Faculty Papers and Publications in Animal Science   Animal Science Department

2002

A genetic evaluation of growth in sheep using random regression techniques

R. M. Lewis
Scottish Agricultural College, West Mains Road, Edinburgh, ron.lewis@unl.edu

S. Brotherstone
University of Edinburgh, West Mains Road, Edinburgh

A genetic evaluation of growth in sheep using random regression techniques

R. M. Lewis[1]† and S. Brotherstone[2]

[1]*Animal Biology Division, Scottish Agricultural College, West Mains Road, Edinburgh EH9 3JG, UK*
[2]*Institute of Cell, Animal and Population Biology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, UK*

† Present addess: Department of Animal and Poultry Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24060-0306, USA. E-mail: rmlewis@vt.edu

Abstract

Repeated measures of live weight in growing animals are used to describe the path by which they travel from birth to maturity. A family of growth functions-the Gompertz is one in particular-has been used successfully to describe this journey with relatively few parameters (most importantly mature size and a rate parameter). However, using these functions to differentiate the genetic merit of individual animals to grow is problematic since the estimates of these parameters are highly correlated and are obtained with varying precision among animals. An alternative is random regression (RR) methodology. It allows environmental effects specific to the time of recording to be accounted for and can accommodate genetic differences in the shape of each animal's growth curve. At present, though, only linear models (polynomials) can pragmatically be fitted with RR. This may be limiting since a priori beliefs about the appropriate form of a growth function, such as the non-linear Gompertz equation, cannot be accommodated. This paper describes the application of RR techniques to describe growth on a population of Suffolk sheep and compares the genetic evaluation predicted from a RR model with that obtained from a more traditional method based on a Gompertz form.

The RR model chosen as providing the best fit (P < 0·01) included additive genetic and permanent environmental (between repeat records of an individual) effects fitted to a fifth order polynomial, and dam effects fitted to a third order polynomial. Measurement error was modelled as six classes. The heritability varied at different points along the growth trajectory (from 0·09 at 15 days to 0·33 at 150 days), suggesting that live weight early in a lamb's life is a different trait to live weight later in life. There was genetic variation in the growth curves of individual animals, which was accounted for by fitting a RR model. Breeding values obtained by RR and a Gompertz approach were moderately to highly correlated (0·81 at 56 days, 0·91 at 150 days). If breeding value for live weight at 150 days of age were the selection criterion, similar individuals would be chosen with both methodologies. The 'better' properties and greater flexibility of the RR approach are discussed.

Keywords: *genetic factors, growth, random regression, sheep.*

Introduction

The idea that an animal follows a prescribed trajectory as it grows towards maturity is a useful one that has been encapsulated in a family of growth equations (Winsor, 1932; Taylor, 1980; Parks, 1982). The desired properties of such functions are that weight tends to a final or asymptotic value with time, that growth rate has a maximum at some intermediate weight, and that the relative growth rate decreases monotonically, preferably in some simple way, as weight increases towards maturity. The Gompertz form is an example of a function with such properties which describes growth as a comparatively simple, single equation (Emmans, 1997). It has three parameters of which the important ones are mature size and a rate parameter. Importantly, the values of such parameters have clear biological interpretation.

Despite their widespread application, there are considerable problems in the estimation of the values of the parameters when fitting growth equations to data from individual animals. In part this is because the estimated values of the parameters of such functions are highly correlated (Cullis and McGilchrist, 1990; Lewis *et al.,* 2002) although this is not necessarily so among the true parameter values. The precision of the estimates of parameter values also varies where the frequency of live weight recording differs between animals, as is commonly the case. Even though growth may be sufficiently summarized by the few parameters fitted in a growth equation, the use of these parameters to delineate, for instance, genetic merit between animals may for these reasons be problematic (Lewis *et al.,* 2002).

The use of random regression (RR) methodology in an animal breeding context is a recent innovation pioneered by researchers working on improving the prediction of genetic merit of dairy cattle (Schaeffer and Dekkers, 1994; Jamrozik and Schaeffer, 1997). The technique is applicable when repeated measures of a trait are available for an animal. Examples are milk yield records taken at various points throughout a cow's lactation, yearly weights of beef cattle or growth data in pigs. No prior assumptions about time trends are required. Environmental effects specific to the time of recording can be accounted for and the shape of each animal's lactation or growth curve can be accommodated in the model.

RR models use a fixed regression to describe the average shape of a lactation or growth curve, and a random regression for each animal to account for deviations from the fixed regression. This allows the repeated records collected on an animal to be directly incorporated into genetic evaluations and, since an animal model is fitted, results in the predicted lactation or growth curve being heritable. Since orthogonal forms of linear models (Legendre polynomials) are typically fitted with RR, correlations between coefficients are generally lower than with ordinary polynomials or parametric curves.

Most countries are now in the process of introducing RR methods for evaluating dairy cattle. RR models have also been used to describe food intake and weight gain in pigs (Andersen and Pedersen, 1996) and growth and mature weight of beef cows (Meyer, 1999 and 2000), but the benefits of the methodology in the analysis of weight data in sheep are as yet unknown.

Table 1 *Data characteristics*

Category	Measure
No. of records	40371
No. of animals	3901
No. of animals with records	2264
No. of dams with progeny	716
No. of sires with progeny	138
Minimum no. of records per animal	7
Maximum no. of records per animal	24
Mean live weight overall (kg)	34·8 (18·1)†
Mean live weight at weaning (56 days; kg)	23·2 (4·30)†
Mean live weight at end of test (150 days; kg)	63·3 (8·48)†

† Standard deviation shown in parentheses.

This paper describes the application of RR techniques to live weights recorded on a population of Suffolk sheep. It assesses how useful they are in evaluating growth curves and compares genetic evaluation predicted from a RR model with that obtained from a more traditional method based on the Gompertz form of the growth equation.

Material and methods
Animal management and data collection
The data comprised live weight records on 2264 Suffolk lambs collected between 1985 and 1994 from a selection experiment at the Scottish Agricultural College (SAC) described by Simm *et al.* (2002). The lambs were reared indoors with free access to a high energy and protein food (12 MJ metabolizable energy and 180 g crude protein per kg dry matter) as part of a performance test regime. The lambs were weaned at 56 days of age and the test ended when they were about 150 days of age. Each lamb was weighed between 7 and 24 times over this period with more than 50% being weighed at least 20 times. Data characteristics, including the mean and standard deviation of live weights, are given in Table 1.

In 1985 the flock was closed with approximately two-thirds of the 140 breeding ewes randomly allocated to a selection line and the remainder allocated to a control line. Selection was thereafter based on an index that combined live weight, and ultrasound measurements of muscle and fat depth, recorded at 150 days of age. The index was designed to increase the rate of lean deposition, with little change in the rate of fat deposition (Simm and Dingwall, 1989). Within the control line lambs were retained that had average index scores. The flock was allowed to increase in size to about 250 ewes by the late 1980s and maintained at that size through 1994. Simm *et al.* (2002) describes in detail the dynamics of the flock.

Table 2 *Fixed effects included in the model, together with the number of levels of each*

Fixed effect	No. of Levels	Description
Year-week-sex	392	
Rearing type	2	Singleton and twin or greater
Birth type	3	Singleton, twin and triplet or greater
Rearing dam status	4	'Natural' mother, foster dam and surrogate dam of two breed types ($\frac{1}{2}$ Suffolk or $\frac{3}{4}$ Suffolk)
Rearing dam age	4	2-year-old, 3-year-old, 4-year-old and 5-year-old and older

From 1991 onwards about 30 ewes from the selection line were mated by artificial insemination to rams used as reference sires in the UK-wide co-operative breeding scheme in the Suffolk breed (the Suffolk Sire Reference Scheme Ltd, SSRS). This was to allow a direct comparison of the genetic merit of the selection and control lines, with flocks involved in the SSRS (Simm and Murphy, 1996).

Model selection and fitting
Preliminary analyses indicated that rearing type, birth type, rearing dam status ('natural' mother, foster dam or surrogate dam of two breed types), and age of rearing dam all removed a significant amount of variation in live weights. These were included in the model as fixed effects. The main contemporary grouping was year-week-sex, where year-week identifies the actual time of recording. A lamb would only be weighed once within a year-week classification. Fixed effects included in the RR model together with the number of levels for each are given in Table 2.

For RR models, weight as a function of age in days at weighing (test day), was included as a fixed regression of order 5 (quartic). This fixed regression describes the 'overall' or 'average' growth curve of all animals with data. Individual lambs were allowed to deviate from this overall curve and so have different coefficients of growth curves at both the genetic and the permanent environmental levels. For each lamb, deviations were modelled using orthogonal polynomials of varying degrees but the same degree of polynomial was fitted at both the genetic and the permanent environmental levels. Orthogonal (Legendre) polynomials were used in all analyses, as they are easy to manipulate, have good convergence properties and correlations between coefficients are lower than between the coefficients of ordinary polynomials. Note that permanent environmental effects, which measure the environmental differences between repeat records of an individual, were also modelled with higher order polynomials. This was done to avoid the assumption that the environmental correlations between all pairs of records were equal.

The earliest weight recorded was at 2 days of age and the latest at 159 days of age. Measurement error variance may not be homogeneous over the test period of 158 days and may vary depending on the age of the lamb. To investigate this, the recording period was arbitrarily split into six classes. The subclasses were days 2 to 25, 26 to 50, 51 to 75, 76 to 100, 101 to 125 and 126 to 159. In order to avoid the assumption of homogeneity of variance in each interval, an attempt was made to model the residual variances using a continuous function. Unfortunately this analysis failed to converge.

Dam effect was included in some models as an additional independent random effect, fitted as a constant (i.e. a constant dam effect over the entire test period) and as a polynomial of order 2 (linear), 3 (quadratic) and 5 (quartic). In order to account for the pre-natal environment of the offspring, we fitted the genetic dam in the model rather than the rearing dam. No attempt was made to partition the maternal variation into a genetic and an environmental component.

Analysis was by animal model restricted maximum likelihood (REML) using the software package 'DxMrr' (Meyer, 1998). The average information (AI) REML algorithm was used to maximize the likelihood (Johnson and Thompson, 1995; Meyer, 1997), and the derivative-free Powell method was employed to check that a global maximum had been reached.

Comparison of breeding values
At convergence of the RR analysis, we backsolved to obtain solutions for the fixed and random effects in the model. Using the solutions for the genetic coefficients obtained for individual animals, breeding values for live weight were predicted for all time points along the growth trajectory. For comparison purposes we chose to use predicted breeding values for lambs at 56 (weaning) and 150 days of age. Note that dam and permanent environmental effects for all time points can be predicted in the same way using the dam and permanent environmental coefficients.

In a related study, the Gompertz function was used to describe the growth of these same lambs (Lewis *et*

al., 2002) and to obtain their breeding values at 56 and 150 days of age. The function fitted was

$$W_t = (Z/B) \cdot \exp(-\exp(G_0 - B \cdot t)) \qquad (1)$$

where W_t is live weight at age t days from birth, B is a rate parameter, Z is the product $A \cdot B$ with A the mature size, and G_0 is a transformed initial weight defined as $G_0 = \ln(-\ln(W_0/A))$ with W_0 the weight at $t = 0$. Phenotypic measures of B, Z, and G_0 were obtained for individual animals based on their own live weight data.

These growth parameter values were taken as the observed values and breeding values estimated by fitting a weighted univariate animal model using an AI REML algorithm (ASReml; Gilmour *et al.,* 1995 and 1998). The model fitted was similar to that for RR. The exceptions were that the week designation no longer applied, and year and sex were fitted as main effects only. The reciprocal of the square of the standard error of the observation was used as the weight to account for variation in the frequency of live weight recording between animals. The breeding values for B, Z and G_0 were added to the overall phenotypic mean for these parameters and, using equation (1), breeding values were predicted for live weight at 56 and 150 days of age.

The simple correlation and the Spearman rank correlation were used to assess the similarity of the breeding values predicted by RR and the Gompertz equation (Genstat 5 Committee, 1998).

Results

In total 9 models were fitted to the data, and a description of each plus the maximum of the log-likelihood function is given in Table 3. The models considered differed in the order of the polynomial used to model the additive genetic, permanent environmental (between repeated records on an animal) and dam effects, and the number of measurement error classes included. For presentation purposes the maximum of the log-likelihood values are expressed as differences from the value obtained from the basic model (model 1). All models have the same fixed effects but different numbers of random components and so goodness-of-fit can be tested using a likelihood ratio test based on the χ^2 – distribution.

The fit improved significantly as the order of the polynomial used to model the additive genetic and permanent environmental effect was increased from 3 to 5. There was also a benefit to increasing the measurement error classes from 1 to 6. Modelling the dam effect as a polynomial of order 3 resulted in a significant improvement in fit of the model to the data, but increasing the order of polynomial to 5 had no significant effect. Further results are therefore presented for where a fifth order polynomial was used to model additive genetic and permanent environmental effects, a third order polynomial was used to model dam effects, and 6 measurement error classes were fitted (model 8).

Analyses using random regression models yield estimates of covariance functions which can be evaluated to provide estimates of genetic and environmental (co)variance components for every age (in days) on test. To simplify presentation, results are given for selected days only.

Table 4 gives phenotypic and genetic correlations between weights on selected test days, chosen at equal intervals throughout the test period. The pattern of both phenotypic and genetic correlations is the same in that correlations decrease as the distance between the tests increases. In particular, the genetic correlation between weight at start of test and weight near completion of test is fairly low suggesting that early weights are not under exactly the same genetic control as weights taken at an older age.

Permanent environmental correlations were slightly higher than phenotypic correlations but followed the same pattern. Between observations on adjacent days the permanent environmental correlation was approximately unity, and declined as the days apart increased, falling to around 0·28 between live weight at age 2 days and live weight at age 159 days.

Table 3 *Comparison of log-likelihood values (LogL) from the various models fitted, categorized by the order of the polynomial used to model the additive genetic and permanent environmental effects (K) and the number of measurement error (ME) classes (the presence of a dam effect in the model and the order of polynomial used to model this effect is also given)*

Model	K	No. of ME	Dam	LogL†
1	3	1	No	0
2	4	1	No	+3273
3	5	1	No	+4550
4	5	1	Yes – constant	+4581
5	5	1	Yes – order 2	+4589
6	5	6	No	+6260
7	5	6	Yes – constant	+6293
8	5	6	Yes – order 3	+6309
9	5	6	Yes – order 5	+6313

† Log-likelihoods are expressed relative to the log-likelihood for model 1.

Table 4 *Phenotypic (below diagonal) and genetic (above diagonal) correlations between live weights at selected days of age, estimated from model 8*

Day	15	30	45	60	75	90	105	120	135	150
15	—	0·81	0·61	0·47	0·40	0·38	0·39	0·40	0·41	0·39
30	0·88	—	0·93	0·82	0·74	0·68	0·64	0·62	0·61	0·61
45	0·80	0·93	—	0·97	0·92	0·87	0·82	0·77	0·75	0·75
60	0·72	0·85	0·94	—	0·99	0·95	0·90	0·86	0·83	0·84
75	0·66	0·79	0·91	0·95	—	0·99	0·96	0·92	0·89	0·90
90	0·63	0·74	0·86	0·92	0·96	—	0·99	0·97	0·94	0·94
105	0·61	0·70	0·82	0·88	0·94	0·97	—	0·99	0·98	0·97
120	0·60	0·67	0·77	0·84	0·89	0·94	0·97	—	1·00	0·99
135	0·58	0·65	0·73	0·79	0·85	0·90	0·94	0·97	—	0·99
150	0·55	0·62	0·71	0·76	0·81	0·86	0·90	0·93	0·96	—

Between live weight at age 15 days and live weight at age 150 days the permanent environmental correlation was 0·64.

Heritabilities estimated from models 6, 7, 8 and 9, together with estimates of the measurement error variance, are given in Table 5 for selected days of age. Heritability estimates were highest from model 6, the model with no dam effect, particularly for early observations. For all models, heritability increased over time. Model 7 included a constant dam effect that reduced the heritability estimates for the first 40 days on test. After day 40, results for these two models were very similar. Models 8 and 9 included a quadratic and quartic dam effect respectively. Results from the likelihood ratio tests had already indicated no difference between these two models and this is confirmed by the virtually identical heritability estimates. Allowing the dam effect to vary across the growth trajectory (model 8) as opposed to fitting a constant dam effect (model 7) allowed more accurate partitioning of the total variance into genetic, dam and environmental variance. Excluding the dam effect from the model (model 6) resulted in the genetic variance being inflated and hence higher heritability estimates. This can be seen clearly in Figure 1, which plots the genetic variance by day on test for models 6 and 8.
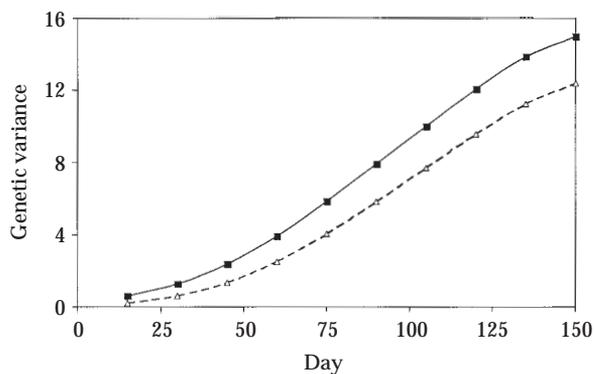
Figure 1 Genetic variance by day of age when fitting (△; model 8) or excluding (■; model 6) a dam effect from the random regression model fitted.

Measurement error variances in Table 5 for selected days on test are taken from model 8, but measurement errors for all models with six measurement error classes were very similar. Measurement error variances were low, ranging from 0·09 kg² to 0·82 kg². Although these variances were, in general, low, Table 3 shows that increasing the number of classes from 1 to 6 resulted in a significant improvement in fit.

Table 5 *Heritabilities of live weight as estimated from models 6 (h^2_6), 7 (h^2_7), 8 (h^2_8) and 9 (h^2_9) and measurement error variances (ME; kg²) on selected test days (estimates of measurement error variances were consistent over the four models†)*

Days	15	30	45	60	75	90	105	120	135	150
h^2_6	0·27	0·23	0·25	0·26	0·28	0·30	0·32	0·35	0·37	0·39
h^2_7	0·15	0·18	0·20	0·23	0·25	0·28	0·31	0·34	0·36	0·38
h^2_8	0·09	0·11	0·14	0·17	0·20	0·22	0·25	0·28	0·31	0·33
h^2_9	0·10	0·12	0·15	0·17	0·20	0·23	0·25	0·28	0·31	0·33
ME	0·09	0·23	0·23	0·64	0·64	0·62	0·67	0·67	0·82	0·82

† Features of models described in Table 3.

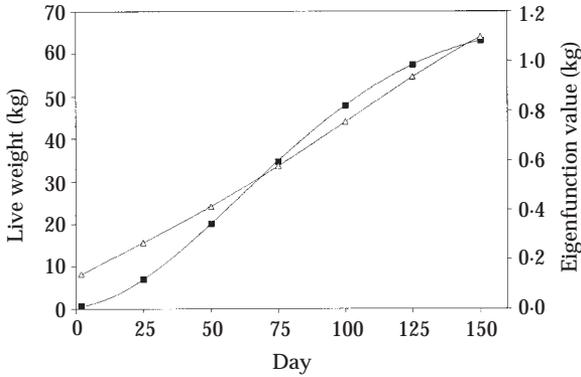**Figure 2** Plot of eigenfunction (△) and of the overall fixed live weight curve (■) by day of age.

Eigenfunctions, estimated from the eigenvectors of the genetic (co)variance matrix (Kirkpatrick *et al.,* 1990), provide an insight into the effects of selection across the growth trajectory. The leading eigenvalue of the genetic (co)variance matrix accounted for around 95% of the trace of the matrix. The corresponding eigenfunction accounts therefore for about 95% of the additive genetic variation and was positive for all ages (Figure 2), showing that positive selection at any point on the trajectory would result in an increase at all other points. A straight-line function parallel to the age axis would indicate that selection at any age results in an equal response across all ages. Our function instead increases with increasing age, which means selected animals would reach mature weight faster and thus grow more quickly at any age. This implies genetic selection for growth rate would be successful. The rate of response to that selection depends on the relative magnitude of the leading eigenvalue of the genetic (co)variance matrix compared with the leading eigenvalue of the phenotypic (co)variance matrix (conceptually similar to a heritability). That ratio is 0·43 indicating that the response to selection would
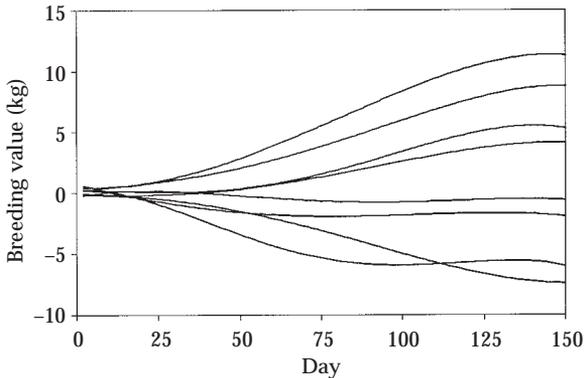

Figure 3 Predicted daily breeding values by day of age for eight rams with more than 20 progeny each.
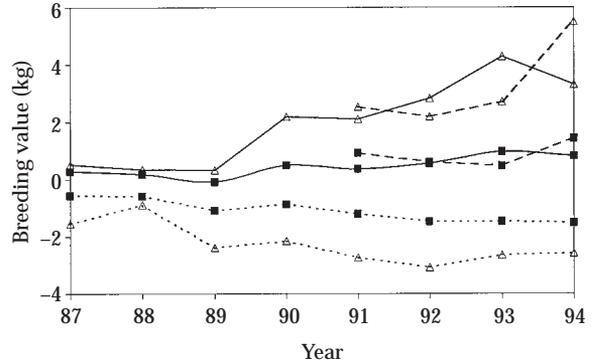

Figure 4 Mean breeding values at day 56 (■) and at day 150 (△) based on random regression analyses for the selection (———) and control (··········) line, and for the sire reference scheme (– – –), by year of birth.

be rapid. In contrast, response to selection based on the function associated with the 2nd, 3rd, 4th and 5th eigenvalues (for a fifth order polynomial as with model 8) would be both small and slow as each accounts for so little of the additive genetic variation.

Taking results from model 8, Figure 2 also shows the overall fixed curve. This is the general curve, common to all lambs with records in the data, whereas the random regressions allow individuals to vary from this curve at both the genetic and the permanent environmental level. Deviations from this curve at the genetic level provide the breeding values. Visual appraisal of Figure 2 suggests that modelling the overall curve with a polynomial of reduced order may be sufficient.

Solutions from model 8 for the curve coefficients for all animals in the analysis were used to calculate predicted daily breeding values (BVs), and these are plotted in Figure 3 for eight randomly chosen rams with more than 20 progeny each. The figure illustrates that the growth curves vary between the rams, and this variation is not limited to differences in height of the curve.

Figure 4 presents the mean BVs by line within year. Over time, the gap in BVs between the selection and control line widened. In part, this was because of an increase in BVs in selection line animals but also due to deterioration in BVs in the control line. The latter was not necessarily expected. The control line was maintained at an average index score across years and thus it could be presumed growth rate would remain unchanged. However, live weight was only one criterion in that index. When compared over contemporaneous years (1991 to 1994), the reference sire and selection line lambs were of similar genetic merit.

Table 6 *Simple (below diagonal) and Spearman rank (above diagonal) correlation coefficients for mean breeding values at day 56 (BV-56) and at day 150 (BV-150) among sire families predicted by random regression (RR) or a Gompertz function (GF)†*

Measure	BV-56 RR	BV-56 GF	BV-150 RR	BV-150 GF
BV-56, RR	—	0·774	0·904	0·750
BV-56, GF	0·808	—	0·780	0·896
BV-150, RR	0·913	0·826	—	0·876
BV-150, GF	0·774	0·920	0·907	—

† Based on 44 sire families with 20 or more progeny. All coefficients differ from zero ($P < 0.001$).

Forty-four rams had 20 progeny or more. For these half-sib sire families, the correlation among predicted BVs at day 56 and day 150 from the RR analyses and from fitting a Gompertz function (Lewis *et al.,* 2002) were calculated (Table 6). The simple and rank correlation coefficients between the prediction methods at both 56 and 150 day were moderate to high (0·77 to 0·91). Particularly at the end of test (150 days), similar individuals would be chosen irrespective of whether the random regression or Gompertz methodology was used to predict breeding value.

Discussion

This investigation has indicated that live weight early in a lamb's life is a different trait to live weight later in life (Tables 4 and 5) and hence to some extent is under different genetic control. RR methodology allows different genetic variances at each point on the trajectory but, unlike multivariate analysis, is a smoothed analysis which takes account of the continuity of the trajectory. Figure 3 demonstrates that there is genetic variation in the growth curves of individual animals and an evaluation model which included only fixed regressions of weight on age would result in less accurate evaluations of a number of animals. RR models allow differences between animals to be accounted for and hence are a useful tool in the evaluation of growth curves.

Researchers have used both linear (Portolano and Todaro, 1997) and non-linear (Detorre *et al.,* 1992; Lewis *et al.,* 2002) representations of the growth curve, but the latter are difficult to employ in variance component estimation and genetic evaluation. We used simple orthogonal polynomials to model both the overall curve and deviations from this curve at both the genetic, permanent environmental and maternal environmental levels. It may be possible to improve the fit of the model by using a mixture of parametric and semi-parametric

curves. Verbyla *et al.* (1999) suggested modelling growth curves with smoothing splines and White *et al.* (1999) used cubic smoothing splines to model lactation curves. Note that the overall curve may vary between males and females. Nesting the fixed regression coefficients within the sex of the animal could result in a lower order of polynomial being sufficient to model deviations from the overall curve.

Currently only linear (including polynomial) models can be fitted pragmatically in RR analyses. This is limiting since the coefficients of such curves often do not have a clear biological interpretation and *a priori* beliefs or hypotheses about the appropriate form of a descriptive function, such as the non-linear Gompertz equation, cannot be accommodated. An alternative could be to transform non-linear functions to their linear analogue. With the Gompertz form this involves two log transformations. When attempting to fit such a model, defining starting values and convergence criteria has proven problematic. Daily breeding values can, however, be expressed in a variety of ways of use to the farmer, and predictions of genetic merit with biological interpretation could be derived either from the daily breeding values or from each animal's (genetic) curve coefficients. For example, we could re-express the genetic curve coefficients in a way that is consistent with, say, mature size or relative growth rate, and the coefficients themselves would then be meaningful to breeders and useful as criteria for selection.

Despite these potential limitations, random regression has 'better' properties for genetic evaluation. Solutions for genetic and environmental effects are obtained simultaneously for all animals allowing family information to be used in the estimation. This was not the case in the two step process used in the Gompertz approach. Environmental effects peculiar to the time of recording also can be accounted for and differences in the frequency of recording between animals do not pose problems. Clearly the RR methodology offers a more powerful and flexible means than the Gompertz approach to evaluate repeated live weight information to determine genetic merit.

When comparing breeding values for 56 and 150 days of age predicted by RR and by the Gompertz approach, the ranking of animals was similar. With both methods, if breeding values predicted at day 150 were used as the selection criterion effectively the same individuals would be chosen. What remains unclear is which technique more accurately reflects the true breeding values for the coefficients or growth parameters evaluated, or the breeding

values predicted from these at specific ages. Undoubtedly addressing this issue requires stochastic simulation where true breeding values are known. A fundamental difficulty would be the way growth was modelled at the genetic level in such simulations. If modelled as a sigmoidal curve, for instance, one would expect the Gompertz approach to be better than it may be if growth was instead modelled as an asymptotic curve (e.g. Brody growth equation). Still, such an investigation is necessary to properly compare these and other approaches for assessing genetic merit for growth.

Acknowledgements

References

Andersen, S. and Pedersen, B. 1996. Growth and food intake curves for group-housed gilts and castrated male pigs. *Animal Science* **63:** 457-464.

Cullis, B. R. and McGilchrist, B. R. 1990. A model of the analysis of growth data from designed experiments. *Biometrics* **46:** 131-142.

Detorre, G. L., Candotti, J. J., Reverter, A., Bellido, M. M., Vasco, P., Garcia, L. J. and Brinks, J. S. 1992. Effects of growth curve parameters on cow efficiency. *Journal of Animal Science* **70:** 2668-2672.

Emmans G. C. 1997. A method to predict the food intake of domestic animals from birth to maturity as a function of time. *Journal of Theoretical Biology* **186:** 189-199.

Genstat 5 Committee. 1998. *Genstat 5, release 4·1 (PC/ Windows NT)*. Rothamsted Experimental Station, Harpenden, UK.

Gilmour, A. R., Cullis, B. R., Welham, S. J. and Thompson, R. 1998. *ASReml user guide*. NSW Agriculture, Orange, NSW, 2800, Australia.

Gilmour, A. R., Thompson, R. and Cullis, B. R. 1995. Average information REML, an efficient algorithm for variance estimation in linear mixed models. *Biometrics* **51:** 1440-1450.

Jamrozik, J. and Schaeffer, L. R. 1997. Estimates of genetic parameters for a test day model with random regressions for yield traits of first lactation Holsteins. *Journal of Dairy Science* **80:** 762-770.

Johnson, D. L. and Thompson, R. 1995. Restricted maximum-likelihood estimation of variance components for univariate animal models using sparse-matrix techniques and average information. *Journal of Dairy Science* **78:** 449-456.

Kirkpatrick, M., Lofsvold, D. and Bulmer, M. 1990. Analysis of the inheritance, selection and evolution of growth trajectories. *Genetics* **124:** 973-993.

Lewis, R. M., Emmans, G. C., Dingwall, W. S. and Simm, G. 2002. A description of the growth of sheep and its genetic analysis. *Animal Science* **74:** 51-62.

Meyer, K. 1997. An 'average information' restricted maximum likelihood algorithm for estimating reduced rank genetic covariance matrices or covariance functions for animal models with equal design matrices. *Genetics, Selection, Evolution* **29:** 97-116.

Meyer, K. 1998. "DxMrr" — a program to estimate covariance functions for longitudinal data by restricted maximum likelihood. *Proceedings of the sixth world congress on genetics applied to livestock production, Armidale, vol. 27*, pp. 465-466.

Meyer, K. 1999. Estimates of genetic and phenotypic covariance functions for postweaning growth and mature weight of beef cows. *Journal of Animal Breeding and Genetics* **116:** 181-205.

Meyer, K. 2000. Random regressions to model the phenotypic variation in monthly weights of Australian beef cows. *Livestock Production Science* **65:** 19-38.

Parks, J. R. 1982. *A theory of feeding and growth of animals*. Springer-Verlag, Berlin.

Portolano, B. and Todaro, M. 1997. Curves and biological efficiency of growth for 100- and 180-day-old lambs of different genetic types. *Annales de Zootechnie* **46:** 245-253.

Schaeffer, L. R. and Dekkers, J. C. M. 1994. Random regressions in animal models for test-day production in dairy cattle. *Proceedings of the fifth world congress on genetics applied to livestock production, Guelph, vol. 18*, pp. 443-446.

Simm, G. and Dingwall, W. S. 1989. Selection indices for lean meat production in sheep. *Livestock Production Science* **21:** 223-233.

Simm, G., Lewis, R. M., Grundy, B. and Dingwall, W. S. 2002. Responses to selection for lean growth in sheep. *Animal Science* **74:** 39-50.

Simm, G. and Murphy, S. V. 1996. The effects of selection for lean growth in Suffolk sires on the saleable meat yield of their crossbred progeny. *Animal Science* **62:** 255-263.

Taylor, St C. S. 1980. Genetic size-scaling rules in animal growth. *Animal Production* **30:** 161-165.

Verbyla, A., Cullis, B. R., Kenwood, M. G. and Welham, S. J. 1999. The analysis of designed experiments and longitudinal data by using smoothing splines (with discussion). *Journal of the Royal Statistical Society, C* **48:** 269-311.

White, I. M. S., Thompson, R. and Brotherstone, S. 1999. Genetic and environmental smoothing of lactation curves with cubic splines. *Journal of Dairy Science* **82:** 632-638.

Winsor, C. P. 1932. The Gompertz curve as a growth curve. *Proceedings of the National Academy of Sciences of the United States of America* **18:** 1–8.