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1 **Heterogeneous variances and genetics by environment interactions in genetic**  
2 **evaluation of crossbred lambs**

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18

19 Short title: Heteroscedasticity and GxE in crossbred lambs

20 **Abstract**

21 Accounting for environmental heteroscedasticity and genetics by environment  
22 interaction (G×E) in genetic evaluation is important because animals may not perform  
23 predictably across environments. The objectives of this study were to evaluate the  
24 presence and consequences of heteroscedasticity and G×E on genetic evaluation.  
25 The population considered was crossbred lambs sired by terminal sires and reared  
26 under commercial conditions in the UK. Data on 6,325 lambs sired by Charollais,  
27 Suffolk, and Texel rams were obtained. The experiment was **conducted** between  
28 1999 and 2002 on three farms located in England, Scotland, and Wales. There were  
29 2,322, 2,137 and 1,866 lambs in England, Scotland and Wales, respectively. A total  
30 of 89 sires were mated to 1,984 ewes of two types (Welsh and Scottish Mules). Most  
31 rams were used for two breeding seasons with some rotated among farms to create  
32 genetic links. Lambs were reared on pasture and had their parentage, birth, 5 wk, 10  
33 wk, and **slaughter** weights recorded. Lambs were **slaughtered** at a constant  
34 fatness, at which they were ultrasonically scanned for fat and muscle depth.  
35 Heteroscedasticity was evaluated in two ways. Firstly, data were separated into three  
36 subsets by farm. Within farm variance component estimates were then compared to  
37 those derived from the complete data (Model 1). Secondly, the combined data were  
38 fitted, but with a heterogeneous (by farm) environmental variance structure (Model  
39 2). To investigate G×E, a model with a random farm by sire (F×S) interaction was  
40 used (Model 3). The ratio of the F×S variance to total variance was a measure of the  
41 level of G×E in the population. Heterogeneity in environmental variability across-  
42 farms was identified for all traits ( $P < 0.01$ ). Rank correlations of sire EBV between  
43 farms differed for Model 1 for all traits. However, sires ranked similarly (rank  
44 correlation of 0.99) for weight traits with Model 2, but less so for ultrasonic measures.

45 Including the FxS interaction (Model 3) improved model fit for all traits. However, the  
46 FxS term explained a small proportion of variation in weights (less than 2%) although  
47 more in ultrasonic traits (at least 10%). **In conclusion**, heteroscedasticity and GxE  
48 were not large for these data, and can be ignored in genetic evaluation of weight but,  
49 perhaps, not ultrasonic traits. Still, before incorporating heteroscedasticity and GxE  
50 into routine evaluations of even ultrasonic traits, their consequences on selection  
51 response in the breeding goal should be evaluated.

52 **Keywords:** crossbred lambs, genetics by environment interaction, heterogeneous  
53 variances, sheep

54

## 55 **Implications**

56 Genetics by environment interaction (GxE) and heterogeneous environmental  
57 variances may impact genetic evaluation. Where appreciable, sheep reared in  
58 different environments may not perform predictably. Different variances across  
59 environments **were found**, with GxE more pronounced for ultrasonic than for weights  
60 traits up to **slaughter**. Still, their impacts were generally small. Genetic evaluation  
61 aims to assist livestock industries to achieve defined breeding goals; environmental  
62 heterogeneity and GxE can slow progress toward that aim. Although incorporating  
63 heteroscedasticity and GxE into genetic evaluation of ultrasonic traits may be  
64 justified, the utility of doing so must be considered within the framework of industry  
65 breeding goals.

66

## 67 **Introduction**

68 An animal's phenotype reflects a combination of its genetics and environment.  
69 Selection often takes place among animals that are reared in different climatic and

70 husbandry conditions, and animals (and their progeny) may not perform uniformly  
71 across them. None-the-less genetic evaluation programs often assume that animals  
72 will perform consistently across environments, and that variability in performance in  
73 different environments will be similar. A wealth of evidence has shown that is not the  
74 case, and that ignoring such effects had unfavorable consequences on genetic  
75 evaluation schemes (Robert-Graniè *et al.*, 1999; Mulder and Bijma, 2005).

76 Differences in phenotypic variances across flocks can arise from differences in  
77 production conditions such as management, nutrition, and climate. Such  
78 environmental heteroscedasticity (sub-populations with different environmental  
79 variances) has been found in several livestock species for a multitude of traits  
80 (SanCristobal-Gaudy *et al.*, 2001; Rowe *et al.*, 2006; Nakaoka *et al.*, 2007). Variable  
81 performance levels across flocks can also arise from sensitivities of genotypes to  
82 their environmental circumstances. Such genotype by environment interactions  
83 (**G×E**) have been observed in sheep and other species (e.g. Maniatis and Pollott,  
84 2002; Pollott and Greeff, 2004; Steinheim *et al.*, 2008).

85 Ignoring environmental heteroscedasticity and G×E can hinder the robustness  
86 of genetic evaluations. Accuracy of selection can be affected, leading to decreases in  
87 genetic response (Mulder and Bijma, 2005). Variance components may be poorly  
88 estimated and EBV biased, leading to re-rankings of animals (Hill, 1984; Garrick and  
89 Van Vleck, 1987). These effects often were greater when animals were selected on  
90 EBV derived from individual phenotypes, which remains the norm in livestock  
91 species, rather than on family mean performance (Hill and Zhang, 2004).

92 In the UK, 70% of the lamb crop has had terminal sire breeding, with  
93 Charollais, Suffolk, and Texel the predominant breeds used (Pollott and Stone,  
94 2004). Environments in which lambs were reared also differ. By performance testing

95 terminal sire rams in several environments, the extent and consequence of  
96 heteroscedasticity and G×E on genetic evaluation can be examined. Such were the  
97 objectives of this study using a population of terminal-sire cross lambs reared under  
98 commercial conditions.

99

## 100 **Material and methods**

### 101 *Animal care and use*

102 The Animal Experiment Committees at the Institute of Biological  
103 Environmental and Rural Sciences (**IBERS**), the Scottish Agricultural College (**SAC**),  
104 and ADAS UK Ltd (**ADAS**) approved all procedures and protocols used in the  
105 experiment.

### 106 *Animal resources*

107 Data on 6,325 crossbred lambs sired by Charollais, Suffolk, and Texel rams  
108 were obtained. There were a total of 89 rams, which came from their breed's sire  
109 referencing schemes. These were cooperative breeding schemes where reference  
110 rams were shared among flocks to create connectedness and facilitate within breed  
111 genetic evaluation. The rams were selected according to a lean growth index  
112 designed to increase carcass lean growth, while constraining fat growth at a constant  
113 age end point (Simm and Dingwall, 1989). Sires were chosen from the top and  
114 bottom 5% of available rams based on index score and categorized as 'high' or 'low'  
115 lean growth index. High vs. low index rams differed in their EBV when evaluated at  
116 approximately 21 week-of-age. In high index rams, live weight EBV were  $6.6 \pm 0.5$  kg  
117 greater, ultrasonic muscle depth (**UMD**) EBV were  $2.3 \pm 0.2$  mm thicker, and  
118 ultrasonic fat depth EBV were  $0.49 \pm 0.12$  mm thinner, than in low index rams  
119 (Márquez *et al.*, 2012).

120 Lambs in this study came from mating of the terminal sires to Scottish or  
121 Welsh Mules. The Mule ewes were developed from the matings of Bluefaced  
122 Leicester rams with Scottish Blackface and (Welsh) Hardy Speckled Face ewes (van  
123 Heelsum *et al.*, 2003; Mekkawy *et al.*, 2009). Matings between Mule ewes and  
124 terminal sires took place between 1999 and 2002 on three farms in the UK (one each  
125 in England, Scotland, and Wales). Most sires were used for two breeding seasons  
126 and were physically moved between farms to create genetic links among farms and  
127 years (Márquez *et al.*, 2012; 2013). Matings were designed so that the number of  
128 rams from high and low index categories, and from the three breeds, were balanced  
129 across farms, years and ewe breeds.

130 At birth, lamb parentage and weight (**BWT**) were recorded. Mule ewes were  
131 turned out to pasture within 48 hours of lambing with at most 2 lambs. Excess lambs  
132 were fostered to other ewes. Singletons and twins were grazed separately. Lamb's  
133 weights were further recorded at approximately 5 wk (**5WT**), and 10 wk (**10WT**) of  
134 age.

135 Once lambs were approximately 10 wk old they were evaluated subjectively  
136 for finishing condition every two weeks. This entailed lambs being restrained and  
137 assessed for fatness by palpation of the vertebral process and ribs. The fatness  
138 score ranged from 1 (devoid) to 5 (extreme), with L and H indicating 'low' and 'high'  
139 condition within a score, respectively. They were **slaughtered** once reaching a target  
140 finished condition of 3L fat score, which corresponded to approximately 11%  
141 subcutaneous fat (Kempster *et al.*, 1986). Lambs were finished to a constant fatness  
142 so they could be compared at equitable levels of physiological maturity. Upon  
143 finishing, lambs' weights, henceforth referred to as **slaughter** weight (**SWT**), were  
144 obtained. The lambs were also ultrasonically scanned for muscle and fat depth. Their

145 UMD was measured at the deepest point of the eye muscle (longissimus lumborum)  
146 at the third lumbar vertebra. Ultrasonic fat depth was measured at the same location  
147 and at 1 and 2 cm lateral to it and averaged. When finished, lambs were processed  
148 at a commercial abattoir. Further details of design and husbandry were provided by  
149 Márquez *et al.* (2012; 2013).

#### 150 *Genetic groups*

151 A pedigree was assembled, which consisted of 1,325,736 animals. There  
152 were six distinct (unrelated) breed types in the pedigree. Unknown parents for each  
153 breed were fitted as a genetic group: one for each terminal sire breed (the sires of  
154 the lambs), one for each Mule ewe breed types (the dams of the lambs), and one for  
155 the Bluefaced Leicester (the maternal grandsires of lambs). Across breeds the  
156 unknown parents were unrelated justifying their fit as separate genetic groups. Also,  
157 by fitting groups, differences in genetic means among breeds were accounted for,  
158 thereby reducing bias in the evaluation (Van Vleck, 1990).

159 Heterosis effects could not be explicitly fit in the analyses as performance and  
160 pedigree data on the hill breeds used to establish the crosses were unavailable.  
161 However, the combination of breed-types ( $\frac{1}{2}$  terminal sire breed,  $\frac{1}{4}$  hill breed,  $\frac{1}{4}$   
162 Bluefaced Leicester) was consistent for all lambs and therefore the expected levels  
163 of heterozygosity. Furthermore, by fitting genetic groups in the analyses, lamb EBV  
164 were adjusted for mean differences in parental breeds. All analyses in this study  
165 were performed using ASReml (Gilmour *et al.*, 2009).

#### 166 *Heteroscedasticity*

167 The traits investigated were BWT, 5WT, 10WT, SWT, UMD and log  
168 transformed ultrasonic fat depth (**logUFD**). Ultrasonic fat depth was transformed to



169 approximate normality. Analyses of the effects of index selection on these traits have  
 170 been reported previously (Márquez *et al.*, 2012; 2013).

171 *Within farm.* Heteroscedasticity due to farm was tested by creating three  
 172 subsets of data based on where lambs were born and reared. There were 2,322,  
 173 2,137, and 1,866 lambs born in England, Scotland, and Wales, respectively. The  
 174 model fitted was:

$$y_i = \mathbf{X}_i\beta_i + \mathbf{Z}_{a_i}a_i + \mathbf{Z}_{d_i}d_i + e_i \quad [\text{Model 1}]$$

175 where  $y_i$  was a vector of observations,  $\beta_i$  was a vector of fixed effects coefficients,  $a_i$   
 176 was a vector of genetic animal effects,  $d_i$  was a vector of rearing dam effects, and  $e_i$   
 177 was a vector of random residual effects. The  $\mathbf{X}_i$ ,  $\mathbf{Z}_{a_i}$ , and  $\mathbf{Z}_{d_i}$  matrices were incidence  
 178 matrices relating to observations in  $\beta_i$ ,  $a_i$  and  $d_i$ , respectively. The  $i$  subscript referred  
 179 to data from each of the three farms. Fixed effects were an overall mean, lamb sex  
 180 (ewe or wether), age of dam (2 to 5-yr), and birth year (2000-2003). For all traits  
 181 except BWT, a birth-rearing rank effect was fitted with four categories: single  
 182 born/single reared, twin or more born/single reared, single or twin born/twin reared,  
 183 and triplet born/twin reared. For BWT, birth rank (single, twin, or triplet) was fitted.  
 184 Covariates for all traits except SWT and UMD were age at measurement. For SWT  
 185 and UMD, the covariate was estimated subcutaneous fat percent at **slaughter**. Fat  
 186 score was transformed to subcutaneous fat percent according to Kempster *et al.*  
 187 (1986).

188 The (co)variance structure of this model was:

$$\text{var} \begin{bmatrix} a_i \\ d_i \\ e_i \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{a_i}^2 & 0 & 0 \\ 0 & \mathbf{I}\sigma_{d_i}^2 & 0 \\ 0 & 0 & \mathbf{I}\sigma_{e_i}^2 \end{bmatrix} \quad [\text{Model 1}]$$

189 where  $\mathbf{A}$  was the numerator relationship matrix among animals in the pedigree and  $\mathbf{I}$   
 190 was an identity matrix of appropriate dimensions,  $\sigma_{a_i}^2$  was the **additive** genetic

191 variance,  $\sigma_{d_i}^2$  was the environmental rearing dam variance, and  $\sigma_{e_i}^2$  was the residual  
192 environmental variance. Genetic groups were considered in **A**. Since the data were  
193 on crossbred animals, estimates of genetic variance were possibly increased by  
194 dominance effects. However, as noted earlier, it was presumed that heterotic effects  
195 were consistent among lambs in these data. Heritabilities were estimated within farm  
196 as the ratio of genetic variance to the sum of the total variances (i.e.,  $h_i^2 = \sigma_{a_i}^2 / (\sigma_{a_i}^2 +$   
197  $\sigma_{d_i}^2 + \sigma_{e_i}^2)$ )).

198 A likelihood ratio test revealed that rearing dam did not explain substantial  
199 variation in **slaughter** traits (SWT, UMD, logUFD;  $P > 0.2$ ), and therefore the rearing  
200 dam random effect was omitted for these traits. A maternal additive effect could not  
201 be fitted because of the lack of pedigree information on Scottish Blackface and Hardy  
202 Specked Face hill breeds, the dam breeds of the Mule ewes.

203 For each trait, log likelihoods for data from each farm were obtained. These  
204 were independent samples, and therefore the log likelihoods were summed and  
205 compared against a model fitted to the combined data. In the combined model,  
206 additional effects of farm and farm by birth year interaction were included. In the  
207 absence of heteroscedasticity, the sum of the log likelihoods from the independent  
208 samples and the log likelihood from the combined data would be expected to be  
209 equal. **A** likelihood ratio test with 2 degrees of freedom **was used** to test whether the  
210 sum of the log likelihoods from the independent samples differed from the log  
211 likelihood from the combined data. Rank correlations of EBV from the combined and  
212 within farm data were obtained to investigate any consequences of variance  
213 heterogeneity. Some sires did not have progeny on all farms. For those that did, re-  
214 rankings of sires were investigated, and correlations between EBV in the different  
215 farms were obtained.

216 *Across farm.* The second method to test variance heterogeneity was by fitting  
 217 heterogeneous residual (farm) variances (Model 2). In this model, the combined data  
 218 were used, but separate residual variances were estimated for each farm. The fixed  
 219 effects of Model 1, in addition to farm, and farm by year interaction, were fitted to all  
 220 the data with a modified (co)variance structure. The (co)variance matrix remained the  
 221 same as in Model 1, except:

$$\text{var} \begin{bmatrix} a \\ d \\ e_1 \\ e_2 \\ e_3 \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 & 0 & 0 & 0 \\ 0 & I\sigma_d^2 & 0 & 0 & 0 \\ 0 & 0 & I\sigma_{e_1}^2 & 0 & 0 \\ 0 & 0 & 0 & I\sigma_{e_2}^2 & 0 \\ 0 & 0 & 0 & 0 & I\sigma_{e_3}^2 \end{bmatrix} \quad [\text{Model 2}]$$

222 where  $\sigma_{e_i}^2$  ( $i = 1,2,3$ ) was the residual variance of farm  $i$ . Within farm heritabilities for  
 223 this model were calculated as  $h_i^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_d^2 + \sigma_{e_i}^2)$ .

224 The log likelihood for this model was obtained for each trait, and was tested  
 225 against a null model with a single residual variance component, with a likelihood ratio  
 226 test with 2 degrees of freedom. The consequences of heteroscedasticity were  
 227 investigated by obtaining rank correlation of EBV calculated assuming either  
 228 heterogeneous or homogeneous environmental variances.

229 *Genotype by environment interaction*

230 To investigate the presence of G×E, an animal model **was fitted** with a  
 231 random farm by sire (**F×S**) interaction term. Fixed effects were the same as in Model  
 232 1. Random effects were animal, farm, F×S and a random residual. A random rearing  
 233 dam was fitted for BWT, 5WT, and 10WT. The (co)variance structure for this model  
 234 was:

$$\text{var} \begin{bmatrix} a \\ f \\ fxs \\ d \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & 0 & 0 & 0 & 0 \\ 0 & I\sigma_f^2 & 0 & 0 & 0 \\ 0 & 0 & I\sigma_{fxs}^2 & 0 & 0 \\ 0 & 0 & 0 & I\sigma_d^2 & 0 \\ 0 & 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix} \quad [\text{Model 3}]$$

235 where **A** was the numerator relationship matrix,  $\sigma_a^2$ ,  $\sigma_f^2$ , and  $\sigma_{fxs}^2$  were the variance  
 236 components associated with animal (**additive genetic**), farm, and F×S, respectively.  
 237 Other variance components were defined as in Model 1 and Model 2. The F×S  
 238 interaction component would indicate the amount of G×E in a population (Dickerson,  
 239 1962). To test for its significance, a likelihood ratio test was performed by comparing  
 240 it to a model without the random F×S interaction term. The ratio of F×S to total  
 241 variance was calculated to quantify the extent of G×E in the population. The  
 242 heritability was calculated as the ratio of genetic variance to total variance.

243 To investigate whether any G×E was caused by heterogeneous phenotypic  
 244 variances, traits were standardized to their within-farm variance, and Model 3 was  
 245 again fitted. Large differences in variance component estimates, and re-ranking of  
 246 sires in standardized as compared to unstandardized data, would indicate the  
 247 importance of variance heterogeneity.

#### 248 *Connectedness*

249 In order to avoid biases in our EBV, the study was designed to establish  
 250 sound genetic links, or connectedness, among farm locations within and across  
 251 terminal sire breeds and index categories. The sufficiency of the design was explored  
 252 by quantifying the strength of connections using prediction error correlations (Lewis  
 253 *et al.*, 2005; Kuehn *et al.*, 2007; 2008). Using 5WT as the example trait, and a  
 254 heritability of 0.20, connectedness correlations were derived among farms and

255 breed-index categories. The mixed linear animal model fitted included farm-year  
256 combination, sex-birth rearing type combination, and age of dam as fixed effects.

257

## 258 **Results**

259 Summary statistics for BWT, 5WT, 10WT, SWT, UMD and logUFD are  
260 provided in Table 1 relative to sire breed. As reported previously (Márquez et al.  
261 (2012; 2013), weights and ultrasound measures differed with respect to sire breed,  
262 although changes in means were generally proportional to changes in s.d. (similar  
263 CV across breeds).

264

265 Please place Table 1 about here

266

267 *Within farm.* When the data were separated by farm, likelihood ratio tests  
268 indicated the presence of heterogeneity in the environmental variance for all traits ( $P$   
269  $< 0.01$ ). However, the estimates of total variance and heritability were similar for the  
270 combined data, and for within each subset of farm data (Table 2).

271

272 Please place Table 2 about here

273

274 Rank correlations between lamb EBV with the full data and farm subsets  
275 ranged from: 0.77-0.81 for BWT; 0.55-0.93 for 5WT; 0.57-0.74 for 10WT; 0.71-0.82  
276 for SWT; 0.70-0.83 for UMD; and, 0.76-0.95 for logUFD. The rank correlations  
277 estimated within a particular farm were not consistently higher or lower than those in  
278 the other farms, nor were there clear patterns among correlations within farms. The  
279 rank correlations among lamb EBV were higher than those among sire EBV,

280 reflecting the fewer numbers of sires than lambs on individual farms (results not  
281 shown).

282 *Across farm.* Allowing for heterogeneous environmental variances among  
283 farms (Model 2) provided a better fit to the data for all traits ( $P < 0.01$ ). However,  
284 when comparing the genetic variances and heritabilities obtained from models with  
285 heterogeneous vs. homogenous variance structures, they were within the standard  
286 error for most traits (except SWT and UMD) (Table 3).

287

288 Please place Table 3 about here

289

290 Rank correlations between EBV obtained from the homogenous and heterogeneous  
291 variance models were 0.99 for all weight traits (both animals and sires), and 0.88 and  
292 0.84 for UMD and logUFD, respectively, among sires. These results indicate that re-  
293 ranking only would be observed for ultrasonic traits, **although they** would not be  
294 substantial. The across farm estimates of heritabilities were similar to the within farm  
295 heritabilities of Model 1.

296 *Genotype by environment interaction*

297 For all traits, including a random F×S interaction in the model resulted in a  
298 better fit ( $P < 0.001$ , except  $P = 0.02$  for SWT). Heritabilities were similar to those  
299 estimated in Models 1 and 2. The proportion of the F×S variance to total variance  
300 was small for weight traits, but more pronounced for ultrasonic measures (Table 4).  
301 Standardizing traits to a common within farm variance did not have an effect on  
302 variance components or rankings (results not shown).

303

304 Please place Table 4 about here

305

306 *Connectedness*

307       Among farm locations, connectedness correlations were between 0.61 and  
308 0.67. Between the high and low index category within a breed, these correlations  
309 ranged from 0.44 for the Suffolk to 0.53 for the Charollais. Values between breeds  
310 were only slightly lower (0.40). Correlations of 0.10 and above were shown to be  
311 indicative of strong connectedness (Kuehn *et al.*, 2008). Although there were only 8  
312 sires shared between Wales and Scotland, 14 between Wales and England, and 13  
313 between Scotland and England, the rotation of rams among farms generated the  
314 well-connected design intended.

315

316 **Discussion**

317 *Variance heterogeneity*

318       Heteroscedasticity was present in this population, especially for ultrasonic  
319 traits. In the combined data, the additive genetic variance was similar to that  
320 estimated within farms (Model 1). These estimates changed little when fitting Model  
321 2. Such was the case even when a homogeneous farm variance was assumed.

322       For both weight and ultrasound traits, accounting for heterogeneous variances  
323 improved model fit. However, for the weight traits, rank correlations between EBV  
324 obtained with homogenous and heterogeneous variances were near one. This  
325 suggested that any consequences of heteroscedasticity were not pronounced for  
326 weight traits, in agreement with previous results (Canavesi *et al.*, 1995). Sire re-  
327 ranking was more evident for UMD and logUFD, suggesting heteroscedasticity would  
328 **have a greater** effect on the genetic evaluation of ultrasound traits.

329 Ignoring heterogeneous variances in genetic evaluation has risks. As  
330 observed in this study, animals may be incorrectly ranked resulting in lower selection  
331 response. Accuracies of EBV may also be affected. By fitting a heterogeneous  
332 variance model, EBV would be scaled, lessening the impact of inaccuracies in the  
333 estimation (Gianola, 1986). Given the presence of heterogeneous variances, several  
334 livestock breeds have developed genetic evaluation models that account for  
335 heteroscedasticity (Wiggans and VanRaden, 1991; Nakaoka *et al.*, 2007).

336 An effective way to mediate bias in EBV due to heterogeneous variances  
337 would be to test progeny in different environments. In progeny testing of dairy cattle,  
338 ranking of bulls was not greatly affected by heteroscedasticity when their daughters  
339 were randomly distributed among farms with high and low variances (Winkelman and  
340 Schaeffer, 1988). Sire referencing schemes, such as those from which the rams used  
341 in this study were drawn, provide another way of distributing genetics of sires to  
342 many flocks. It has been reported that assumptions of homogeneity may not lead to  
343 substantial decreases in selection response when heritabilities are higher in more  
344 variable populations (Garrick and Van Vleck, 1987). No such pattern was found in  
345 these data.

346 Evidence for heterogeneity of variances within individual sheep breeds has  
347 been reported. SanCristobal-Gaudy *et al.* (2001) found that selecting for increased  
348 litter size led to increases in variability of the trait, and that using a heterogeneous  
349 variance model resulted in increased selection response. In a study comparing  
350 different breeds, Tosh and Kemp (1994) found variable estimates of heritability for  
351 weights up to 100 d in 3 breeds (Hampshire, Polled Dorset, and Romanov). They  
352 also report heterogeneous breed variances, and suggested accounting for breed



353 specific variance estimates may be necessary when comparing different breeds in an  
354 across-breeds genetic evaluation.

### 355 *Genetics by environment interactions*

356 The ratio of F×S to total variance was shown to be indicative of the presence  
357 and influence of G×E within a population (Dickerson, 1962; Meyer, 1987). For weight  
358 traits, F×S explained approximately 1% of the total variation. For ultrasonic traits, this  
359 percentage was greater (10 – 13%), indicating that G×E has a larger influence on  
360 body composition traits. For weight traits, our results were similar to Maniatis and  
361 Pollott (2002), also in sheep; however, they reported a lower proportion of variance  
362 due to F×S in ultrasonic traits than in the current study.

363 In our case, including the F×S effect in the analyses decreased estimates of  
364 heritability. Such was also the case for Maniatis and Pollott (2002). Here, as in their  
365 study, ignoring F×S may have inflated estimates of **additive** genetic variance. They  
366 hypothesized that some of the additive **genetic** variance was being partitioned into  
367 the F×S variance component, yielding downwardly biased heritabilities. Shrunk  
368 additive **genetic** variances were also found by Hagger (1998) for ADG in sheep  
369 when fitting an F×S effect. Therefore levels of G×E in production traits appear to be  
370 low but real in sheep populations.

371 Misztal (1990) suggested that an explanation for a significant F×S interaction  
372 was poor representation of sires across-flocks, where genetic evaluations were more  
373 severely regressed. In our study, sires were well represented across flocks, with a  
374 proportion of sires having progeny in two of the three farms. The connectedness  
375 among farms was also strong. Another reason for the F×S interaction may be  
376 preferential treatment of some half-sib groups (Meyer, 1987). However, given the

377 design of this experiment, with management intentionally standardized across farms,  
378 such would not be anticipated.

379 Ultrasonic traits had greater indication of heteroscedasticity than weight traits,  
380 and also had a higher proportion of variation explained by the F×S interaction.  
381 Dickerson (1962) and Canavesi *et al.* (1995) found that F×S interaction may be  
382 caused by, or at least inflated by, heterogeneous variances. When **variances were**  
383 standardized across farms, the variance component estimates, and the proportion of  
384 F×S interaction variance to total variance, did not change. Notter *et al.* (1992) and  
385 Maniatis and Pollott (2002) reported similar results.

#### 386 *Effects on genetic evaluation*

387 Weight at **slaughter** reflects an animal's growth to a certain end point, such as  
388 a target level of fatness. As such, it is a combination of the bone, fat, lean, and other  
389 tissues deposited in an animal as it grows. **Evidence of** heterogeneity and G×E **was**  
390 **not observed** in SWT, or in earlier weights, but **it was** in ultrasonic traits. Ultrasonic  
391 measures were shown to be indicative of fat and lean tissue deposition in an animal  
392 (Emenheiser *et al.*, 2010), and therefore can be thought of as components of SWT.  
393 Perhaps when considering the components rather than the culmination of growth,  
394 heterogeneity and G×E become more apparent. Our findings indicate that accounting  
395 for heterogeneity and G×E in genetic evaluation of ultrasonic measures, at least in  
396 progeny of terminal sires, will reduce such bias.

397 In selection regimes, where animals were often reared in environments that  
398 differed, ignoring G×E when estimating variance components in genetic evaluation  
399 led to reductions in selection response (Garrick and Van Vleck, 1987; Mulder and  
400 Bijma, 2006). Mulder and Bijma (2005) found that progeny testing schemes were  
401 more robust to G×E than sib-testing schemes: when including information on

402 progeny, in the presence of any G×E, the rate of genetic change was greater. The  
403 current data were derived from a progeny testing scheme. **It was** therefore  
404 anticipated **that it would have** less of an impact of G×E than otherwise.

405 In the presence of G×E, the breeding objective of selection programs in  
406 different environments may differ. The construction of selection tools may also differ  
407 because genetic (co)variances between traits may vary across environments. With  
408 the presence of G×E, a way to optimize selection programs would be to have an  
409 overall breeding goal yet test progeny in more than one environment, as was **the**  
410 **case** in the current study.

411 Clearly the consequences of heteroscedasticity or G×E on genetic evaluation  
412 programs must be carefully considered before being incorporated into genetic  
413 evaluation. The limited extent of environmental heteroscedasticity observed in this  
414 study may justify it being ignored even for ultrasonic traits, as re-ranking of sires was  
415 trivial. Accounting for any G×E in the genetic evaluation of ultrasonic traits may be  
416 more important: the F×S random component explained at least 10% of the variation  
417 in these traits. Still, to robustly estimate the F×S effect, the number of offspring per  
418 sire needs to be large enough and connectedness among their offspring needs to be  
419 sufficient. Such was the case in this study but may not be so in industry breeding  
420 schemes.

421 Even where heteroscedasticity or G×E may be important, incorporating them  
422 into genetic evaluation schemes could be complicated. Firstly, environments must be  
423 delineated. In the current study this was straightforward; by its design, lambs were  
424 reared in three distinct locations within the UK. However, in genetic evaluation  
425 schemes, environments may be less easily distinguished, may overlap, and may vary

426 gradually across geographic regions and climates. Furthermore, environmental  
427 conditions would not be static over time, even on individual farms.

428 **When** deciding whether to incorporate G×E or heterogeneous variances into  
429 genetic evaluation, the efficacy of running such evaluations **also** deserves  
430 consideration. When fitting models with more random effects, solutions may be more  
431 difficult to obtain. Furthermore, the amount of data in current routine genetic  
432 evaluations would be large, with computational time a constraint. Therefore the costs  
433 of accounting for heteroscedasticity and G×E in routine, particularly multivariate,  
434 genetic evaluations need to be considered.

#### 435 *Conclusions*

436 The aim of genetic evaluation programs is to assist livestock industries  
437 achieve defined breeding goals. The presence of environmental heterogeneity or  
438 G×E may hinder progress toward these goals. However, before incorporating such  
439 factors into routine genetic evaluations, their extent and consequence on reaching  
440 breeding goals need to be carefully evaluated. **In the present study, incorporating**  
441 **such comprehensive statistical models for weight traits was not warranted.**

442

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456

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543 **Table 1.** Summary statistics for birth, 5 wk, 10 wk and **slaughter** weights, and for ultrasonic  
 544 muscle (UMD) and log-transformed fat (logUFD) depths, by sire breed.

Trait	Mean	s.d.	CV%	Minimum	Maximum
<b>Birth weight (kg)</b>					
Charollais	4.7	0.93	19.6	2.0	8.3
Suffolk	4.8	0.94	19.6	2.2	8.5
Texel	4.7	0.96	20.3	2.0	8.2
<b>5 wk weight (kg)</b>					
Charollais	16.3	3.69	22.6	5.8	31.5
Suffolk	16.9	3.68	21.8	5.5	28.8
Texel	16.6	3.85	23.2	5.5	29.5
<b>10 wk weight (kg)</b>					
Charollais	26.3	5.36	20.4	7.6	44.2
Suffolk	26.9	5.04	18.8	11.3	43.0
Texel	26.4	5.32	20.1	9.0	44.3
<b>Slaughter weight (kg)</b>					
Charollais	42.2	4.62	11.0	29.0	62.0
Suffolk	42.5	4.68	11.0	29.8	61.0
Texel	40.7	4.43	10.9	28.0	59.2
<b>UMD (mm)</b>					
Charollais	24.8	2.20	8.9	17.5	33.0
Suffolk	24.6	2.19	8.9	18.3	32.3
Texel	24.9	2.25	9.1	17.0	36.2
<b>logUFD (mm)</b>					
Charollais	1.4	0.31	22.6	0.2	2.4
Suffolk	1.3	0.29	22.2	0.4	2.2
Texel	1.3	0.30	22.8	0.1	2.5

545

546 **Table 2.** Estimates of genetic and environmental variance and heritability for growth and **slaughter** traits in sheep. Combined  
 547 model includes all data, and country subsets includes data only from farm in that country.

	Trait					
	BWT (kg <sup>2</sup> ) <sup>1</sup>	5WT (kg <sup>2</sup> )	10WT (kg <sup>2</sup> )	SWT (kg <sup>2</sup> )	UMD (mm <sup>2</sup> )	logUFD (mm <sup>2</sup> )
Genetic variance						
Combined	0.110 ± 0.023	0.69 ± 0.15	1.68 ± 0.36	5.29 ± 0.64	1.33 ± 0.15	0.019 ± 0.003
England	0.094 ± 0.034	0.59 ± 0.24	2.01 ± 0.63	5.86 ± 0.95	1.31 ± 0.23	0.027 ± 0.004
Scotland	0.097 ± 0.033	1.25 ± 0.37	1.81 ± 0.63	6.46 ± 1.18	1.43 ± 0.24	0.015 ± 0.003
Wales	0.094 ± 0.034	0.67 ± 0.26	1.32 ± 0.53	4.39 ± 0.98	1.60 ± 0.29	0.027 ± 0.005
Environmental variance						
Combined	0.27 ± 0.02	3.61 ± 0.12	8.07 ± 0.26	10.67 ± 0.47	2.67 ± 0.11	0.046 ± 0.002
England	0.29 ± 0.01	2.89 ± 0.17	5.84 ± 0.41	7.61 ± 0.66	2.69 ± 0.18	0.035 ± 0.003
Scotland	0.26 ± 0.02	2.54 ± 0.21	5.73 ± 0.41	11.79 ± 0.89	1.96 ± 0.17	0.046 ± 0.003
Wales	0.29 ± 0.02	4.20 ± 0.23	9.73 ± 0.51	11.76 ± 0.81	3.19 ± 0.23	0.046 ± 0.003
Heritability <sup>2</sup>						
Combined	0.22 ± 0.04	0.13 ± 0.03	0.14 ± 0.03	0.33 ± 0.04	0.33 ± 0.04	0.30 ± 0.04
England	0.18 ± 0.06	0.12 ± 0.05	0.19 ± 0.06	0.43 ± 0.06	0.33 ± 0.05	0.43 ± 0.06
Scotland	0.20 ± 0.06	0.26 ± 0.07	0.17 ± 0.06	0.35 ± 0.06	0.42 ± 0.06	0.24 ± 0.05
Wales	0.18 ± 0.05	0.12 ± 0.05	0.10 ± 0.04	0.27 ± 0.06	0.33 ± 0.05	0.38 ± 0.06

<sup>1</sup>BWT= birth weight; 5WT = five week weight; 10WT = ten week weight; <sup>1</sup>SWT = **slaughter** weight; UMD = ultrasonic muscle depth; logUFD = log ultrasonic fat depth

<sup>2</sup>Heritabilities are without units

548

549 **Table 3.** Genetic and environmental variances and heritabilities for homogeneous and heterogeneous variance models for growth  
 550 and **slaughter** traits.

	BWT (kg <sup>2</sup> ) <sup>1</sup>	5WT (kg <sup>2</sup> )	10WT (kg <sup>2</sup> )	SWT (kg <sup>2</sup> )	UMD (mm <sup>2</sup> )	logUFD (mm <sup>2</sup> )
Genetic variance						
HOM <sup>2</sup>	0.12 ± 0.03	0.91 ± 0.18	2.11 ± 0.41	6.01 ± 0.67	1.50 ± 0.16	0.024 ± 0.003
HET	0.13 ± 0.02	0.94 ± 0.19	2.14 ± 0.42	6.00 ± 0.67	1.34 ± 0.15	0.020 ± 0.003
Environmental variance						
HOM	0.27 ± 0.01	3.16 ± 0.12	6.87 ± 0.26	10.22 ± 0.49	2.58 ± 0.12	0.004 ± 0.002
England	0.28 ± 0.02	2.88 ± 0.16	5.85 ± 0.32	12.44 ± 0.66	2.02 ± 0.13	0.005 ± 0.002
Scotland	0.24 ± 0.02	2.73 ± 0.15	5.98 ± 0.32	7.72 ± 0.53	2.69 ± 0.14	0.004 ± 0.002
Wales	0.30 ± 0.02	3.96 ± 0.19	9.03 ± 0.43	10.82 ± 0.64	3.41 ± 0.17	0.053 ± 0.003
Heritability <sup>3</sup>						
HOM	0.24 ± 0.04	0.17 ± 0.03	0.18 ± 0.03	0.37 ± 0.04	0.36 ± 0.03	0.34 ± 0.04
England	0.24 ± 0.04	0.19 ± 0.04	0.20 ± 0.04	0.33 ± 0.03	0.39 ± 0.04	0.30 ± 0.04
Scotland	0.26 ± 0.05	0.20 ± 0.04	0.20 ± 0.04	0.44 ± 0.04	0.33 ± 0.03	0.33 ± 0.04
Wales	0.23 ± 0.04	0.16 ± 0.03	0.15 ± 0.03	0.35 ± 0.04	0.28 ± 0.03	0.27 ± 0.03

<sup>1</sup>BWT= birth weight; 5WT = five week weight; 10WT = ten week weight; <sup>1</sup>SWT = **slaughter** weight; UMD = ultrasonic muscle depth; logUFD = log ultrasonic fat depth

<sup>2</sup>HOM = homogeneous variances model; HET = heterogeneous variances model

<sup>3</sup>Heritabilities are without units

551

552 **Table 4.** Variance components estimates for the genetics by environment interaction **models for growth and slaughter traits**.

	BWT (kg <sup>2</sup> ) <sup>1</sup>	5WT (kg <sup>2</sup> )	10WT (kg <sup>2</sup> )	SWT (kg <sup>2</sup> )	UMD (mm <sup>2</sup> )	logUFD (mm <sup>2</sup> )
Genetic variance	0.18 ± 0.03	1.02 ± 0.02	2.31 ± 0.53	6.60 ± 0.74	1.41 ± 0.20	0.026 ± 0.003
F×S <sup>2</sup> variance	0.009 ± 0.004	0.09 ± 0.04	0.19 ± 0.09	0.22 ± 0.14	0.47 ± 0.11	0.013 ± 0.002
Heritability <sup>3</sup>	0.30 ± 0.05	0.15 ± 0.05	0.15 ± 0.05	0.37 ± 0.04	0.30 ± 0.04	0.28 ± 0.05
G×E <sup>3,4</sup>	0.015 ± 0.007	0.013 ± 0.007	0.012 ± 0.007	0.012 ± 0.008	0.10 ± 0.02	0.13 ± 0.03

<sup>1</sup>BWT = birth weight; 5WT = five week weight; 10WT = ten week weight; <sup>1</sup>SWT = **slaughter** weight; UMD = ultrasonic muscle depth; logUFD = log ultrasonic fat depth

<sup>2</sup>F×S = sire by farm interaction

<sup>3</sup>heritability and G×E are without units

<sup>4</sup>**G×E = genetics by environment interaction, defined as F×S variance as a proportion of total variance**

553