon 1983, Sæther 1985, Solberg & Sæther 1994, Langvatn *et al.* 1996, Hjeljord & Histøl 1999, Weladji *et al.* 2003b), and relations to several weather parameters are reported (review in Weladji *et al.* 2002). General patterns are hard to detect, but low summer temperatures seem to enhance weights of northern ungulates (Sæther 1985, Solberg & Sæther 1994, Langvatn *et al.* 1996, Hjeljord & Histøl 1999, Weladji *et al.* 2003b). Sæther (1985) also reported that autumn slaughter weights of sheep (*Ovis aries*) were correlated with temperature-related carcass weights of calves from a sympatric moose (*Alces alces*) population. For effects of precipitation on ungulate weights there appears to be no clear pattern under temperate conditions (Sæther 1985, Solberg & Sæther 1994, Sand *et al.* 1996, Hjeljord & Histøl 1999).

Despite the availability of long time-series of data on Norwegian sheep, studies of local climate influences on domestic sheep are not internationally published. Importantly, the fact that sheep in Norway are fed indoors during winter gives us the opportunity to test for direct relationship between sheep performance and weather condition during spring and summer.

Autumn live weights of Norwegian sheep lambs, taken at the end of the free-ranging summer grazing period, show marked between-year variation (Eide 1981, Eggen 1992, Garmo & Skurdal 1998, Lind & Karlsen 1998). Between birth and weighing in autumn, lambs spend approx. 70% of the time on rangeland pastures, and the lambs' spring body conditions are fairly stable from year to year (within flock). The observed variations in autumn live weights will thus to a large extent reflect the inherently variable rangeland environmental conditions. A large part of the environmental variation is caused by weather conditions, which should thus be expected to influence the body weight of the animals. The weather's influence on plant quality and quantity has been studied in most detail in the crop sciences, where weather is considered the most important external effect behind annual variations in harvest: weather conditions may account for more than 50% of differences in yield between years and locations (Skjelvåg 1981b).

The objective of this study was to investigate (i) relationships between autumn live weights of Norwegian free-ranging lambs and weather conditions as described by one or several simple weather indices previously found to be — or deemed to be — important for ungulate body weights, and (ii) to test whether the response of sheep to a given weather parameter varies between locations. To do so, we use 11 years of lamb body weight records from six Norwegian grazing areas with a wide latitudinal and altitudinal distribution (Fig. 1).

Materials and methods

Sheep husbandry practice and study areas

During winter, sheep are kept indoors and fed roughage and concentrates. Feeding and care schemes during the winter period are stable over years. Most lambs are born indoors during the spring, and shortly after released onto pastures together with their mothers, which they follow during the entire outdoor season. More than 93% of all Norwegian sheep lambs spend from three to four months free-ranging on unfenced mountain or forest pastures, most in the alpine or sub-alpine zone (Skurdal 1997, Garmo & Skurdal 1998).

In selecting grazing areas we employed the national database Organisert Beitebruk, in which data on location of grazing area, animal density, losses of livestock, and identity of participating farmers are found. To be included, areas should have some natural boundaries (rivers, steep hills etc.) deterring the sheep from utilising other areas. Further, a weather station had to be situated less than 25 km from the area, and there should not be high losses (> 10%) of lambs. Altogether, the areas were to represent several different regions in Norway. Six grazing areas, ranging in size from 40 to 230 km^2 were chosen (Fig. 1). The areas are distributed along a latitudinal range from 58°52´N to 68°36´N. Additional information on the areas is given in Table 1.

Climatic conditions were quite different among the areas and years; e.g., during the study period mean July temperature varied between 5.6 °C (Steinsdalen, 1995) and 20.1 °C (Kolbu, 1994), while the sum of July rainfall varied between 7 mm (Kolbu, 1994) and 315 mm (Steinsdalen, 1992). For details on climatic conditions in the areas, *see* Appendix 1. Three of the grazing areas were situated in regions with Köppen's classical type C climate (Johannessen 1977), here: an advectively determined, maritime, mesothermal climate with cool summers and mild winters (Table 1). The other three areas were in Köppen's type D climates, here: a radiation influenced, maritime, microthermal climate with warm summers and cold winters.

Sheep production data

Sheep production data were retrieved from the Norwegian Sheep Recording System, where approximately one third of the Norwegian sheep population is registered. Only lambs of the prevalent, long-tailed breeds Dala and Steigar were included. The breeds were pooled in the analyses, as they are quite similar in performance and in many ways today may be considered one breeding population.

To ensure that lambs had experienced a normal free-ranging period we excluded all hand-reared lambs, and furthermore all that did not meet the following criteria: (1) litter size (spring) of one, two or three lambs, (2) date of autumn weighing between 10 September and 10 November (in accordance with the end of the rangeland period), and (3) age of ewe between one and seven years (very few are older). Retrieved and calculated parameters for each lamb were: lamb's date of birth, litter size in spring, lamb autumn live weight (kg), date of weighing, age of lamb (days) at weighing, litter size in autumn, flock identity, year and grazing area. To limit the number of terms in the models we did not use ewe's age, due to its high correlation with litter size (Mysterud *et al.* 2002, Steinheim *et al.* 2002). The final dataset consisted of 56 584 lambs (for numbers per area and year *see* Table 2).

Table 1. Characteristics of the study areas, including altitude of the weather stations (WS). Climatic regions from Johannessen (1977); subdivisions relate to winter temperature: subscripts indicate three to four (3) or one to two (4) months with average temperature > 10 °C.

Area name	Altitude area (m)	Altitude WS (m)	Climatic region	Size (km^2)	Latitude (North)
S-Langøya	0–700	12 (30)	CM_4	45	68°36´
Krutfjell	400–1400	265	D_4	180	65°45´
Kvitdalen	950–1600	974	D_4	230	62°15´
Kolbu	500–700	204	D_3	60	60°30´
Steinsdalen	400–1100	408	CM_3	80	60°24´
Handeland	600–1000	500	CT_3	40	58°55´

Meteorological data

Daily observations of temperature, precipitation and snow depth, from April through August, were obtained from the Norwegian Meteorological Institute (DNMI), Oslo. Codes of DNMI weather stations at which the weather conditions were measured are presented in Fig 1. For the northernmost area, S-Langøya, data from weather station no. 86760 (12 m a.s.l.) were missing for 1995, and for this year data from the nearby station no. 86780 (30 m a.s.l.) were used instead. Weather stations were located from 0 to 300 m below the lower parts of the grazing areas (Table 1). No correction of temperature according to the general temperature lapse (Ahrens 1991) of 0.6 °C per 100 m altitude from the weather stations to the grazing areas was done, because the analyses were all conducted over years within areas. Precipitation usually increases with altitude, and precipitation, as related to potential evapotranspiration and soil moisture supply, is usually considered a less limiting factor for plant growth in mountainous areas than in lowlands (Baadshaug *et al*. 1987). Thus, neither precipitation data were corrected for difference in altitude.

The weather indices (Table 3) are combinations of monthly sums of the weather parameters. The sum of daily snow depth values for April was used as an indicator of quantity and persistence of snow in the spring/early summer.

Table 2. Number of lamb autumn weights used in the analyses, per area and year. * = data missing.

Grazing area	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
S-Langøya	843	887	982	1053	1142	1251	1202	1443	1666	1686	1744
Krutfjell	239	634	766	629	562	786	823	411	369	470	*
Kvitdalen	1082	1236	1221	1450	1355	1737	1729	1653	1582	1271	1104
Steinsdalen	306	366	348	462	529	649	708	440	523	563	609
Kolbu	777	870	914	964	1058	1244	1276	1405	1284	1473	1476
Handeland	*	425	366	265	312	393	372	342	544	313	*

Table 3. The 19 weather indices, with information on previous use. The table should not be regarded as an exhaustive review. nr = results not reported.

Previously used by (or * use motivated by)	Weather index related to (month in parentheses)	Species	Time series (years)	Effect on ungulate production traits
Hjeljord & Histøl 1999*	Snow depth (4)	Moose	15/24	
Sæther 1985	Temperature (5)	Moose	13	nr
Sæther 1985	Temperature (6)	Moose	13	Yes
Sæther 1985	Temperature (7)	Moose	13	nr
Sæther 1985	Temperature (8)	Moose	13	nr
Langvatn *et al*. 1996	Temperature (5 + 6)	Red deer	22	Yes
Solberg & Sæther 1994	Temperature (6 + 7)	Moose	22	Yes
Sand *et al*. 1996	Temperature (7 + 8)	Moose	13	Yes
Hjeljord & Histøl 1999	Temperature (5 + 6 + 7)	Moose	15/24	Yes
Sæther 1985	Temperature (6 + 7 + 8)	Moose	13	Yes
Sæther 1985	Precipitation (5)	Moose	13	nr
Sæther 1985	Precipitation (6)	Moose	13	nr
Sæther 1985	Precipitation (7)	Moose	13	Yes
Sæther 1985	Precipitation (8)	Moose	13	nr
Solberg & Sæther 1994	Precipitation (5 + 6)	Moose	22	Yes
Solberg & Sæther 1994*	Precipitation (6 + 7)	Moose	22	
Eide 1981	Precipitation (7 + 8)	Sheep	6	Yes
Hjeljord & Histøl 1999	Precipitation (5 + 6 + 7)	Moose	15	No
Sæther 1985	Precipitation (6 + 7 + 8)	Moose	13	Yes

Statistical analyses

The lamb autumn weights (kg) were ln transformed to achieve constant variance, and corrected for age of lamb (days), sex of lamb (male/female) and litter size (1, 2, or 3 lambs), using the model

$$\mathrm{Ln(Weight_{LAMB})} = \mathrm{age_{LAMB}} + \mathrm{sex_{LAMB}} + \mathrm{lsize_{LAMB}} + \mathrm{year} + \mathrm{error} \quad (1)$$

All variables were defined as fixed; all except age of lamb (continuous) were defined as categorical. Whilst $\mathrm{age_{LAMB}}$ is age (days; defined as continuous; mean = 141, min. = 106, max. = 169) of lamb at weighing, $\mathrm{sex_{LAMB}}$ is sex of lamb (male or female, categorical), $\mathrm{lsize_{LAMB}}$ is the size (in spring) of the litter the lamb was born into (1–3 lambs, categorical). Least square means (lsmeans) for lamb body weight by year, for each area, were calculated for illustrational and comparative purposes, using the GLM procedure in SAS Release 8.02 (SAS 1999). We checked for synchronicity of yearly lsmeans of the autumn weight between areas by computing Pearson's correlation coefficients (SAS Institute Inc. 1985) in the CORR procedure of the software.

For the main analyses, we applied linear mixed models (Littell *et al.* 1996, Montgomery 1997, for applications similar to ours *see* e.g. Kruuk *et al.* 1999, Milner *et al.* 1999, Steinheim *et al.* 2002) with a structure of variance designed to take into account dependency among observations caused by flock and year, thus avoiding pseudo-replication (Kruuk *et al.* 1999), and achieving a desired potential for extending our results (Montgomery 1997), in this case to any farm or any year. Using the Mixed procedure (for theory and applications *see* Littel *et al.* 1996) in SAS Release 8.02, we tested the effects of weather variables on the lambs' body weights for each area separately by applying the model:

$$\mathrm{Ln(Weight_{LAMB})} = \mathrm{W} + \mathrm{age_{LAMB}} + \mathrm{sex_{LAMB}} + \mathrm{lsize_{LAMB}} + \mathrm{flock} \times \mathrm{year} + \mathrm{error} \quad (2)$$

where $\mathrm{Weight_{LAMB}}$ is the lamb's autumn live weight (kg) and W is one of the 19 weather variables from Table 3. The weather indices were included as continuous variables. The interaction term between flock and year (flock × year) and the error were defined as random factors, with flock being included as a categorical term and year as a continuous variable (*see* also Weladji *et al.* 2003a, 2003b for applications). The other terms are as in Eq. 1.

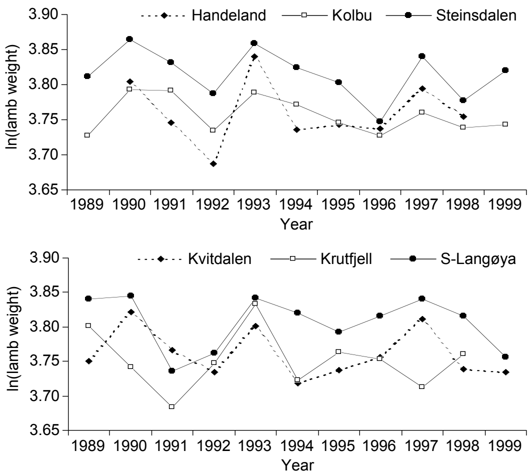

Fig. 2. Corrected means (lsmeans) of ln-transformed lamb autumn live weights for each area and year.

Density of sheep was known only for the years 1992–1999 (Appendix 2). Inclusion of the term *sheep density* (sheep km^{-2}; as continuous and fixed) in the above model (Eq. 2) instead of the weather index for the four areas with some variation in density (Handeland, Kolbu, Steinsdalen and S-Langøya) yielded one instance of density having a significant ($p < 0.01$) effect. The area was Kolbu, where the density varied between 73 and 100 animals km^{-2}, and the density was negatively (est: –0.0009 ± 0.0002) related to the lamb weights. Still, to be able to utilise the complete 11 years of data, we chose to conduct our analyses without including sheep density in the models.

Results

Interannual patterns

The interannual variation in corrected lamb weights (lsmeans from Eq. 1), area-wise, was substantial (Fig. 2). The correlation analysis gave one negative, non-significant (between areas

Kolbu and Krutfjell), and 14 positive relationships between the lamb weight time-series for the six grazing areas (Table 4). The lamb weights of the four southern areas were all positively and substantially correlated to each other (all correlation coefficients > 0.50, all $p < 0.07$).

Relationship between local weather conditions and lamb weight within area

The variance component for the term flock × year ranged from 2.14×10^{-10} to 1.84×10^{-9} for the different weather models (Eq. 2). The residual variance was estimated to be between 0.021 and 0.027 (SE < 0.0005) for all analyses. Consistently, the effects of "lamb sex", "litter size" and "lamb age" were significant ($p < 0.001$) and had similar estimates for all areas and for all runs of the model (Eq. 2). Further presentations of the results are restricted to the effects of individual weather variables in the six areas.

The results indicated that the weather of the grazing season influenced the lamb weight, as each of the 19 weather parameters was significantly ($p < 0.05$) related to the live autumn weights of the lambs in at least two (on average 4.6) of the study areas (Table 5). Four weather variables were significantly related to the lamb weights in all six locations, namely temperature in May, temperature in July, precipitation in May, and precipitation in July. Temperature in May was positively related to the autumn weight except in one area, and temperature in July positively related to the autumn weight in half of the areas. Higher precipitation in May led to lower autumn weights in four areas and higher weights in two. More precipitation in July was favourable to lamb weights in three areas but not beneficial in the three others.

Whenever significant, precipitation in June was negatively, and the three month average temperature in May–June–July was positively related to lamb weights (Table 5). Considering significant as well as non-significant correlations, a readily observable pattern was found in Steinsdalen, where all temperature indices were positively, and all precipitation indices negatively, correlated to the lamb weights. In Krutfjell the precipitation indices were all positively correlated with the weights, while in the neighbouring area, S-Langøya, all the precipitation indices, except the one for August, showed a negative relationship with the weights. In the Kvitdalen area, increasing temperature was associated with increasing weights except for temperature in July, whereas most (seven out of nine) of the temperature indices were negatively related to lamb weights in the southernmost area, Handeland.

Site-specific responses of sheep to climatic variability

As shown in the previous section, our results are inconsistent over areas in terms of direction of relationships between weather variables and autumn live weight of the lambs: positive weather index estimates in Table 5 implying positive relationships with the lamb body weights, and negative estimates the opposite. Indeed, none of the weather variables used showed the same relations in all areas. However, temperature in May displayed an almost consistent pattern: it had a positive effect on lamb weights in five out of six areas, increasing May temperature being associated with declining lamb weights only in S-Langøya (the northernmost, coastal area). This case, in spite of statistical significance, can

Table 4. Correlations (Pearson's) between time-series of corrected means (lsmeans) and ln-transformed lamb live autumn weights for area × year.

	Handeland	Kolbu	Steinsdalen	Kvitdalen	Krutfjell
Kolbu	$r = 0.64$, $p = 0.06$				
Steinsdalen	$r = 0.71$, $p = 0.03$	$r = 0.82$, $p < 0.01$			
Kvitdalen	$r = 0.81$, $p = 0.01$	$r = 0.59$, $p = 0.06$	$r = 0.64$, $p = 0.04$		
Krutfjell	$r = 0.43$, $p = 0.25$	$r = -0.22$, $p = 0.53$	$r = 0.01$, $p = 0.99$	$r = 0.04$, $p = 0.91$	
S-Langøya	$r = 0.70$, $p = 0.03$	$r = 0.09$, $p = 0.79$	$r = 0.24$, $p = 0.46$	$r = 0.49$, $p = 0.13$	$r = 0.52$, $p = 0.13$

Table 5. Parameter estimates (± SE), describing the effect of the weather indices on autumn live weight of lambs in different areas. Significant coefficients ($p < 0.05$) are given in boldface.

Weather index (month numbers in brackets)	Handeland (A1)	Kolbu (A2)	Steinsdalen (A3)	Kvitdalen (A4)	Krutfjell (A5)	Søndre–Langøya (A6)
Snow depth (4)	**0.00012 ± 0.00005**	0.00015 ± 0.00013	**0.00006 ± 0.00003**	**–0.00040 ± 0.00010**	0.00009 ± 0.00016	Missing
Temperature (5)	**0.00777 ± 0.00191**	**0.00324 ± 0.00080**	**0.00287 ± 0.00133**	**0.00683 ± 0.00080**	**0.02651 ± 0.02370**	**–0.02074 ± 0.00207**
Temperature (6)	**–0.00566 ± 0.00181**	**–0.00502 ± 0.00088**	0.00027 ± 0.00130	**0.00346 ± 0.00090**	–0.00024 ± 0.00162	**–0.00084 ± 0.00102**
Temperature (7)	**–0.00330 ± 0.00128**	**0.00494 ± 0.00079**	**0.00247 ± 0.00072**	**–0.00231 ± 0.00075**	**–0.01176 ± 0.00160**	**0.01077 ± 0.00079**
Temperature (8)	**–0.00377 ± 0.00130**	0.00036 ± 0.00074	0.00102 ± 0.00133	**0.00465 ± 0.00074**	**–0.01537 ± 0.00174**	**0.01636 ± 0.00096**
Temperature (5 + 6)	0.00067 ± 0.00130	–0.00046 ± 0.00055	0.00115 ± 0.00080	**0.00425 ± 0.00053**	**0.00643 ± 0.00119**	**–0.01049 ± 0.00090**
Temperature (6 + 7)	**–0.00527 ± 0.00118**	0.00046 ± 0.00060	**0.00212 ± 0.00066**	0.00091 ± 0.00072	**–0.00882 ± 0.00137**	**0.00294 ± 0.00057**
Temperature (7 + 8)	**–0.00273 ± 0.00080**	**0.00173 ± 0.00045**	0.00152 ± 0.00053	**0.00088 ± 0.00045**	**–0.00936 ± 0.00098**	**0.00880 ± 0.00050**
Temperature (5 + 6 + 7)	–0.00196 ± 0.00109	**0.00167 ± 0.00051**	**0.00185 ± 0.00053**	**0.00343 ± 0.00056**	–0.00008 ± 0.00137	**0.00131 ± 0.00056**
Temperature (6 + 7 + 8)	**–0.00317 ± 0.00072**	0.00029 ± 0.00039	**0.00136 ± 0.00050**	**0.00157 ± 0.00043**	**–0.00861 ± 0.00094**	**0.00468 ± 0.00042**
Precipitation (5)	**–0.01760 ± 0.00435**	**–0.00275 ± 0.00117**	**–0.00340 ± 0.00095**	**0.02689 ± 0.00232**	**0.03853 ± 0.00358**	**–0.12860 ± 0.00153**
Precipitation (6)	0.00295 ± 0.00185	0.00084 ± 0.00083	–0.00083 ± 0.00057	**–0.01212 ± 0.00167**	0.00460 ± 0.00255	**–0.00446 ± 0.00154**
Precipitation (7)	**0.00710 ± 0.00207**	**–0.00293 ± 0.00147**	**–0.00289 ± 0.00094**	**0.02656 ± 0.00170**	**0.03412 ± 0.00352**	**–0.02434 ± 0.00114**
Precipitation (8)	**–0.00790 ± 0.00162**	**0.00338 ± 0.00097**	**–0.00279 ± 0.00065**	–0.00078 ± 0.00116	**0.03634 ± 0.00327**	**0.00337 ± 0.00127**
Precipitation (5 + 6)	–0.00036 ± 0.00234	–0.00066 ± 0.00090	**–0.00151 ± 0.00049**	0.00299 ± 0.00220	**0.01917 ± 0.00247**	**–0.01163 ± 0.00126**
Precipitation (6 + 7)	**0.00538 ± 0.00146**	–0.00090 ± 0.00079	**–0.00249 ± 0.00065**	**0.01603 ± 0.00184**	**0.01117 ± 0.00180**	**–0.01431 ± 0.00084**
Precipitation (7 + 8)	–0.00183 ± 0.00117	**0.00197 ± 0.00094**	**–0.00270 ± 0.00052**	**0.00881 ± 0.00102**	**0.02154 ± 0.00187**	**–0.01527 ± 0.00097**
Precipitation (5 + 6 + 7)	**0.00398 ± 0.00158**	–0.00126 ± 0.00076	**–0.00279 ± 0.00054**	**0.02126 ± 0.00147**	**0.01552 ± 0.00162**	**–0.01467 ± 0.00075**
Precipitation (6 + 7 + 8)	–0.00053 ± 0.00010	**0.00291 ± 0.00092**	**–0.00250 ± 0.00045**	**0.01210 ± 0.00171**	**0.01467 ± 0.00146**	**–0.01084 ± 0.00078**

easily be disregarded, because of its very narrowest range of 2.5 °C in May temperature, as compared with the other areas with range widths of 3.2 to 6.2 °C and a similar variation in lamb weight (Appendix 1 and Fig. 3).

Discussion

The within-area weight variation over years was large from one year to the next, indicating a strong temporal variation in environmental resources, which lends support to the "range quality hypothesis" (Sæther & Heim 1993). Considering the lsmeans for areas and years, there appeared to be some degree of synchronicity in the year-to-year weight variation patterns of the six grazing areas. The correlation analysis suggested that the weight variations over years in the areas Kvitdalen, Kolbu, Steinsdalen, and Handeland were all related to each other, and also that there might be a dependent relationship in annual weight variations between so distant areas as the northernmost (S-Langøya) and southernmost (Handeland) one (~1200 km apart). Yet, the latitudinal range of Norway, and the apparent site-specific effects of weather variables make the synchrony-inducing mechanisms hard to explain. One plausible explanation to such a "large spatial scale" synchrony in annual variation in lamb weight might be an effect of large-scale climatic conditions. Indeed, the effects of large-scale climatic fluctuations on terrestrial ecosystems are manifold (*see* reviews by Stenseth *et al.* 2002 and Walter *et al.* 2002), including body weight of grazing animals. Furthermore, large-scale winter weather, as indexed by the North Atlantic Oscillation Index (NAO), is related to autumn live weights of lambs along Norway's western coast (Mysterud *et al.* 2001). It seems doubtful, however, that global winter weather effects are strong enough to result in the pattern observed in this study.

The weather's strong effect on both quantity and quality of forage plants (*see* e.g. Torssell & Kornher 1983, Deinum 1984, Van Soest 1994, Langvatn *et al.* 1996, Sand *et al.* 1996) is likely to be the major component of its influence on the lamb weights. However, due to the lack of data on biomass and chemical composition of plants in our study areas, we do not discuss specific mechanisms in detail.

Our results are, in general, inconsistent among the areas in terms of whether a weather index had a significant effect on the lamb autumn weights, and in terms of its direction (both for significant and non-significant effects). Within areas, the direction of relationships of lamb weights to temperature and precipitation indices also varied with month or combinations of months. The May temperature index showed a significant effect in all areas; in five out of the six areas the direction of the effect was positive. Finstad *et al.* (2000) found May–June growing degree days to have a positive effect on reindeer reproductive performance in the Seward Peninsula (but *see* Langvatn *et al.* 1996). We found a negative, but inconclusive, relationship only in the northernmost area, S-Langøya. In the inland areas at higher altitudes higher temperature as well as more precipitation in the month of May may have accelerated snow thaw and improved early season grazing conditions. Indeed, Kvitdalen had the lowest May temperature and Krutfjell the second lowest one (Appendix 1 and Fig. 3), and just those two areas showed the positive relationships between both temperature and precipitation in May and lamb weights. Otherwise, May precipitation was negatively and, mostly, weakly related to the lamb weights. Lack of soil moisture for grass growth this short a time after snow thaw is not much expected. Frequently, also the seasons with the highest lamb weights were associated with years with high temperature and low precipitation in the month of May (Fig. 3).

The two other weather variables showing consistently significant relationships to lamb weights, but with varying signs, were July temperature and precipitation. However, there were consistently opposite signs of the two variables within areas (Table 5 and Fig. 3). By inspection of Fig. 3 it is seen that years with a low July temperature frequently had a high July precipitation and *vice versa*. In the area with the most precipitation, Steinsdalen, July temperature seems to be the more limiting factor, whilst rainfall is abundant. The other more typical coastal area, S-Langøya, exhibited similar relationships (Fig. 3). The third area showing some of the same relationships was Kolbu: this being the case

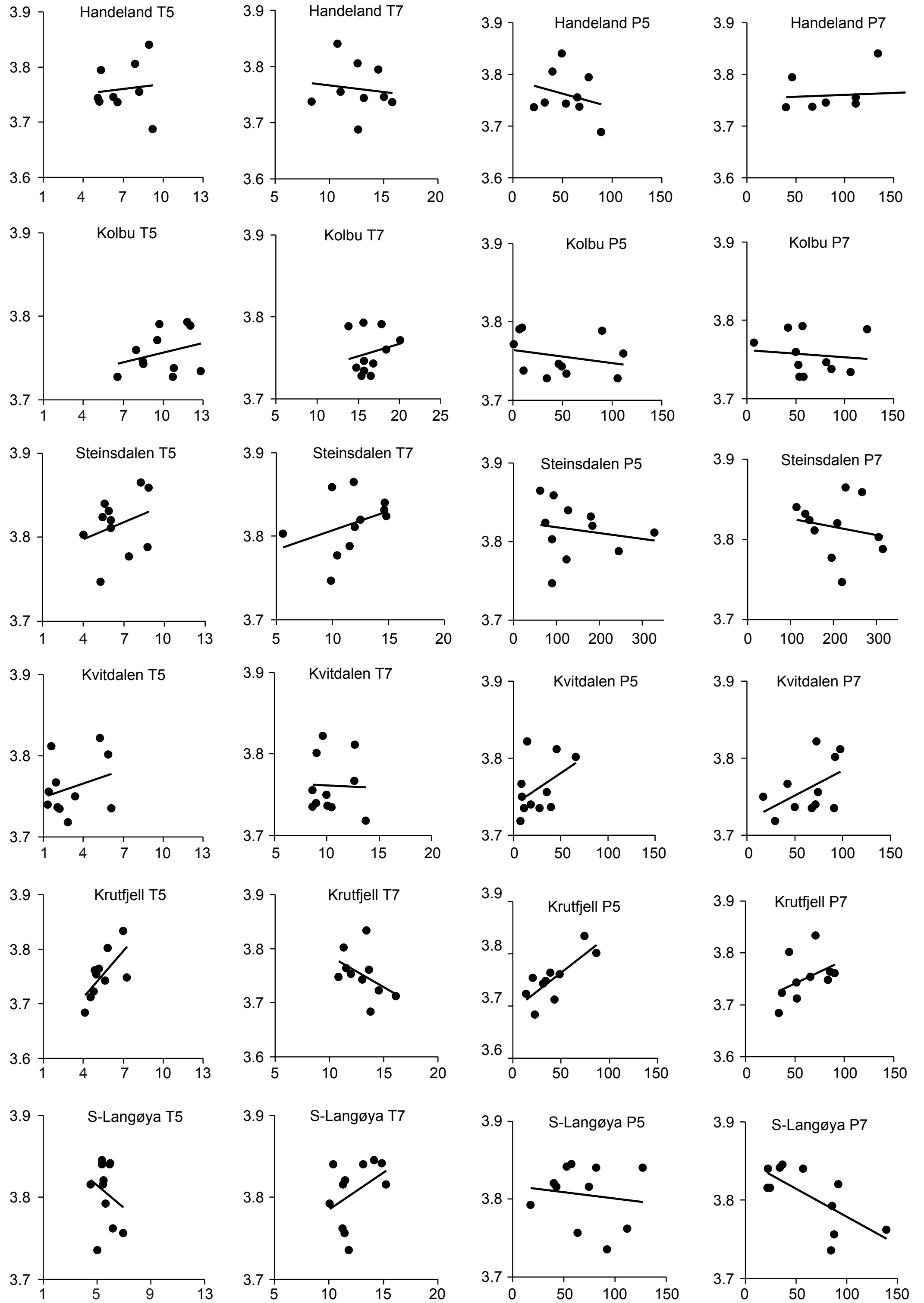

Fig. 3. Area-wise plots, vertical axes are ln-transformed lamb weights per year (least square means, corrected for sex, litter size and lamb age), and horizontal axes are the corresponding weather indices for temperature (°C) in May (T5), and in July (T7), precipitation (mm) in May (P5) and July (P7).

even with the highest July temperature of all areas. However, inspection of Fig. 3 shows that the eleven years of Kolbu lamb weights could rather be grouped into five years with high lamb weights and six years with lower ones, and the relation to temperature in July may thus be a little fortuitous. Four of the high ones had received less than average July rainfall, whilst the lower group had gotten below as well as above average rainfall. Thus, in case the soil moisture capacity in this area has been sufficient to sustain plant growth, which may be possible with its moraine deposits at least at the lower altitudes (Skogan 2000), neither temperature nor rainfall in the month of July is necessarily an important lamb weight determinant. Later in the season, August rainfall was positively correlated to lamb weight in this inland region, as well as in another inland region, Krutfjell.

The three areas exhibiting negative relationships between July temperature and lamb weights clearly indicated a positive relation of weight to July rainfall. Krutfjell with its strong temperature response indicated that cool seasons had received more rainfall than the warmer ones. Thus, this may indicate that the lamb weights had been limited by lack of rainfall and subsequently reduced plant growth in July, and not by temperature whose level did not deviate conspicuously from those of the other regions (which were showing negative as well as positive relationships to lamb weights). Kvitdalen is also an inland region, and the positive relation between precipitation in July and lamb weight appears stronger than the slightly negative one of July temperature. The Handeland area is climatically classified as a coastal CT_3 region (Johannessen 1977). Still, the amount of rainfall in July varied considerably, and the rainfall in June and July indicates that a shortage of soil moisture supply during summer may have limited lamb growth.

The direction, and significance, of the effect of all weather indices seem to be area-specific. This is hardly a surprising result as the areas are situated in different climatic zones (Table 1 and Appendix 1), and exhibit large differences in topography, soil characteristics, vegetation and geology. A few relationships between weather variables and autumn lamb weights, consistent as well as inconsistent ones, are discussed above, and we may, indeed, be able to continue putting forward some sensible explanations for the inconsistencies. It may, however, be a more sound approach to conclude that the interactions between the summer weather and the area-specific characteristics in topography, vegetation etc. are important, but so complex that much more research is needed before one should conclude on specific mechanisms.

We applied a general linear mixed model, testing the effects of weather against a variance structure designed to take dependency within observations into account. This approach has not been common when analysing weather–ungulate relationships (but *see* Milner *et al.* 1999). We tested each weather index on its own, in contrast to model selection approaches where significant relationships often are presented from models including more than one weather index, and where it is often not reported whether each index would have had a significant effect if tested alone. Our method is easier to use for hypothesis testing, but we have certainly not taken into account complex interactions between weather indices: it is likely that such interactions are ecologically important, e.g. low temperature could have a certain effect only if the precipitation level is high. Furthermore, soil moisture status is a much better determinant of plants' water supply than is precipitation (Skjelvåg 1981a).

The stable winter environment of our sheep should have strengthened the influences of summer weather conditions, which have been indicated as especially important to wild grazers (Sæther 1985, Sand *et al.* 1996, Weladji *et al.* 2003). As our study animals spent approx. 70% of their lives before weighing unmanaged (Skurdal 1997, Steinheim unpubl. data), it is not likely that management should have greatly influenced the effects of weather. If ewes were in good condition after the indoor season, their stored resources could function as a buffer against environmental variation. This is, however, counter-indicated by results of Mysterud *et al.* (2001), who found that weather conditions during winter affected sheep (housed and fed during winter) and wild red deer autumn weights in a similar manner, both in terms of relationship patterns and magnitude. It cannot be ruled out that domesticated ungulates' evolutionary histories have altered the way they respond to weather. However, behavioural differences between livestock breeds and wild ancestors are, as a rule, not qualitative (Price 1998), and domestic sheep are unlikely to be less affected, directly, by summer weather than wild ungulates are. Being selected by Man for an efficient production (e.g. fast body growth, low age of sexual maturity), domestic sheep lambs should be as limited by environmental resources as wild ungulates (Beilharz 1998, Rauw *et al.* 1998, Mysterud *et al.* 2002). It thus seems likely that monthly average-based weather indices found appropriate for moose and red deer (*Cervus elaphus*) should work similarly for sheep, especially as these wild ungulates' summer diets have a substantial overlap with that of free-ranging domestic sheep (Mysterud 2000). Thus, the domestic sheep, for which high quality data exist, is a well-suited animal for studying summer weather-ungulate relationships.

Unfortunately, due to the limited time series, we were unable to include density of sheep in the analyses. The consequent omission of an interaction term between density and climate may also be important (Aanes *et al.* 2000, Gaillard *et al.* 2000, *see* also Coulson *et al.* 2001). A challenge for further research is to determine the relative contributions of the two factors, and how they interact (Sæther 1997, Gaillard *et al.* 2000, Coulson *et al.* 2001, Patterson & Power 2002).

The known importance of weather conditions for quantity and quality of forage (*see* e.g. Torssell & Kornher 1983, Deinum 1984, Van Soest 1994, Langvatn *et al.* 1996, Sand *et al.* 1996), and for animal behaviour and thermoregulation, makes it imperative, both from a theoretical and a management/production viewpoint, to develop a better understanding of how weather conditions influence the autumn body weights of lambs. This calls for further studies using more sophisticated approaches. The goal should be to develop models able to disentangle direct and indirect effects of weather conditions, using weather parameters derived along the lines of Langvatn *et al.* (1996): from knowledge of important periods in the study animals' life history. Models should be able to demonstrate non-linear effects of environmental variables on animal traits (Brereton *et al.* 1994, Mysterud *et al.* 2001) and should take into account interactions between weather variables, and between weather and other environmental variables. Also, further studies should focus on spatial scale of effects of weather variables: how far may we move along altitudinal, latitudinal and longitudinal gradients before size and/or direction of the effects change?

The spatial variation in climate and other environmental characteristics, the weather's potential of having both direct and indirect effects, and the animals' abilities to respond to weather conditions by adjusting their behaviour (e.g. by altering habitat use), suggest that a linking of weather variables and production parameters of ungulates will be an arduous task. Still, the demonstrated relationships indicate possibilities in, for instance, predictions of autumn lamb meat production already during the summer. There are several options for improved approaches at various resolution levels. Modern technology in geographical information systems (GIS) may allow for interpolation of weather variables to the real grazing areas. This may substitute observations from a more or less representative nearby weather station, and it may open for a combined and meaningful use of data on weather, quarternary geology, and vegetation as environmental characteristics (O. E. Tveito *et al.* unpubl. data).

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Appendix 1. Monthly mean, minimum (Min.) and maximum (max.) values of observed weather parameters during the study period 1989–1999. Snow = monthly averages of daily April snow depth (cm) including days with no snow. Precipitation = means of monthly sums.

			Temperature (°C)				Precipitation (mm)			
		Snow	May	June	July	August	May	June	July	August
Handeland	Mean	7.8	7.0	10.7	12.7	11.7	55	93	101	126
	Min./max.	1.7/16.9	5.1/9.2	8.1/13.6	8.4/15.8	7.6/15.4	21/89	17/162	40/162	19/250
Kolbu	Mean	0.8	9.9	13.7	16.4	14.8	47	84	65	89
	Min./max.	0.0/4.0	6.6/12.8	10.2/17.2	13.8/20.1	11.9/19.2	1/111	10/173	7/123	15/182
Steinsdalen	Mean	6.1	6.5	10.2	11.6	11.5	146	191	208	247
	Min./max.	0.3/18.3	4.1/8.9	7.6/12.9	5.6/14.8	9.4/14.6	63/328	52/396	114/315	105/459
Kvitdalen	Mean	3.6	3.1	7.8	10.4	9.1	26	56	66	68
	Min./max.	1.3/5.7	1.3/6.1	5.3/10.8	8.7/13.8	6.8/12.7	8/67	6/94	17/98	22/119
Krutfjell	Mean	3.2	5.4	10.6	13.1	12.0	42	60	62	69
	Min./max.	0.8/5.01	4.1/7.3	8.0/13.1	10.9/16.2	10.3/15.0	14/87	20/107	34/91	29/116
S-Langøya	Mean	0.0	5.7	10.3	12.3	12.2	69	45	62	81
	Min./max.	0.0/0.0	4.5/7.0	8.0/12.2	10.1/15.2	9.6/13.8	18/127	9/83	22/140	43/134

Appendix 2. Number of ewes and lambs per km^2 in the study areas, 1992–1999. * = area and year without corresponding lamb weight data or meteorological data.

	Year							
Area	1992	1993	1994	1995	1996	1997	1998	1999
Handeland	43	39	48	51	54	54	46	*38
Kolbu	73	77	81	86	92	92	100	95
Steinsdalen	27	28	29	29	26	25	22	23
Kvitdalen	16	15	16	16	15	16	16	16
Krutfjell	9	9	10	10	10	8	8	*8
S-Langøya	95	99	101	105	104	106	104	110