SHORT COMMUNICATION

Genotype by environment interaction for lamb weaning weight in the Norwegian White Sheep breed

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Abstract: Genotype by environment (GxE) interaction effects influence phenotypic expressions of a trait and may be of importance for sheep breeding. Interaction effects are more likely to be present when there are large environmental differences. Norwegian sheep usually graze mountain or forest pastures during summer. In this study, we estimate GxE interactions in Norwegian White Sheep as genetic correlation between area-specific traits (autumn lamb weight) in three ram circles located in two different counties; two in Buskerud in the south and one in Troms to the north of the country. 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 correlations were significantly different from unity indicating the absence of GxE interaction effect for weaning weight. To gain further insight, studies should include a breeding-goal level aggregation of all traits thought to contribute to profitability.

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Introduction

Norway has diverse rangeland pastures, ranging from southern lowland forests to the transition zone between alpine vegetation and arctic tundra in the north (Austrheim & Eriksson, 2001). This large environmental variation, together with a national breeding scheme with intensified use of artificial insemination (AI) (Eikje et al., 2011), stress the need to investigate whether genotype by environment (GxE) interaction effects important for breeding, exist within the most prevalent Norwegian sheep breed, the Norwegian White Sheep (NWS).

Steinheim et al. (2004, 2008) found significant breed by environment interactions effects on lamb autumn weights when comparing NWS and the Spælsau breed, with lower environmental sensitivity (deJong & Bijma, 2002) for Spælsau than for NWS, and suggested that this was due to breed differences in digestive anatomy (Steinheim et al., 2003) and diet choice (Steinheim et al., 2005). We now present the first attempt to estimate GxE interactions within-breed in Norwegian sheep, using the NWS. This recently founded, composite breed (Eikje et al., 2008), is mainly made up of the Norwegian breeds Dala, Rygja, and Steigar (these hail from old Norwegian breeds and UK breeds, with some imports of Finnish Landrace and Texel) (descriptions, see: Oklahoma State University, 2011: www.ansi.okstate.edu/breeds/sheep).

We estimated genotype by environment (GxE) interaction effects on lamb weaning weight in the NWS using a bivariate animal model, with the GxE effect modelled as the genetic correlation between environment-specific weaning weight traits.

Material and methods

Sheep data and study areas

The Norwegian sheep breeding scheme is based on ram circles (Gjedrem, 1969) made up of several flocks (in 2011 a total of 122 circles; 92 of these keep NWS) that exchange promising rams for progeny testing. Rams producing high quality offspring are selected as elite rams, and some of these are chosen for national use through AI. Data are collected through the Norwegian Sheep Recording System in which today approximately 4,500 sheep flocks (of a total of 14,000) participate.

Ram circles included in this study were 1) Lier, Modum and Eiker (hereafter termed: LME), grazing their sheep on forest pasture in Buskerud county, 2) Uvdal, also in Buskerud, using mountain pastures, and 3) Alperingen using coastal mountain pasture in Troms County (Fig. 1). Animals from flocks belonging to these circles were selected from the Recording System. A requirement for inclusion in the study was that the summer range pastures should be relatively free from large predators, and within a circle only sheep from farms using the same rangeland area for all sheep (verified through communication with the circles) were included.

Data included observations from 1990 through 2010, on 37,530 lambs in LME (11 flocks), 17,040 in Uvdal (10 flocks) and 21,540 in Alperingen (5 flocks); in total 76,110 lambs. Selection criteria for including lambs in the dataset were similar to those used in the national BLUP evaluations (Eikje et al., 2008), e.g. weaning weight 15-85 kg, age at weighing 90-180 days, with birth in spring and weighing in autumn. Due to few older ewes in our dataset we included only dams aged 1 - 8 years. A 12-generation pedigree was constructed for all lambs.

Statistical analysis

Data management and descriptive statistics, including number of sires used across >1 of the circles (for indication of genetic ties between the environments) was done in SAS 9.2 (SAS Institute Inc., 2008). Using ASReml-W v3.0 (Gilmour et al., 2009) we fitted a bivariate general mixed linear animal model, with the GxE effect modelled as the genetic correlation between weaning weight in environments *I* and *II* and tested through comparing log likelihoods of a (reduced) model with the correlation set to unity and a (full) model with the correlation estimated from the data. In the following, environment *I* and *II* represent two of the in total four environment classes (LME, Uvdal, LME and Uvdal pooled, and Alperingen). The model was

$$\begin{bmatrix} y_I \\ y_{II} \end{bmatrix} = \begin{bmatrix} X_I & 0 \\ 0 & X_{II} \end{bmatrix} \begin{bmatrix} b_I \\ b_{II} \end{bmatrix} + \begin{bmatrix} Z_{w_I} & Z_{p_I} & 0 & 0 \\ 0 & 0 & Z_{w_I} & Z_{p_I} \end{bmatrix} \begin{bmatrix} u_{w_I} \\ u_{p_I} \\ u_{w_{II}} \\ u_{p_{II}} \end{bmatrix} + \begin{bmatrix} e_I \\ e_{II} \end{bmatrix},$$

where **y** is the vector of all weaning weight observations in environment *I* or *II*; **b** is a vector of environment-specific fixed effects included to correct for environmental and demographic effects and **X** an incidence matrix relating **b** to the environment-specific observations. Fixed effects included <u>ram circle</u>, <u>birth rank</u> (combinations of litter size at birth 1-5, litter size in autumn 1-4, and sex of lamb), <u>age of dam</u> (1-8 years), and <u>flock by year</u>. <u>Age at weighing</u> (80-180 days) was included as a regression variable. The incidence matrix **Z** relates observations in environment *I* or *II* to their random effects in **u**, a vector representing random effects for direct (**w**) additive effect and maternal permanent environmental (**p**) effects for environment *I* or *II*. Variance-covariance structure for **w** was

$$\begin{bmatrix} A\delta^2_{BV_I} & A\delta_{BV_{I,II}} \\ A\delta_{BV_I,BV_{II}} & A\delta^2_{BV_{II}} \end{bmatrix}$$

where **A** is the additive relationship matrix between animals; correspondingly sized maternal (environmental) and residual variance matrices were diagonal but heterogeneous.

Results

Mean weaning weights and descriptive statistics per ram circle are given in Table 1. The heaviest lambs were found in Uvdal and the lightest in Alperingen.

Log-likelihood tests of explanatory gains of including estimated-from-data correlations between weaning weights in the pair-wise environment classes (Table 2) did not find any of the correlations to be significantly different from unity (all $p > 0.05$). Heritabilities and genetic and residual variance components are given in Table 3.

From use of AI sires and exchange of live animals within Buskerud, LME and Uvdal shared 83 sires, LME and Alperingen 49 sires, and Uvdal and Alperingen 43 sires. Of these rams, 30 had sired lambs in all three ram circles.

Discussion

None of the obtained correlations were significantly different from unity. The smallest estimate was 0.85 for weights in the southern forest area (LME) versus weights in the northern mountain grazing area (Alperingen): this environmental pair, with a north-south distance of approximately 2000 km, is likely the one with the largest between-environment contrast in pasture conditions. The correlation is, however, not even approaching significance and is not an appropriate basis for a discussion on possible interactions.

The pattern of genetic correlations from the bivariate model may seem counterintuitive: $\mathbf{r_g}$ is at unity between environments LME and Uvdal, and between Uvdal and Alperingen, but estimated to 0.85 between LME and Alperingen. Estimating the correlations simultaneously through a trivariate model would likely have given more tidy results; we do however believe the bivariate approach to be the most valid in our case: when investigating GxE interaction effects between a southern forest environment and a northern mountainous environment, information from a third, separate area (southern mountain) should not make the level of the estimate more correct.

The estimates of heritability for weaning weight ranged from 0.14 to 0.19 with a tendency towards being highest in Uvdal and lowest in Alperingen. The size of these estimates correspond well with previous studies: Larsgard and Olesen (1998) estimated a heritability of 0.12 ± 0.11 in Norwegian White sheep. From the genetic and residual variance components it is clear that the phenotypic variance and (substantially) the residual (micro-environmental) variance were higher in Alperingen than in Uvdal, with LME at an intermediate level. This may be due to sheep achieving a more homogenous pasture environment in Uvdal, or, possibly, to different weighing practices. In theory the different variation could be due to differences in environmental plasticity (de Jong & Bijma, 2002); this should be addressed in further studies

When performing GxE studies across environments, strong genetic ties (connectedness) are needed; otherwise there is risk of bias in genetic comparisons (Kennedy & Trus, 1993; Kuehn et al., 2008). We found a considerable overlap in use of sires between the circles, as reflected in the reasonable standard errors of the estimates of the genetic correlations.

To determine the environmental factors that are relevant in a GxE context is not straightforward. From our selected material and locations, it seems likely that interactions could be related to genetic differences in foraging behaviour; e.g. on mountain pastures sheep usually take advantage of the altitudinal gradient by following the snow melt and thus getting prolonged access to fresh, newly emerged plant growth. Another possible reason for GxE interactions could be different occurrence of heat stress: even in Northern Norway sheep will often reduce their foraging time on hot summer days [even in the northernmost part of Norway temperatures may rise as high as 30°C, see *e.g.* Meteorologisk institutt (2011)] and resistance to heat stress is likely to have a genetic basis. Overall, when comparing such diverse environment classes as rangeland pasture types it is likely that GxE interaction effects, if present, are due to combinations of several environmental factors.

Unlike the reaction norm approach (Kolmodin, 2003), which is based on defined environmental gradients, genetic correlations are estimated without the need to define what specific 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 relevant environmental gradients may turn out to be a complex task.

Further GxE research within sheep breed in Norway should appreciate all production traits that are important for industry profitability in a wide range of environments. Even with small GxE effects for individual traits, the effect through aggregated genotypes could still be considerable.

Conclusion

This is the first attempt to estimate genotype by environment interaction (GxE) within-breed for sheep in Norway. The results do not indicate the presence of a GxE interaction effect for the lamb weaning weight. Further attempts to gain industry-relevant insight into GxE interaction effects within sheep breed, should carry out studies on a breeding goal level, i.e. for an aggregated economic genotype.

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TABLE HEADINGS

Table 1. Number of records (N), mean, standard deviation (SD) and range of autumn lamb weight in the four environments studied (LME = ram circle “Lier, Modum og Eiker”)

Table 2. Genetic correlations (r_g) ± SE, between lamb weaning weights in Lier, Modum og Eiker (LME), Uvdal, and Alperingen ram circles; no r_g differed significantly from 1.0: the χ^2 statistics (df= 1) in italics for the log-likelihood test must be ≥ 3.84 to reach a 0.05 level of significance.

Table 3. Genetic (**δ^2_{BV}**), maternal permanent environmental (**δ^2_{PE}**), and residual environmental (**δ^2_{E}**) variation, with estimated heritabilities (**h^2**) for each environment (LME= Lier, Modum and Eiker), for each bivariate analysis.

FIGURE CAPTION

Figure 1. Location of study areas are indicated on the map; these are the summer grazing areas of the ram exchange circles Lier, Modum og Eiker (LME), Uvdal (U) and Alperingen (A).