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Modelling growth in Suffolk and Charollais sheep populations using random regression models and validation of constrained polynomial correlation values



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ABSTRACT

Random regression modelling has been used across multiple animal species to model longitudinal data. The random regression model for growth accounts for the genetic correlation between measures of the same trait over time and the wide environmental variability in growth, but this requires adequate weight records across the age range. However, contemporary management practices in sheep in the United Kingdom generally focus on growing lambs and neglect mature weight recordings. This study examined modelling strategies for growth data in Suffolk and Charollais sheep, provided by the Agriculture and Horticulture Development Board, with polynomial random regression modelling with many early life weight recordings but limited weight recordings in mature animals. Two methods were employed to model the data. In Method A, missing mature weight records were predicted for those animals that did not have a recorded mature weight. The animals were sorted into groups based on the identity of their sires and the year in which the animal was born. Mature weight values were predicted within each group with a multiple regression model. The dataset, including predicted values, was analysed with random regression models using polynomials and simple linear regression for animal and permanent environmental (PE) effects. In Method B, the dataset with missing mature weight records was analysed using a random linear regression animal model with random animal and PE effects. Due to problems of convergence because the parameters were close to the boundary space, fixing the correlation between the intercept and slope of the Legendre polynomial at different levels was investigated. The heritability values resulting from the model with a fixed correlation between intercept and slope parameters at 0.5 for the Suffolk dataset resulted in heritability values ranging from 0.2 to 0.5 from 1 to 619 days of age. Corresponding estimates for the Charollais dataset ranged from 0.18 to 0.49 from 1 to 640 days of age. For the Suffolk data, the genetic correlations ranged from 1.00 to 0.08 between weight at day 1 to weight at day 619, while for the Charollais, the correlations ranged from 1.00 to 0.05 from 1 to 640 days of age. Validation procedures were undertaken using a multitrait approach to examine the estimated breeding values when the correlation between the intercept and slope are fixed at different levels. The results indicated that fixing the correlation at 0.5 gave the most appropriate estimates for the Suffolk and Charollais datasets.

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Implications

This research investigates modelling strategies for sheep data with a sparsity of mature weight records relative to early life records. Modelling such data is an important step for geneticists and animal breeders as most sheep production systems do not record mature weights thereby impacting the ability to accurately

model growth over the life course and select for more appropriate growth profiles. The methods used in this research may allow genetic research on a wider range of datasets, therefore improving the efficiency of the sector and contributing to long-term profitability and sustainability.

Introduction

There are around 30 million sheep and lambs in the United Kingdom (UK) as of 2020 with a production value of £1.3 billion. Employment in the sheep sector contributes about £290 million

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to the UK economy. Sheep production contributes substantially to the UK food supply. The UK is the world's fifth largest producer and third largest exporter of sheep meat. Annually, the UK produces 300 000 tonnes and exports 80 000 tonnes valued at £373.8 million (Agriculture and Horticulture Development Board, 2021). Clearly, the sheep sector is one of the most substantial areas of agriculture in the UK. However, the industry is facing multiple challenges. The global population is increasing and is estimated at 8 billion people (World Population Clock, 2022). Additionally, meat consumption across the world has increased at an even higher rate over the past 50 years and is expected to continue to do so (Vranken et al., 2014). Improving sustainability of production is vital.

Animals that obtain their optimal slaughter weight earlier also emit less greenhouse gas thereby limiting their impact on the environment. Animal science has an important role to play in identifying and selecting animals that grow optimally. Genetic selection has contributed to sheep production by modelling growth and identifying those animals with superior genetic potential to grow optimally and pass on this potential to their offspring. Until recently, repeatability models were used to model growth relying on two prominent assumptions: that the mean and covariance structure of the growth trait remains constant with time or age, and that each measurement of the growth trait is genetically different from but correlated to all other measurements of the growth trait (Amer et al., 1997; McLaren et al., 2014). Multivariate models are then created to produce estimated breeding values (EBVs) at fixed age points which are then used to create a selection index (Jones et al., 2004; Mrode, 2005).

However, this methodology is problematic. It has three main issues: (1) impracticality; (2) neglecting wide random variability in environmental effects; and (3) overparameterisation. The first issue arises because the current methodology relies on weights taken at specific points in time or within certain windows which may or may not coincide with the normal rearing procedures of the producer (Bullock et al., 1993). Consequently, the model represents a very specific subset of the animal's entire growth cycle rather than the entire growth trajectory (Schnyder et al., 2001; Lewis and Brotherstone, 2002). On the second issue, environmental fixed effects are fit to the age or point in time of the weight measurement. This means that the only environmental effect included is the one available at the time the weight was recorded. This makes it impossible to capture the way environment may impact an animal's growth the entire time it is growing (Hermesch et al., 2003; Jones et al., 2004). Finally, the models run the risk of being overparameterized wherein there are more parameters than can be estimated from the data (Ashfield et al., 2014).

There are three distinctive advantages to the infinite dimensional method. The first is it describes the trait at all points in time during the animal's life rather than a finite number of landmarks. Second, it eliminates the errors in predicting the evolutionary response to selection made by conventional methods that neglect the impact of selection on other traits or other components of the same trait. Third, it is more efficient at estimating parameters of interest (Kirkpatrick and Heckman, 1989; Schaeffer, 2004).

The random regression model has been used to model growth in sheep and estimate genetic parameters. Lambe et al. (2006) also found random regression models applied to growth in Scottish Blackface and Texel sheep resulted in different heritabilities across the growth curve and between breeds. The resulting heritability values ranged from 0.14 to 0.74 in Texel and 0.07 to 0.34 in Scottish Blackface, which suggests that modelling growth requires a model that allows for changing variance structures. Similarly, Sallam et al. (2019) found that heritability, and therefore genetic variability, changed across the growth curve in sheep data. Their study used 16 496 records that included five weights for each individual. The Legendre Polynomial random regression model

included third order for a fixed effect of lamb age and permanent environmental effect and a fourth order for the animal genetic effect. The heritability estimates were 0.06 for birth weight, 0.42 for weight at nine months, and 0.27 for weight at one year of age. The study compared the random regression model with a multitrait model and found generally lower heritability estimates in the multitrait model. The random regression model also showed higher accuracy of the predicted breeding values which indicates the random regression model is more suited to analysing longitudinal growth data in sheep (Sallam et al., 2019). The growing body of research suggests heritability values from 0.10 to 0.40 for growth in most breeds of sheep (Fossceco and Notter, 1995; Jannoune et al., 2015; Lalit et al., 2016; Zeljic et al., 2019).

The key concerns when applying random regression models to growth traits are the number of times an animal's weight needs to be recorded, when those recordings need to be taken, and what the upper limit on age should be. Additionally, current management practices may introduce accidental bias. Records are kept on only a subset of animals which tend to be managed more closely and those animals which are kept past standard market weight for breeding tend to be the highest performing animals. These sources of bias must be accounted for to ensure the accuracy of the models. The cost of collecting weights is also practically important for the use of random regression. Now, random regression offers more freedom in the timing of recording than the repeatability model, but the number of weights is still an important consideration (Meyer, 1999). The more data that are available, the more precise the model can be.

Additionally, most random regression models are used successfully in highly managed flocks with equal or high numbers of weight records across the age distribution. Despite the fact that performance of the random regression model is not as well tested in environments with unequal spacing or sparse weight records, there are a few studies that have successfully tested random regression models in actual production environments (Sarti et al., 2015; Arthy et al., 2020). Most production systems in the UK do not regularly record weight records throughout a sheep's life and there is particular sparsity towards maturity. As indicated earlier, the use of a random regression model offers producers more flexibility on when to weigh their animals and on the availability of EBVs at various time periods to suit their production system (Coffey et al., 2006). The preliminary results from this paper have been published in a poster presented at the British Society of Animal Science conference 2022 (Mutch et al., 2022). Thus, this study aimed to investigate the use of random regression models with data collected from production environments across the UK which have comparatively few records in maturity relative to the number of individuals in the dataset. Although mature weight is generally not a focus for genetic research, it is difficult to accurately model the growth curve, and hopefully identify the genetic and environmental factors contributing to optimized early growth rates or slaughter weights, without a mature weight acting as an anchor point for the model. This research may expand the utility of the random regression model to datasets which previously would not be feasible.

Material and methods

Description of data

This study was conducted with two datasets provided by the Agriculture and Horticulture Development Board (AHDB); one with Suffolk sheep and their F1 crosses, and the other with Charollais sheep and their F1 crosses. The Suffolk dataset had records from 14 870 Suffolk sheep. It included multiple weight records

for each animal, resulting in a total of 42 244 records. Four possible weight records were identified for the analysis including birth weight, weaning weight (about 9 weeks), scan weight (about 21 weeks), and mature weight which was defined as any weight after 180 days. There were 14 870 animals with a birth weight, 14 823 with a weaning weight, 11 548 with a scan weight, and 94 with a mature weight. From birth weight to mature weight, the number of animals with records began at 100%, dropped to 99.6% for weaning weight, 77.7% for scan weight, and 0.63% for mature weight. The Charollais dataset contained 148 334 individuals with 353 958 records with weights available at birth, weaning, scanning and maturity. There were 148 334 animals with a birth weight, 148 321 with a weaning weight, 146 331 with a scan weight, and 921 with a mature weight, and these details are summarised in Table 1. Initial attempts to use the whole data for genetic parameter estimation resulted in problems with convergence of model. In an attempt to achieve a balanced distribution of weight at the various ages and hence enhance convergence, only individuals with all four weight recordings were kept for use in the model for genetic parameter estimation. This resulted in a total of 3 685 records from 921 animals being used.

The data were collected from farms across the UK over a duration of 22 years from 1997 to 2019 from multiple production environments including lowland, upland, and hill flocks. Summaries of the fixed effects of interest for both datasets are included in Table 2. The Suffolk dataset included both male and female animals born in 33 seasons, a contemporary grouping for animals born within the same season of the same year and raised in 30 flocks. Animals were classified into four management groups. The Charollais dataset included only females from 16 different flocks which were born in 22 seasons and were classified into seven different management groups.

There was minimal intentional selection used during the data collection phase as the data were collected from production environments operating as they would normally operate. Both rams and ewes are included in the datasets. However, all animals with a mature weight record are ewes due to the normal production procedure wherein most male sheep are usually slaughtered upon reaching the appropriate slaughter weight for the breed while ewes are often kept into maturity for breeding purposes. Thus, these data are representative of general Suffolk and Charollais populations in the United Kingdom.

Statistical analysis of data

Data were subjected to quality measures by first excluding records with missing birth weight using the “filter” function in R. Additionally, the mean and variance structure of each weight variable were analysed and then records which were more than three standard deviations away from the mean were excluded from the dataset using the “filter” function in R. For the Suffolk dataset, animals were excluded from the analysis dataset if they had fewer than two weight records. For the Charollais dataset, there were sufficient animals with all four weight records; thus, the Charollais analysis dataset only included animals with all four weight records. Each of the variables was investigated for content and then used in a linear model for each weight record using the “glm” function in R (Rstudio Team, 2012). The linear models were used to identify those variables which were significant as fixed effects for each weight record. A version of the data was then organised for random regression analysis. In the case of Charollais sheep, all animals had a weight record at the four different ages but for the Suffolk, the number of weights per animal ranged from one to four recorded at various ages. This was done using the “filter”, “select” and “nrow” functions in R (Rstudio Team, 2012).

Mature weight prediction

This study used two methodologies to model the data. The first method (Method A) can be considered a prediction method where the missing mature weight records were predicted and then analysed. The second method (Method B) modelled the data with only the recorded mature weight records; no records were predicted. Method A used the same Suffolk dataset described previously to predict missing mature weights. The missing mature weights were predicted for the dataset based on those animals that did have a recorded mature weight. To make these predictions, the data were filtered in R using the “filter” function to include only animals with a mature weight.

The sires and birth years of these animals were identified and a prediction model for each of the sire groups and each of the year groups was made. In the first instance, predictions were made within sire groups because it was thought that the mature weights were likely influenced by the impact of sire’s genetic merit on the weight, growth rate, or carcass characteristics of offspring (Held

Table 1
Summary of records for each weight recording point in the Suffolk and Charollais datasets.

Dataset	Birth Weight Count	Weaning Weight (avg 9 weeks) Count	Scan Weight (avg 21 weeks) Count	Mature Weight (above 180 days of age) Count
Suffolk	14 870 (100%)	14 823 (99.7%)	11 548 (77.7%)	94 (0.63%)
Charollais	148 334 (100%)	148 321 (99%)	146 331 (98.6%)	921 (0.006%)

Abbreviations: avg = average.

Table 2
Summary of variables for Suffolk and Charollais datasets.

Dataset	Sex No	Season No	Flock No	Management Groups No	Mean BW (kg)	Mean WW (kg)	Mean WW Age (days)	Mean SW (kg)	Mean SW Age (days)	Mean MW (kg)	Mean MW Age (days)
Suffolk	F: 6 392 M: 8 478	33	30	4	M:5.3 ± 1.2 F:5.0 ± 1.2	M:30.5 ± 8.6 F:27.8 ± 7.8	M:65.4 ± 11.7 F:65.2 ± 11.7	M:57.5 ± 13.4 F:48.2 ± 11.0	M:145.8 ± 16.4 F:144.1 ± 16.6	M:67.9 ± 7.2 F:75.9 ± 12.0	M:218.5 ± 8.7 F:479.7 ± 124.5
Charollais	F: 3 685 M: 0	22	16	7	5.2 ± 0.9	26.3 ± 5.4	62.9 ± 10.1	46.35 ± 7.6	137.4 ± 18.5	75.94 ± 12.4	522.4 ± 91.1

Abbreviations: F = female, M = male, BW = birth weight, WW = weaning weight, SW = scan weight, MW = mature weight.

et al., 1997; Elizalde et al., 2019). However, due to the small number of animals with a mature weight record, it was impossible to predict the mature weight within sire groups for every animal. Therefore, prediction models were made within year groups as animals born in the same year are likely to be of similar genetic merit. The prediction model was based on a multiple regression model with the following equation:

Mat weight = birthweight + weaning weight + scan weight.

The multiple regression model assumes there must be a linear relationship between the outcome variable and the independent variables. In this case, this would mean there is a linear relationship between the mature weight and the three other weights. It also assumes that residuals are normally distributed. The model also assumes that the independent variable, the three weights, are not highly correlated with each other to create any major collinearity problems in predicting mature weight. This assumption is generally tested by using variance inflation factor values. The average inflation factor value for birth weight was 1.91, 2.65 for weaning weight, and 2.24 for scan weight. The model variance will inflate by these values compared to a model without collinearity.

The prediction modelling was done using the “lm” function in base R (Rstudio Team, 2012). These models were then used to predict the mature weights for the entire dataset using the “predict” function in RStudio within sire groups and year groups for animals without recorded mature weights (Rstudio Team, 2012). This methodology was performed only with the Suffolk dataset due to the genetic model from Method A failing to converge and the fact that the Charollais dataset did not include any individuals with missing mature weight records.

Genetic modelling

The availability of mature weights in 0.63% of the data implies that the implementation of a multitrait model is not feasible for this data set. Therefore, a random regression model offers the only opportunity to model growth along the whole age trajectory in the dataset for these two breeds. Initial investigations of random regression models for these both data sets included a genetic maternal component in the models. However, these did not converge, and this may be attributed to the data structure or data size that makes it difficult to accurately partition this component. However, the inclusion of maternal effect is being investigated in further studies due to its potential importance for early growth. Genetic modelling began after a three-generation pedigree was formed in R using a “match” function and a full pedigree provided by AHDB (Rstudio Team, 2012). In Method A, the Suffolk dataset with predicted mature weights were analysed in a random regression model (Model 1) with Legendre polynomials of order 1 for animal and PE effects. The fixed effects for this model were sex, season of birth, flock, and management group.

The structure of the model was as follows:

$$Y_{ijkn:t} = F_i + g(t)_j + r(a, x, m1)_k + r(pe, x, m2)_k + e_{ijkn:t} \quad (1)$$

where y is the n th weight observation of the k th animal at time t belonging to the i th fixed factors and the j th group; F_i represents fixed effects consisting of sex of animal (two levels), season of birth (33 levels), flocks (30 levels), and management groups (four levels). The next variable, $g(t)_j$, is a function that accounts for the phenotypic trajectory of the average observation across all animals belonging to the j th group. The next term $r(a, x, m1)_k$ is the notation adopted for the random regression function, denoting in this case the additive genetic effect for the k th animal, x is the vector of

age in days, and $m1$ is the order of the regression function which is 1 in this model; $r(pe, x, m2)_k$ is PE effect for the k th animal and lastly, e is the random residual effect.

Model 1 failed to converge. It was determined this was due to there being too few mature weight records to accurately predict mature weight records for the entire dataset. At this point, Model 1 was no longer considered to be a candidate model for the data because it was determined that it was unrealistic to predict mature weights for the dataset from such a small number of recorded mature weights. Method B used an animal model without any prediction of missing records. For Suffolk, a random regression model (Model 2) with Legendre polynomial of order 1 for the random animal effect, random PE effects and fixed effects of sex season of birth, a fixed regression on age, flock, management group, and PE effect was fit.

This model had the following structure:

$$Y_{ijkn:t} = F_i + g(t)_j + r(a, x, m1)_k + r(pe, x, m2)_k + e_{ijkn:t} \quad (2)$$

where terms in Eq. (2) were defined as in Eq. (1).

Although other studies on random regression modelling for growth in sheep report a Legendre polynomial of order 3–5 as the best fitting, in this study, a Legendre polynomial of order 1 was considered to be a sufficient model because the models failed to converge when the order of the Legendre polynomial was increased above 1 or set to 0 (Arthy et al., 2020; Jannoune et al., 2015; Lewis and Brotherstone, 2002).

However, for the model fitted, there were inflated genetic parameters which were not biologically probable, because the correlation between the intercept and slope parameters of the Legendre polynomial was close to unity. When these parameters are approaching unity, this indicates that the model is unable to estimate a value for each of the weight recording points. In the case of the Suffolk model, this is likely due to the lack of records in maturity which could cause the model to be unable to partition the variance between each weight recording point. The biological expectation is that the weight records should be correlated but not identical; thus, the correlation between the parameters of the Legendre polynomial was fixed at three levels to indicate minimal correlation, medium correlation, and high correlation. This allowed for the comparison of the resulting genetic parameters from these three levels of correlation. The resulting genetic parameters should be more accurate when a model with a more biologically plausible correlation value is used compared to the correlation close to unity because the latter deviates both from the biological expectation and from the assumptions of the model. Therefore, the correlation between the intercept and slope was fixed at three different levels of 0.2, 0.5 and 0.7. These three levels of correlations investigate the impact of fixing this correlation at a low, medium and high values. Genetic parameters were estimated from the estimates of the random regression coefficients. All genetic analyses were conducted in ASREML (Gilmour et al., 2016).

For the Charollais dataset, only Method B was used initially in which a model (Model 3) was fit with Legendre polynomial of order 1 for the random animal effect, random permanent environmental effect and the following fixed effects: fixed regression on age, season of birth, and flock was fit.

This model had the following mathematical structure:

$$Y_{ijkn:t} = F_i + g(t)_j + r(a, x, m1)_k + r(pe, x, m2)_k + e_{ijkn:t} \quad (3)$$

where terms were as defined in Eq. (1) but with F_i consisting of the fixed effects season of birth (22 levels), fixed linear regression on age and flocks (16 levels).

Again, a Legendre polynomial of order 1 was deemed to be the most preferable because the models failed to converge above an order of 1. Model 3 resulted in biologically improbable heritability

values initially, again due to the correlation between the intercept and slope parameters of the Legendre polynomial approaching unity. Again, the three fixed correlations between the intercept and slope coefficients were investigated and genetic parameters were estimated from the results. All genetic analyses were conducted in ASREML (Gilmour et al., 2016).

Correlation validation

Attempts were made to validate the genetic parameters obtained from the random regression models with the correlation between the intercept and slope parameters fixed to 0.2, 0.5 and 0.7. The predictive ability of the genetic parameters from the three fixed levels was examined by using a multitrait prediction of EBVs for birth weight, weaning weight, scan weight and mature weight. This was done by implementing the multi trait model using the genetic and residual variances and covariances obtained from the models when the correlation between intercept and slope was fixed at three different levels, fitting the fixed effects as listed in Model 2 (Suffolk) and Model 3 (Charollais), with animal and PE effects fitted as random effects. Additionally, a univariate fixed effect model was implemented for birth weight, weaning weight, scan weight and mature weight individually. These models included only fixed effects and no random animal effect. This analysis was aimed at obtaining records for each of these traits corrected for all fixed effects apart from the random animal effect such that the only components in these corrected records were the genetic merit of the animals and residual error.

The predictive ability and accuracy of the breeding values from the multitrait analysis, using the genetic parameters when the correlations were fixed at three levels, were estimated by correlating the EBVs with corrected records, regression of the corrected records on EBVs and estimating bias for each weight trait for the 94 animals that had observations for all four weight traits. These calculations were all performed in Excel. It should be noted here that bias is represented as mean and standard deviations of the difference between corrected records and EBV.

The validation method applied in this study is similar to the validation approach employed in genomic studies where genomic breeding values are compared with corrected yield in terms of correlations, regression and computations of bias and mean square error (Pryce et al., 2012; Kalaldehy et al., 2021). Also, the method used to compute bias has been used in other studies (Schenkel et al., 2002; Sood et al., 2020). The validation method used in this study examined the ability of the genetic parameters and breeding values generated from the random regression model when the correlation between the intercept and the slope is fixed to predict the performance (corrected for all fixed effects) of animals with actual observations in the validation set. The approach may suffer for the limitations that the validation animals were part of the dataset

used in estimating the random regression parameters. However, such a limitation will equally affect the three scenarios considered and may therefore have no major influence in terms of choosing the most appropriate fixed correlation. In addition, given the data structure, these animals could not be excluded from the model as these were the animals with data along the complete trajectory of the age in the study.

Attempts were made to examine the impact of fixing the correlation between the intercept and the slope using dairy cattle data in which a random regression model has been successfully implemented (Mrode et al., 2021). The model in Mrode et al (2021) was modified such that Legendre polynomial of order 1 was fitted for both animal and PE effects to mimic the model for this sheep study. The correlation between the intercept and slope was 0.1 after convergence of the model. The analysis was then repeated with the correlations fixed at 0.2, 0.5 and 0.7 and estimates of genetic parameters compared with the original method with a correlation of 0.1. Estimates of heritabilities were then generated for 10 stages of lactation ranging from day 4 to day 364. The results from these analyses are in the discussion section for this paper as the main focus of this study is the sheep data.

Results

Genetic parameters for the Suffolk and Charollais breeds

Method A for the Suffolk dataset failed to converge, meaning any resulting genetic parameters are unlikely to be accurate. Therefore, results have not been presented. The results from Method B, Model 2, for Suffolk are shown in Table 3. These results are presented for the model using the fixed correlation of 0.5 between intercept and slope parameters. Prior to fixing the correlation, Model 2 resulted an additive genetic variance of 0.02 for BW, 13.58 for WW, 68.68 for SW, and 990.92 for MW. This corresponded to heritabilities of 0.02, 0.49, 0.69, and 0.76, respectively. The genetic correlations were BW-WW = 0.46, BW-SW = 0.02, BW-MW = 0.01, WW-SW = 1.0, WW-MW = 1.0, MW-SW = 1.0. Table 3 shows that the heritability values resulting from the fixed correlation of 0.5 were between 0.20 and 0.50 for ages ranging from 1 to 619 days of age. The table also includes genetic (0.1–1.00) and phenotypic (0.03–0.60) correlations which follow the anticipated trend of decreasing as the difference between ages increases. The PE effect accounted for 15.41 kg² out of a total variance of 2 984.41 in the 0.2 model, 0.52 kg² out of 54.04 in the 0.5 model, and 1.26 kg² out of 61.45 in the 0.7 model.

The results from Model 3, the Charollais model, are shown in Table 4. These are also reasonably consistent with the published estimates between 0.10 and 0.40. The heritability values range from 0.18 to 0.49. The table also includes genetic (0.05–1.00) and phenotypic (0.01–0.44) correlations which follow the anticipated

Table 3 Genetic (below diagonal) and phenotypic (above diagonal) correlations among several ages in days (along the top and left side) with heritabilities on the diagonal from the random regression model for Method B¹ for Suffolk.

Day	1	30	60	120	180	200	244	460	530	619
1	0.23	0.22	0.21	0.19	0.17	0.17	0.15	0.08	0.05	0.03
30	1.00	0.22	0.21	0.20	0.18	0.17	0.16	0.10	0.08	0.05
60	0.98	1.00	0.21	0.20	0.18	0.18	0.17	0.12	0.10	0.08
120	0.92	0.95	0.98	0.20	0.19	0.19	0.19	0.16	0.15	0.14
180	0.82	0.87	0.91	0.98	0.20	0.20	0.20	0.21	0.21	0.20
200	0.78	0.83	0.88	0.96	1.00	0.20	0.21	0.22	0.22	0.22
244	0.68	0.74	0.80	0.91	0.98	0.99	0.22	0.25	0.26	0.26
460	0.26	0.34	0.43	0.61	0.77	0.81	0.88	0.37	0.60	0.42
530	0.17	0.26	0.35	0.54	0.70	0.75	0.84	1.00	0.43	0.46
619	0.08	0.17	0.26	0.46	0.64	0.69	0.78	0.98	1.00	0.50

¹ Method B refers to the Methodology in which only recorded mature weights were used in Model 2 and then, parameters were constrained to a correlation of 0.5.

Table 4

Genetic (below diagonal) and phenotypic (above diagonal) correlations among several ages in days (along the top and left side) with heritabilities on the diagonal from the random regression model for Method B¹ for Charollais.

Day	1	31	60	120	182	200	255	460	530	640
1	0.22	0.21	0.20	0.18	0.16	0.16	0.14	0.07	0.05	0.01
31	1.00	0.20	0.20	0.18	0.17	0.16	0.15	0.09	0.07	0.04
60	0.98	1.00	0.19	0.18	0.17	0.17	0.16	0.11	0.09	0.07
120	0.92	0.95	0.98	0.18	0.18	0.18	0.17	0.15	0.14	0.13
182	0.81	0.86	0.91	0.98	0.19	0.19	0.19	0.19	0.19	0.19
200	0.78	0.83	0.88	0.96	1.00	0.19	0.20	0.21	0.21	0.20
255	0.65	0.72	0.78	0.89	0.97	0.98	0.21	0.24	0.25	0.25
460	0.25	0.34	0.42	0.60	0.76	0.80	0.90	0.35	0.37	0.40
530	0.16	0.24	0.34	0.53	0.70	0.74	0.85	1.00	0.40	0.44
640	0.05	0.14	0.23	0.43	0.62	0.67	0.79	0.98	0.99	0.49

¹ Method B refers to the Methodology in which only recorded mature weights were used in Model 3 and then, parameters were constrained to a correlation of 0.5.

trend of decreasing as the difference between ages increases. Thus, the results for the Suffolk and Charollais models are similar and reasonably similar to published estimates for heritability of weight.

Validation results for the Suffolk breed

The results for the Suffolk validation procedure are shown in Table 5. For the Suffolk dataset, the correlations from the fixed correlation of 0.2 and 0.5 indicate similar correlations between corrected record and EBV for the four traits while the correlations were generally higher at 0.70. The higher correlations between EBVs from the parameters obtained from a correlation of 0.7 with corrected record may be due to the high heritability estimates (0.26–0.63) obtained at this fixed correlation compared to the heritability estimates of (0.23–0.50) at the fixed correlation of 0.5. The regression coefficients for 0.7 are closest to 1, suggesting a regression of unity wherein the EBV and corrected records values are the most similar, for birth weight, scan weight, and mature weight. The regression coefficients are generally similar for 0.2 and 0.5 across all four weights points. The bias between 0.2 and 0.5 is generally similar for each weight trait except for birth weight where the bias for 0.20 is much further away from 0 when it is compared to the bias for 0.5. A value of 0.7 produces biases that are closer to 0, except the bias for mature weight comparing to a value of 0.5. The validation results seem to indicate that 0.7 is the correlation of choice for the Suffolk dataset. However, the estimates of genetic correlation among weight traits were negative in some cases. Thus, in addition to the validation results, comparison of genetic parameters to published estimates was employed as an additional measure to select the most appropriate estimates. This leads to the selection of a fixed correlation of 0.5 as the most correlation given the validation results and the genetic parameters resulting from this fixed correlation.

Table 5

Validation results for fixed correlations between intercept and slope at three different levels for the Suffolk breed.

Item	BW			WW			SW			MW		
	0.20	0.50	0.70	0.20	0.50	0.70	0.20	0.50	0.70	0.20	0.50	0.70
Cor ¹	0.28	0.27	0.36	0.74	0.71	0.81	0.47	0.45	0.55	0.70	0.72	0.89
Reg ²	0.04	0.05	0.50	0.76	0.68	1.31	0.33	0.32	0.50	0.74	0.73	0.88
Bias ³	-2.46	-1.99	-0.80	-2.22	-2.45	-1.14	-3.69	-3.70	-3.03	-4.16	-4.29	-4.47
SD of bias	2.46	2.02	1.61	3.45	3.59	3.50	4.95	5.02	4.69	6.60	6.32	5.20

Abbreviations: BW = birth weight, WW = weaning weight, SW = scan weight, MW = mature weight, CY = corrected record, EBV = estimated breeding value.

¹ Cor is the correlation between CY and EBV.

² Reg is the regression coefficient.

³ Bias is calculated as the mean difference between the CY and EBV.

Validation results for the Charollais breed

The results for the validation for the Charollais dataset are given in Table 6. The bias was generally better, that is, closest to 0, for the fixed correlation of 0.5 across all four traits. While the correlations were higher for the fixed correlation at 0.2 for scan weight, the correlations tended to be similar across the fixed correlations for the other three weights traits. No clear pattern can be observed for the regression coefficients as they showed under or over predictions for the various traits at each of the three fixed correlation levels. However, given the lowest bias for the fixed correlations at 0.5, and the similar or slightly higher correlations, compared to the fixed correlation of 0.2 or 0.7, the results from the fixed correlations at 0.5 were chosen as most appropriate for the Charollais dataset.

Discussion

The random regression model has been useful in modelling growth in several animal populations. However, research continues to investigate ways to overcome the constraints of the model when it is applied to field data from more realistic production environments. The results from this study contribute to a growing body of research that establishes the need for many records across an animal's entire growth cycle to accurately model growth using random regression modelling. In this study, with limited mature weights in less than 0.63% of the Suffolk data and 0.006% of the Charollais data initially, the implementation of a multitrait model is not feasible for this data set. Therefore, a random regression model offers the only opportunity to model growth along the whole age trajectory in the dataset for these two breeds. However, this study also used a multi trait validation on constrained estimates of genetic parameters from random regression models as a potential strategy to model growth in animals with few or

Table 6
Validation results for fixed correlations between intercept and slope at three different levels for the Charollais breed.

Item	BW			WW			SW			MW		
	0.20	0.50	0.70	0.20	0.50	0.70	0.20	0.50	0.70	0.20	0.50	0.70
Cor ¹	0.05	0.36	0.32	0.70	0.68	0.68	0.87	0.78	0.74	0.88	0.87	0.87
Reg ²	0.01	0.18	0.18	0.53	1.36	1.33	0.63	2.14	1.74	1.32	1.86	1.25
Bias ³	-6.46	-0.19	-0.35	-0.46	-0.08	-0.41	-3.27	-0.35	-0.90	-1.46	-0.04	-1.66
SD of bias	61.52	1.37	1.27	3.35	2.71	2.75	3.35	4.58	4.68	5.23	6.06	5.24

Abbreviations: BW = birth weight, WW = weaning weight, SW = scan weight, MW = mature weight, CY = corrected record, EBV = estimated breeding value.

¹ Cor is the correlation between CY and EBV.

² Reg is the regression coefficient.

³ Bias is calculated as the mean difference between the CY and EBV.

unequally distributed weight recordings throughout the growth cycle. These results will hopefully allow more data to be used in random regression modelling which will expand the potential benefits of genetic selection and growth modelling to a larger portion of the UK sheep population.

Genetic parameters for the Suffolk breed

Method A is not useful because the model failed to converge in the first place suggesting that although the predicted parameters are biologically plausible, the model was not able to accurately predict a growth curve for the dataset. The results from constraining the estimates of the genetic parameters in Method B for the Suffolk are similar to current literature estimates. However, prior to fixing the correlation, the results from Method B have a highly inflated heritability ranging up to 0.76 at the top of the age range at 619 days. This heritability most likely reflects the very small dataset available to predict mature weight with only 0.63% of the animals having a mature weight record. The prevalence of edge effects in which the random regression model struggles to accurately fit a growth curve at the extreme ends of the age distribution or where there are limited records has been documented in other studies (Lambe et al., 2006). However, from a biological standpoint, one would not expect the genetic heritability of the growth trait to increase so sharply from 0.02 to 0.76 as it does in Method B prior to fixing the correlation.

One of the potential reasons the initial genetic parameters are inflated in Method B may be due to the inability of the model to partition the genetic variation adequately along the trajectory. The inability of the model to partition the genetic variance could be due to data size and structure in this study, given that random regression models have been successfully fitted in some sheep studies. The biological expectation is that the measurements are correlated to but not identical to each other. However, fixing the correlation may introduce some bias into the model's predictions. Thus, the validation was an attempt to verify if the model predicted accurate genetic values for each animal.

When comparing the accuracy of the constrained parameter levels for Suffolk, the better predictive ability produced from a value of 0.7 as indicated by some of the regressions because the regression coefficients for 0.7 are closer to 1 for some of the weights. The corrected record from the fixed effect models represents the animal's genetic value for the growth trait and residual error. They therefore provide an independent variable to assess the accuracy of predictions when the correlation is fixed at different levels. If the constrained parameter models are accurately predicting the genetic merit of the animals for the growth trait, then these EBVs should have a high correlation as the actual genetic merit obtained from the fixed effect models and should have high predictive ability. Thus, when the corrected records are regressed on the EBVs for each fixed correlation model, the most accurate model will have a regression closest to unity represented by a

value of 1. However, it must be noted that the Suffolk dataset had very few (94) animals. The validation results do not clearly distinguish which correlation is the most accurate as the results were similar for each constrained model. Thus, the validation results can be used to support a constrained estimate of genetic parameters only as long as the genetic parameters from the constrained model are biologically reasonable.

The parameters obtained from a correlation of 0.5 were considered more biologically appropriate compared to the results from the fixed correlation of 0.7 for the Suffolk breed. This was due to two main considerations. First, there were a small number of animals available for the validation, at only 94 animals with all four weight records, which may have caused similarity between the correlations and regression at 0.5 and 0.7. Second, the range of heritability values from a correlation of 0.5 were more consistent with the published estimates, which range from 0.10 to 0.40. Lewis et al. (2002) reported a heritability value of 0.37 for mature size in sheep, 0.38 for growth rate, and 0.31 for weight at 150 days of age. Other studies report values between 0.10 and 0.40 (Fossceco and Notter, 1995; Jannoune et al., 2015; Lalit et al., 2016; Zeljic et al., 2019).

Genetic parameters for the Charollais breed

The heritability values displayed in Table 4 are in keeping with the findings of other studies. Additionally, the Charollais heritability values are very slightly lower than those for Suffolk, remaining slightly more consistent with current literature estimates. However, this difference is minimal and likely due to a larger number of records in maturity present in the Charollais dataset rather than any difference in model accuracy. For the Charollais dataset, the high correlations cannot be due to a sparsity of mature weight records because all the animals included in the dataset have mature weight records. However, the animals that possessed mature weight records were all female animals from similar production environments. Additionally, it is possible that because all weight records were taken at different ages for each animal, the model was unable to converge because it had to predict weights for a wide range of individual ages. Further studies could investigate condensing the age points into weeks or months rather than days to aid convergence.

The results for the validation for the Charollais dataset more strongly support the selection of the 0.5 fixed correlation. The bias was, generally, closest to 0 for the fixed correlation of 0.5 across all four weight traits. Although the regression coefficients did not indicate a regression of unity consistently for 0.5 across all four weight traits, there is no clear pattern for either of the other fixed correlations. Given the lowest bias at a fixed correlation of 0.5 and the generally higher correlations, 0.5 was chosen as the best fixed correlation. Additionally, the heritability values for 0.5 are more consistent with published estimates, making 0.5 the more appropriate choice for Charollais sheep. As previously discussed, the cur-

rent literature estimates for growth in sheep range from 0.1 to 0.4 (Fossco and Notter, 1995; Jannoune et al., 2015; Lalit et al., 2016; Zeljic et al., 2019).

The validation procedure

The validation procedure was used to determine if the constrained estimates of genetic parameters predicted accurate genetic trends for each animal. The validation helps to determine estimates that are usable and that the estimates from the chosen levels, in this case the genetic parameters from the constrained correlation level of 0.5, corresponds to the animal's expected genetic merit for growth represented by the corrected yields. In this procedure, the corrected yields should be highly correlated to the EBVs from the most accurate model. This is because, ideally the model is producing EBVs that are identical to the corrected records. Additionally, as stated, the regression coefficient for the corrected record regressed on the EBV should indicate unity for the most accurate correlation level. The bias estimates should be close to 0 as they are calculated as the mean and standard deviation of the difference. The difference for the correct correlation level should be minimal.

This approach is rather pragmatic, but it yields estimates that are practically useful given the limitations of these datasets. The fixed levels and their validation will be further studied in a beef data set that contains complete records. The limitations of the sheep dataset will be mimicked in the analysis of beef data by omitting records in the beef dataset. Additionally, as more data become available for these particular sheep breeds, the parameters can be further validated even though the estimates are practically useful for now.

The impact of fixing the correlation between the intercept and slope in the dairy models showed that the mean difference between heritabilities at the 10 stages of lactation as a deviation from the original model were -0.009 , -0.04 and -0.08 for correlations fixed at 0.2, 0.5 and 0.7, respectively. However, mean difference was very close to that for the fixed correlation of 0.5, if estimates from the original model were deviated from estimates averaged across the three fixed correlations. Differences in estimates of genetic correlation followed the same pattern. The results showed that as the difference between the actual and the fixed correlations increases, there was a corresponding increase in estimates of genetic parameters. However, the differences were, on average, not very large. In addition, the fixed correlation of 0.5 seems to give estimates that are similar to estimates averaged across the fixed regression. In the case of the sheep data, the high correlation between the intercept and the slope resulted in estimates that were not biologically feasible. It seems that fixing the correlation at 0.5 provided average genetic parameters that reasonably span the age trajectory for the data set.

Conclusions

The availability of mature weights in only 0.63% of the Suffolk dataset and 0.006% of the Charollais dataset implies that the implementation of a multitrait model is not feasible using these data sets. Therefore, a random regression model offers the only opportunity to model the growth data for these two breeds. The approach of constraining the genetic parameters from the parameter space and validating these genetic parameters offers a pragmatic method to obtain genetic parameters for BW across the growth trajectory that are consistent with literature estimates. However, as more data become available, the method may need to be further investigated. Further studies using beef data are currently underway to investigate the impact of limited weight

records at various ages of the growth trajectory on genetic parameters when fitting a random regression using Legendre polynomials.

Ethics approval

Not applicable.

Data and model availability statement

The data/models were not deposited in an official repository. The data/models that support the study findings are available from the authors upon request.

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Declaration of interest

None.

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