

Scotland's Rural College

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Published in:
Animal

DOI:
[10.1017/S1751731114002717](https://doi.org/10.1017/S1751731114002717)

Print publication: 19/11/2014

Document Version
Peer reviewed version

[Link to publication](#)

Citation for published version (APA):

Marquez, GC., Haresign, W., Davies, MH., Roehe, R., Bunger, L., Simm, G., & Lewis, RM. (2014). Heterogeneous variances and genetics by environment interactions in genetic evaluation of crossbred lambs. *Animal*, 9(3), 380 - 387. <https://doi.org/10.1017/S1751731114002717>

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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 F×S interaction (Model 3) improved model fit for all traits. However, the
46 F×S 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 G×E
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 G×E
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 (G×E) 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 G×E 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 G×E can slow progress toward that aim. Although incorporating
63 heteroscedasticity and G×E 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 ± 0.5 kg
117 greater, ultrasonic muscle depth (**UMD**) EBV were 2.3 ± 0.2 mm thicker, and
118 ultrasonic fat depth EBV were 0.49 ± 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, β_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 β_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, σ_a^2 , σ_f^2 , and σ_{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

443 **Acknowledgements**

444 We would like to acknowledge the Meat and Livestock Commission [now English
445 Lamb and Beef Executive (EBLEX), Quality Meats Scotland (QMS), and Hybu Cig
446 Cymru – Meat Promotion Wales (HCC); the UK Department of Environment, Food
447 and Rural Affairs, The British Charollais Sheep Society (Norfolk, UK), the Suffolk
448 Sheep Society (Ballymena, UK) and the British Texel Sheep Society (Kenilworth, UK)
449 for funding of this study. We would also like to thank the technical staff at
450 Aberystwyth University, ADAS Rosemaund and the Scottish Agricultural College

451 (now Scotland's Rural College) for their support of the experimental program, and E.
452 Stephens for technical editing. We also acknowledge Advanced Research
453 Computing at Virginia Tech for providing computational resources and technical
454 support that have contributed to the results reported within this paper. URL:
455 <http://www.arc.vt.edu>

456

457 **References**

458 Canavesi F, Schaeffer LR, Burnside EB, Jansen GB and Rozzi P 1995. Sire-by-herd
459 interaction effect when variances across herds are heterogeneous. I. Expected genetic
460 progress. *Journal of Animal Breeding and Genetics* 112, 95-106.

461 Dickerson GE 1962. Implications of genetic-environmental interaction in animal breeding.
462 *Animal Science* 4, 47-63.

463 Emenheiser JC, Greiner SP, Lewis RM and Notter DR 2010. Validation of live animal
464 ultrasonic measurements of body composition in market lambs. *Journal of Animal Science*
465 88, 2932-2939.

466 Garrick DJ and Van Vleck LD 1987. Aspects of selection for performance in several
467 environments with heterogeneous variances. *Journal of Animal Science* 65, 409-421.

468 Gianola D 1986. On selection criteria and estimation of parameters when the variance is
469 heterogeneous. *Theoretical and Applied Genetics* 72, 671-677.

470 Gilmour AR, Gogel BJ, Cullis BR and Thompson R 2009. *ASReml User Guide Release 3.0*
471 VSN International Ltd, Hemel Hempstead, UK.

472 Hagger C 1998. Litter, permanent environmental, ram-flock, and genetic effects on early
473 weight gain of lambs. *Journal of Animal Science* 76, 452-457.

474 Hill WG 1984. On selection among groups with heterogeneous variance. *Animal Production*
475 39, 473-477.

476 Hill WG and Zhang XS 2004. Effects on phenotypic variability of directional selection arising
477 through genetic differences in residual variability. *Genetical Research* 83, 121-132.

478 Kempster AJ, Cook GL and Grantley-Smith M 1986. National estimates of the body
479 composition of British cattle, sheep and pigs with special reference to trends in fatness. A
480 review. *Meat Science* 17, 107-138.

481 Kuehn LA, Lewis RM and Notter DR 2007. Managing the risk of comparing estimated
482 breeding values across flocks or herds through connectedness: a review and application.
483 *Genetics Selection Evolution* 39, 225-247.

484 Kuehn LA, Notter DR, Nieuwhof GJ and Lewis RM 2008. Changes in connectedness over
485 time in alternative sheep sire referencing schemes. *Journal of Animal Science* 86, 536-544.

486 Lewis RM, Crump RE, Kuehn LA, Simm G and Thompson R 2005. Assessing
487 connectedness in across-flock genetic evaluations. *Journal of Animal Science* 83(Suppl.1),
488 101.

489 Maniatis N and Pollott GE 2002. Genotype by environment interactions in lamb weight and
490 carcass composition traits. *Animal Science* 75, 3-14.

491 Márquez GC, Haresign W, Davies MH, Emmans GC, Roehe R, Bünger L, Simm G and
492 Lewis RM 2012. Index selection in terminal sires improves early lamb growth. *Journal of*
493 *Animal Science* 90, 142-151.

494 Márquez GC, Haresign W, Davies MH, Roehe R, Bünger L, Simm G and Lewis RM 2013.
495 Index selection in terminal sires improves lamb performance at finishing. *Journal of Animal*
496 *Science* 91, 38-43.

497 Mekkawy W, Roehe R, Lewis RM, Davies MH, Bünger L, Simm G and Haresign W 2009.
498 Genetic relationship between longevity and objectively or subjectively assessed performance
499 traits in sheep using linear censored models. *Journal of Animal Science* 87, 3482-3489.

500 Meyer K 1987. Estimates of variances due to sire x herd interactions and environmental
501 covariances between paternal half-sibs for first lactation dairy production. *Livestock*
502 *Production Science* 17, 95-115.

503 Misztal I 1990. Restricted maximum likelihood estimation of variance components in animal
504 model using sparse matrix inversion and a supercomputer. *Journal of Dairy Science* 73, 163-
505 172.

506 Mulder HA and Bijma P 2005. Effects of genotype x environment interaction on genetic gain
507 in breeding programs. *Journal of Animal Science* 83, 49-61.

508 Mulder HA and Bijma P 2006. Benefits of cooperation between breeding programs in the
509 presence of genotype by environment interaction. *Journal of Dairy Science* 89, 1727-1739.

510 Nakaoka H, Narita A, Ibi T, Sasae Y, Miyake T, Yamada T and Sasaki Y 2007. Effectiveness
511 of adjusting for heterogeneity of variance in genetic evaluation of Japanese Black cattle.
512 *Journal of Animal Science* 85, 2429-2436.

513 Notter DR, Tier B and Meyer K 1992. Sire x herd interactions for weaning weight in beef
514 cattle. *Journal of Animal Science* 70, 2359-2365.

515 Pollott GE and Greeff JC 2004. Genotype x environment interactions and genetic parameters
516 for fecal egg count and production traits of Merino sheep. *Journal of Animal Science* 82,
517 2840-2851.

518 Pollott GE and Stone DG 2004. Mating structure of the sheep industry. In *The Breeding
519 structure of the British sheep industry 2003* (eds RD Eglin, A Ortiz Pelaez and CJ Cook), pp.
520 18–22. Department for Environment Food and Rural Affairs, London, U.K.

521 Robert-Graniè C, Bonaôti B, Boichard D and Barbat A 1999. Accounting for variance
522 heterogeneity in French dairy cattle genetic evaluation. *Livestock Production Science* 60,
523 343-357.

524 Rowe SJ, White IMS, Avendaño S and Hill WG 2006. Genetic heterogeneity of residual
525 variance in broiler chickens. *Genetics Selection Evolution* 38, 617-635.

526 SanCristobal-Gaudy M, Bodin L, Elsen J-M and Chevalet C 2001. Genetic components of
527 litter size variability in sheep. *Genetics Selection Evolution* 33, 249-271.

528 Simm G and Dingwall WS 1989. Selection indices for lean meat production in sheep.
529 Livestock Production Science 21, 223-233.

530 Steinheim G, Ødegård J, Ådnøy T and Klemetsdal G 2008. Genotype by environment
531 interaction for lamb weaning weight in two Norwegian sheep breeds. Journal of Animal
532 Science 86, 33-39.

533 Tosh JJ and Kemp RA 1994. Estimation of variance components for lamb weights in three
534 sheep populations. Journal of Animal Science 72, 1184-1190.

535 van Heelsum AM, Lewis RM, Davies MH and Haresign W 2003. Growth and carcass
536 characteristics in wether lambs of a crossbred dam line. Animal Science 76, 45-53.

537 Van Vleck LD 1990. Breeding value prediction with maternal genetic groups. Journal of
538 Animal Science 68, 3998-4013.

539 Wiggans GR and VanRaden PM 1991. Method and effect of adjustment for heterogeneous
540 variance. Journal of Dairy Science 74, 4350-4357.

541 Winkelman A and Schaeffer LR 1988. Effect of heterogeneity of variance on dairy sire
542 evaluation. Journal of Dairy Science 71, 3033-3039.

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
Birth weight (kg)					
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
5 wk weight (kg)					
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
10 wk weight (kg)					
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
Slaughter weight (kg)					
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
UMD (mm)					
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
logUFD (mm)					
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 ²) ¹	5WT (kg ²)	10WT (kg ²)	SWT (kg ²)	UMD (mm ²)	logUFD (mm ²)
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 ²						
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

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

²Heritabilities 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 ²) ¹	5WT (kg ²)	10WT (kg ²)	SWT (kg ²)	UMD (mm ²)	logUFD (mm ²)
Genetic variance						
HOM ²	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 ³						
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

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

²HOM = homogeneous variances model; HET = heterogeneous variances model

³Heritabilities are without units

551

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

	BWT (kg ²) ¹	5WT (kg ²)	10WT (kg ²)	SWT (kg ²)	UMD (mm ²)	logUFD (mm ²)
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 ² 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 ³	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 ^{3,4}	0.015 ± 0.007	0.013 ± 0.007	0.012 ± 0.007	0.012 ± 0.008	0.10 ± 0.02	0.13 ± 0.03

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

²F×S = sire by farm interaction

³heritability and G×E are without units

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

553