

Scotland's Rural College

## The effects of different farm environments on the performance of Texel sheep

McLaren, A; Brotherstone, S; Lambe, NR; Conington, JE; Mrode, R; Bunger, L

*Published in:*  
Animal

*DOI:*  
[10.1017/S1751731115001123](https://doi.org/10.1017/S1751731115001123)

Print publication: 01/01/2015

*Document Version*  
Peer reviewed version

[Link to publication](#)

### *Citation for published version (APA):*

McLaren, A., Brotherstone, S., Lambe, NR., Conington, JE., Mrode, R., & Bunger, L. (2015). The effects of different farm environments on the performance of Texel sheep. *Animal*, 9(10), 1624 - 1634.  
<https://doi.org/10.1017/S1751731115001123>

### **General rights**

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

### **Take down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1 **The effects of different farm environments on the performance of Texel sheep**

2

3 A. McLaren<sup>1</sup>, S. Brotherstone<sup>2</sup>, N.R. Lambe<sup>1</sup>, J. Conington<sup>3</sup>, R. Mrode<sup>3</sup> and L.  
4 Bunger<sup>3</sup>

5

6 <sup>1</sup>*SRUC, Hill & Mountain Research Centre, Kirkton Farm, Crianlarich, FK20 8RU, UK*

7 <sup>2</sup>*Institute of Evolutionary Biology, University of Edinburgh, West Mains Road,  
8 Edinburgh, EH9 3JT, UK*

9 <sup>3</sup>*Animal & Veterinary Sciences, SRUC, Easter Bush, Midlothian, EH25 9RG, UK*

10 Corresponding author: Ann McLaren. E-Mail: [Ann.McLaren@sruc.ac.uk](mailto:Ann.McLaren@sruc.ac.uk)

11

12 **Running head:** Reaction norm analyses in Texel sheep

13 **Abstract**

14 In order to assess the extent of genotype by environment interactions (GxE) and  
15 environmental sensitivity in sheep farm systems, environmental factors must be  
16 identified and quantified, after which the relationship with the traits(s) of interest can  
17 be investigated. The objectives of this study were to develop a farm environment  
18 scale, using a canonical correlation analysis, which could then be used in linear  
19 reaction norm models. Fine-scale farm survey data, collected from a sample of 39  
20 Texel flocks across the UK, was combined with information available at the national  
21 level. The farm survey data included information on flock size and concentrate feed  
22 use. National data included flock performance averages for 21 week old weight  
23 (21WT), ultrasound back-fat (UFD) and muscle (UMD) depths, as well as regional  
24 climatic data. The farm environment scale developed was then combined with  
25 181555 (21WT), 175399 (UMD) and 175279 (UFD) records from lambs born  
26 between 1990-2011, on 494 different Texel flocks, to predict reaction norms for sires  
27 used within the population. A range of sire sensitivities estimated across the farm  
28 environment scale confirmed the presence of genetic variability as both “plastic” and  
29 “robust” genotypes were observed. Variations in heritability estimates were also

30 observed indicating that the rate genetic progress was dependent on the  
31 environment. Overall, the techniques and approaches used in this study have proven  
32 to be useful in defining sheep farm environments. The results observed for 21WT,  
33 UMD and UFD, using the reaction norm models, indicate that in order to improve  
34 genetic gain and flock efficiency, future genetic evaluations would benefit by  
35 accounting for the GxE observed.

### 36 **Keywords**

37 Sheep; Reaction Norms; Genotype x Environment Interactions; Environmental  
38 Sensitivity

### 39 **Implications**

40 Although there are a wide range of different sheep farming systems in the UK, there  
41 is relatively little information with regards to the extent of genotype by environment  
42 interactions and environmental sensitivity present within the industry. This study has  
43 demonstrated an approach for defining sheep farm environments, which was then  
44 used in the reaction norm analyses of Texel sheep. A range of sire sensitivities were  
45 observed across the different environments. The ability to identify this variation in  
46 sensitivities could allow the identification and selection of sires predicted to best suit  
47 specific farm environments, thus improving flock performance.

### 48 **Introduction**

49 The subject of genotype by environment interactions (GxE), and their effect on  
50 livestock breeding across the globe, can be complex and dependent on a number of  
51 different factors. In addition to identifying the presence of GxE, by methods such as  
52 the inclusion of an interaction term in the traditional quantitative genetic model or by  
53 estimating genetic correlations between different individual environments, the degree

54 by which genotypes vary across environments is also of interest. This is often  
55 referred to as *phenotypic plasticity* (Bradshaw, 1965; de Jong and Bijma, 2002) or  
56 *environmental sensitivity* (Falconer, 1990; Kolmodin *et al.*, 2002). Genotypes are  
57 considered “plastic” if they demonstrate highly variable phenotypes across  
58 environments or “robust” if they remain relatively constant (de Jong and Bijma, 2002;  
59 Bryant *et al.*, 2005). In addition to methods such as those described by SanCristobal-  
60 Gaudy *et al.* (2001), Hill and Zhang (2004) and Mulder *et al.* (2007) regarding  
61 selection based on genetic heterogeneity of environmental variance in order to  
62 estimate environmental sensitivity an alternative method is the use of reaction  
63 norms, obtained by random regression on environmental descriptors (Strandberg *et*  
64 *al.*, 2000; Kolmodin *et al.*, 2002; Fikse *et al.*, 2003). In other words, the model  
65 describes the phenotype expressed by a certain genotype over a number of different  
66 environments and can be particularly useful when environments are described along  
67 a continuous scale or gradient (de Jong and Bijma, 2002). The use of a continuous  
68 scale to define the environment also means that there is less reliance on genetic  
69 connections between each individual environment, thus removing some of the  
70 problems observed by McLaren *et al.* (2014). When environments were not well  
71 connected, the estimation of reliable genetic correlations proved difficult.

72 The regression of sire breeding values on a continuous measure of environment, in  
73 which records from their offspring exist, allows reaction norms to be predicted for  
74 individual sires (Kolmodin *et al.*, 2002). In terms of animal breeding, early studies for  
75 lactation in dairy cattle used random regression test day models to predict the  
76 lactation curves of individual dairy cows (Schaeffer and Dekkers, 1994). However  
77 more recently, interest has grown with regards to their use to describe the variation  
78 of performance across environmental gradients such as those in dairy cattle (Calus

79 *et al.*, 2002; Kolmodin *et al.*, 2002; Strandberg *et al.*, 2009), beef cattle (Mattar *et al.*,  
80 2011; Santana *et al.*, 2013a), pigs (Knap and Su, 2008) and sheep (Pollot and  
81 Greeff, 2004; Santana *et al.*, 2013b).

82 In order to assess the extent of environmental sensitivity, and any associated GxE,  
83 environmental factors need to be identified and quantified, after which the  
84 relationship with the trait(s) of interest can be investigated. In experimental  
85 situations, environments can often be clearly defined, allowing relatively  
86 straightforward analyses. However, in commercial animal breeding circumstances,  
87 analyses can become more complicated, with a range of different factors  
88 determining each farm environment (FE). This is particularly true for sheep systems,  
89 which can differ in a number of aspects such as climatic conditions, flock size, health  
90 status and level of inputs. There are a number of different methods to determine FE,  
91 including the use of specific environmental descriptors such as rainfall and  
92 temperature (Ravagnolo and Misztal, 2000; Fikse *et al.*, 2003), the use of phenotypic  
93 means or deviations (Calus *et al.*, 2002; Kolmodin *et al.*, 2002) as well as the  
94 identification of contemporary groups (Pollott and Greeff, 2004; Mattar *et al.*, 2011;  
95 Santana *et al.*, 2013b).

96 Alternatively, a method similar to the one used by Haskell *et al.* (2007), while  
97 assessing the effect of different environments on the lifespan of dairy cattle, may  
98 prove useful in defining sheep FE. This method involves establishing a relationship  
99 between fine-scale information provided by a sample of farms with information  
100 available nationally for all farms. The scale developed by Haskell *et al.* (2007) has  
101 also been used by Strandberg *et al.* (2009) while investigating fertility traits in dairy  
102 cattle. The development of a similar scale, applicable to sheep systems, would

103 potentially allow future genetic evaluations to take GxE into account. Farmers could  
104 identify where their system would lie along an environmental scale, from which they  
105 could select animals predicted to suit their FE. Any negative effects from GxE that  
106 may be evident would potentially be reduced, thus enabling farmers to improve their  
107 production level through the increased knowledge of predicted animal performance.

108 The aims of this study were therefore to a) relate fine-scale, farm-level data,  
109 collected from a sample of UK Texel flocks, with information available at the national  
110 level, using a canonical correlation analysis in order to provide a definition of a FE  
111 scale and b) to assess the effect of FE on individual Texel sires for lamb  
112 performance traits, across the UK, using the analysis of reaction norms. The  
113 heritability of lamb performance traits across the FE scale and correlations between  
114 different points along the FE scale were also investigated.

## 115 **Materials and methods**

### 116 *Farm environment definition*

117 In order to obtain greater insight into the different management systems used on  
118 each farm, and therefore overall farm environments, a survey was carried out  
119 involving members of the UK's national sheep improvement programme, 'Signet  
120 Sheepbreeder' ([www.signetfbc.co.uk](http://www.signetfbc.co.uk)). A questionnaire was developed and sent to all  
121 515 members across the UK, in 2009. Questions posed covered aspects such as  
122 farm location and land cover; sheep numbers and breed; management of the flock  
123 throughout the year; health treatments and the use of labour. The questionnaire and  
124 results have been discussed in detail by McLaren *et al.* (2014). Data collected from  
125 the 40 Texel flocks that responded were used in the current study. The data  
126 collected regarding the use of concentrate feed was selected to provide information

127 on the level of feed inputs for each flock, from which an FE scale could be  
128 developed. The use of concentrate feed information allowed the identification of  
129 purely pasture-based systems and those that used additional feeding throughout the  
130 year.

131 Traits chosen to describe all farm environments across the UK were selected on the  
132 basis that they were readily available for all flocks. They included flock averages for  
133 21 week old weight (21WT), ultrasound back-fat (UFD) and muscle (UMD) depths,  
134 as well as annual averages for rainfall, number of sun hours and temperature values.  
135 The flock averages for 21WT, UFD and UMD were calculated using performance  
136 records available from the Signet Sheepbreeder programme. The Texel breed  
137 performance record their flocks using the terminal sire index which places a heavy  
138 emphasis on these lamb carcass related traits in order to increase the overall yield of  
139 lean meat in the carcass whilst attempting to reduce and associated increase in fat  
140 levels (Simm and Dingwall, 1989). Unlike some other breeds and breeding indexes,  
141 less emphasis is placed on maternal traits. A total of 183153 pure Texel lamb  
142 performance records, from 536 different flocks, between 1990 and 2011, were  
143 analysed. For each flock, adjusted averages for 21WT, UMD and UFD were  
144 obtained by applying the following fixed effects model, using ASReml (Gilmour *et al.*,  
145 2002):

146 Trait = mean + sex + age + litter size at birth + birth year + rearing dam age + (sex x  
147 age) + flock

148 Age was the age of the lamb (in days) at measurement, treated as a covariate.  
149 Rearing dam age was included as a fixed effect measured in years (7 levels: 1 to

150  $\geq 7$ ). Other factors included lamb birth year (22 levels: 1990 to 2011); sex (2 levels:  
151 male and female); litter size at birth (4 levels: 1 to  $\geq 4$ ) and flock (536 levels).

152 Farm postcodes were used to identify the farm location and subsequently the  
153 relevant weather data available from the 10 regions across the UK, as provided by  
154 the Met Office (<http://www.metoffice.gov.uk/climate/uk/datasets/>). Average annual  
155 means were calculated for the 5-year period between 2005 and 2009 for regional  
156 temperature, rainfall and number of sun hours. This time period was the 5-year  
157 period prior to the questionnaire being distributed and was used as representative of  
158 the environmental conditions experienced by the flocks throughout the time span of  
159 the data. Only 3% of records in the dataset were from animals born outside the  
160 spring months of March, April and May, therefore the majority of farms followed a  
161 similar calendar of production.

#### 162 *Canonical correlation analysis*

163 With the aim of assessing the relationship between the variables obtained from the  
164 questionnaire (the criteria variables P) and the weather and production variables  
165 available for all flocks in the UK (the predictor variables Q), a canonical correlation  
166 analysis (Clark, 1975), was carried out using Genstat (11<sup>th</sup> edition, VSN International  
167 Ltd, 2008), similar to the method used by Haskell *et al.* (2007). The Q-variables, in  
168 this analysis, were available for all farms and were the adjusted averages for 21WT,  
169 UMD and UFD as well as the overall 5-year average annual rainfall, temperature and  
170 number of sun hour values. The P-variables were from the flocks involved in the  
171 initial survey and were: the size of the flock (number of breeding ewes) recorded; the  
172 number of weeks lambs had access to concentrate feeding before weaning (0 to  $\geq 12$   
173 weeks); the number of months concentrate feeding was fed to the ewes (0 to 6



174 months) and whether or not the rams were fed concentrates during the month before  
175 mating (0 = no, 1 = yes). Overall, the analysis was based on P- and Q-variables from  
176 39 out of the original 40 Texel flocks that responded to the questionnaire, due to one  
177 farm having no records for 21WT, UMD or UFD in the dataset.

### 178 *Reaction norm analysis*

179 The original data set was reduced to 181555 individual lamb records after removing  
180 records that had no sire allocated as well as data from farms without data for all  
181 three traits studied (Table 1). The best linear combination of Q-variables, identified  
182 by the canonical correlation analysis, was then used to calculate a FE score for 494  
183 flocks in the national data set. Of the 5938 different sires represented in the data,  
184 4572 were used in only one flock whereas 1366 were used in multiple flocks,  
185 including 3 that were used in 30 flocks or more.

### 186 **Table 1 here**

187 Sire models, along with a sire pedigree file containing 9775 records, were used to  
188 analyse the data. The base model (A) included *sire*, *flock* and a *sire by flock*  
189 interaction as random effects (as shown in bold and italics):

190 Trait = mean + sex + age + litter size at birth + birth year + rearing dam age + (sex x  
191 age) + ***sire + flock + (sire x flock)***

192 Following on from this, the covariate of FE was added to model A to form model B.  
193 Phenotypic observations of lamb performance were then regressed, within sire, on  
194 FE by adding an environmental variable to the random effects in the model, thus  
195 allowing the level (intercept) and slope of a linear reaction norm to be estimated for  
196 each sire (model C). By fitting FE as a fixed covariate, FE fits the overall regression

197 and therefore removes/corrects its effect. The inclusion of the *sire x FE* random  
198 effect allows the deviations from the overall trend line to be represented for each  
199 sire. Model C was therefore:

200 Trait = mean + sex + age + litter size at birth + birth year + rearing dam age + FE +  
201 (sex x age) + ***sire*** + (***sire x FE***) + ***flock*** + (***sire x flock***)

202 The *flock* and *sire x flock* terms represented residual effects that were unexplained  
203 by the reaction norm for each sire. Although two flocks may have the same FE value  
204 in the regression for the reaction norm, they may have different *sire x flock* terms.  
205 Haskell *et al.* (2007) commented that retaining these terms is important in order to  
206 preserve the correct variance-covariance structure in the mixed model.

207 Preliminary analysis indicated that the environmental variance was not constant  
208 across environments. In order to estimate the heterogeneity of environmental  
209 variance, and based on the preliminary analyses, FE values were grouped into 6  
210 environmental classes and separate residual variances estimated for each, using  
211 model D (derived from model C). The environmental classes were based on different  
212 sections of the FE scale. For each trait, the classes were: a (-1.40 to -0.5); b (-0.5 to  
213 0); c (0 to 0.6); d (0.6 to 1.2); e (1.2 to 1.7) and f (1.7 to 2.66). Class c and d  
214 represented an average environment, centring on the middle point of the FE scale  
215 (0.6). Classes a and b represented environments at the low end of the scale,  
216 whereas classes d and f represented environments at the high end of the scale.  
217 Models B, C and D were tested using the log likelihood ratio test (*LR*) to determine if  
218 they were significantly different. Model B was tested against model C in order to  
219 identify if the inclusion of the *sire x FE* random effect was significant. The test  
220 statistic,  $LR = 2(\log L_0 - \log L_1)$ , had a  $X^2$  distribution with 1 degree of freedom.

221 Additionally, in order to test the significance of accounting for heterogeneity of  
222 environmental variance, model D was tested against model C. Model C assumed a  
223 constant environmental variance, whereas model D allowed for different  
224 environmental variances for each environmental class (n=6). Therefore the test  
225 statistic, when model C was tested against model D, had a  $\chi^2$  distribution with 5  
226 degrees of freedom.

### 227 *Sensitivity and heritability analysis*

228 The use of reaction norm models allow the estimation of sire sensitivities, as well as  
229 genetic variances and heritabilities, across the environment FE values, similar to the  
230 methods used by Kolmodin *et al.* (2002) and Pollott and Greeff (2004) The sensitivity  
231 for each sire represents the extent to which the sire effect is dependent on the FE  
232 score. The values estimated for the slope of each sire reaction norm were used to  
233 represent the sensitivity. The genetic variance at each point along FE scale ( $\sigma^2_{g|FE}$ ),  
234 was calculated using the following equation:

$$235 \sigma^2_{g|FE} = \sigma^2_a + FE^2 \sigma^2_b + 2FE\sigma_{ab}$$

236 Where  $\sigma^2_a$  represents the reaction norm intercept variance,  $\sigma^2_b$  represents the  
237 reaction norm slope variance and  $\sigma^2_{ab}$  represents the covariance. Similarly,  
238 heritability estimates at each point along the FE scale ( $h^2|FE$ ) were estimated using  
239 the equation:

$$240 h^2|FE = 4\sigma^2_{g|FE} / (\sigma^2_{g|FE} + \sigma^2_f + \sigma^2_{sf} + \sigma_e^2)$$

241 Where  $\sigma^2_{g|FE}$  represents the genetic variance at each point on the FE scale,  $\sigma^2_f$   
242 represents the flock variance,  $\sigma^2_{sf}$  represents the sire x flock variance and  $\sigma_e^2$   
243 represents the residual environmental variance. The heritability estimates for Model

244 C were adjusted by replacing  $\sigma_e^2$  with the residual variance for each of the 6  
245 environmental classes (a-f).

246 Genetic correlations between each point along the FE scale (two levels,  $FE_1$  and  
247  $FE_2$ ), for each trait, were also calculated using the equation:

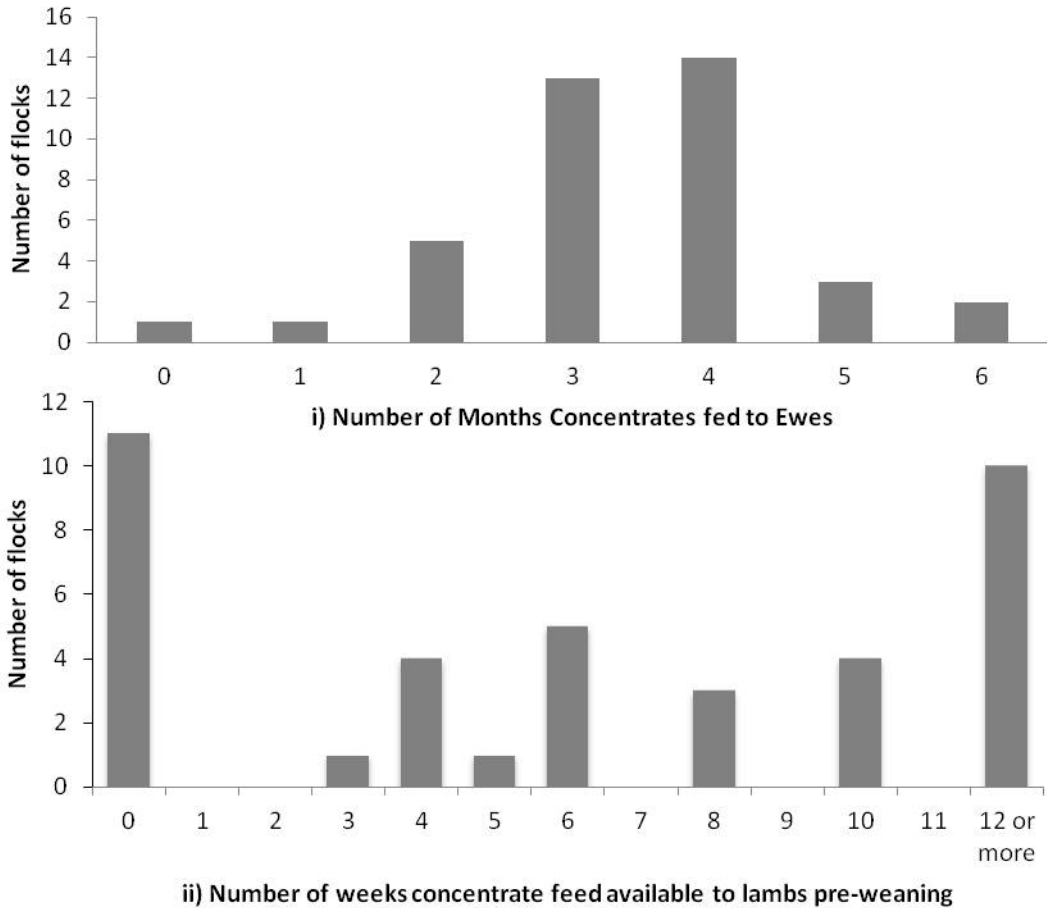
$$248 \quad r_{gFE_1FE_2} = [\sigma_a^2 + FE_1FE_2\sigma_b^2 + (FE_1+FE_2)\sigma_{ab}] / \sqrt{\sigma_{g|FE_1}^2 \sigma_{g|FE_2}^2}$$

249 Where  $\sigma_{g|FE_1}^2$  and  $\sigma_{g|FE_2}^2$  are the genetic variances in  $FE_1$  and  $FE_2$  respectively,  
250 ( $\sigma_{g|FE_1}^2 = \sigma_a^2 + FE_1^2 \sigma_b^2 + 2FE_1\sigma_{ab}$  and  $\sigma_{g|FE_2}^2 = \sigma_a^2 + FE_2^2 \sigma_b^2 + 2FE_2\sigma_{ab}$ ).

## 251 **Results**

### 252 *Questionnaire data*

253 The results of the questionnaire, in relation to the concentrate feed used for ewe and  
254 pre-weaned lamb feeding, are shown in Figure 1. Rams were provided with  
255 concentrate feed during the month prior to mating in 34 out of the 39 flocks. The  
256 majority of flocks lambed during February and March. When asked to classify their  
257 overall farm, in terms of the stratified production levels, 64% classed their farms as a  
258 lowland system, 33% as an upland system and 3% as a hill system. The average  
259 flock size was 80 ewes, ranging from 12 to 220.



260

261 **Figure 1.** Concentrate feed use for (i) ewes and (ii) lambs.

262

263 *Canonical correlation analysis*

264 The first canonical variables were scaled so that the maximum coefficient in each  
 265 case was  $\pm 1$  resulting in the following equations:

266  $P \text{ Value} = +1.00 \times \text{Rams fed concentrates} + 0.002 \times \text{Number of weeks concentrate}$   
 267  $\text{feed available to lambs pre-wean} - 0.005 \times \text{Recorded ewe flock size} - 0.432 \times$   
 268  $\text{Number of months ewes fed concentrates.}$

269  $Q \text{ Value} = -1.00 \times \text{UFD} - 0.0001 \times \text{Rainfall} - 0.001 \times \text{Sun Hours} + 0.104 \times \text{21WT} +$   
 270  $0.235 \times \text{UMD} + 0.249 \times \text{Temperature.}$

271 The corresponding canonical correlation between P and Q was 0.73. The first  
272 canonical P-variate represented the level of concentrate used in each system, with  
273 large, positive, values representing farms that fed their rams and lambs prior to  
274 mating and weaning respectively. In addition, they had a lower flock size and the  
275 ewes were fed for fewer months throughout the year. Low, negative, values  
276 represented larger flocks which fed their ewes for a longer period during the year.  
277 They did not, however, feed their rams or lambs prior to mating and weaning  
278 respectively. The corresponding Q-variate, which utilised data available for all farms,  
279 had large, positive, values for farms with high performance averages for 21WT and  
280 UMD as well as high average temperatures and low average rainfall. The highest  
281 values along the scale were also associated with low UFD averages, as well as low  
282 rainfall and number of sun hours. Conversely, low values were associated with low  
283 temperatures and low performance averages for 21WT and UMD, as well as high  
284 average rainfall and UFD averages. Table 2 shows the correlations between all  
285 variables. Temperature and sun hours were highly correlated ( $r = 0.90$ ), which may  
286 explain the change in direction for sun hours when compared to the coefficient  
287 estimated in the canonical correlation analysis.

288 **Table 2 here**

289 *Reaction norm analysis*

290 The FE scale was then calculated using the weather and production information  
291 available for all 494 nationally recorded farms. By using the Q-value equation  
292 developed, the values estimated along the FE scale ranged from -1.40 to 2.66, with  
293 the average estimated across the population being 0.70. Overall, the scale went from  
294 low performance averages and poorer weather conditions to high performance

295 averages and improved weather conditions. To illustrate, the average FE data for the  
296 ten farms located at both extremes of the FE scale are shown in Table 3. The  
297 average values for 21WT, UMD and UFD were calculated using the original flock  
298 solutions (as estimated using the fixed effect model and that were used to calculate  
299 each Q-value) plus the average values across all levels of each fixed effect in the  
300 model.

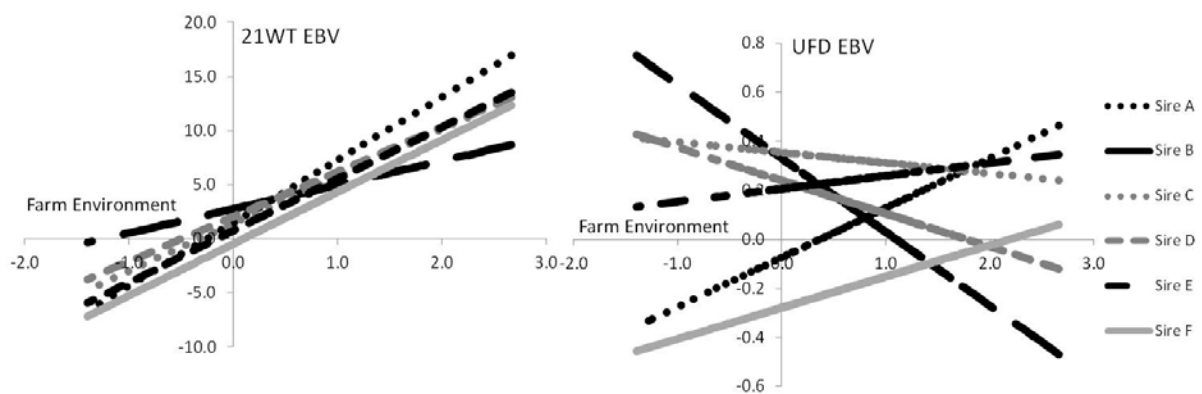
301 **Table 3 here**

302 The variance component estimates obtained by models A, B, C and D are shown in  
303 Table 4. When models C and D were fitted, for each trait, two breeding values were  
304 produced, representing the intercept and slope of the reaction norm for each sire.  
305 The intercept value represented the average sire effect on each trait across all farm  
306 environments. The slope represented the environmental sensitivity, or in other words  
307 the amount to which the sire effect was dependent on the farm environment value.

308 **Table 4 here**

309 Based on the *LR*, model C, when compared with model B, significantly improved the  
310 fit of the model for 21WT and UFD ( $P < 0.001$ ), but not for UMD. Model D was found  
311 to be the best model for all traits ( $P < 0.001$ ). The results demonstrate that the  
312 inclusion of the sire x FE effect was significant for all traits, although only for UMD  
313 when heterogeneity of environmental variance was accounted for. The correlations  
314 between the intercept and slope, using model D, were all less than one and  
315 negative, 21WT (-0.49) and UMD (-0.58) and UFD (-0.49), implying the re-ranking of  
316 sires. Similar results were also obtained using model C. The reaction norms  
317 estimated for a sample of sires (the six sires with the most offspring in the data) in  
318 terms of their estimated breeding values (EBVs) for 21WT and UFD, are shown in

319 Figure 2. The results for UMD were similar to those observed for 21WT. Overall, for  
 320 21WT and UMD, the EBVs of all sires improved as the FE improved. However, of the  
 321 5853 sires with UFD information, the EBVs of 61% of sires increased and 39% of  
 322 sires decreased as the FE improved.



323  
 324 **Figure 2.** Reaction norms, for a sample of 6 sires (A-F), for 21 week old weight  
 325 (21WT) and ultrasound fat depth (UFD) estimated breeding values (EBVs) across  
 326 the farm environment (FE) scale (using model B).  
 327

328 *Heritability and correlation analysis*

329 The heritabilities estimated using model B, for 21WT, UMD and UFD were 0.15  
 330 ( $\pm 0.01$ ), 0.19 ( $\pm 0.02$ ) and 0.17 ( $\pm 0.02$ ) respectively. When using model D, the range  
 331 of heritability estimates for 21WT, UMD and UFD, along the FE scale were, 0.15 -  
 332 0.50, 0.18 - 0.55 and 0.15 - 0.63 for each trait respectively. Similar estimates were  
 333 observed when using model B also. The heritabilities estimated for 21WT and UMD,  
 334 using model D, are shown in Figure 3. The heritability estimates for UFD followed a  
 335 similar pattern as 21WT. The highest heritability estimates for 21WT and UFD were  
 336 observed at each end of the FE scale and lowest at the mid-point, at approximately  
 337 FE value 0.6. The heritability estimates for UMD followed a similar pattern, although  
 338 the estimates at the high end were slightly lower than those estimated at the low  
 339 end. It should also be noted that the largest standard errors, for all traits, were



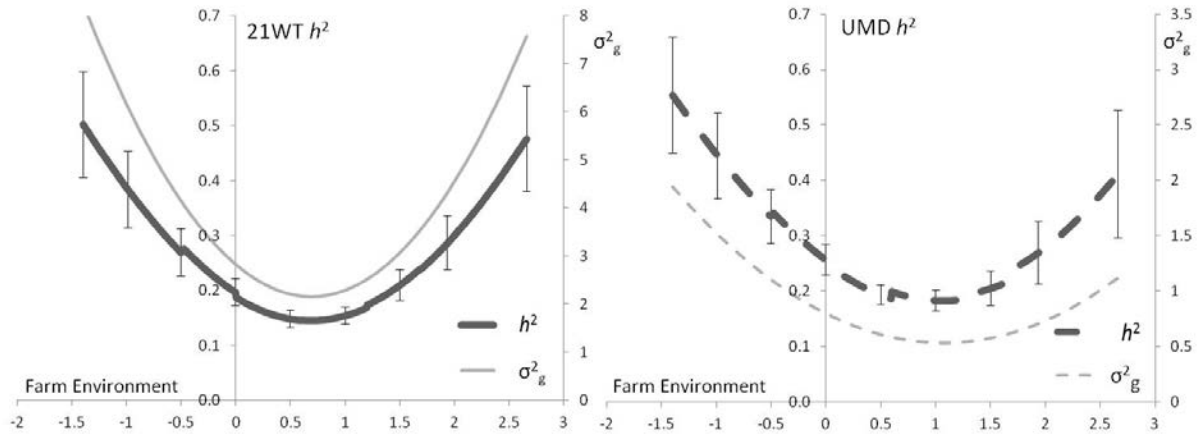
340 associated with heritability estimates at both extremes of the FE scale. The genetic  
341 variances estimated followed a similar pattern as the heritability estimates (Figure 3).  
342 The genetic correlations estimated across the FE scale are shown in Figure 4. The  
343 correlations estimated ranged from -0.42 to 1 for 21WT, -0.22 to 1 for UMD and -  
344 0.51 to 1 for UFD. The correlations shown in Figure 4, for UMD and UFD, are  
345 estimated for flocks with an average Q-value in the population (0.7) as well as those  
346  $\pm 1$  standard deviation (SD) from the average. Similarly, those in Figure 5 for UMD  
347 and UFD demonstrate how the correlations change between all environments. The  
348 results for 21WT were similar to those observed for UMD and UFD.

349 Spearman's rank correlations were also calculated using the breeding values  
350 estimated for all 5938 sires represented in the data, between environments  $\pm 0.5$ ,  
351  $\pm 1.0$  and  $\pm 1.5$  SD from the average Q-value. The results observed for 21WT,  
352 between -0.5 and +0.5; -1.0 and +1.0; and -1.5 and +1.5 SD from the average were  
353 0.97, 0.90 and 0.79 respectively. The correlations estimated UMD and UFD between  
354 -0.5 and +0.5, -1.0 and +1.0 and -1.5 and +1.5 SD from the average were 0.99, 0.96  
355 and 0.94 and 0.96, 0.86 and 0.72 respectively.

356

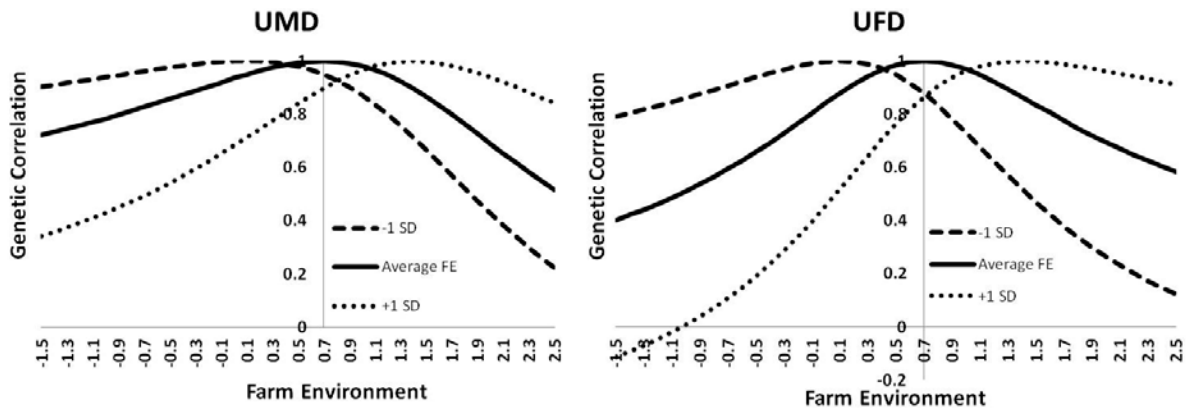
357

358



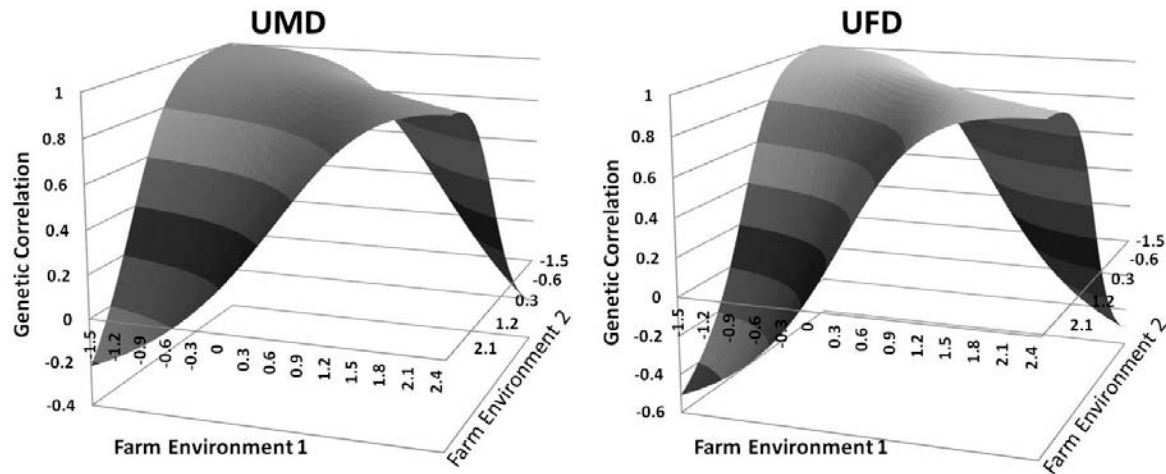
359 **Figure 3.** Heritability ( $h^2$ ) and genetic variance ( $\sigma^2_g$ ) estimates, for 21 week old  
360 weight (21WT), ultrasound muscle depth (UMD) as functions of the farm  
361 environment (FE) scale (using model D).

362



363 **Figure 4.** Genetic correlations estimated for ultrasound muscle depth (UMD) and  
364 ultrasound fat depth (UFD) across the farm environment (FE) scale. Graphs shown  
365 are between flocks with environment values of -1 SD from the average, average and  
366 +1 SD from the average, respectively, and all other environments along the FE  
367 scale.

368



369

370 **Figure 5.** Genetic correlations estimated across the farm environment (FE) scale  
 371 between pairs of farm environments (FE1 and FE2) for ultrasound muscle depth  
 372 (UMD) and ultrasound fat depth (UFD).  
 373

374 **Discussion**

375 *Defining farm environment*

376 The canonical correlation analysis used in the present study provided an opportunity  
 377 to relate fine scale information gathered from a sample of farms, with information  
 378 available from farms at a national level. The concentrate feed-related variables  
 379 obtained from the farm survey were selected for further analysis in order to improve  
 380 our knowledge of the effects that different feeding regimes may have. When using  
 381 canonical correlation analysis it is important to be aware of the sensitivity of the  
 382 method with regards to any changes to the variables used (Hair *et al.*, 2006).  
 383 Although the results should be treated with a certain level of caution, due to the fact  
 384 that the analysis was based on 40 randomly selected farms, they are still worthy of  
 385 consideration. The canonical correlation estimated was reasonably high (0.73),  
 386 therefore suggesting that the first canonical Q-variable was a useful measure of  
 387 system input (in terms of the use of supplementary feed), and thus FE overall. The

388 correlation estimated by Haskell *et al.* (2007), when defining dairy farm FE, using a  
389 similar method, was 0.62. An interpretation of the first Q variable suggests, in terms  
390 of the production averages, that high FE values were associated with high  
391 performance averages for 21WT and UMD, and low averages for UFD. The Terminal  
392 Sire Index, within which the majority of Texel breeders record, has weightings on  
393 each of these traits in order to improve 21WT and UMD while reducing any  
394 associated rise in UFD (Simm and Dingwall, 1989; Macfarlane and Simm, 2007).  
395 Therefore the FE scale developed is a relatively good reflection of the overall aim of  
396 the breeding index. Similarly, the direction of the weather variables, in general,  
397 suggests that the highest FE values are associated with higher average  
398 temperatures and lower rainfall. This would agree with the general assumption that  
399 areas with better weather conditions have improved environments in terms of  
400 aspects such as pasture availability and quality.

401 The first canonical P-variable, using data from the survey farms, provided an  
402 interesting result when compared with the corresponding canonical Q-variable.  
403 Farms with a high P value were associated with a higher use of ram and pre-weaned  
404 lamb concentrate feeding, but less so with ewe feeding and the overall flock size.  
405 The majority of flocks fed their rams during the month before mating. However, there  
406 was quite a range in the number of weeks before weaning, during which lambs had  
407 access to supplementary feed. The increased use of concentrate feed, particularly  
408 for pre-weaned lambs, is likely to have helped improve the production averages.  
409 However, when considered alongside the weather variables, it would seem that  
410 these farms already had a favourable FE and therefore these farms have chosen to  
411 try and improve the environment further by allowing their lambs access to feed  
412 before they are weaned.

413 Farms with a lower P value fed their ewes for a longer period during the year than  
414 those at the other end of the scale. This could again be related to the weather  
415 variables. In areas with lower average temperatures and higher rainfall, the  
416 increased use of feeding could be used to help maintain the condition of the ewe  
417 throughout pregnancy, and possibly post-pregnancy. This could be because the  
418 ewes have been kept outside in potentially poorer conditions where grass growth  
419 can be limited for a greater number of months. Alternatively, in order to remove the  
420 effects of the poorer weather conditions, they may have been housed for a longer  
421 period of time before and during lambing. Whatever the system used, both rely on  
422 the use of substantial amounts of supplementary feed for the ewes. The emphasis  
423 has therefore moved from improving lamb performance further, to perhaps better  
424 maintaining the ewe throughout pregnancy. With the variation over the past few  
425 years in the price of concentrate feed, both nationally and worldwide, if feed prices  
426 increase, while the price of lamb does not increase at a similar rate, farmers may  
427 decide to make adjustments to their management system. Should they cut back on  
428 the level of feed that they provide to their flocks, by using the scale described in the  
429 present study, farmers could potentially identify sires best suited to which ever  
430 system they choose to pursue.

431 Although the initial aim of the analysis was to identify a way of measuring the level of  
432 concentrate feed use, the resulting FE scale, as estimated using the first canonical  
433 Q-value, was not dissimilar to a production level-type scale. Similar scales have  
434 been used in studies such as those by Strandberg *et al.* (2009), who, in addition to  
435 using the FE scale developed by Haskell *et al.* (2007), also used herd averages for  
436 production and fertility-related descriptors to define environments. Kolmodin *et al.*  
437 (2002), defined environments as the deviation from the overall herd-year averages of

438 protein production (production environment) and days open (fertility environment).  
439 Studies using sheep, such as Pollot and Greeff (2004), defined Merino production  
440 environments using the average value of each trait analysed, for each contemporary  
441 group identified. Similar methods have also been used by Santana *et al.* (2013b)  
442 when studying Santa Ines sheep in Brazil.

443 However, it should be noted that before any scale can be introduced to the industry,  
444 further investigation would be required in order to identify an appropriate method by  
445 which the farmers could use this information. The scale used in the present study  
446 uses adjusted performance averages for a number of traits, therefore it may be more  
447 appropriate for the farmers to receive information with regards to a pre-calculated FE  
448 score when they receive their flock genetic evaluation data. It should also be noted  
449 that the scale discussed here was for a specific breed and specific lamb traits. It may  
450 be that the scale would be different if other breeds or traits were involved.

#### 451 *Reaction norm analysis*

452 The reaction norms estimated for each trait suggest GxE was evident, in terms of  
453 both re-ranking and scaling. The sensitivities estimated, as represented by the slope  
454 value for each sire reaction norm, indicated that all sires represented in the dataset  
455 increased their performance, for 21WT and UMD, as the FE improved. When the  
456 overall regression coefficient was removed, there was a mix of positive and negative  
457 values indicating variation in the level of improvement across the scale. In other  
458 words some improved at a quicker rate than others. However, for UFD, the EBVs of  
459 some sires increased as the FE improved while others decreased as the FE  
460 improved. Overall, the range of slope gradients observed for each sire reaction norm  
461 indicated the presence of both scaling and re-ranking. It should be noted though that

462 a number of sires had sensitivities close to, or equal to, zero, indicating that there  
463 was very little variation in their performance across environments and they were  
464 therefore not influenced as much by changes in feeding regimes. Similar examples  
465 of scaling and re-ranking were observed by both Pollot and Greeff (2004) and  
466 Santana *et al.* (2013b), when using random regression models to investigate a  
467 number of sheep performance traits including faecal egg counts, wool, body and  
468 growth characteristics. Overall, as suggested by Haskell *et al.* (2007), the presence  
469 of environmental sensitivity provides an opportunity for farmers to choose sires  
470 based on the FE of their farm.

471 When heterogeneous residual variances were investigated, their inclusion  
472 significantly improved the fit of the overall random regression model for all traits.  
473 Similar results were also observed by Pollot and Greeff (2004), Cardoso and  
474 Tempelman (2012) and Santana *et al.* (2013b). Strandberg (2006) comments that  
475 this is not unexpected, particularly when using sire models. The 6 environmental  
476 classes (a-f) used for the analyses were kept consistent across the traits, and were  
477 selected based on the different sections of the FE scale, representing low, average  
478 and high environments. Although these classes provided significant improvements to  
479 the fit of the model, it may be that the fit could be improved further by adjusting the  
480 classes and using different classes for different traits. Nonetheless, the results  
481 presented here highlight that it may be beneficial for any similar analyses in the  
482 future to account for such heterogeneous variances.

#### 483 *Heritability of traits across different environments*

484 When using environment scales based on production levels, such as those used by  
485 Kolmodin *et al.* (2002) and Strandberg *et al.* (2000), the heritabilities estimated often

486 increased as the environment improved. Heritabilities previously estimated, using  
487 data available for Texel lambs in the UK, for 21WT, UMD and UFD were 0.38, 0.29  
488 and 0.38 respectively (Jones *et al.*, 2004). When the heritabilities of the three traits  
489 were estimated across the FE scale, in the present study, the highest values were  
490 estimated at the extremes of the scale for 21WT and UFD. However, it should be  
491 noted that these estimates were also associated with the highest standard errors  
492 therefore they should be treated with caution. The lowest values, and lowest  
493 standard errors, for these traits were estimated at the mid-point of the scale, possibly  
494 due to the distribution of the farms on the scale. These results are similar to those  
495 estimated by Pollot and Greeff (2004) for faecal egg count across environments. The  
496 estimates for UMD were slightly different than those for 21WT and UFD. The highest  
497 values estimated at the low end for the scale and the lowest values slightly above  
498 the mid-point, but again the standard errors were larger at the extremes of the FE  
499 scale and smaller nearer the mid-point.

500 The heritability estimates for 21WT, UMD and UFD at the low end of the FE scale  
501 (poorer FE environment in terms of production and weather), indicated that the  
502 genetic variation for these traits was high. This would suggest that some rams have  
503 the ability to produce lambs with high 21WT, UMD and UFD values even when the  
504 environment is classed as poorer. Similarly, and perhaps somewhat more expected,  
505 at the higher end of the FE scale, the heritability estimates increased as the  
506 environment improved. The rate of increase was the highest for UFD, followed by  
507 21WT, suggesting that the genetic control over these traits was affected more by the  
508 improvement in environment than UMD. The observed rate of increase should be  
509 treated with some caution due to the increased size of the standard errors  
510 associated with these estimates. At the mid-point of the scale, the animals were



511 generally more similar in their genetic control of each trait. The lowest heritability  
512 values for UMD were estimated just above the mid-point of the scale. This, along  
513 with the fact that the UMD heritability estimates were the highest overall at the  
514 poorer end of the scale, indicates that improvements in this trait can also be made  
515 when environmental conditions are not so favourable.

516 In terms of the different feeding levels, the results suggest that by increasing the  
517 amount of feed available to lambs, although improvements will be found with regards  
518 to all traits, the rate of genetic progress associated with UFD will be the greatest.  
519 This may prove costly if carcasses become over-fat and result in a financial penalty  
520 to the farmer. At the lower end of the FE scale, if the lambs are fed less feed, but the  
521 ewes are fed more, the rate of genetic progress of all three traits will also improve at  
522 a similar rate.

#### 523 *Genetic correlations between farm environments*

524 A wide range of genetic correlations were estimated within each trait, between pairs  
525 of environments across the FE scale. The results suggest that there would be less  
526 GxE evident, in terms sires ranking, if the environmental conditions of the two  
527 environments were similar. For example, flocks with below average Q-values on the  
528 FE scale were relatively highly correlated with similar flocks located at that end of the  
529 FE scale and similarly, flocks with above average Q-values were more highly  
530 correlated with other flocks at the top end of the FE scale. However, as the  
531 environments become more divergent (e.g. the lowest points of the FE scale and the  
532 highest points on the FE scale) the genetic and Spearman's rank correlations fell.  
533 Sires suitable for flocks at the lower end of the FE scale are therefore not necessarily  
534 as suitable for those at the higher end of the FE scale and this further emphasises

535 that GxE is evident in the population. These results were similar to those reported by  
536 Santana *et al.* (2013b) for the body weight of Santa Ines sheep at 180 days of age  
537 as well as Cardoso and Tempelman (2012) for post-weaning weight gain of Angus  
538 cattle.

#### 539 *Accounting for GxE in genetic evaluations*

540 Overall, the use of reaction norm analyses provide an opportunity for future genetic  
541 evaluations to take into account any interactions that may be present between  
542 genotypes and environments. The reduced requirement for each individual  
543 environment to be genetically linked, such as those required when using the multi-  
544 trait method and groups of environments, potentially allows the prediction of an  
545 animal's performance across a greater number of environments. Providing a suitable  
546 "measure of environment" can be agreed, the method can allow the prediction of  
547 unique rankings for each level of environment.

548 The method presented in the current study combined fine-level detail, with particular  
549 emphasis on the use of concentrate feed, with information available nationally for all  
550 flocks that are members of Signet Sheepbreeder programme. By using the  
551 environment scale developed, GxE was observed for all Texel lamb traits  
552 investigated, both in terms of re-ranking and scaling. The variation in heritability  
553 estimates across different environments, as well as the range of genetic correlations  
554 estimated between environments, all need consideration in future selection  
555 programmes. Mulder *et al.* (2006) recommended, while investigating the presence of  
556 GxE in dairy cattle, that when genetic correlations between environments were  
557 below 0.61, different breeding programmes should be used. However, whether this  
558 specific value is relevant to the sheep breeding situation of the present study, or

559 economically viable, would be worthy of further investigation. It may also be useful to  
560 investigate if the FE scale developed in this study is applicable to other traits and  
561 breeds, or if another way of quantifying FE should be considered.

## 562 **Conclusions**

563 The techniques and approaches used in this study have proven to be useful in  
564 defining sheep farm environments and have the potential to be adopted across the  
565 globe in relation to different farming systems. Although the environment scale  
566 identified in the current study may perhaps be more relevant to terminal sire breeds  
567 and traits, there is no reason why variables better suited to other breed types, such  
568 as hill breeds for example, cannot be identified and used in a similar manner. The  
569 range of sire sensitivities estimated across the environment scale, using the reaction  
570 norm methods, confirmed the presence of genetic variability, as both “plastic” and  
571 “robust” genotypes were observed in the population. The ability to identify  
572 differences in sensitivity allows farmers to select animals best suited to specific  
573 environments as well those that will perform consistently across a range of  
574 environments. The variation in heritability and correlation estimates also suggests  
575 that the rate genetic progress will vary depending on the environment. Overall, the  
576 results from this study indicate that in order to improve genetic gain and flock  
577 efficiency, future genetic evaluations would benefit by accounting for the GxE  
578 observed.

## 579 **Acknowledgements**

580 The author wishes to acknowledge EBLEX, HCC & QMS for funding this research.  
581 Many thanks also to the farmers who responded to the questionnaire, Ian White  
582 (University of Edinburgh) and Sebastian Mucha (SRUC) for their advice in regards to

583 the data analysis and Sam Boon (Signet Breeding Services) and Kirsty Moore  
584 (EGENES) for their help with providing the data.

585 **References**

- 586 Bradshaw AD 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in*  
587 *Genetics* 13, 115-155.
- 588 Bryant J, Lopez-Villalobos N, Holmes C and Pryce J 2005. Simulation modelling of dairy  
589 cattle performance based on knowledge of genotype, environment and genotype by  
590 environment interactions: current status. *Agricultural Systems* 86, 121-143.
- 591 Calus MPL, Groen AF and de Jong G 2002. Genotype x environment interaction for protein  
592 yield in Dutch dairy cattle as quantified by different models. *Journal of Dairy Science* 85,  
593 3115-3123.
- 594 Cardoso FF and Tempelman RJ 2012. Linear reaction norm models for genetic merit  
595 prediction of Angus cattle under genotype by environment interaction. *Journal of Animal*  
596 *Science* 90, 2130-2141.
- 597 Clark D 1975. Understanding canonical correlation analysis. *Concepts and Techniques in*  
598 *Modern Geography* 3, University of East Anglia, Norwich, England.
- 599 de Jong G and Bijma P 2002. Selection and phenotypic plasticity in evolutionary biology and  
600 animal breeding. *Livestock Production Science* 78, 195-214.
- 601 Falconer DS 1990. Selection in different environments: effects on environmental sensitivity  
602 (reaction norm) and on mean performance. *Genetical Research* 56, 57-70.
- 603 Fikse WF, Rekaya R and Weigel KA 2003. Assessment of environmental descriptors for  
604 studying genotype by environment interaction. *Livestock Production Science* 82, 223-231.
- 605 Gilmour AR, Cullis BR, Welham SJ and Thompson R 2002. *ASReml Reference Manual*.  
606 NSW Agriculture, Orange, NSW, Australia.
- 607 Hair JF, Tatham RL, Anderson RE and Black W 2006. *Multivariate data analysis (Volume 6)*.  
608 Pearson Prentice Hall, Upper Saddle River, New Jersey, USA.
- 609 Haskell MJ, Brotherstone S, Lawrence AB and White IMS 2007. Characterization of the dairy  
610 farm environment in Great Britain and the effect of the farm environment on cow life span.  
611 *Journal of Dairy Science* 90, 5316-5323.
- 612 Hill WG and Zhang XS 2004. Effects on phenotypic variability of directional selection arising  
613 through genetic differences in residual variability. *Genetical Research* 83, 121-132.
- 614 Jones HE, Lewis RM, Young MJ and Simm G 2004. Genetic parameters for carcass  
615 composition and muscularity in sheep measured by X-ray computer tomography, ultrasound  
616 and dissection. *Livestock Production Science* 90, 167-179.
- 617 Knap PW and Su G 2008. Genotype by environment interaction for litter size in pigs as  
618 quantified by reaction norms analysis. *Animal* 2, 1742-1747.
- 619 Kolmodin R, Strandberg E, Madsen P, Jensen J and Jorjani H 2002. Genotype by  
620 environment interaction in Nordic dairy cattle studied using reaction norms. *Acta Agriculturae*  
621 *Scandinavica, Section A, Animal Science* 52, 11-24.

- 622 Macfarlane JM and Simm G 2007. Genetic improvement programme meat type sheep: an  
623 experience from the United Kingdom. Proceedings of the 3<sup>rd</sup> International Symposium about  
624 Goat and Sheep Meat Type – 3<sup>rd</sup> SINCORTE, Joao Pessoa, Paraiba, Brazil.
- 625 Mattar M, Silva LOC, Alencar MM and Cardoso FF 2011. Genotype x environment  
626 interaction for long-yearling weight in Canchim cattle quantified by reaction norm analysis.  
627 Journal of Animal Science 89, 2349-2355.
- 628 McLaren A, Lambe NR, Morgan-Davies C, Mrode R, Brotherstone S, Conington J, Morgan-  
629 Davies J and Bunger L 2014. Characterisation of UK terminal sire sheep farm systems,  
630 based on a range of environmental factors: A case study in the context of genotype by  
631 environment interactions using Charollais lambs. Animal 8, 867-876.
- 632 Mulder HA, Veerkamp RF, Ducro BJ, van Arendonk JAM and Bijma P 2006. Optimization of  
633 dairy cattle breeding programs for different environments with genotype by environment  
634 interactions. Journal of Dairy Science 89, 1740-1752.
- 635 Mulder HA, Bijma P and Hill WG 2007. Prediction of breeding values and selection  
636 responses with genetic heterogeneity of environmental variance. Genetics 175, 1895-1910.
- 637 Pollot GE and Greeff JC 2004. Genotype x environment interactions and genetic parameters  
638 for fecal egg count and production traits of Merino sheep. Journal of Animal Science 82,  
639 2840-2851.
- 640 Pollot GE and Stone DG 2006. The breeding structure of the British sheep industry 2003.  
641 DEFRA publications, London, UK. Retrieved on 25 April 2012,  
642 from [http://archive.defra.gov.uk/evidence/economics/foodfarm/reports/documents/pollott200](http://archive.defra.gov.uk/evidence/economics/foodfarm/reports/documents/pollott2003.pdf)  
643 [3.pdf](http://archive.defra.gov.uk/evidence/economics/foodfarm/reports/documents/pollott2003.pdf))
- 644 Ravagnolo O and Misztal I 2000. Genetic component of heat stress in dairy cattle, parameter  
645 estimation. Journal of Dairy Science 83, 2126-2130.
- 646 SanCristobal-Gaudy M, Bodin L, Elsen JM and Chevalet C 2001. Genetic components of  
647 litter size variability in sheep. Genetics Selection Evolution 33, 249-271.
- 648 Santana ML, Eler JP, Cardoso FF, Albuquerque LG and Ferraz JBS 2013a. Phenotypic  
649 plasticity of composite beef cattle performance using reaction norms model with unknown  
650 covariate. Animal 7, 202-210.
- 651 Santana ML, Bignardi AB, Eler JP, Cardoso FF and Ferraz JBS 2013b. Genotype by  
652 environment interaction and model comparison for growth traits of Santa Ines sheep. Journal  
653 of Animal Breeding and Genetics 130, 394-403.
- 654 Schaeffer LR and Dekkers JCM 1994. Random regressions in animal models for test-day  
655 production in dairy cattle. Proceedings of the 5<sup>th</sup> World Congress on Genetic Applied to  
656 Livestock Production, Guelph, Canada, pp. 443-446.
- 657 Simm G and Dingwall WS 1989. Selection indices for lean meat production in sheep.  
658 Livestock Production Science 21, 223-233.
- 659 Strandberg E, Kolmodin R, Madsen P, Jensen J and Jorjani H 2000. Genotype by  
660 environmental interaction in Nordic dairy cattle studied by the use of reaction norms. Interbull  
661 Bulletin 25, 41-45.

662 Strandberg E 2006. Analysis of genotype by environment interaction using random  
663 regression models. 8<sup>th</sup> World Congress on Genetics Applied to Livestock Production, Brazil,  
664 13-18 August, pp. 25-05. Retrieved November 3, 2013, from <http://www.cabi.org/>

665 [cabdirect/FullTextPDF/2006/20063170059.pdf](http://cabdirect.org/FullTextPDF/2006/20063170059.pdf).

666 Strandberg E, Brotherstone S, Wall E and Coffey P 2009. Genotype by environment  
667 interaction for first-lactation female fertility traits in UK dairy cattle. *Journal of Dairy Science*  
668 92, 3437-3446.  
669

**Table 1.** Summary of lamb traits included in the data set.

	Lamb Records	Sires Represented	Min.	Max.	Average	s.d.
21WT (kg)	181555	5938	12.0	90.0	46.0	9.2
UMD (mm)	175399	5853	5.0	46.2	28.4	3.7
UFD (mm)	175279	5853	0.1	16.0	2.7	1.4

670 21WT = 21 Week Old Weight; UMD = Ultrasound Muscle Depth; UFD = Ultrasound Fat  
671 Depth

672

673



**Table 2.** Correlations between all variables used in the canonical correlation analysis and the resulting P- and Q-variates.

	P Value	Q Value	Rams Fed	Months ewes fed	Flock size	Weeks lambs fed	Rain	Sun Hours	Temp.	Adjusted average 21WT	Adjusted average UFD
Q Value	0.73										
Rams Fed	0.49	0.36									
Months ewes fed	-0.73	-0.53	0.07								
Flock size	-0.32	-0.23	-0.02	-0.13							
Weeks lambs fed	0.23	0.16	0.24	0.03	-0.24						
Rain	-0.13	-0.20	-0.08	0.00	0.22	0.01					
Sun Hours	0.08	0.12	0.15	0.12	-0.22	0.07	-0.72				
Temperature	0.11	0.16	0.17	0.12	-0.28	0.06	-0.64	0.90			
Adjusted average 21WT	0.58	0.80	0.23	-0.43	-0.25	0.21	-0.17	-0.06	0.00		
Adjusted average UFD	0.25	0.35	0.11	-0.10	-0.26	0.23	-0.14	-0.11	0.00	0.78	
Adjusted average UMD	0.54	0.74	0.30	-0.32	-0.28	0.26	-0.07	-0.08	-0.02	0.84	0.80

P-value and Q-value = Values estimated using the P- and Q-variable equations, respectively, derived during the canonical correlation analyses.

**Table 3.** Average descriptors for Texel sheep farms located at the 10 highest and 10 lowest points on the farm environment (FE) scale

	Rainfall (mm)*	Sun (hours)*	Temperature (°C)*	21WT (kg)	UMD (mm)	UFD (mm)	Q-value
High FE score	1189	1393	9.4	52.9	28.8	0.1	2.3
Low FE score	1421	1431	9.2	40.1	25.7	0.3	-1.1

675 21WT = 21 Week Old Weight; UMD = Ultrasound Muscle Depth; UFD = Ultrasound Fat Depth;  
 676 Q-value = Value estimated using the Q-variable equation derived during the canonical correlation analyses.  
 677 \*Weather variables = overall 5 year annual averages

**Table 4.** Estimates of fixed regression coefficients and variance components for intercept ( $\sigma^2_a$ ), slope ( $\sigma^2_b$ ), flock ( $\sigma^2_f$ ), sire x flock interaction ( $\sigma^2_{sf}$ ), error variance ( $\sigma_e^2$ ), log likelihood (LogL) and correlation (r) between intercept and slope from the reaction norm models for 21 week old weight (21WT), ultrasound muscle depth (UMD) and ultrasound fat depth (UFD) (s.e. in parenthesis).

Trait	Regression coefficient	$\sigma^2_a$	$\sigma^2_b$	r	$\sigma^2_f$	$\sigma^2_{sf}$	$\sigma_e^2$	LogL
21WT								
Model A	-	2.26 (0.22)	-	-	27.12 (1.88)	6.89 (0.22)	31.87 (0.11)	
Model B	-	2.24 (0.22)	-	-	18.82 (1.34)	6.91 (0.22)	31.87 (0.11)	-412492.87
Model C	4.58 (0.33)	2.80 (0.36)	1.33 (0.38)	-0.48 (0.09)	18.49 (1.32)	6.63 (0.23)	31.87 (0.11)	-412483.62
Model D	4.58 (0.33)	2.82 (0.36)	1.39 (0.39)	-0.49 (0.09)	18.48 (1.32)	6.61 (0.23)	6 classes	-412446.59
UMD								
Model A	-	0.58 (0.05)	-	-	3.56 (0.26)	1.53 (0.05)	7.84 (0.03)	
Model B	-	0.57 (0.05)	-	-	2.18 (0.17)	1.53 (0.05)	7.84 (0.03)	-275205.93
Model C	1.89 (0.12)	0.82 (0.09)	0.23 (0.08)	-0.61 (0.08)	2.14 (0.17)	1.47 (0.05)	7.84 (0.03)	-275209.80
Model D	1.89 (0.12)	0.80 (0.09)	0.23 (0.08)	-0.58 (0.08)	2.14 (0.17)	1.47 (0.05)	6 classes	-275028.60
UFD								
Model A	-	0.08 (0.01)	-	-	0.52 (0.04)	0.28 (0.01)	1.09 (0.004)	
Model B	-	0.08 (0.01)	-	-	0.52 (0.04)	0.28 (0.01)	1.09 (0.004)	-103340.25
Model C	0.01 (0.06)	0.10 (0.01)	0.06 (0.02)	-0.47 (0.09)	0.51 (0.04)	0.27 (0.01)	1.09 (0.004)	-103320.03
Model D	0.01 (0.06)	0.10 (0.01)	0.06 (0.02)	-0.49 (0.08)	0.51 (0.04)	0.27 (0.01)	6 classes	-103123.83

678 Model A = Sire model with *sire, flock and sire x flock* fitted as random effects.

679 Model B = Sire model, similar to Model A, but with FE fitted as a covariate.

680 Model C = Sire model, similar to Model B but with *sire, flock, sire x flock and sire x FE environment* fitted as random effects.

681 Model D = Sire model, similar to Model C, but also accounting for heterogeneity of environmental variance.

682 6 classes = Environmental classes a, b, c, d, e and f used for heterogeneity of environmental variance analysis

