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Analyzing Genotype by Environment Interaction on the pre- weaning growth rate of Norwegian white sheep using a two-stage reaction norm approach.

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ANALYZING GENOTYPE BY ENVIRONMENT INTERACTION ON THE PRE-WEANING GROWTH RATE OF NORWEGIAN WHITE SHEEP USING A TWO-STAGE REACTION NORM APPROACH.

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PREFACE

This is the master's thesis "Analyzing genotype by environment interaction on pre-weaning growth rate of Norwegian white sheep using a two-stage reaction norm approach". This study is part of the PhD project "Robust, resilient and sustainable ruminant production for future resource constraints and climatic conditions" It has been submitted to fulfill the requirements of the European Master's in Animal Breeding and Genetics an Animal Science master's program at the Norwegian University of Life Sciences, Department of Animal and Aquacultural Science (IHA). I was responsible for researching and writing this thesis.

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Abstract

This study was aimed at using the two-stage reaction norm approach to analyze genotype by environment interaction in the pre-weaning growth rate of Norwegian white sheep. The NWS sheep data from 2010 to 2021 (12 production years) containing 66 999 sheep data and a pedigree file of 1406 sires and 18051 dams from municipalities Ål and Hol of old Bruskerud county was used in this study. An animal model was used to create an environmental gradient based on the herd year effects, and that environmental variable was then used in an interaction effect in the sire model to determine the presence of genotype by environment interaction. The fixed effects of the animal model (herd year, age of the dam, the month of lambing, and sex) all showed great significance in their predictive ability ($p < 0.05$). The descriptive statistics of the herd year indicated that the average pre-weaning growth rate is $0.344\text{kg/d} \pm 0.06$. It was evident that male lambs grow 0.028kg/d more than female lambs, lambs born in May grow at 0.005kg/d more than those born in April, and lambs born to ewes aged 4 years have the highest weaning growth rate (0.042kg/d) compared to those born to other ewe ages. Two models were run all extending the basic model with additive animal genetic effects and either (1) dam genetic effects or (2) the dam's common environment effects. Extending the model with both maternal genetic effects and the permanent environment of the dam was tried but the model could not converge. The (co) variances and genetic parameters were estimated for the pre-weaning growth rate. The variance component for animal genetic effect was 0.000234 ± 0.018 , for dam genetic was 0.000625 ± 0.013 , and the permanent environment of the dam was 0.00048 ± 0.010 . The direct animal genetic heritability of pre-weaning growth rate was unexpectedly high (0.388 ± 0.011), for the dam genetic effects heritability was 0.209 ± 0.006 , and the dam's common environment heritability was 0.169 ± 0.005 . Offspring yield deviations were predicted using Legendre polynomial coefficients, their interaction with the genotype as a fixed effect showed a p-value of 0.02 each (ie $p < 0.05$) which is significant. The Legendre coefficients were used to provide independent intercepts and linear growth rates along the environmental gradient of each sire. Several sires showed an increase in offspring yield deviations with increasing herd year gradient while other sires showed a decrease in offspring yield deviations across the herd year gradient. These noticeable changes in the ranking of the sires could demonstrate the presence of genotype by environment interaction for pre-weaning growth rate.

TABLE OF CONTENTS

Abstract	ii
List of tables	iv
List of Figures	v
1 Introduction	1
2 Materials and methods	3
2.1 Animal Data	6
2.2 Statistical Models and genetic analysis	9
3 Results	13
3.1 Fixed effects	13
3.2 Estimation of (co) variance component and genetic parameters	13
3.3 Estimation of breeding value	15
3.4 Offspring yield deviations	16
3.5 Genotype by environment interaction	16
4 Discussions	19
5 Conclusion	22
6 References	23

LIST OF FIGURES

Figure 1: Old Buskerud County with its municipalities Ål and Hol indicated with arrows.....	8
Figure 2: Distribution of the estimates of pre-weaning growth rate(wean_grate)	8
Figure 3: Distribution of pre-weaning growth rate, weaning weight, weaning age, and the age of the dam.....	9
Figure 4: Distribution of Estimated breeding values	15
Figure 5: The offspring yield deviations.....	16
Figure 6: Offspring yield deviations plotted against herd year solutions for Sire 1 and Sire 2....	17
Figure 7: Offspring yield deviations plotted against herd year solutions for Sire 3 and Sire 4.....	18

LIST OF TABLES

Table 1: Descriptive statistics of the herd year.....	8
Table 2: The effects of fixed effects on pre-weaning growth rate and standard.....	8
Table 3: Estimation of (co)variance components and genetic parameters for each model.....	14

1 INTRODUCTION

Breeding of domestic sheep in many parts of the world takes place across a substantial range of farming systems and natural environments (McLaren 2014). Sheep production contributes immensely to the economies of several countries by providing a considerable proportion to the livelihoods of many smallholder farmers (Alsheikh 2019). Even though sheep production in Norway is mostly a part-time occupation, it is an important form of rural livelihood sustenance that contributes to local economies (Bhatti 2019). Amongst Nordic countries, Norway is the biggest producer of lamb and mutton with 13 million sheep and lamb slaughtered in 2017 (Bhatti 2019). Sheep breeds in Norway may be classified into two types: short-tailed and long-tailed breeds. The long-tailed Norwegian White Sheep (NWS) is the most prominent sheep breed in Norway accounting for 80% of the total sheep population (Eikje 2008). The NWS is a relatively new composite, and dual-purpose breed made by crossing several local Norwegian breeds some of which are influenced by the UK breeds (Marković 2014). The NWS is popular for its high fecundity and rapid growth rate (Steinheim et al.,2004), therefore it is widely disseminated through considerably diversified environments (Hinayah Rojas De Oliveira 2020). NWS is a dual-purpose breed producing meat and wool but today most focus is on meat production attributes (Hinayah Rojas De Oliveira et al.,2020). Selection indexes used in Norwegian sheep breeding include those termed by Eikje (2008) as “The nine traits that make up the aggregate phenotype”. These include traits like percentage carcass, litter sizes at the first to the third years of age, and maternal effect on weaning weight. Most traits except fat grade have seen substantial genetic improvement (Eikje 2008). Currently, with the introduction of genomic selection (GS) and concerns for climate change, selection scheme designs are anticipated to change. For example, Jakobsen et al. (2022) proposed the selection for less methane emission to be incorporated into the breeding goals for NWS breeding schemes. Selection for maternal traits and fitness, in general, will also be more efficient with the use of GS (Lillehammer 2020). The breeding scheme is based on local ram evaluation circles, with some Artificial Insemination in later decades, and multi-trait breeding goals with estimated breeding values for all individuals (Eikje 2008). Sheep farming in Norway differs sharply between quite intensive in winter when animals are reared indoors and extensive in spring and summer when lambs are allowed to graze first on-farm and later range land pastures. Production is thus restricted by the requirement for indoor feeding throughout winter and to a

lesser extent by available rangeland grazing during summer. Grazing of sheep in the mountains and forests is prominent with over 2 million ewes and lambs foraging in these areas throughout summer (Lind et al., 2020). The range lands consist chiefly of boreal forests or areas of alpine and subalpine terrain (Géraldine 2015). During summer free-range grazing, a lack of close monitoring and no fencing or herding means predation from predators such as wolves, brown bears, golden eagles, Eurasian lynx, and many wolverines is a common problem (Géraldine 2015). Though the production system in Norway is characterized by the expansive use of unfenced forests and mountain pastures in summer, there is an increasing trend towards using cultivated pastures for the whole season in some places partly due to the increased predation (Eikje 2008). The results of the genetic versus phenotypic change as shown by Eikje (2008) indicate that environmental conditions have not been good enough for the sheep to realize their full genetic lamb body growth potential. This is because, in the uncultivated, free-range pasture environments where lambs spend most of their life non-supplemented before weaning, they are as exposed to natural variation and stochasticity as the often sympatric, wild ruminants (Steinheim 2008). In the initial on-farm environment during the lamb's first few weeks of life for example, the feed supply may be well managed, ewes and lambs are fed indoors or grazed on good-quality cultivated pastures and given supplementary feed (Eikje 2008). Subsequently, most ewes and lambs are transferred to forest or mountain pastures where the environment varies a lot from year to year, mainly due to between-year variations in temperature and precipitation and thus pasture quantity and quality (Eikje 2008). With the wide range of climate, topography, and vegetation communities and therefore genotype by environment interaction is potentially important for rangeland-based sheep production. This study thus investigates if there is a GxE interaction effect on lamb growth rate(pre-weaning) in NWS.

1.1 Pre-weaning growth rate

Pre-weaning growth rate significantly affects productivity in any meat-producing business particularly meat sheep because it is strongly correlated to the eventual market weight as the early measure of the eventual market weight (Mandal 2006; Lupi et al., 2015; Mousa et al., 2010). Sheep breeders thus try to enhance growth rate performance in lambs (Mellado, et al., 2016). Growth is a complicated quantitative trait that has been found to be impacted by both the genes and

environment and the interaction of those factors (Sharif et al.,2022). Several factors have impacts on the early growth of lamb like environmental effects provided by the dam, the duration of the suckling of the lamb, and the milking productivity of the ewe (Sharif et al.,2022). According to Sharif et al. (2022), maternal environmental influences are every effect provided for by the dam to the offspring excluding genetic factors. The growth rate of the lamb is also influenced by the genotype of the ewe for motherly effects such as milk production. Farm, birth year, parity, sex of the lamb, and weight of the ewe at lambing are just some of the non-genetic aspects influencing lamb growth (Jawasreh, et al.,2018). Therefore, there is a need to modify the above-mentioned aspects when estimating breeding values (Mahala et al., 2019). Rapid growth means attaining market weight early and thereby ensuring quick earnings for the farmers (Momoh et al.,2019). It is very important to enhance lamb for a profitable breeding program.

1.2 Genotype by environment interactions

Genotype-by-environment interactions are common in livestock and have been a concern in animal breeding for quite some time because they can reduce the effectiveness of selection schemes (MacLaren 2014; Moulder 2016). According to Wakchaure (2016), genotype by environment interaction (GxE) is a shift in the comparative performance of two or more genotypes observed in two or more conditions or circumstances. When a change in the expression of a trait of a genotype is due to the environment, we say a GxE interaction has occurred (Waters 2022) and one will often assume that the trait is to some degree affected by different genes in different environments (Wallenbeck 2009). This indicates that if a genotype performs well in one environment it may not do so in another environment. Phenotypic plasticity, which is the capability of an organism to react to variation in the environment, is a way to view GxE (DeJong Birma et al.,2000). GxE interactions may lead to scaling effects or even substantial re-ranking of breeding values and thus major economic consequences to producers if the genetic assessment relies on data from only one environment (Wallenbeck 2009). Through the study of GxE interactions breeders can establish whether a genotype is robust and suited to a broad range of environmental conditions or sensitive and needs to be selected for specific environments (Bondari 2003). In many industrialized or 'modern' schemes, it is perhaps a problem that animals are selected in optimal or very good environments, but genes are then and then distributed across not-so-good conditions (Bondari

2003). It is important that breeding plans be observant of GxE interactions to select relevant production environments (Bondari 2003).

Climatic conditions, quality of nutrition, disease prevalence, or overall animal management decisions are some of the environmental factors that can influence genotype performance (McLaren 2014). There are several ways for breeders to deal with GxE interactions. These approaches include ignoring it, avoiding it, and exploiting it (McLaren 2014). Studying GxE is relatively complex because it involves methodologies that integrate several fields such as biology, agriculture, genetics, statistics, life history theory, and many more (Bondari 2003). Models for genetic evaluation of GxE interactions in animal breeding are complicated and may have low precision in extreme environments (Moulder 2016). The complexities lead to animal breeders often choosing the ‘ignore’ approach (McLaren 2014; Moulder 2016). McLaren (2014) outlined three approaches to identifying genotype -by environment interaction: the classical quantitative model, the multi-trait approach, and the reaction norm method. A multi-trait approach regards a trait as different traits in different environments and then estimates the among-environment genetic correlations (McLaren 2014). For this study, a two-step reaction norm approach is used. The reaction norms method involves analyzing a genotype’s phenotypic expressions along continuous environmental gradients example as shown by Daniela Bustos-Korts (2019) and Christina Sartori (2022). This method is preferred when the environment is defined as a continued variable rather than a set of categories (Hayes et al.,2016). In this case, the occurrence of GxE interaction can be investigated by defining the pre-weaning growth rate of an individual as a function of the environment. According to G. Su (2006), the reaction norm model is appealing also due to its ability to fit a decent number of environmental levels with a small number of parameters. There are several GxE case studies where the environmental forms are continuous, for instance, Hayes et al. (2003) considered farm input levels, and herd average production levels as a continuous environment. Even though it is common practice to portray the reaction norm as a linear regression it is also possible to use polynomials. In this case, the polynomial coefficients are thought to be affected by genetics. The selection of appropriate environmental specifiers is of main significance when using reaction norms. The average herd production level of the phenotype in question is utilized oftentimes as the environmental descriptor seeing that it integrates several concealed environmental aspects influencing the phenotype (Streit et al.,2013). The main aim of this study is

to investigate potential genotype-by-environment interaction on the pre-weaning growth rate of NWS. The genotype is a series with many offspring in many flocks, many of which are used for artificial insemination. The environmental gradient is based on flock-by-year production levels determined by natural environmental and management factors on the pre-weaning growth rate but also correcting the gradient for animal genetic effects through including an animal model in the calculation. I used data from sheep flocks in two municipalities in the old Buskerud County. This led to the production of two estimated breeding values for each individual sire (1) the intercept, representing the performance through environments, and (2) the gradient which represents the variation of estimated breeding values through the respective environment (Waters et al.,2022). The intercept represents the average environment, and the slope expresses the individual genotype's reaction to the environmental variation. A difference in slope indicates a GxE interaction.

2 MATERIALS AND METHODS

2.1 Animal data

The data set used in the study is from the Norwegian Sheep Recording Scheme. The breed chosen is the Norwegian White sheep and the data used is from the years 2010 to 2021 (twelve production years) containing 66 999 sheep data from two municipalities; Ål and Hol in the old Buskerud County now Viken, shown in Figure 2.1 below. This database has records of lamb growth, and lamb weights (live and carcass), with the pedigree of almost all animals. A pedigree file of 73156 observations consisting of 1406 sires and 18051 dams was used.



Source (<https://www.oldmapsonline.org/en/Buskerud>)

Figure 1. Old Buskerud County with its municipalities Ål and Hol indicated with arrows.

Animals that appeared to have experienced a normal Norwegian sheep production cycle were used in the analysis example: only lambs born in April and May because those are the typical lambing months in Norway. The following variables were extracted from the main data set; animal identity, sex, birth year, litter size, dam identity, sire identity, weaning weight, weaning age, lambing date,

how the lamb was raised (bottle-fed lambs were removed), and others. Herd-years with more than 13 observations of pre-weaning growth rates were used. Animals from litter with 1 to 3 sizes were included. A subset of farms that were members of the ram circle system (have genetic ties due to the use of AI) were used.

The pre-weaning growth rate (wean_grate)

The pre-weaning growth rate was obtained by dividing the weight of the lamb at weaning in kilograms by the age in days of the lamb at weaning.

$$pre - weaning \ growth \ rate \left(\frac{kg}{d}\right) = \frac{weaning \ weight \ (kg)}{weaning_age(days)}$$

The pre-weaning growth rate values were pre-adjusted prior to estimating mean values for the random regression model using SAS software. Solutions of the model estimates showed that for the herd year, the pre-wean growth rate ranged from -0.1062 kg/d to 0.560 kg/d and the average was 0.3443 kg/d.

The figure below shows the distribution of the estimates of the trait pre-weaning growth rate (wean_grate)

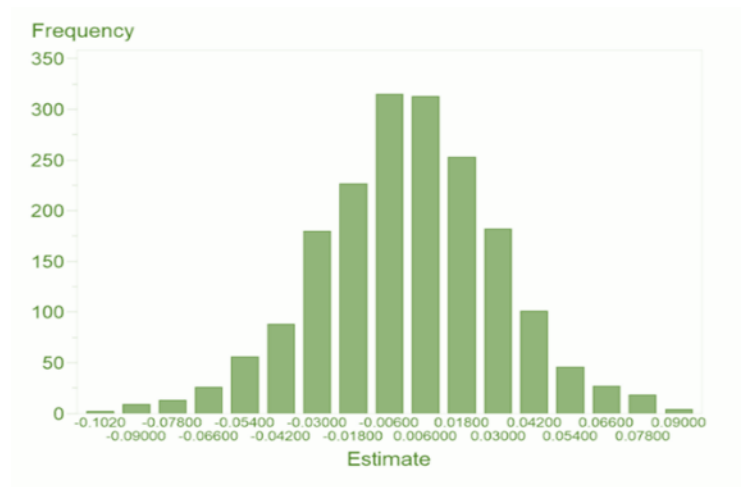


Figure 2. Distribution of the estimates of pre-weaning growth rate(wean_grate)

Descriptive statistics of the herd-year

The table below shows the proc means of pre-weaning growth rate, weaning weight, weaning age, age of the dam, litter size, herd year, number of herd years, and lambing month.

Table 2.1: Descriptive statistics of the herd year

Variable	N	Mean	SD	Min	Max
Wean_grate	66999	0.344	0.06	0.096	0.56
Wean_weight	66999	43.75	7.91	11.00	79.00
Wean_age	66999	127.30	10.98	90.00	179.00
Mom_age	66999	2.60	1.48	1.00	9.00
Litter size	66999	2.26	0.62	1.00	3.00
N_herd*year	66999	304.5	211.97	13.00	944.00
Lambing month	66999	4.66	0.47	4.00	5.00

The figures below show the distribution of some traits in the data set. The pre-weaning growth rate(wean_grate), weaning weight, and weaning age show a normal distribution. The age of the dam shows a decreasing frequency with increased age of the dam.

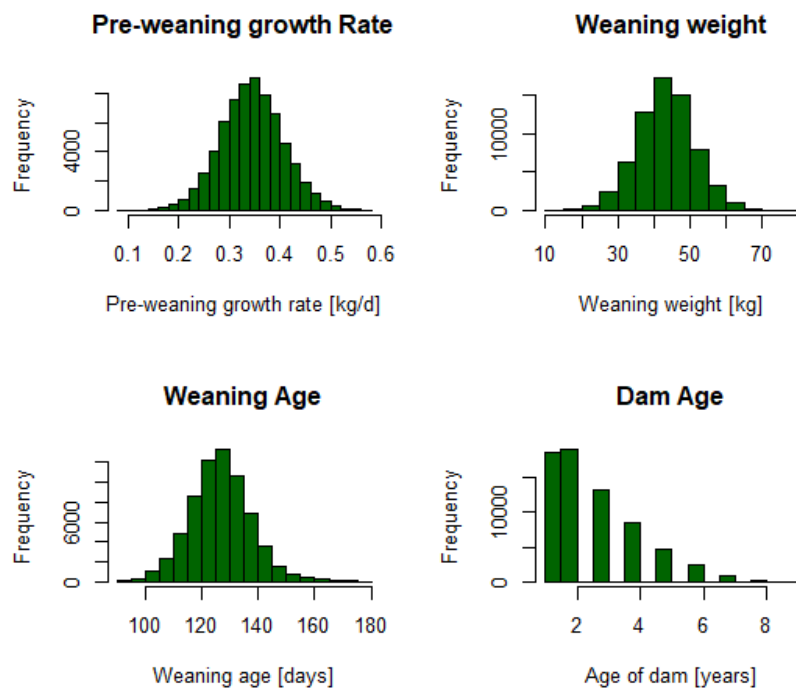


Figure 3. Distribution of pre-weaning growth rate, weaning weight, weaning age, and the age of the dam

2.2 Statistical Models and Genetic Analysis

Evaluation of (co)variance components and of genetic parameters as well as estimating breeding values for pre-weaning growth rate was done using the ASReml-R software (Butler et al., 2023). Animal models were run to obtain the gradients to the herd year effect. The analysis was executed in 2 steps, (1) creating an environmental continuous variable based on herd-year effects on traits with an animal model to correct for genetic levels, and (2) using this environment variable in an interaction effect with offspring yield deviations of sires with more than 100 offspring and range herd-year solutions more than the average range herd year solutions (range hysol more than 0.66) in a sire model to determine if there is GxE. There was the initial testing of the significance of fixed effects on a basic model, estimating the breeding values of each individual and the offspring yield deviations for each sire, and. The model was fitted using the sigma parameterization in ASReml-R.

Analysis of data with animal models

Model 1

Basic model to test the significance of fixed effects with the Wald test.

$$Y_{ijkl} = hy_i + sex_j + birthmonth_k + damAge_l + e_{ijkl}$$

Where Y_{ijk} is the vector of observations of the pre-weaning growth rate hy_i is the fixed effect of the herd*year, sex_j is the fixed effect of the j^{th} sex ($j= 1,2$) $birthmonth_k$ is the fixed effect of the k^{th} month ($j=4,5$), $damAge_l$ the fixed effect of the l^{th} age of the dam ($l=1,2,\dots,9$), and e_{ijkl} is the error term, $(0, v_1)$.

Model 2

Model 2 is an extension of model 1 by introducing the random animal genetic effects,

$$Y_{ijklm} = hy_i + sex_j + birthmonth_k + damAge_l + animal_m + e_{ijklm}$$

Where Y_{ijklm} is the vector of observations of the pre-weaning growth rate, hy_i is the fixed effect of the herd*year, sex_j is the fixed effect of the j^{th} sex ($j= 1,2$), $birthmonth_k$ is the fixed effect of the k^{th} month ($k=4,5$), $damAge_l$ is the fixed effect of the l^{th} age of the dam ($l=1,2,\dots,9$), a_m is the random individual effects of the m^{th} animal, $(0, v_1)$, and e_{ijklm} is the error term.

The heritability of the pre-weaning growth rate was estimated using the formula,

$$h^2 = \frac{v_1}{v_1 + v_2}$$

Where v_1 is the random genetic effects of the animal and v_2 is the error variance.

Model 3

Addition of random genetic effects of the dam

$$Y_{ijklmn} = hy_i + sex_j + birthmonth_k + damAge_l + animal_m + dam_n + e_{ijklmn}$$

Where Y_{ijklm} is the vector of observations of the pre-weaning growth rate, hy_i is the fixed effect of the herd*year, sex_j is the fixed effect of the j^{th} sex ($j= 1,2$), $birthmonth_k$ is the fixed effect of the k^{th} month ($k=4,5$), $damAge_l$ is the fixed effect of the l^{th} age of the dam ($l=1,2,\dots,9$) and a_m is the random individual effects of the m^{th} animal, $(0,v1)$, dam_n is the random genetic effects of the n^{th} dam, $(0,v2)$, and e_{ijklmn} is the error term.

The heritability of pre-weaning growth rate for animal genetic effects was calculated as:

$$h^2 = \frac{v_1}{v_1 + v_2 + v_3}$$

The heritability of pre-weaning growth for the dam genetic effects was then calculated using:

$$h^2 = \frac{v_2}{v_1 + v_2 + v_3}$$

Where v_1 is the random genetic effects of the animal, v_2 is the random genetic effects of the dam and v_3 is the random error effects

Model 4

Animal genetic effects and the permanent environmental effect of the dam

$$Y_{ijklmn} = hy_i + sex_j + birthmonth_k + damAge_l + animal_m + dam_n + e_{ijklmn}$$

Where Y_{ijklm} is the vector of observations of the pre-weaning growth rate, hy_i is the fixed effect of the herd*year, sex_j is the fixed effect of the j^{th} sex ($j= 1,2$), $birthmonth_k$ is the fixed effect of the k^{th} month ($k=4,5$), $damAge_l$ is the fixed effect of the l^{th} age of the dam ($l=1,2,\dots,9$) and a_m is the random individual effects of the m^{th} animal, $(0,v2)$, dam_n is the random permanent environment of the n^{th} dam, $(0,v1)$, and e_{ijklmn} is the error term. The permanent environmental effects of the dam heritability for pre-weaning growth rate were calculated by the formula,

$$c^2 = \frac{v_1}{v_1 + v_2 + v_3}$$

Where c^2 is the permanent environment of the dam heritability, v_1 is the random permanent environmental effects of the dam, v_2 is the random individual effects of the animal and v_3 is the random error effect.

Estimation of breeding values

Breeding values were calculated from model 3 using summary of the model and the coefficients of the random animal genetic effects with summary function in ASReml-R. The estimated breeding values and the herd year solutions from model 3 were used to determine the regression coefficients of the Legendre polynomials with orders leg 0 and leg 1 (ie a straight line) using the function Legendre polynomial in R. The coefficients of the Legendre polynomial used were 0.0787893 and 0.0968482.

Multiple polynormal Legendre

A subset data set of 101 sires was used through the Legendre polynomial function using the minimum and maximum herd year solution to calculate the Legendre coefficients 0 and 1 for each sire were used in the model to give independent intercepts and linear growth rates along the environmental gradient of each sire.

Calculation of the offspring yield deviations

The observed pre-weaning growth rates were corrected for the fixed effects in model 3, and for the direct and maternal effect. The offspring yield deviations are remaining residuals which are assumed to contain the sire's genetic effects.

Model 4

Model 4 was used to estimate the interaction of the sire's offspring yield deviations with the herd-year. The Wald test was used to test the significance of the fixed effects,

$$oy_i = \beta_0_i * leg0_i + \beta_1_i * leg1_i + e_i$$

where is oy_i the yield deviation for $sire_i$ ($i= 1, \dots, 101$), β_0_i is the 0th order fixed regression coefficient for $sire_i$ on $leg0_i$ is and correspondingly for the first order regression ($\beta_1_i * leg1_i$), while e_i is the error term ,distr(0, σ^2e)

3 RESULTS

3.1 Fixed effects

Model 1 showed that all the fixed effects significantly affect the pre-weaning growth rate of lambs. The Wald tests for fixed effects of the animal model, (age of the dam, herd year, sex of the lamb, and lambing month showed significance($p < 0.05$). The results show that a female lamb has a pre-weaning growth rate of 0.028 kg/d less than a male, lambs born in May grow 0.005kg/d more than those born in April, and lambs born to ewes aged 4 years have the highest pre-weaning growth wean growth rate of 0.042kg/day.

Table 3.1 The effects of fixed effects on pre-weaning growth rate and standard error

Fixed effect	Effect	Std error
Sex		
Male	0.000	N/A
Female	-0.028	0.0004
Lambing month		
April	0.000	N/A
May	0.005	0.0004
Age of dam		
1	0.000	N/A
2	0.335	0.0004
3	0.409	0.0005
4	0.421	0.0006
5	0.389	0.0007
6	0.329	0.0007
7	0.285	0.0010
8	0.115	0.0023
9	0.397	0.006

3.2 Estimation of (co)variance components and genetic parameters

Variance components for additive direct, maternal genetic, and maternal permanent environmental and their standard error were estimated from model 2, model 3, and model 4.

Genetic parameters

The inheritability of the wean grate (h^2 wean_grate) and common environment of the dam on the pre-weaning growth rate (c^2 wean_grate) and their standard errors were estimated. Table 3.2 shows the estimation of variance components and genetic parameters for the pre-weaning growth rate.

Table 3.2. Estimation of (co)variance components and genetic parameters for each model

	Model1	SE	Model2	SE	Model 3	SE	Model 4	SE
Variance component								
Residual	0.0027	0.010	0.00186	0.009	0.002121	0.012	0.0020	0.0128
Dam genetic	-	-	-	-	0.000625	0.013	-	-
Animal genetic	-	-	0.00118	0.0225	0.000234	0.018	0.00030	0.01756
PEM dam	-	-	-	-	-	-	0.00048	0.00966
Genetic parameters								
Heritability	-	-	-	-	-	-	-	-
Animal	-	-	0.3880	0.0105	0.078586	0.0077	0.108656	0.0089
Dam genetic	-	-	-	-	0.209734	0.0058	-	-
PEM dam	-	-	-	-	-	-	0.168603	0.00475

Model 1 was used to test the significance of the fixed effects. For model 2 the variance component of the animal genetic effects was 0.00118 ± 0.0225 . The variance component of the residual variance, the dam genetic, and the direct animal genetic effects were 0.002121, 0.000625, and 0.000234 respectively for model 3. For model 4 the following variance components were observed 0.0020, 0.00030 and 0.00048 for residual variance, animal genetic, and permanent environment of the dam effects respectively.

Heritability (h^2 . Pre-weaning growth rate)

The heritability of the pre-weaning growth rate was 0.388 with a standard error of 0.0105 for the direct animal effect in model 2, 0.0786 ± 0.0077 for model3 and 0.108656 ± 0.0089 for model 4. The heritability of pre-weaning growth rate for dam genetic effects is 0.209734 ± 0.0058 .

3.3 Estimated Breeding Values

The minimum and maximum estimated breeding values were -0.026 and 0.045 respectively. The highest and lowest herd-year solutions were herd year effects were 0.097 and -0.008 respectively. The histograms below show the distribution of the estimated breeding values of the individual animals. From figure 4, the breeding values are clearly approaching a normal distributed.

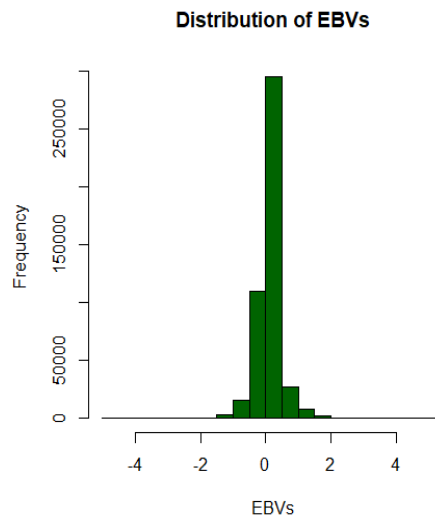


Figure 4. *Distribution of Estimated breeding values Distribution of herd year*

3.4 Offspring yield deviations

The highest offspring yield deviation obtained was 0.203, the minimum offspring yield deviation was -0.250 and the standard deviation was 0.003. The figure below depicts the distribution offspring yield deviation estimates.

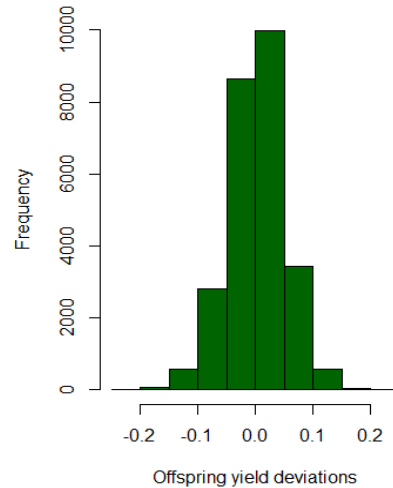


Figure 5. Distribution of the offspring yield deviation estimates

3.5 Genotype by environment interactions

The Wald test was used to test the significance and their p-values were all 0.02, thus they all showed to be significant ($p \text{ value} < 0.05$). The Legendre coefficients allow for each sire to have an independent intercept estimated. Four sires were chosen for visual presentations (Figures 6 and 7), and their offspring yield deviations were plotted against herd year solutions. The selected sires were sire with the highest number of offspring (sire 1 and sire 4) and those with widest range of herd year solutions (sire 2 and sire 3).

Sires with the highest number of offspring and highest range of herd year (sire1 and sire 2)

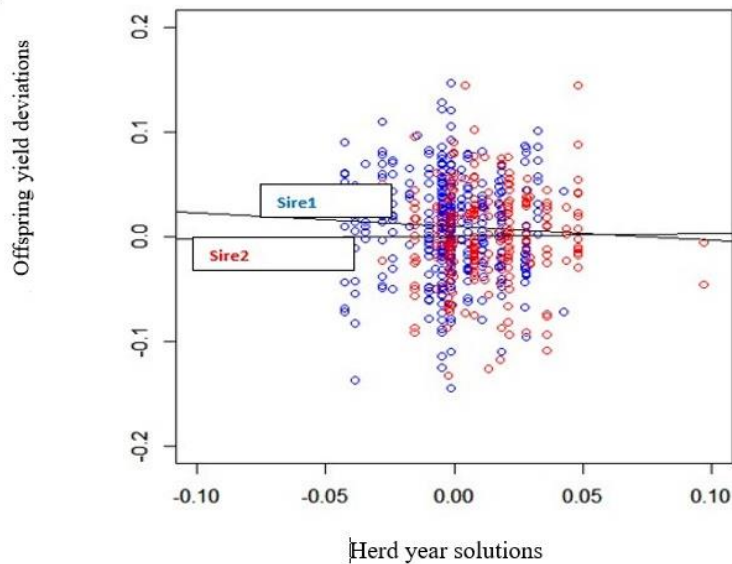


Figure 6. Offspring yield deviations plotted against herd year solutions for Sire 1 and sire 2.

For the offspring yield deviations against herd-year solutions for sire 1 and sire 2 there was a slight increase in offspring yield deviations from low environmental category (0.0 oy at -0.10 herd year solution to approximately 0.003 oy at 0.10). Sire 1 started at 0.003 offspring yield deviations at -0.10 herd year and decreased offspring yield deviation as the herd year solution increases.

Sires second widest range of herd-year solutions while and the second highest number of offspring (sire 3 and sire 4).

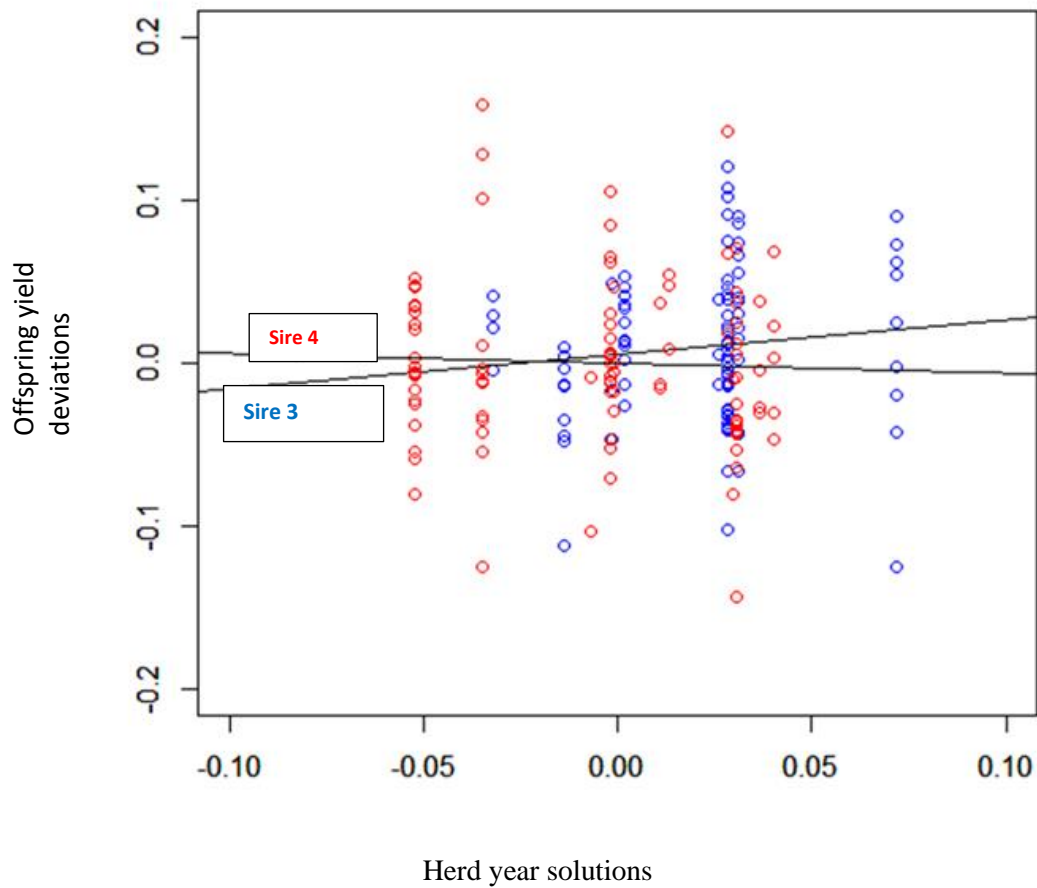


Figure 7. Offspring yield deviations plotted against herd year solutions for Sire 3 and sire 4

For sire 3 and sire 4, there was slightly more variability between the sire’s offspring yield deviations interaction with the environment. Sire 3 showed a noticeable increase in offspring yield deviations from below 0.0 to around 0.04 as the herd year solutions increased and sire 4 showed vice versa.

4. DISCUSSION

Overall, all the fixed effects; sex, lambing month, and age of the dam have significantly affected the pre-weaning growth rate. Gardner et al. (2007) reported the season or month of lambing, age of the ewe, lambing year, number of lambs per birth, and sex of the lamb as additional factors that influence the growth capacity of lambs to varying degrees. The effect of 1 year old was set to zero and the other ages estimated relative to it while ewes aged 4 had the highest effect on lamb pre-weaning growth rate (0.389kg/d) higher than 1-year olds. These results are similar to Kuchtik (2006), who reported a remarkable effect of the age of the ewe on most growth attributes. Age of the dam may reflect her level of resources available for investment in her offspring (Freitas-de-Melo et al., 2022). Male lambs showed a pre-weaning growth 0.028 kg/d higher than that of female lambs Peeters et al (1996) found ram lambs to have greater birth weight and growth data. The animal heritability of the pre-weaning growth rate was unexpectedly higher (0.388) as compared to Faid-Allah E (2016) who reported estimated direct animal heritability of 0.20+/-0.074 for Romney sheep pre-weaning growth. Each of the chosen sire 's estimated offspring yield deviations was plotted against the herd year solutions to determine their breeding values across the environmental gradient. The offspring yield solutions from the sire model were used to illustrate the magnitude of performance of each sire across the herd-year gradient. The herd year solutions were used to capture the total resulting in numerous abiotic and biotic as well as management related factors. Because our genotype equaled sires and sires were not evenly distributed in the data set, sires with the widest range in herd year solutions were picked to reduce biases in the estimation of the environmental aspect. Some sires showed an increase in offspring yield deviation across increasing herd-year solutions while others showed the opposite. Any noticeable scaling or re- between with changing environmental quality points to presence of genotype by environment interaction (Osorio-Avalos et al.,2012). The estimates of GxE were done with a fixed regression model since the random regression model of first order did not run. This could be because too many (co)variance components had to be estimated; one for β_0 , one for the covariance between β_0 and β_1 , one for β_1 and one for the error term, all in a rather limited data set (about 16 000 records). Yet, another explanation could be due to models used being sensitive to heterogeneous variances. Heterogeneity can be described as any difference between animals that leads to differences between them in any one of the vital predictions like the growth rate encountered

(Caswell and Vindenes 2018). Again, rather than treating herd year as fixed, it could have been considered random. Then, the herd year effects estimated as extreme in a fixed model and with only few data would have become constricted towards zero, meaning a smaller correction of the yield deviations, alleviating a larger effect to be estimated for the genotype by environment interaction (than when HY is considered fixed). Computational limitations hindered further expansion of models and also comprehensive articles accessible concerning the impacts of GxE on sheep production are scarce. This is probably because of inadequate global proliferation in the enterprise, the utilization of the first-off regionally acclimatized breeds in several places, and the shortage of satisfactory data present (McLaren et al., 2012).

5. CONCLUSION

Lamb's pre-weaning growth rate is important for farm productivity and financial gains. My results show that this trait is influenced by the genotype, the environment and the interaction of the two. The heritability of the trait is moderate so there is a possibility to select for the trait. There are significant variations in offspring yield deviations of elite NWS sires across different herd-year effects. It is safe to conclude that there is a significant presence of genotype by environment interaction on the pre-weaning growth rate, but I acknowledge that the models should be developed and refined, including introducing heterogeneous variances along the herd-year gradient. The effect of increasing the number of observations in total and the minimum observations per herd-year solutions should also be tried, an alternative to the latter may be defining by as a random factor. In this study, limited computational resources may have precluded this to work in our analyses in general need for verifying and developing models, but I have demonstrated that the two-step reaction norm approach model seems appropriate for analyzing GxE in Norwegian white sheep. Need for further evaluation verification models, especially in terms of heterogeneous variances and expand models to include the random permanent environment of dam.

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