Indian Journal of Animal Sciences **91** (9): 696–705, September 2021/Review Article
https://doi.org/10.56093/ijans.v91i9.116456

Genetic evaluation of growth using random regression models

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Received: 28 July 2021; Accepted: 5 August 2021

ABSTRACT

The variability in growth traits provides enormous scope for improvement through selection and breeding. However, growth is a longitudinal trait measured repeatedly on the animal and random regression models (RRM) have been found to be suitable for modeling the trait as a growth curve. RRM accommodate repeated records for traits which change gradually and continually, over time, and do not require stringent assumptions about constancy of variances and correlations. RRM has the advantage that, variance components can be estimated for any point in the trajectory of the growth curve and genetic parameters could be estimated for any age class within the range of ages included in the study. RRM is suitable for group breeding schemes and field performance recording systems where the growth data will be uneven and for varying age points. Worldwide, several studies on use of the tool, RRM in growth of various livestock species are available, but literature on such studies is scanty from India. The methodology used, data requirement, assumptions, validity, software available and application of RRM in the field are discussed based on the earlier reports.

Keywords: Eigen value, Genetic parameters, Growth curve, Repeatable data

Growth is the most important economic trait especially in small ruminants as the primary utility from these species is meat. India is diverse with respect to sheep and goat genetic resources. The variability in growth traits provides enormous scope for improvement in growth through selection and breeding. Nevertheless, growth traits are moderate to highly heritable in nature and thus response to selection is also expected to be good. Precise and unbiased estimates of genetic parameters are essential to obtain accurate predictions of breeding value. Numerous studies including detailed reviews on estimation of genetic parameters for growth in small ruminants are available (Fogarty *et al.* 2005, Safari *et al.* 2005, Bhatia and Arora 2005). Majority of these studies have considered growth at different ages as separate traits and the estimation has been dealt with through univariate and multivariate analyses. However, growth is a longitudinal trait measured repeatedly on the animal and random regression models (RRM) have been found to be suitable for modeling the trait as a growth curve. RRM is based on a covariance function which could be defined as "a continuous function to give the variance and covariance of traits measured at different points on a trajectory" (van der Werf 2001). Kirkpatrick *et al.* (1990) showed that variance components for longitudinal data can be modelled through covariance functions. Random regression models (RRM) and the resulting covariance function have been recognized as ideally suited for analysis of longitudinal data (Hill 1998, Meyer 1998). In particular, RRM accommodate repeated records for traits which change gradually and continually, over time, and do not require stringent assumptions about constancy of variances and correlations. In addition, RRM provide insights about temporal variation of biological processes and physiological implications underlying the studied traits (Strucken *et al.* 2015).

In general random regressions have been extensively used for test day records in dairy cattle (Schaeffer and Dekkers 1994, Jamrozik *et al.* 1997, Prakash *et al.* 2017). Worldwide, several studies on use of the tool, RRM in growth of various livestock species are available (Table), but literature on such studies are scanty from India (Venkataramanan 2015, Arthy *et al.* 2020, Mahala *et al.* 2020). RRM has the advantage that, variance components can be estimated for any point in the trajectory of the growth curve and genetic parameters could be estimated for any age class within the range of ages included in the study. In a country like India small ruminants are reared under small holding systems and field performance recording is done through ICAR network projects. Data from these units are available only on the days of visit to the villages and the age at measurement varies between contemporaries. Random regression could form a very good tool to analyse such data without need for correction of ages. Repeated measures of live weight in growing animals are used to describe the path by which they travel from birth to maturity. RRM allows environmental effects specific to the time of recording to be accounted for and can accommodate genetic

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differences in the shape of each animal's growth curve.

The objective of this paper is to review the use of RRM for growth traits. The details of various studies carried on RRM for growth traits worldwide in different livestock species are presented in Table. The methodology used, data requirement, assumptions, validity, software available and application of RRM in the field are discussed based on the earlier reports.

Earlier studies on growth using RRM

Growth is a repeatable trait suitable for RRM as it changes gradually with time (Anderson and Pederson 1996, Meyer 1998, Meyer 2000, Van der Werf 2001). In a pioneering study by Meyer (2000) on RRM, weights of beef cows recorded on a monthly basis were analysed. Records between 19 and 84 months were analysed and phenotypic random regressions for animal effects, ignoring relationships, were considered. One of the early studies to analyse body weight in sheep using RRM was that by Lewis and Brotherstone (2002). The earliest weight recorded was at 2 days of age and the latest at 159 days of age. Fischer *et al.* (2004) used RRM to model the variance in weight of Polled Dorset lambs from 50–500 days of age. Growth in Spanish Merino sheep up to three months of age was modelled with RRM (Molina *et al.* 2007). Growth data of Mehraban sheep were used to estimate direct and maternal additive genetic effects together with direct and maternal permanent environmental effects on body weight from birth to 270 days of age using RRM (Ghafouri-Kesbi *et al.* 2008). Variance components for five consecutive measurements of body weight from 5 to 150 days of age in Polish sheep were estimated using random regression and multi-trait animal models (Wolc *et al.* 2011). Vatankah (2013) analysed adult ewe body weight (1.5 to 8 years) of Lori-Bakhtiari sheep using RRM with homogenous and heterogeneous error variances. Sarti *et al.* (2015) estimated the genetic parameters for weight from 60–450 days at a performance test conducted on the breed Appenninica using RRM. This study was based on data from field performance recording system. Venkataramanan (2016), modelled growth of Nilagiri sheep of South India for the body weights at 3-month, 6-month, 9-month, 12-month, 18-month and 24-month using RRM with 9 classes for heterogeneous error variance. This was one of the first studies available for RRM in Indian breeds of sheep conducted on data from an organized farm. Arthy *et al.* (2020) used RRM for evaluation of growth in a cooperative breeding scheme (ICAR-Network Project on Sheep Improvement) where field performance recording system in farmers' flocks is practiced. Mahala *et al.* (2020) compared the estimates of heritability and ranking of sires for growth traits as obtained from RRM and the conventional univariate animal models. This was one of the first attempts to interpret genotype x environment interaction using RRM. All these studies indicate substantial genetic variation in the shape of growth curve and proved that RRM facilitates modeling of growth data over a range of ages. However, as seen from majority of the studies, RRM is found to be more appropriate during the growing phase of the animal when there is change in body weight with time.

Methodology, analyses and software used

The detailed methodology of the use of RRM is explained by Van der Werf (2001). The ability of the RRM to model the growth curve is based on the Legendre polynomials. According to Meyer (2005) and Silva *et al.* (2013), orthogonal polynomials are the most appropriate to estimate covariance functions of growth traits, and Legendre is the most commonly used one due to the correlation reduction between estimated regression coefficients (Table 1). The regression on orthogonal polynomials do not require prior assumptions about the shape of curves to be modelled and can be recommended as general purpose functions, especially if higher orders of fit are feasible. Other functions for modeling included the spline function (Iwaisaki *et al.* 2005, Zamani *et al.* 2016, Nemutandani *et al.* 2018, Scalez *et al.* 2018).

The RRM is done using the Legendre polynomial and standardized ages as—

$\Phi_i = \ddot{E}_i\,(t_{ij})$, where, $\ddot{E}_i$ are the coefficients of Legendre polynomial, and t_{ij} are the ages standardized between –1 and +1, derived as—

$$t_{ij} = \left[2 \times \frac{(T - T_{min})}{(T_{max} - T_{min})}\right] - 1$$

where, T_{min} is the earliest date (or the youngest age) and T_{max} is the latest date (or oldest age) represented in the data. 'T' is the age in original scale for which t_{ij} is calculated.

A sequence of analyses with different orders of fit for the random effects are carried out to determine the most parsimonious model describing the data. Different types of random effects have been used in the analyses of growth traits. The list of random effects and order used for RRM of growth is presented in table.

Error variances

Another important aspect of the RRM model is that heterogeneity of error variance with the control variable age could be modelled by use of heterogeneous error variance classes in the model (Table). According to Mota *et al.* (2013) and Menezes *et al.* (2013), assuming homogeneity of residual variance may create considerable distortions in the total variance, i.e. the residual variance can be affected by many factors along the growth. In the RRM, error variances could be modelled as heterogeneous for different age classes. Meyer (2004) used rrm for growth from birth to 730 days in beef cattle and the error variances were modelled as a step function with 19 classes (0, 1–30, ..., 271–300, 301–360, ..., 661–720 and 721–730 days).

In a study done in India (Arthy *et al.* 2020) error variance was modelled as a step function with four and ten different heterogeneous classes and the model with ten classes was found to have better fit.

Table 1. Reports on the use of Random regression models (RRM) for growth in various species of livestock

Breed	Location	Total No.of records	No. of records per animal	Age range	Random effects with best order of fit				Number of error classes	NP	Heritability estimates	Method of estimation-Software used	References
					A	M	P	W					
Sheep													
Suffolk	UK	40371	17.83	2–159 days	5	–	5	–	6	–	0.09–0.33	REML-ASReml	Lewis and Brotherstone (2002)
Poll Dorset	Australia	16826	3.10	50–500 days	3	2	3	3	9	30	1.5–4.8	REML-ASReml	Fischer *et al.* (2004)
Spanish Merino	Spain	88727	2.94	2–92 days	3	3	3	2	10	39	0.123–0.186	REML-ASReml	Molina *et al.* (2007)
Mehraban	Iran	2746	3.43	Birth-270 days	3	3	4	4	1	36	0.28–0.58	REML-DxMRR	Ghafouri-Kesbi *et al.* (2008)
Dorper	Kenya	8922	3.38	20–380 days	2	2	2	2	7	19	0.9–2.44	REML-Wombat	Kariuki *et al.* (2010)
Polish	Poland	112396	3.54	Birth-150 days	–	–	–	–	1	–	0.08–0.23	REML-ASReml	Wolc *et al.* (2011)
Zandi	Iran	5573	3.66	Birth-300 days	4	5	4	–	8	43	0.06–0.52	REML-Wombat	Bohlouli *et al.* (2013)
Lori-Bakhtiari	Iran	22153	9.96	371–3416 days	6	–	6	–	9	51	0.37–0.50	REML-Wombat	Vatankhah (2013)
Sardi	Morocco	131110	2.95	Birth-85 days	3	3	3	2	12	64	0.11–0.37	REML-ASReml	Jannoune *et al.* (2015)
Appenninica	Italy	8546	4.43	2–15 months	–	–	–	–	1	–	0.34–0.52	REML-VCE	Sarti *et al.* (2015)
Santa Ines	Brazil	17767	4.22	Birth-196 days	7	5	7	3	6	82	0.12–0.21	REML-DFREML	Sarmento *et al.* (2016)
Nilagiri	India	10792	3.32	3–48 months	4	4	4	4	9	–	0.068–0.275	REML-Wombat	Venkataramanan (2016)
Moghani	Iran	9165	3.26	60–365 days	3	3	3	2	5	26	0.14–0.32	REML-Wombat	Zamani *et al.* (2016)
Kordi	Iran	7875	2.67	Birth-360 days	4	–	5	5	1	41	0.11–0.56	REML-Wombat	Mohammadi and Farhadian (2017)
Zandi	Iran	9699	2.32	60–365 days	3	3	3	3	1	29	0.15–0.39	REML-Wombat	Ghafouri-Kesbi (2018)
Baluchi	Iran	22179	3.1	50–400 days	4	4	4	4	1	47	0.09–0.42	REML-Wombat	Ghafouri-Kesbi and Gholizadeh (2018)
Makouei	Iran	8733	4.43	Birth-270 days	5	–	4	5	7	47	0.10–0.42	REML-Wombat	Naderi (2018)
Grootfontein Merino	South Africa	58214	3.61	Birth-6 years	2	2	–	–	1	14	0.00–1.00	REML-ASReml	Nemutandani *et al.* (2018)
Kordi	Iran	23720	3.53	Birth-360 days	4	3	4	3	5	38	0.133 0.391	REML-Wombat	Saghi *et al.* (2018)
Santa Ines	Brazil	4608	5.17	180–720 days	3	–	3	–	5	17	0.02–0.40	REML-Wombat	Freitas *et al.* (2019)
Ghezel	Iran	39288	2.94	Birth-360 days	5	3	5	2	1	22	0.22–0.55	REML-Remlf90	Ghahri *et al.* (2019)
Barki	Egypt	16496	4.93	Birth-12 months	4	–	3	–	5	21	0.06–0.42	REML-Wombat	Sallam *et al.* (2019)
Madras Red	India	9361	1.74	66–365 days	–	–	4	–	10	–	0.16–1.54	REML-Wombat and Bayesian-GIBBSF90	Arthy *et al.* (2020)
Avikalin	India	27555	3.79	Birth-365 days	4	4	3	4	5	41	0.18–0.45	REML-Wombat	Mahala *et al.* (2020)
Afshari	Iran	–	–	98–525 days	3	2	3	2	14	38	0.05–0.45	REML-Wombat	Ghafouri-Kesbi and Eskandarinasab (2021)
Goat													
Raini	Iran	10606	2.72	20–360 days	5	5	4	4	6	56	0.14–0.38	REML-Wombat	Barazandeh *et al.* (2012)
Markhoz	Iran	12116	3.94	Birth-365 days	4	–	3	2	7	36	0.17–0.34	REML-Wombat	Kheirabadi and Rashidi (2016)

Continued

(Table 1. *Concluded*)

Breed	Location	Total No. of records	No. of records per animal	Age range	Random effects with best order of fit: A	M	P	W	Number of error classes	NP	Heritability estimates	Method of estimation-Software used	References
Cattle													
Brazilian	Nelore Australia	74591	6.65	Birth-730 days	4	4	6	3	4	51	0.14–0.32	REML-DxMRR	Albuquerque and Meyer (2001)
Nellore	Brazil	74601	–	Birth-733 days	4	4	4	4	1	–	0.10–0.35	REML-Wombat	Nobre *et al.* (2003)
Nellore	Brazil	79849	4.94	1–733 days	4	4	4	4	1	–	0.12–0.27	Bayesian-GIBBS2F90	Nobre *et al.* (2003)
Japanese	Japan	11815	4.94	Birth-365 days	4	3	4	3	10	–	0.38–0.65	Bayesian-RRGIBBS	Aziz *et al.* (2005)
Black Gelbvieh cattle	Japan	36193	1.92	Birth-1 year	–	–	–	–	1	–	0.36–0.59	Bayesian-GIBBSF90	Iwaisaki *et al.* (2005)
Nelore	Brazil	82064	10.08	Birth-550	4	3	6	3	5	50	0.34–0.42	REML-Wombat	Boligon *et al.* (2009)
Canchim	Brazil	49011	20.13	Birth- 3542 days	4	3	6	2	4	44	0.15–0.40	REML-Wombat	Baldi *et al.* (2010)
Simmental beef	Brazil	29510	2.77	60–819 days	3	3	3	3	1	25	0.14–0.46	REML-Wombat	Mota *et al.* (2013)
Polled Nellore	Brazil	10839	5.63	63–653 days	4	2	2	2	6	25	0.42–0.73	REML-Wombat	Barros *et al.* (2017)
Turkish Holstein	Turkey	1475	3.73	32–725 days	–	–	–	–	1	–	0.03–0.90	REML-Wombat	Galic and Takma (2018)
Nellore	Brazil	16291	4.85	262–642 days	6	–	5	–	1	42	0.375–0.90	REML-Wombat	Scalez *et al.* (2018)
Nellore	Brazil	10002	3.99	60–499 days	4	4	4	4	1	40	0.09–0.28	REML-Wombat	Teixeira *et al.* (2018)
Pig													
Landrace * Desi		India	10792	2.55	Birth-32 weeks	4	4	3	4	16	–	0.011–0.582	REML-Wombat Chaudhary *et al.* (2019)

A, Direct genetic; M, Maternal genetic; P, Permanent environmental; W, Maternal permanent environmental; NP, Number of parameters estimated; 1 in number of error classes indicates homogeneous error variance

Method of estimation: Frequentist and Bayesian approaches

Most of the studies using RRM have been analysed using restricted maximum likelihood analyses (REML). Few studies (Nobre *et al.* 2003b, Iwaisaki *et al.* 2005, Arthy *et al.* 2020) performed through the Bayesian approach indicate better scope for convergence, especially for higher orders of fit and more no. of parameters to be estimated. Arthy *et al.* (2020) compared both frequentist and Bayesian approaches for modeling of growth and similar estimates were obtained. However, certain problems with convergence faced in REML are overcome by the Bayesian Gibb's sampling, which helps in obtaining smoother curve of variance components estimates as compared to the conventional REML. WOMBAT (Meyer 2007) was the predominant software used for REML and GIBBSF90 (Misztal *et al.* 2018, Masuda 2018) for Gibbs sampling. Other software used are presented in Table

Deciding the best model of fit

The best model is decided based on Log likelihood, Akaike's information criterion (AIC) and the Bayesian information criterion (BIC) for REML estimation and Deviance information criterion (DIC) is used to decide the models analysed using Bayesian approach. The AIC and BIC can be useful as guides because they adjust for the number of parameters and sample size (Foulley and Robert-Granie, 2002).

The orders for random regression could initially be fixed based on recommendations from previous studies on RRM in growth. Meyer (1999) used a RRM to analyze monthly weights of 2 to 10 years old (19 to 119 months) in Australian Hereford and Wokalup cows. She concluded that orders of fit of 'n = 3' and 'n = 4' were appropriate for Herefords and Wokalups, respectively. Fischer *et al.* (2004) and Molina *et al.* (2007) found orders of fit of 3 to be most suitable for growth in lambs. Orders of fit of 3 for additive and direct maternal, and 4 for permanent environmental effects was best suited for modeling of growth in Mehraban sheep (Ghafouri-Kesbi *et al.* 2008). Venkataramanan (2016) observed that the model with best fit based on LRT was 4444b, which had orders of fit of 4 for all random effects and heterogeneous error variance (9 classes). The orders of fit for different random effects considered in various studies are presented in Table.

The Eigen function of the random regression matrix will also help identifying the required order of fit. In the study of Arthy *et al.* (2020) more than 97% of the Eigen value for sire and individual permanent environmental effect were determined by the first three orders of fit, and thus the order of fit of 4 was regarded sufficient for the data set used.

Estimation of (co)variance components

The genetic (co)variance between ages were estimated by the general expression

$$G_x = \Phi_{xj} K_{xj} \Phi'_{xj}$$

where, G_x is the (co)variance matrix for random effect x which may be the animal, sire or individual permanent environment.

Φ_{xj} is the vector of Legendre polynomials for the random effect of x and j^{th} age group. Since this matrix is fixed for a particular age, genetic variance and covariance could be obtained for any age point by using the particular vector and constant random regression matrix. The matrix of genetic variance-covariance thus obtained is then used to estimate the genetic correlation for various ages as ratio of covariance to square root of product of respective variances.

Number of records per animal

Fischer and Van der Werf (2002) showed that RRM could be useful even when the data structure has very few records per animal. However, according to Meyer (2004), the full potential of RRM could be achieved when more number of repeated records are available. Table gives information on the number of records per animal used in various studies on RRM done earlier. The total no. of growth observations varied from a few thousands to more than 1.30 lakh, while the average number of records per individual varied from 1.7 to 27.3. Successful estimation of variances with Legendre polynomials is possible with large data sets, even distribution of data points on the trajectory, and careful modeling of other effects (Druet *et al.* 2003). Similarly the no. of records per animal is also important to obtain precise estimates of random regression coefficients. In a study on Madras Red sheep, the period of growth with lesser no. of observations led to sudden disruption in the shape of the variance estimation curve (Arthy *et al.* 2020). The study reports that the standard error was high for 12W, which was the end point for range of ages studied, indicating the 'effect of extreme ages'. This difference can also be attributed to the variation in the number of observations, which is usually lower for the later ages. Curves at points of the trajectory with few records are likely to contain artefacts (Misztal *et al.* 2000, Nobre *et al.* 2003a, Meyer 2005). More number of observations per age point for the growth data resulted in smoother curve for the variance and better estimates of variance components.

Estimates of genetic parameters using RRM for growth

The main advantage of RRM is that variance components and genetic parameters could be obtained for any age point in the trajectory of the growth curve. This also helps in obtaining the breeding value and genetic trend for bodyweights at various ages. The modeling of the growth curve helps in making decisions for unique selection objectives which could vary for each of the growth periods. Similarly breeding values could be obtained for any age point in the trajectory and selection based on multiple traits (weight at different ages) could be done based on weightages given to each trait. Recent papers have attempted use of RRM to study genotype x environment interaction using a reaction norm gradient of the traits over control variable (Chiaia *et al.* 2015, Mahala *et al.* 2020).

As seen from the Table, RRM is able to model growth traits and estimates of heritability have been obtained for various age ranges. A continuously increasing trend over ages up to 10 months of age was generally noticed for the additive genetic variance and thus the heritability estimates also was found to increase in most of the studies. Ghafouri-Kesbi *et al.* (2008) found that in Mehraban sheep heritability of growth traits, especially at later ages, were overestimated in RRM. Most of the earlier studies (Lewis and Brotherstone, 2002; Fischer *et al.* 2004, Molina *et al.* 2007, Ghafouri-Kesbi *et al.* 2008, Vatankah 2013, Kheirabadi and Rashidi 2016, Venkataramanan 2016) reported an increase in additive genetic variance with age. As far as growth is concerned, the estimates of heritability from univariate and multivariate analyses also indicated a similar trend (Mota *et al.* 2013, Arthy *et al.* 2018, Mahala *et al.* 2020).

However, RRM suffers from problems associated with polynomials at the ends of trajectory caused by absence of constraints at the end (Fischer and Van der Werf 2002). Nobre *et al.* (2003) reported that parameter estimates obtained by fitting polynomials could be affected by sparse data and extremes of trajectory. Arango *et al.* (2004) reported inadequacy of RRM to model genetic variability at later ages. Ghafouri-Kesbi *et al.* (2008) in Mehraban sheep, found that heritability of growth traits especially at later ages were overestimated in RRM. The potential overestimation was possibly due to ‘end effect of polynomials’ or “Runge’s phenomenon” (Meyer 2005).

In general RRM estimates for individual age points were slightly higher than those obtained through multitrait models. The comparatively higher value of estimates could be due to variation in the kind of random effect (especially the additional individual permanent environmental effect) included and ability of RRM to fit the growth curve by taking in to consideration the relationship between weights at various ages.

The maternal influence is usually found in early growth due to the influence of maternal permanent environmental effect. However, RRM facilitates modeling for the maternal genetic effect and helps in understanding the role of maternal effect in growth of the animal. Maternal heritability estimates increased after birth to a maximum around 120 days of age in Mehraban sheep and decreased thereafter (Ghafouri-Kesbi *et al.* 2008). In a study in Nilagiri sheep maternal genetic influence was found to be present until 18 months of age (Venkataramanan 2016). Similarly other variance components including permanent environmental and phenotypic variances could be modelled using the RRM.

The total phenotypic variance increased with age until around 300 days where it reached a plateau (Fischer *et al.* 2004).

Another important use of RRM has been the ability to use partial records of growth at different age points to obtain information on the complete growth curve. This enables its use for field performance recording especially in a country like India where the animal holdings are in small number. Group breeding schemes are being implemented and RRM is very much suitable for such recording systems where the growth data will be uneven and for varying age points. Arthy *et al*. (2020) have found the technique very much suitable for such programmes. The study was based on use of RRM in a group breeding scheme involving several farmers for the Madras Red breed of sheep.

RRM forms an excellent method to study correlation between weights at different ages as the modeling of growth curve helps in obtaining valuable estimates of correlation. The compound symmetry structure of growth traits is clearly seen from the results of earlier studies on growth using RRM. Estimates of direct genetic correlation showed a declining trend with increase in difference between ages. As expected, genetic correlation was found to decrease with widening of the age interval. The genetic correlation between subsequent ages approached unity, while that between the extreme ages were moderate. Most of the earlier studies indicated similar pattern for genetic correlation (Lewis and Brotherstone 2002, Fischer *et al.* 2004, Aziz *et al.* 2005, Ghafouri-Kesbi *et al.* 2008). This has implications for potential to select on the shape of the growth curve as an animal can be above average weight at younger ages, but can be below average weight at older ages or vice versa.

Maternal genetic correlations showed a similar pattern to that of direct genetic correlation. The values for 3W with body weight at other ages were lower while those among weights at later ages were almost 1. Ghafouri-Kesbi *et al.* (2008) observed similar results indicating that same set of maternal genes acted at later ages, while those responsible for maternal effect during birth were different. Fischer *et al.* (2002) reported high values of maternal genetic correlation throughout the period of study (50–500 days) and concluded that the same set of genes were responsible for maternal effect during this period.

Breeding values obtained through RRM and conventional univariate analyses

RRM provides breeding value estimates for the entire growth curve and several studies have compared ranking of animals from the two methods. Lewis and Brotherstone (2002) obtained estimates ranging from 0.70 to 0.91 for correlation between breeding values for 56 and 150 day body weight obtained through RRM and Gompertz approach in Suffolk lambs. Similarly, Fischer *et al.* (2002) obtained correlation coefficients of 0.82 and 0.87 for body weight at 100 and 200 days of age, respectively. Meyer (2004) made a comparative study between the MTM and RRM for the body weight traits of beef cattle which included the birth weight, weaning weight, yearling weight and final weight and found that RRM estimates were more accurate than MTM. Molina *et al.* (2007) found changes in ranking of the animals based on the breeding value estimation with the conventional method and with the random regression procedure, however, the authors recommend use of RRM to analyze the genetic trajectory of growth in the population of Merino sheep studied, on account of its benefits discussed earlier. Mene´ndez-Buxadera *et al.* (2008) studied the weaning weight (WW) using a multitrait animal model (MAM) and a RRM in order to estimate the variance components and the breeding value of the animals. The authors concluded that the small specific differences between RRM and MAM are due to the fact that the exact age was used in RRM whereas a class is used in MAM. The correlation (Pearson's correlation) between breeding values estimated from RRM and conventional REML methods were 0.904, 0.331, 0.774 and 0.771 for 3W, 6W, 9W and 12W, respectively (Venkataramanan, 2016). All the values were positive and estimates were significantly (P<0.01) different from zero. Similarity in ranking of animals could be expected for 3W, 9W and 12W, thus validating the RRM technique. However, since the values are sufficiently different from unity, ranking of animals from the two methods will not be exactly the same. Compared to the animal model ranking from RRM is more reliable as information obtained is from the growth curve and not the weight at individual age as is used in the univariate model.

Eigen function

The Eigen values (λ_i) and their associated Eigen vectors of the genetic regression coefficients matrix are used to analyse the patterns of variation existing in growth over ages (Van der Werf 2001). Kirkpatrick and Heckman (1989) and Kirkpatrick *et al*. (1990) show that covariance functions can be used to analyze 'patterns of inheritance' in the covariance matrix ~ G. For this purpose they determined eigenvalues and eigenfunctions from the coefficient matrix for a given covariance function. The trajectories of these eigen functions obtained from the random regression coefficients will give an idea about the possible variation in the particular function over the entire range of ages.

Several studies indicate majority of the random sources of variation due to the intercept and linear order. Lewis and Brotherstone (2002) found that Eigen function of genetic variance – covariance matrix indicated positive and increasing trend for first Eigen function with age. Venkataramanan (2016) observed that the trajectories for first and second eigen value, which account for more than 97% genetic variation showed a uniform trend with positive values and slight increase with age. Selection on these factors will improve weight at all ages, with more response at later ages after 9 months of age.

RRM in genomic selection

Genomic selection is practiced for improvement of livestock and genomic RRM can provide an opportunity to unravel genomic regions significantly associated with traits of interest at specific time points, as well as the trajectory of biological processes during the animal's life or production cycle. Oliviera *et al.* (2019) have reviewed the advances in use of RRM and provided insight on the incorporation of genomic information in the use of RRM. By analyzing marker associations over time, regions with higher effects in specific stages are more likely to be identified, which could contribute to better detection of the genetic variation of longitudinal traits (Strucken *et al.* 2015). Including genomic information to evaluate longitudinal traits using RRM is a feasible alternative to yield more accurate selection and culling decisions, because selection of young animals may be based on the complete pattern of the production curve with higher accuracy compared with the use of traditional parent average (i.e. without genomic information). However, further research in this field is recommended by the author for application.

Conclusion

Growth curve has been successfully modelled using the RRM and the main utility of the technique is that variance components which could be obtained for any point in the trajectory of growth. The heritability estimates obtained through RRM was similar or higher than those obtained through univariate analysis, which is due to the additional information obtained through the growth curve. RRM is able to provide more information for breeding programmes to improve longitudinal traits as that of growth, and additional information from Eigen functions predicts the response to selection based on particular Eigen function. Correlation of breeding values obtained by RRM and conventional BLUP analysis was positive, significant and high, which is indicative of the ability of RRM to model growth. Similarity of results with multitrait animal model is suggestive of favourable results using RRM, as use of RRM brings in the advantages of multitrait analyses with lesser computational requirements. Compared with a multi-trait model, RRM estimates (co)variances form a smooth curve and are less biased. Similarly, RRM is able to provide more information for breeding programmes to improve longitudinal traits as that of growth, and additional information from Eigen functions predicts the response to selection based on particular Eigen function. In a country like India, RRM is suitable for modeling growth traits especially in a field performance recording system where the number of records will not be evenly distributed for all age groups.

ACKNOWLEDGEMENTS

The author acknowledges the support of Dr. Murugan, Professor, TANUVAS and help of Dr. Ambike Vrinda Bindumadhav in compilation of the table on studies of RRM.

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