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

2

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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). 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 ≥ 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 ≥ 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 (11th 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 ≥ 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 χ^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 σ^2_a represents the reaction norm intercept variance, σ^2_b represents the
237 reaction norm slope variance and σ^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, σ^2_f
242 represents the flock variance, σ^2_{sf} represents the sire x flock variance and σ_e^2
243 represents the residual environmental variance. The heritability estimates for Model

244 C were adjusted by replacing σ_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:

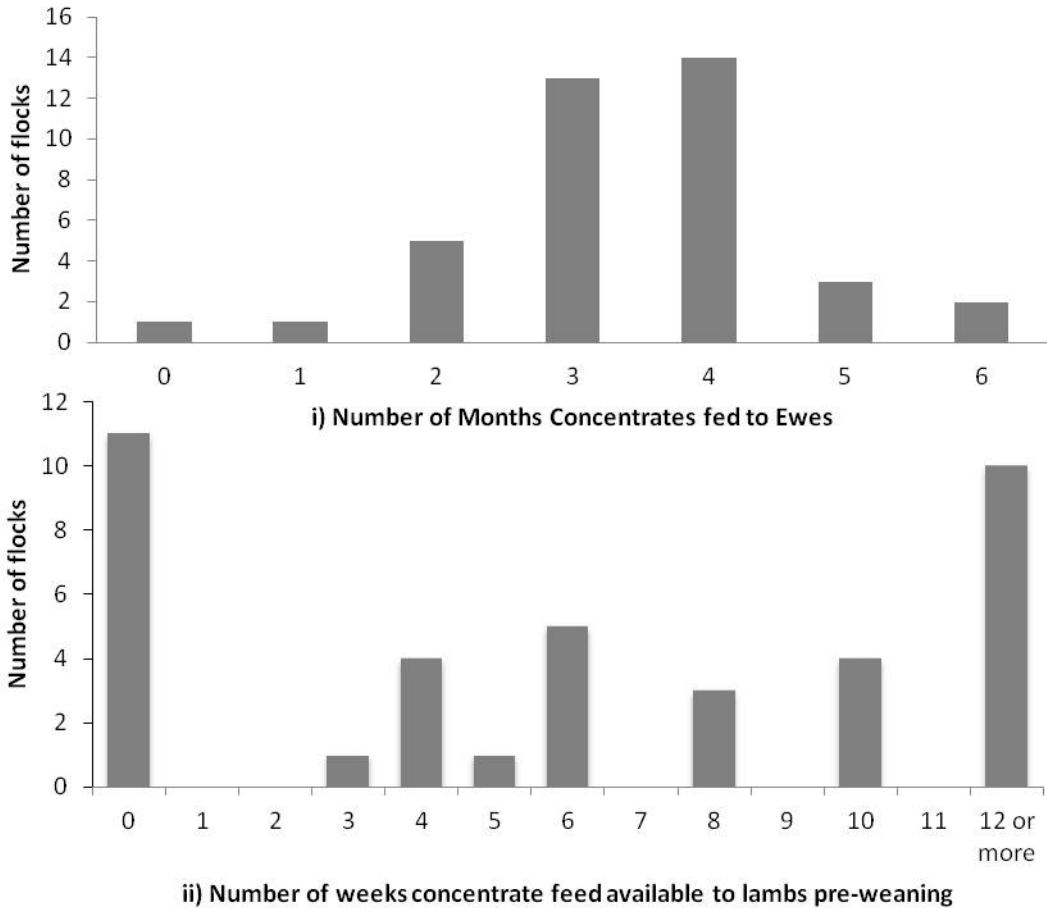
$$248 \quad r_{gFE_1FE_2} = [\sigma_a^2 + FE_1FE_2\sigma_b^2 + (FE_1+FE_2)\sigma_{ab}] / \sqrt{\sigma_{g|FE_1}^2 \sigma_{g|FE_2}^2}$$

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 ± 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.

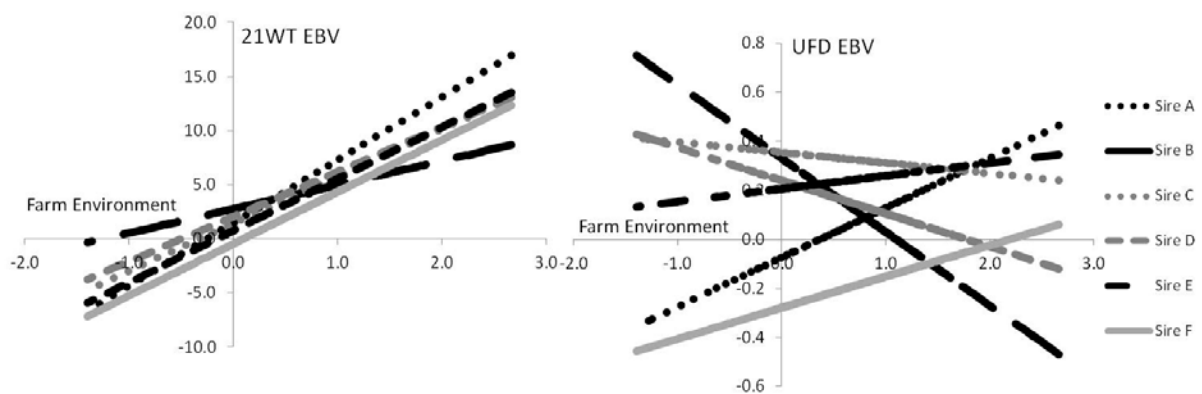
301 **Table 3 here**

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 (± 0.01), 0.19 (± 0.02) and 0.17 (± 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

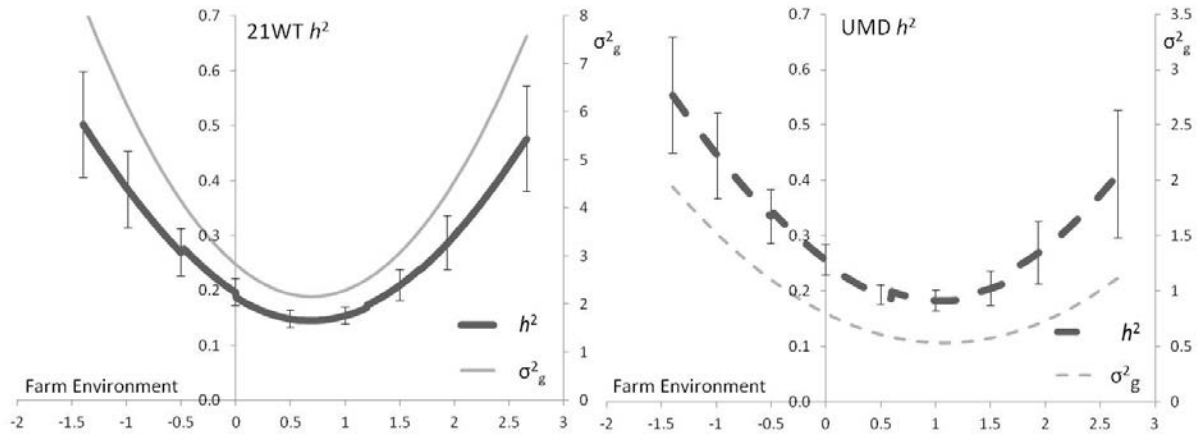
340 associated with heritability estimates at both extremes of the FE scale. The genetic
341 variances estimated followed a similar pattern as the heritability estimates (Figure 3).
342 The genetic correlations estimated across the FE scale are shown in Figure 4. The
343 correlations estimated ranged 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 ± 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 ± 0.5 ,
351 ± 1.0 and ± 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

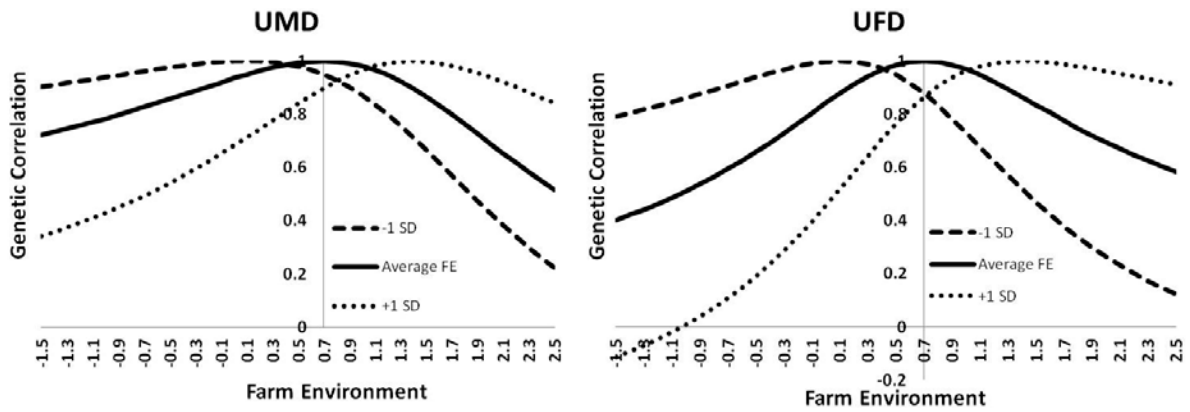
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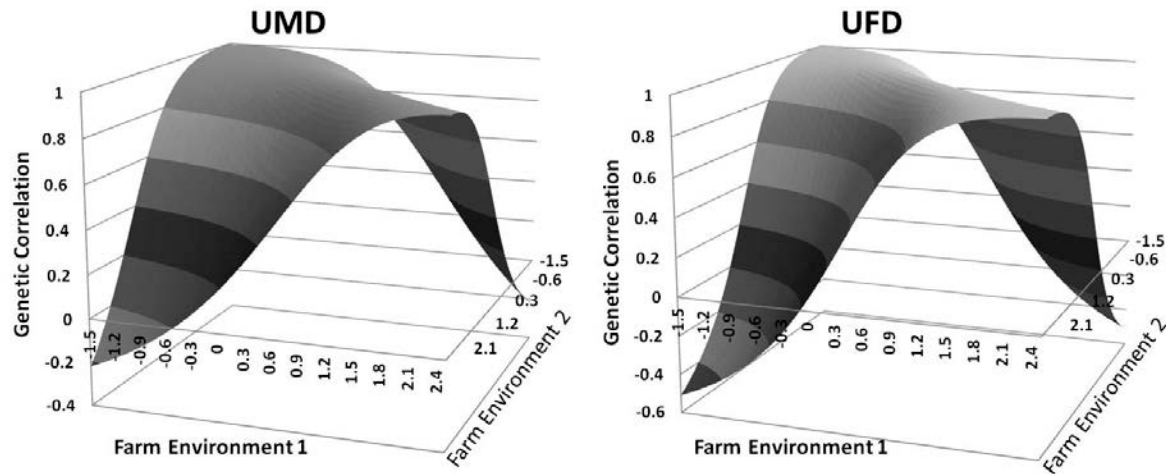
359 **Figure 3.** Heritability (h^2) and genetic variance (σ^2_g) estimates, for 21 week old
360 weight (21WT), ultrasound muscle depth (UMD) as functions of the farm
361 environment (FE) scale (using model D).

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.

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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 (σ^2_a), slope (σ^2_b), flock (σ^2_f), sire x flock interaction (σ^2_{sf}), error variance (σ_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	σ^2_a	σ^2_b	r	σ^2_f	σ^2_{sf}	σ_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

