

Genotype by environment interaction effect on lamb weaning weight in Norwegian White Sheep.

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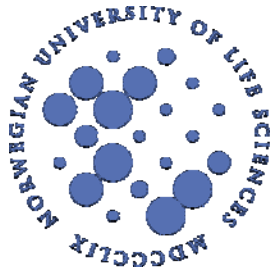
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SUMMARY

Genotype by environment (G x E) interactions influence the phenotypic expression of a trait and the presence of these interactions can have economic consequences for sheep breeding. These interactions are more likely to be present when there are huge environmental differences. Norwegian sheep usually graze in local mountain or forest pastures during summer. In this study, we aimed to estimate genotype by environment (G x E) interactions in Norwegian White Sheep as genetic correlations between area-specific traits (autumn lamb weight) in three ram circles located in two different counties from Norway: southern county of Buskerud and northern Troms. Using data from the National Sheep Recording System, a bivariate animal model was fitted and genetic correlations for each trait were obtained. None of the obtained correlations present a threat to the current breeding scheme. However, further studies including other important production traits and an increase of the representative flock data are suggested.

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DEDICATION

To my parents (Pablo and Guadalupe) and brothers (Zahir and Zarel) who I love on top of everything and always encourage me to reach my goals.

To my friends at home and the ones I've made through this past 2 years, for being always there for me and for sharing countless adventures.

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ABBREVIATIONS

G x E	Genotype by environment interaction
NWS	Norwegian White Sheep (in Norwegian: “Norsk kvit sau”)
NSG	Norwegian Sheep and Goat Association
LME	Lier, Modum and Eiker (ram circle)
masl	Meters above sea level

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1. INTRODUCTION

Norwegian White Sheep (NWS) is the predominant breed kept in Norway. To improve the genetic gain and breeding strategies, the Norwegian Sheep Breeding Scheme was established in 1968 by the Norwegian Sheep and Goat Association (NSG). This scheme is in charge of the recording system and breeding program for the NWS (Eikje et al., 2008).

To select the best animals in a population, breeding plans take into account several aspects (e.g. carcass conformation, maternal performance, inbreeding, etc). A factor that may also impact sheep productivity is genotype by environment (G x E) interactions. When these interactions occur, the phenotypic expression of a trait is influenced by factors present in both the environment and the genetic constitution of an animal (Bondari, 2003).

Norway has very diverse rangeland resources (Figure 1); it is possible to find in the southern part large forest areas, as well as a vast range of mountains; while in the north, alpine vegetation changes gradually into arctic tundra (Austrheim and Eriksson, 2001). According to Austrheim et al. (2008a) about 93% of the Norwegian rangelands are not suitable for agriculture, only for grazing. Value of feed harvested through rangeland grazing in 2005 was estimated to \approx 145 million US\$, of which sheep contributed with about 68 % (Asheim and Hegrenes, 2006).

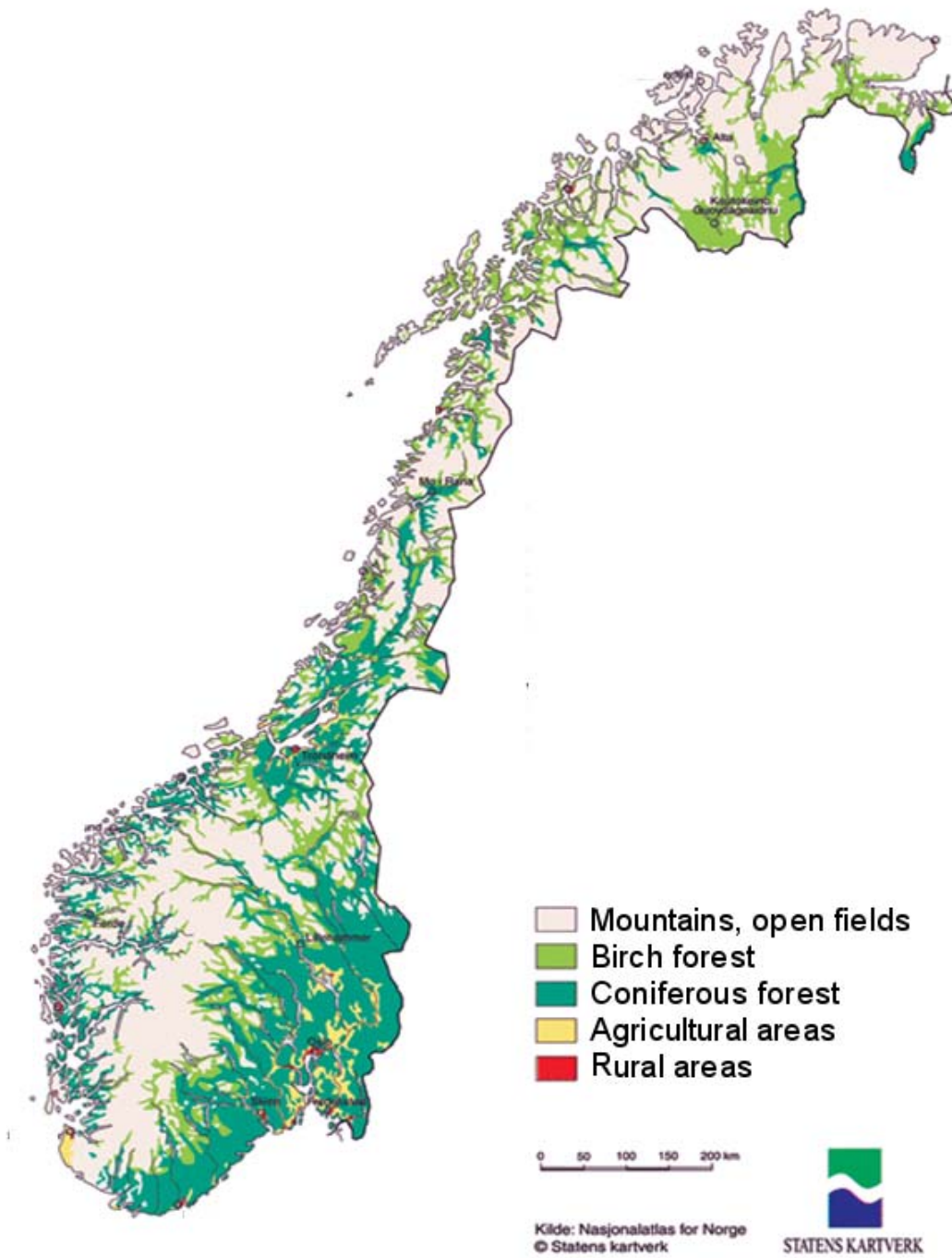


Figure 1. Norway's forest and agricultural land areas.

Source: Statens Kartverk (2011)

Because of these variations in environments across Norway's rangeland areas (mountain or forest pastures) and the increasing use of artificial insemination (AI), genotype by environment (G x E) interactions could be important for sheep production (Steinheim et al., 2008b).

In this study we estimated genotype by environment (G x E) interactions in Norwegian White Sheep as genetic correlations between area-specific traits (autumn lamb weight) in three ram circles of two counties from Norway: two in the southern county of Buskerud and one in northern Troms.

Ram circles were chosen because their grazing areas represent common types of northern and southern mountain pastures and southern forest pastures, without a significant amount of predators (which increases sheep mortality), and with farmers that are members of the National Sheep Recording System (ensuring good recorded data) and have similar management practices.

In the southern county of Buskerud, both mountain and forest pastures can be found. Therefore, two ram circles out of this county were selected: Lier, Modum and Eiker (LME - consist in three municipalities) and Uvdal, the first on which farmers graze their flocks locally in the forest and the second in the mountains. The farms from the ram circle of Alperingen - located in the Lyngen Alps from the northern county of Troms - graze their flocks in the mountains. Information about grazing areas was collected through contacts in the circles: only flocks grazing pastures representative of the circle's "normal" area were included in the datasets.

Most studies estimating G x E interactions have been performed for cattle. Only a few studies have focused on G x E interactions in sheep. For example, Steinheim et al. (2008a; 2004) found significant breed by environment interactions on lamb autumn weights while comparing two Norwegian sheep breeds (Dala and Spæl), and also found lower environmental sensitivity for Spæl lambs than for NWS; concluding that it may be related to differences in digestibility and foraging behavior. This is the first attempt to estimate genotype by environment interactions within-breed in Norway.

2. LITERATURE REVIEW

2.1 Norwegian White Sheep

The long-tailed Norwegian White Sheep (NWS) (Figure 2) is a synthetic cross-breed, for meat and wool production (15%) (Austrheim et al., 2008b; Vatn, 2009). The breed comprises about 80% of the sheep population in Norway (Eikje et al., 2008). It was accepted as an own breed in 2000-2001, but it is basically a mix from three Norwegian breeds: Dala, Steigar and Rygja. Norwegian White Sheep are quite heterogeneous; compared to the original Dala sheep they are a bit smaller but more muscular, having higher fertility and higher growth rate (NORDGEN, 2011; NSG, 2011).



Figure 2. Typical Norwegian White Sheep (NWS)

Source: <http://www.123hjemmeside.no/Solhaug-gardstun/40877305>

Other breeds, such as Spæl, Merino, Texel, Suffolk, etc. can be also found in Norway but are kept in a much smaller scale. Along with the Norwegian White Sheep, 13 of these other breeds participate in the national recording system (Eikje et al., 2008; NSG, 2011).

Some of the trait means of NWS population recorded in the years 2003-2007 are shown in Table 1.

Table 1. Trait means in NWS for the years 2003-2007 (Eikje, 2008).

Trait	Trait mean
Litter size at birth (at 1 yr of age ^a)	1.63
Litter size at birth (at 2 yrs of age)	2.10
Litter size at birth (at 3 yrs of age and older)	2.36
Litter size at weaning (at 1 yr of age)	1.46
Litter size at weaning (at 2 yrs of age)	1.86
Litter size at weaning (at 3 yrs of age and older)	2.02
Weaning weight (kg)	43.43
Carcass weight (kg)	19.60
Carcass grade (EUROP-system) ^b	47.44
Fat grade (EUROP-system) ^c	5.69
Lambs' fleece weight (kg) ^d	2.12

^a) Litter size at weaning is per ewe lambing, ^b) 41(P-)/55(E+), ^c) 1(1-)/15(5+), ^d) for the years 1998-2002

2.2 Sheep breeding in Norway

Sheep in Norway are generally kept on rangeland pastures from May to October (average period of 99 days (Skurdal, 1995) and inside, with feeding, the rest of the year. The ewes are mated in early winter (first time, when they are 7 – 8 months old) and give birth in spring while they are still indoors (Austrheim et al., 2008b). During winter, feeding is based on roughage

(silage, hay) with concentrate supplements (Austrheim et al., 2008a). During summer, lambs follow the dams in the mountain or forest pastures until weaning at the age of ≈ 5 months.

The Norwegian Sheep Breeding Scheme was established by the Norwegian Sheep and Goat Association (NSG) in the 60's in order to maximize genetic gain in all regions (Eikje et al., 2008). It provides information about pedigree and production data from the flocks that participate in this system, which accounts for about 30% of the total sheep population of Norway (Vatn, 2009). The scheme is based on progeny tested ram lambs in ram circles. The total breeding population comprises about 1,300 flocks with 110,000 ewes recorded. The National Sheep Recording Service receives traits information recorded by the farmers and the slaughterhouse. During the mating season, the test rams are moved among the cooperating flocks for testing and to create genetic relationship between flocks. The ram lambs are selected according to their pedigree and own performance and the ewes according to selection index (Eikje, 2008). By using selection indices, rams can also be selected for mating as elite rams. Some of the most promising (based on first year results) are selected for artificial insemination (AI) which helps to increase the genetic gain (Eikje et al., 2008) and creates additional genetic ties, that are beneficial when doing genetic analyses across regions.

Artificial insemination in Norwegian sheep breeding has become more common since the 90's, and from 2002 onwards the annual numbers of AI matings have increased from 30,000 to 45,000. Semen is also collected for long-term storage from AI-rams at two of the AI-stations (NORDGEN, 2011). Non-return rates in 2007 after use of AI were 63% for frozen semen and 78% for fresh semen (Eikje et al., 2008).

The main traits included in the NSG multi-trait breeding goal are: litter sizes, carcass weight, carcass class, fat percentage, maternal effect on spring weight, and maternal effect on carcass weight (Table 2).

Table 2. Weight (%) given to traits in the national sheep breeding goal (NSG, 2011).

Trait	Percentage
Litter sizes	12 %
Carcass weight	20 %
Carcass class	23 %
Fat percentage	12 %
Maternal effect on spring weight	8 %
Maternal effect on carcass weight	25 %

2.3 Genotype by environment interactions

A genotype, as defined by Falconer and Mackay (1996) is the combination of alleles at a single locus in a diploid organism. The visible characteristics (e.g. physical) that are due to the interaction between the genotype and the environment of an organism are referred to as the phenotype. Although all animals in principle have the same genotypes, environmental conditions such as weather fluctuations and feed quality may influence their genetic potential if there are environmental variations. A way to see this it is as phenotypic plasticity, which refers to the ability of organisms to respond to changes in the environment and the differences in phenotypic plasticity between genotypes result in genotype by environment interactions (G x E) (Kolmodin, 2003b; Strandberg, 2005).

A genotype by environment interaction (G x E) determines if the genotype is adapted to a range of environmental conditions or if, otherwise, different genotypes must be selected for different environments (Bondari, 2003). This means that the best genotype in one environment is not necessarily the best in another one; therefore, if this interaction exists, a trait in two different environments should be regarded as two different traits (e.g. to improve a breeding program).

Lin and Togashi (2002) classify the following types of G x E interactions:

- Breed by environment interaction (between-breed interaction)
- Individual by environment interaction (within-breed interaction)
- Gene by environment interaction (within-individual interaction)

To understand this better, it is important to know the possible effects that can result from G x E interactions (Bondari, 2003; Brdaric, 2010; Hammami, 2009; Kolmodin, 2003a):

1. Absence of G x E interaction.

The example represented in Figure 3 shows that the phenotype for genotype 1 (G1) and genotype 2 (G2) are equally different in two different environments (E1 and E2). This means that the animal that has better performance in E1 also performs better in E2.

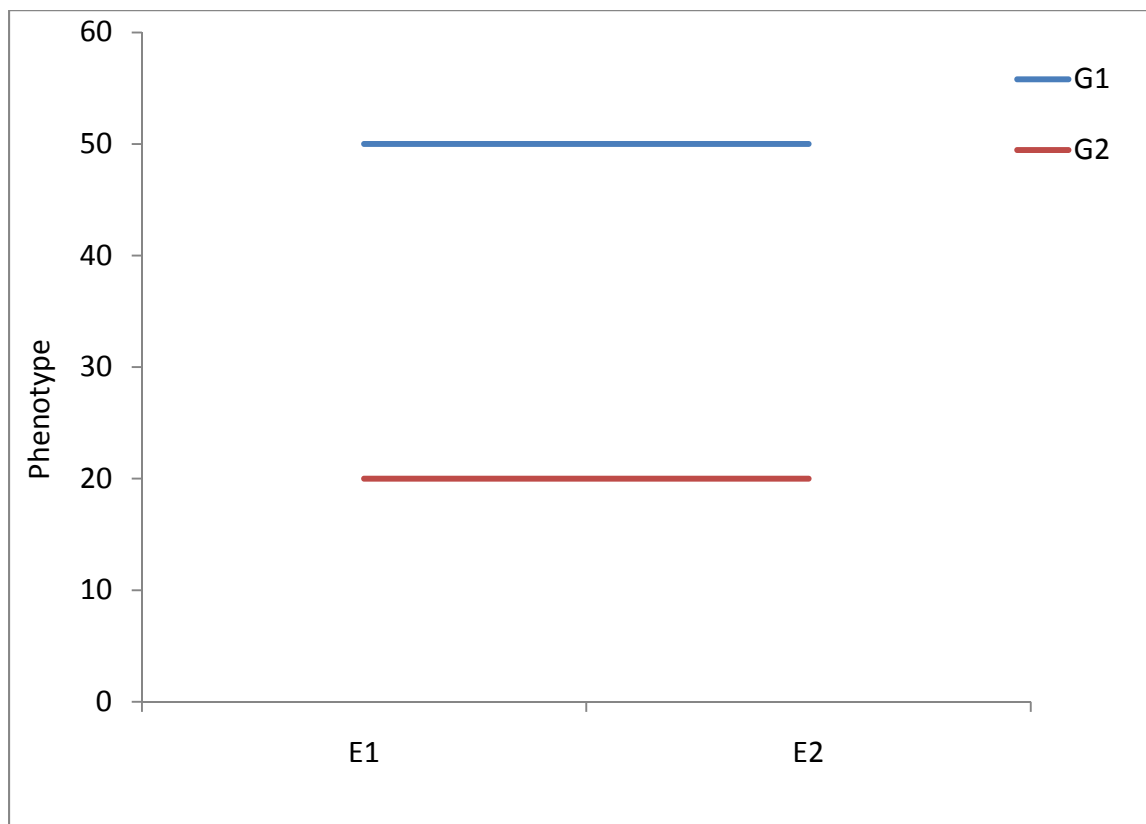


Figure 3. Example of absence of G x E interaction.

2. G x E interaction due to an effect of scaling.

Presence of scaling implies a difference between the genotypes in the different environments but the best animal in one environment will still be the best in the other one (Figure 4).

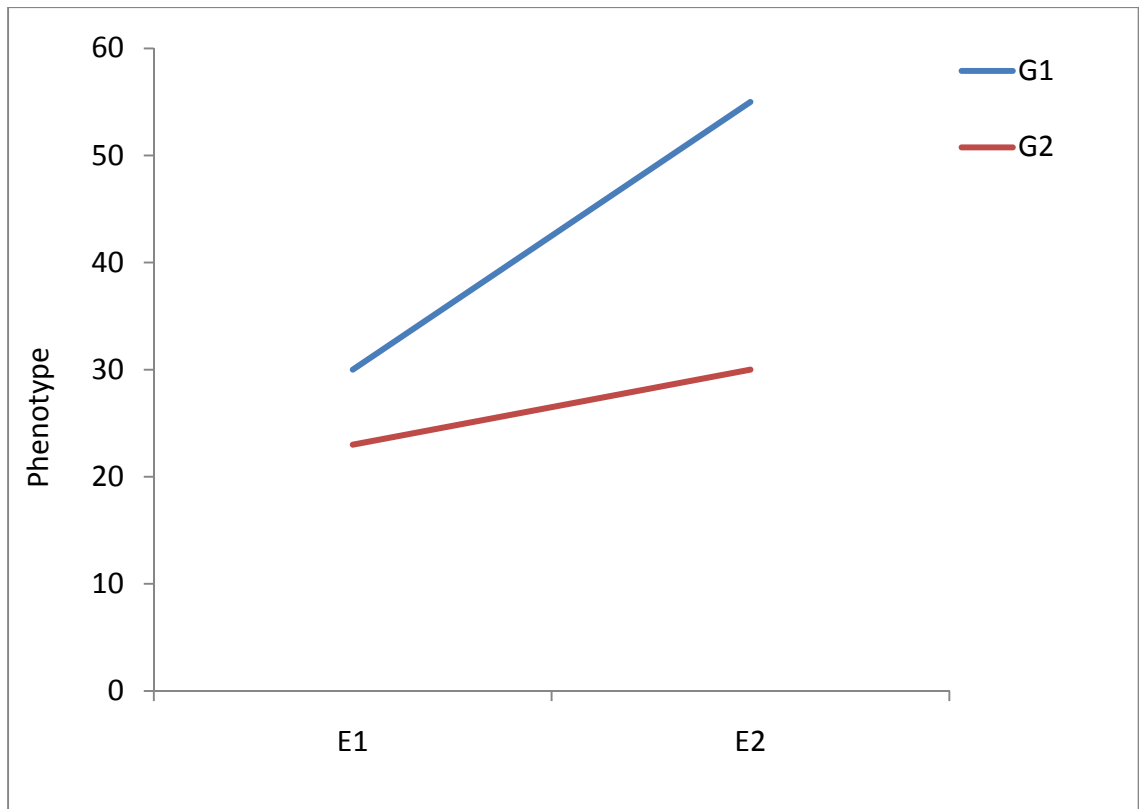


Figure 4. Example of scaling.

3. G x E interaction due to an effect of re-ranking.

In the example (Figure 5) it is possible to see that genotype 1 (G1) performs better on environment 2 (E2), while genotype 2 (G2) is superior on environment 1 (E1). Additionally to this example, it is possible to observe G x E with both effects of scaling and re-ranking.

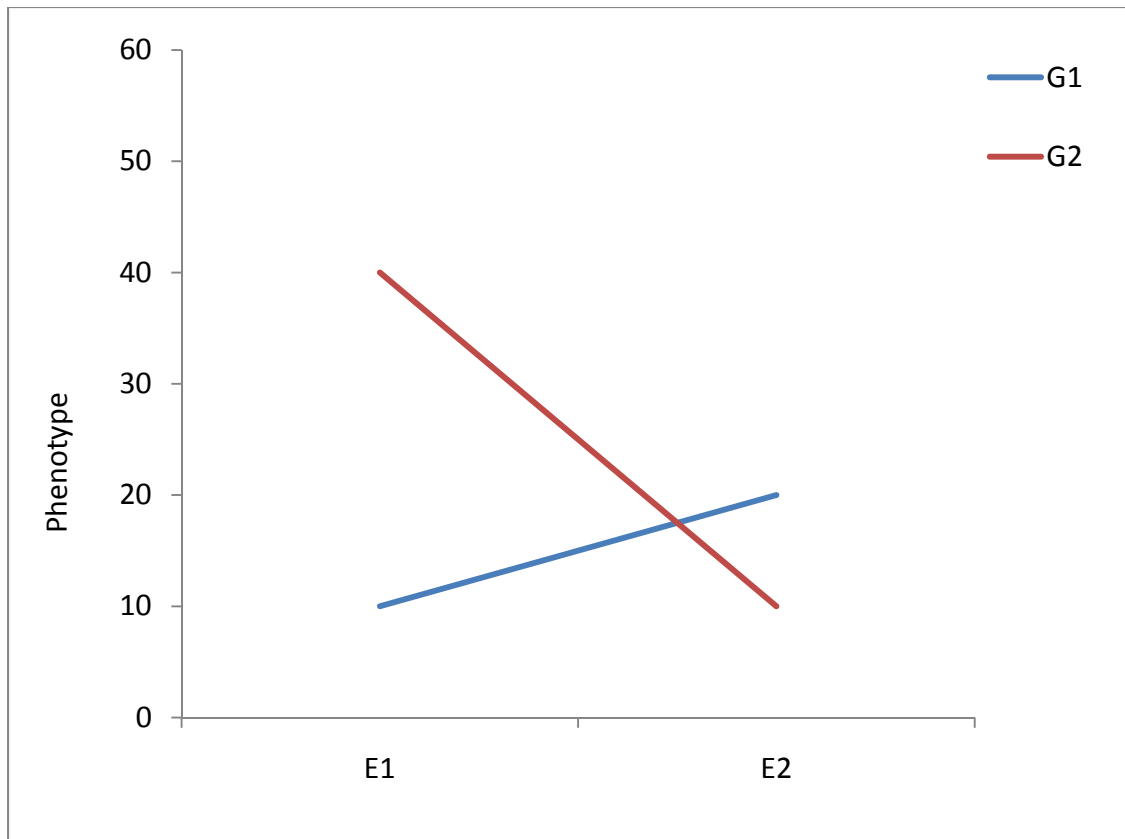


Figure 5. Example of G x E due to re-ranking.

For animal breeders it is of concern if a significant genotype by environment (G x E) interaction occurs (for example, causing a re-ranking). Hence, knowledge of genotype by environment interactions may be useful in order to calculate genetic values more accurately and improve the breeding strategies (Steinheim et al., 2004).

2.4 Methods to study G x E interactions

The equation $P = G + E + e$ (P = phenotype, G = genotype, E = environment, e = residual) explains the phenotype effects of both the genotype and the environment. Environmental effects are usually assumed to be random (de Jong and Bijma, 2002). If there is G

x E, an interaction term will add up to the equation ($P = G + E + GxE + e$) (Strandberg and Kolmodin, 2010).

Normally, in a multiple trait model, G x E can be estimated based on the genetic correlation (r_G) between a trait measured in different environments (Falconer, 1996; Lin and Togashi, 2002):

$$r_G = \frac{\sigma_{G_1G_2}}{\sqrt{\sigma^2_{G_1} * \sigma^2_{G_2}}}$$

where $\sigma_{G_1G_2}$ is the genetic covariance between environments 1 and 2, $\sigma^2_{G_1}$ and $\sigma^2_{G_2}$ are the genetic variances of the same trait in the two environments, respectively. The genetic correlation across environments is expected to be one if there is no G x E interaction (Hammami, 2009). If the correlation is low, an interaction is present, meaning that the expressed phenotypes between different environment may be determined by different genes (Strandberg and Kolmodin, 2010). According to Robertson (1959), correlations lower than 0.8 indicates that the G x E interactions are of biological and agricultural relevance, due to re-ranking of breeding animals.

A reaction norm model it is also useful to study G x E interactions because reaction norms can be used to describe the gradual changes on a trait in an environmental gradient. In this sense, this model would measure how sensitive is an individual if there is a change in the environment (Kolmodin, 2003a).

Other statistical methods and modeling are available in order to study G x E interactions. Some of them are: Analysis of Variance (e.g. least squares, restricted maximum likelihood (REML)), regression, variance components, cluster analysis, factor analysis, Additive Main Effects and Multiplicative Interaction effects (AMMI) (Bondari, 2003).

Consequences for breeding, such as loss of genetic gain (Mulder and Bijma, 2005), may arise due to the presence of genotype by environment (G x E) interactions. For breeders, dealing with a G x E with scaling effect would be easier because it would not generally affect selection strategies (Hammami, 2009). On the other hand, if a re-ranking effect exists, especially when environments are not controllable, which is the case in Norwegian sheep grazing; then specific genotypes for each environment should be selected. This would allow maintaining genetic diversity and optimizing the use of the pasture but problems such as inbreeding and low selection response may arise (Hammami, 2009). According to Lin & Togashi (2002), the solution for each type of G x E interaction is unique and depends on the combination of six factors: G x E interaction intensity, relative economic weights, environment sizes, nature of environments as well as nature of G x E interaction and selection intensity.

3. MATERIAL AND METHODS

3.1 Data and data preparation

3.1.1 Flock data

The data used for this study was provided by the National Sheep Recording Service (Norwegian Sheep and Goat Association).

The data comprised information on the Norwegian White Sheep recorded between 1990 and 2010 in three ram circles (“Uvdal” and “Lier, Modum and Eiker” located in the southern county of Buskerud and “Alperingen” located in the northern county of Troms) (Figure 6).



Figure 6. Map representing the locations of the three selected ram circles.

A=Alperingen, U= Uvdal, LME= Lier, Modum and Eiker.

From the information provided, a dataset was made comprising the following variables: circle (“Uvdal”, “Lier, Modum and Eiker” or “Alperingen”), unique identification number (ID) for the 26 flocks (10 flocks from “Uvdal”, 11 flocks from “Lier, Modum and Eiker” and 5 from “Alperingen”), year (between 1990 and 2010), flocks by year (average of 19.9 farms present each year), lamb ID (unique number for the 76110 lambs recorded), age at weighing (90-180 days), age of the dam (1-8 years), litter size at birth (1, 2, 3, 4 or 5 lambs), litter size in

autumn (1, 2 or 3 lambs), sex (1=male, 2=female), birth rank (30 classes comprising litter size at birth, litter size at autumn and sex), and autumn weight for each circle (Uvdal: 17 – 84 kg, Lier, Modum and Eiker: 17 – 75 kg, and Alperingen: 17 – 81 kg). The selection criteria for including lambs in the dataset are the same as used in the national sheep breeding scheme (Eikje, 2008; Eikje et al., 2008).

Thus, the final dataset comprised records from 76110 animals. Additionally, pedigree information was provided, altogether 9,712,338 records, and by including 12 generations back for those with data, a final pedigree file of 166,703 animals was considered for the analyses.

Data preparation and editing were done using SAS software, version 9.1 for Windows (SAS Institute Inc., 2004).

3.2 Study areas and pasture environments

Overviews of the main characteristics where the ram circles are located are described below.

- LME ram circle:

Lier, Modum and upper-/lower-Eiker, (Øvre-Eiker and Nedre-Eiker) municipalities, Buskerud county, 56°E 66°N, Norway. Located at an altitude of 100-650 meters above sea level (masl). Average temperature in summer (June – August) ranges from 14.3°C to 18°C, receiving from 33-225 mm of precipitation (YR, 2011). Grazing takes place in two neighboring areas: Finnemarka and Vestmarka. The forest pasture is strongly dominated by coniferous forest (Fir and Pine), where many small lakes and ponds can be found. All areas are below the tree line. According to the Norwegian Forest and Landscape Institute (2011b), Finnemarka has an average

sheep density of < 25 sheep/km² and Vestmarka of 25-50 sheep/ km². Also, the mortality while on rangeland pasture of both dams and lambs during 2009 was 5-6%.

- Uvdal ram circle:

Nore og Uvdal municipality, Buskerud county, 49°E 66°N, Norway. Located at 850-1200 masl with an average summer temperature of 10.6°C, receiving from 62-130 mm of precipitation (YR, 2011). Grazing areas are characterized by sub-alpine forest (a mix of coniferous and deciduous tree species) and open areas above the tree line (≈ 1050 masl) (Norwegian Forest and Landscape Institute, 2011a). These areas have an average sheep density of < 25 sheep/km² and rangeland losses in 2009 were 0-0.4% of both dams and lambs (Norwegian Forest and Landscape Institute, 2011b).

- Alperingen ram circle:

Lyngen municipality, Troms county, 93°E 77°N, Norway. Located at 100-1200 masl. In summer it has an average temperature of 13°C. Grazing areas are dominated by deciduous forest, mainly birch and some Willow trees (*salix spp.*). The tree line is located at ≈ 400 masl (Norwegian Forest and Landscape Institute, 2011a). The average density of sheep is 26-50/km². During 2009, losses of sheep accounted for a 7-8% (Norwegian Forest and Landscape Institute, 2011b).

Normally, the large altitudinal gradient allows grazers to follow the snow melt upwards during summer where the fresh, high quality forage is located.

3.3 Data analysis

Genotype by environment (G x E) interactions estimates were made as a genetic correlation (r_G) between a trait measured in different environments (Falconer, 1996; Lin and Togashi, 2002).

3.3.1 Model

For each of two traits (weaning weight in the two environments), the follow bivariate linear mixed model was fitted using the Restricted Maximum Likelihood (REML) method in the ASReml Software release 2.0 (Gilmour et al., 2006);

$$Y_{ijklmno} = \mu + C_j + \beta_1 X_k + R_l + AM_m + FY_n + dam_o + a_i + e_{ijklmno}$$

Where

$Y_{ijklmno}$ is the autumn weight for lamb i

μ is the overall mean

C_j is the fixed effect of the j th ram circle ($j = 1, 2$)

$\beta_1 X_k$ is the regression (β_1) of the age at weighing in days (X_k)

R_l is the fixed effect of l th litter size at birth, litter size in autumn and sex (up until 30 classes)

AM_m is the fixed effect of the m th age of mother of the i th lamb (from 1 to 8 years old)

FY_n is the fixed effect of n th flock by year

dam_o is the random effect of the common environmental effect of the o th dam for the i th lamb

a_i is the random additive genetic effect of lamb i , with $a = [a_1 \dots a_p] \sim N(0, A\sigma_a^2)$, p is the number of animals contained in relationship matrix A and σ_a^2 is the additive genetic variance component (for the circles Uvdal, LME and Alperingen, respectively).

$e_{ijklmno}$ is the random residual for lamb i , $e = [e_1 \dots e_N] \sim N(0I\sigma_e^2)$, where N is the number of observations for autumn lamb weight in one environment, I is an identity matrix of dimension N , and σ_e^2 is the variance component in one environment.

3.3.2 Likelihood-ratio test

A likelihood-ratio test was performed in order to test whether the genetic correlations obtained were significantly different from unity. This was made by comparing both log likelihoods from the model with the correlation fixed at 0.99 (≈ 1) and that from the model with the correlation estimated from the data. The test statistic is twice the difference in these log-likelihoods: $LR = -2[(\log \text{likelihood for null model}) - (\log \text{likelihood for full model})]$ (Lynch and Walsh, 1998). The statistic has a chi-square (χ^2_r) distribution with r degrees of freedom; in our case $r = 1$.

4. RESULTS

4.1 Descriptive statistics

Least-square means of autumn lamb weight (corrected for age at weighing, age of ewe, sex, litter size in autumn and year) were plotted per circle in order to observe the variation of weights across the selected environments. As shown in Figure 7, weights vary substantially across the environments, with the northern ram circle “Alperingen” having the lowest and the southern mountain ram circle “Uvdal” having the highest lamb weights.

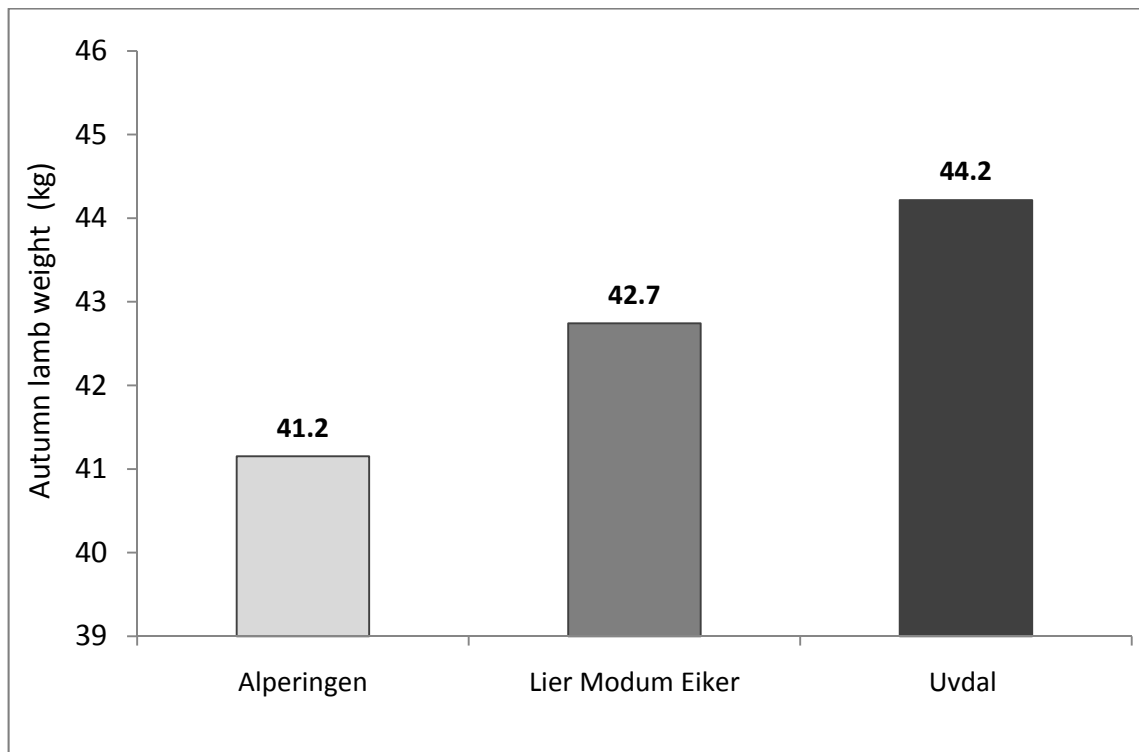


Figure 7. Least-square means of autumn lamb weights from selected ram circles.

Number of records, minimum and maximal values, and standard deviation of autumn lamb weight in the three test environments are described in Table 3.

Table 3. Number of records, mean, standard deviation (SD) and range of autumn lamb weight in the three test environments.

Ram circle	N	Autumn lamb weights		
		Mean	SD	Range
Uvdal	17040	44.05	7.67	17-84
LME	37530	43.76	7.26	17-75
Alperingen	21540	42.46	7.76	17-81
Uvdal + LME	54570	43.96	7.60	17-84
Total	76110	43.54	7.67	17-84

N= number of records (lambs), LME= Lier, Modum and Eiker.

4.2 Genetic correlations and likelihood-ratio test

Estimates of genotype by environment interactions as genetic correlations (r) for autumn lamb weight between pairs of environments (ram circles), including their standard error (se) and results from likelihood-ratio test (LR) to test whether the obtained genetic correlations were significantly different from one are presented in Table 4.

Table 4. Genetic correlations (r) for autumn lamb weight between pairs of environments (ram circles), with standard error (se) and results from likelihood-ratio test (LR) of whether the genetic correlations are significantly different from one.

Tested ram circles			LR	
			X^2 of LR	Significance
Uvdal	LME	0.99±0.00 ^a	0.04	NS
Uvdal	Alperingen	0.99±0.00 ^a	0.16	NS
LME	Alperingen	0.85±0.13	1.84	NS
Uvdal + LME	Alperingen	0.89±0.11	1.00	NS

LME= Lier, Modum and Eiker, NS= not significant ($P > 0.05$, $X^2 = 3.84$).

^aASReml restriction: r may not be > 0.99 .

None of the estimated genetic correlations are significantly different from one.

5. DISCUSSION

None of the obtained correlations were significantly different from unity. The smallest estimate was 0.85, when comparing the southern forest with the northern mountain grazing areas, which are obviously environmentally different.

When performing G x E studies across environments, strong genetic ties (connectedness) are needed; otherwise there would be risk of bias in genetic comparisons (Kuehn et al., 2008). In this study, flocks are assumed to be well connected due to the use of the same AI rams in the different circles. Indication of this is shown in the low standard error of estimates of genetic correlation.

When using the genetic correlation approach, precise estimates depend on the amount of data. It is important to have enough data. Increasing our material by grouping “Alperingen” data with information from similarly environmental ram circles (e.g. “Senja” ram circle – located at the coast of the county of Troms-) and also data from other ram circles that represent the typical southern forest while avoiding strong presence of predators; would ultimately result in more precise correlation estimate.

To determine the environmental factors that are actually causing correlations lower than 1 is not straightforward. From our selected material and locations, it is possible to think that these interactions could be related to foraging behavior, e.g. in the mountains, sheep usually start grazing following the snow melt where they find fresh pasture. Another possible reason for G x E interactions could come from the fact that in comparison of mountains’ high altitude where the climate is cooler, southern forest has warmer conditions, that could facilitate the incidence of heat stress. Overall, it is likely that these interactions are due to combination of several environmental factors.

Unlike the reaction norm approach (Kolmodin, 2003a), essentially based on defined environmental gradients, genetic correlations are estimated without the need to define exactly what environmental traits (e.g. altitude, precipitation, etc.) are relevant. Because of the high number of potentially important environmental traits shaping the Norwegian sheep grazing areas, defining environmental gradients may turn out to be a complex task.

Further G x E research should take into account a combination of important production traits such as carcass weight, number of lambs born and survival, and should include a wide range of environments. G x E should be studied for aggregated genotype (using the relative economic values of the traits) which may help to clarify whether a significant G x E interaction exist in the level of the breeding goal.

6. CONCLUSION

This is the first attempt to estimate genotype by environment interaction (G x E) within-breed in Norway. This study shows the possible presence of G x E interaction but with no consequences for the current sheep breeding program (estimates for weaning weight were equal to or higher than 0.85). Further studies should be carried out on the level of the breeding goal, for an aggregated economic genotype.

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