

Estimation of direct and maternal genetic and permanent environmental effects for weights from birth to 356 days of age in a herd of Japanese Black cattle using random regression

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ABSTRACT: A total of 11,815 weight records from 23,94 Japanese Black calves was used to estimate direct, maternal, direct permanent environmental, and maternal permanent environmental effects on growth from birth to 356 d of age. The data were collected from a herd of Japanese Black cattle in Shirosi city, Miyagi prefecture, Japan. A random regression model, including parity of dam and year-season of calving-sex of calf as fixed effects and animal, dam, animal permanent environmental, and maternal permanent environmental as random effects, was fitted to the data using Legendre polynomials for age of calf. Direct heritability estimates increased from 0.38 at birth to 0.65 at 120 d of age, decreased to 0.38 at 300 d, and then increased again up to 0.47 at 356 d. The ratio of animal permanent environmental variance to phenotypic variance de-

creased from 0.41 at birth to 0.12 at 90 d, and then increased gradually up to 0.40 at 270 d and oscillated around this value up to the end of the test period. Maternal genetic heritabilities increased from 0.04 at birth to 0.09 at 120 d and then decreased to 0.06 thereafter, whereas the variance ratios due to maternal permanent environment were fairly constant across the age trajectory, fluctuating around the value of 0.03. Direct genetic, phenotypic, maternal genetic, animal permanent environmental, and maternal permanent environmental correlations between different ages were all positive, and they generally decreased as the interval between ages increased. These correlations were lower between weights from nonadjacent ages than those between weights from adjacent ages. Results suggest that selection on preweaning weights would have a positive effect on weights at later ages.

Key Words: Genetic Effects, Growth, Japanese Black Cattle, Random Regression

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Introduction

Random regression models are a popular choice for modeling traits that change gradually and continually with time and are measured repeatedly on individuals. Kirkpatrick et al. (1990) showed that phenotypic changes with age could be represented by a function of time. Growth is a typical example of such traits. Random regression models have been applied to growth of beef cattle by Albuquerque and Meyer (2001a), Schenkel et al. (2002), and Nobre et al. (2003). Traditionally, animal growth measured at various ages is analyzed with a multitrait model defining the phenotypic values at distinct ages as different traits. One advantage of

random regression models is the possibility of calculating variances for every age and covariances between any pair of ages. Kirkpatrick et al. (1990) stated that random regression models could estimate variances and covariances more smoothly and with less bias than multivariate models.

Japanese Black cattle are famous for the high marbling score of their beef. Genetic studies for carcass traits are numerous for this breed (Mukai, 1994; Kitamura et al., 1999; Uchida et al., 2001). However, there are comparatively few studies dealing with parameter estimates for growth traits (Shimada et al., 1995; Mukai et al., 2000). Estimates of genetic parameters for weights in a sequence of small age intervals are not available. Of interest are genetic parameters that describe the change of such traits in time. From an animal breeding point of view, these genetic parameters reflect to what extent and how genetic changes in growth patterns over time can be achieved by selection.

The objectives of this study were 1) to estimate coefficients of covariance functions for direct and maternal

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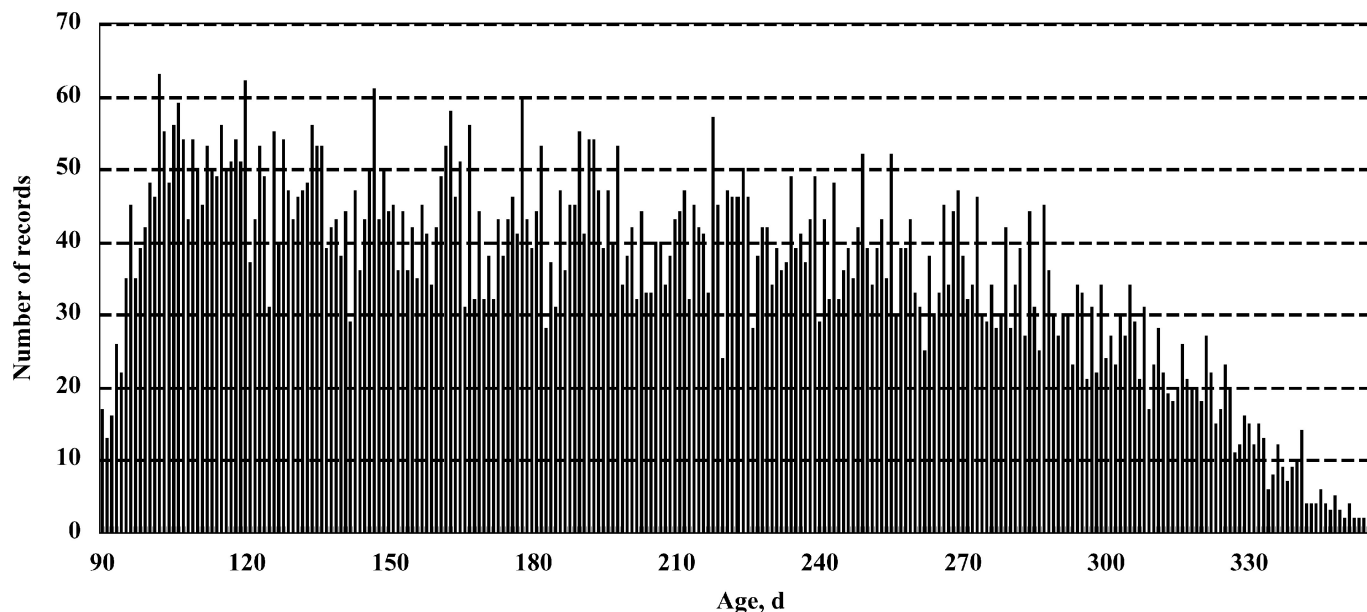


Figure 1. Distribution of number of records by age, from 90 to 356 d of age.

genetic and permanent environmental effects, and 2) to use random regression to estimate genetic, environmental, and phenotypic parameters of the aforementioned effects for weights taken from birth to 356 d of age in a herd of Japanese Black calves.

Materials and Methods

Data

Japanese Black is the most common cattle breed in Japan. Japanese Black cattle were established in 1944 by crossing Japanese native cattle with various breeds such as Shorthorn, Simmental, and Brown Swiss. The breeds used and the structure of the crossbreeding program varied among prefectural populations. Even after the establishment of the breed, most breeding programs continued to be carried out separately within each prefecture, although there has been some genetic flow among the various subpopulations (Nomura and Sasaki, 1988). In fact, the breed is genetically divided into several subpopulations, each with a different genetic background. The current breed is characterized by high meat quality, with prominent i.m. fat deposition (i.e., marbling).

The initial data set comprised 17,368 weight records on 3,272 Japanese Black calves. These data were collected from 1997 to 2003 in a farm located in Shiroshi city, Miyagi prefecture, Japan. This farm has an operational genetic improvement program that considers growth, marbling score, fertility, and maternal ability traits. Calves are weighed at birth and subsequently at monthly intervals. They are weaned at approximately 6 mo of age. Calves are given free access to concentrate mixed with 10% chopped rice straw by weight. The concentrate comprised 20% ground barley, 35% ground

yellow corn, 20% wheat bran, 17% defatted rice bran, 6% soybean meal, 1% NaCl, and 1% calcium carbonate (as-fed basis). In addition, roughage (in the form of green forage, silage, or hay) and water are supplied ad libitum. A unique number assigned by the Wagyu Registry Association, which maintains pedigree records, identifies animals. Information available is animal name and number, parental identifications, and date and place of birth. Traits included in this study were birth weight and nine consecutive monthly weights up to 356 d of age. There were few records after 356 d, and these were eliminated to avoid computational problems due to small numbers of records per subclass. Records with implausible dates or weights were also eliminated. The edited data set included 11,815 weights from 2,394 calves, offspring of 45 sires, and 631 dams. Calves were born year round. All animals had records for birth weight. The number of age subclasses including birth weight was 269. Contemporary groups (CG) were defined as year and season of birth-sex of calf. The number of animals in the relationship matrix was 3,082. All calves and dams had their parents identified. The percentage of dams with at least two progeny was 90. There was some overlapping of ages for different measurements. Figure 1 shows the distribution of weight recordings over age in days. Table 1 contains number of records, unadjusted means, standard deviations, and CV for the 10 consecutive weights and their corresponding age subclasses. Figure 2 depicts BW means throughout the complete test period.

Random Regression Model

The model considered for fitting repeated weights of calves included parity of dam as a fixed effect and fixed regressions of weights on fourth-order orthogonal Leg-

Table 1. Number of records, unadjusted means, SD, and CV of the 10 weight intervals (W1 to W10) and their corresponding age subclasses

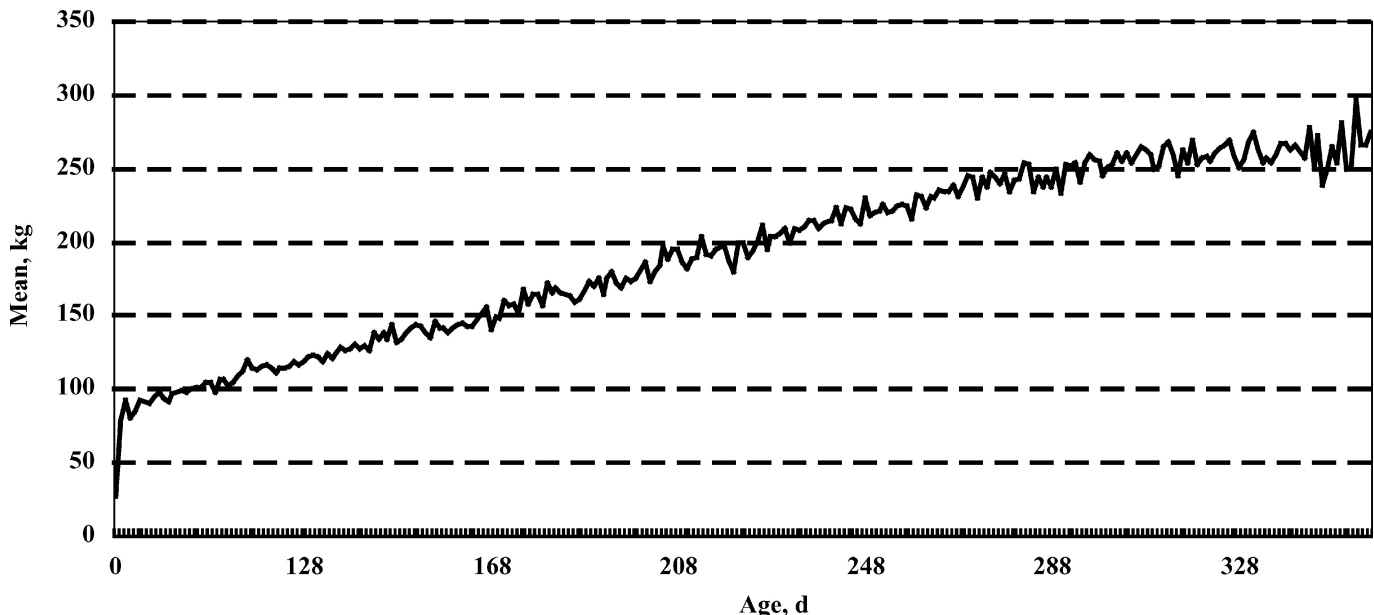
Interval	No.	Weight, kg			Age, d		
		Mean	SD	CV	Mean	SD	CV
W1 ^a	2,394	27.45	4.79	0.17	—	—	—
W2	1,545	105.26	21.49	0.20	112.51	16.94	0.15
W3	1,194	128.24	28.46	0.22	135.78	13.59	0.10
W4	1,246	151.02	31.87	0.21	165.29	15.71	0.10
W5	1,243	175.57	35.20	0.20	194.81	18.31	0.09
W6	1,213	201.14	37.34	0.19	224.12	18.20	0.08
W7	1,146	223.38	38.82	0.17	253.77	19.03	0.07
W8	919	240.46	38.12	0.16	280.81	18.19	0.06
W9	623	252.78	33.62	0.13	305.38	19.72	0.06
W10	292	257.74	33.66	0.13	326.06	20.41	0.06
Total	11,815	147.40	81.00		159.99	100.61	

^aW1 is birth weight.

endre polynomials of actual day of age for CG effects. Random regressions on fourth-order Legendre polynomials were included for animal additive genetic and animal permanent environmental effects, whereas third-order Legendre polynomials were used for maternal genetic and maternal permanent environmental effects. The model was as follows:

$$\begin{aligned}
 y_{ij} = & \sum_{n=1}^9 b_{n(j)} P_n + \sum_{m=0}^{N_G-1} \beta_{m(j)} \phi_m(t_{ij}) \\
 & + \sum_{m=0}^{N_G-1} \alpha_m \phi_m(t_{ij}) + \sum_{m=0}^{N_P-1} \gamma_m \phi_m(t_{ij}) \\
 & + \sum_{m=0}^{N_G-1} \delta_m \phi_m(t_{ij}) + \sum_{m=0}^{N_P-1} \tau_m \phi_m(t_{ij}) + \varepsilon_{ij}
 \end{aligned}$$

where y_{ij} is the j th weight of the i th calf, $b_{n(j)}$ is the fixed linear regression coefficient of the n th parity for the j th measurement, P_n is the n th parity of dam effect, t_{ij} is the ij th actual day of age at recording for which Legendre polynomials are defined, standardized to the range -1 to $+1$, and $\phi_m(t_{ij})$ is the corresponding m th Legendre polynomials, β_m is the m th fixed regression coefficient for CG, α_m , γ_m , δ_m , and τ_m are the m th-order random regression coefficients for animal additive genetic (**G**), maternal genetic (**M**), animal permanent environmental (**P**), and maternal permanent environmental (**C**) effects, respectively, N_G and N_P denote the orders of fit ($G = 4$ and $P = 3$), and ε_{ij} is the ij th temporary random environmental effect (residual) that was assumed to be independently distributed with heterogeneous variances. Heterogeneity of variances was modeled as a step function of the covariable, defining $e =$

**Figure 2.** Mean weights from birth to 356 d of age.

10 classes, including a separate class for birth weight, (0, 1 to 90, 91 to 120, 121 to 150, 151 to 180, 181 to 210, 211 to 240, 241 to 270, 271 to 300, and 301 to 356 d). The ranges specified assumed that a separate error variance needed to be fitted for records taken at birth (0 d), and subsequently every month (30 d), except for the second and the last classes, which span 90 and 56 d, respectively.

The model written in matrix notation was:

$$\mathbf{Y} = \mathbf{X}\beta + \mathbf{Z}_1\alpha + \mathbf{Z}_2\gamma + \mathbf{Z}_3\delta + \mathbf{Z}_4\tau + \mathbf{e}$$

where y is the vector of records; β is the vector of fixed effects, including parity of dam and CG; α , γ , δ , and τ are vectors of animal additive genetic, maternal genetic, animal permanent environmental, and maternal permanent environmental effects, respectively; \mathbf{X} is an incidence matrix for fixed effects; \mathbf{Z}_1 , \mathbf{Z}_2 , \mathbf{Z}_3 , and \mathbf{Z}_4 are incidence matrices for G, M, P, and C effects, respectively; and \mathbf{e} is the residual vector.

The set of orthogonal polynomials for age can be arranged in the following matrix (Φ):

$$\Phi = \mathbf{M}\mathbf{A}$$

where \mathbf{M} is a matrix containing the polynomials of the corresponding standardized ages and \mathbf{A} is a matrix containing the coefficients of the Legendre polynomials of a given order. The elements of the additive genetic covariance matrix \mathbf{G} can be expressed as follows:

$$\mathbf{G} = \Phi\mathbf{K}\Phi' = \mathbf{M}(\mathbf{A}\mathbf{K}\mathbf{A}')\mathbf{M}'$$

where \mathbf{K} is a matrix of coefficients that define the covariance function. Covariance matrices for the other random effects (M, P, and C) can be expressed in similar fashion.

The first and second moments of the model are:

$$\mathbf{E}(\mathbf{y}) = \mathbf{X}\beta$$

$$\mathbf{Var}(\mathbf{y}) = \mathbf{Z}_1(\mathbf{K}_\alpha \otimes \mathbf{A})\mathbf{Z}_1' + \mathbf{Z}_2(\mathbf{K}_\gamma \otimes \mathbf{A})\mathbf{Z}_2' + \mathbf{Z}_3(\mathbf{K}_\delta \otimes \mathbf{I})\mathbf{Z}_3' + \mathbf{Z}_4(\mathbf{K}_\tau \otimes \mathbf{I})\mathbf{Z}_4' + \mathbf{R}$$

where \mathbf{A} and \mathbf{I} are the numerator relationship matrix and the identity matrix, respectively; \mathbf{K}_α , \mathbf{K}_γ , \mathbf{K}_δ , and \mathbf{K}_τ are the matrices of coefficients of the covariance functions for animal additive genetic, maternal genetic, animal permanent environmental, and maternal permanent environmental effects, with dimensions equal to the order of the covariances matrices in the analysis; and \mathbf{R} is the variance of the residual effects, which is a diagonal matrix allowing for different variances for each age t .

The data allowed permanent environmental and maternal genetic effects to be separated, as there was a large number of dams with more than one progeny with records. The random regression model (**RRM**) was fitted on Legendre polynomials of age. A fourth-order poly-

nomial was fitted for G and P effects, whereas a third-order polynomial was fitted to M and C effects. A preliminary analysis indicated that higher order polynomials were unnecessary. Covariances between random regression coefficients pertaining to different random factors were assumed to be zero. Matrices \mathbf{K}_α , \mathbf{K}_γ , \mathbf{K}_δ , and \mathbf{K}_τ corresponding to G, M, P, and C effects were estimated as covariance matrices for the corresponding random regression coefficients. Elements of \mathbf{K}_α , \mathbf{K}_γ , \mathbf{K}_δ , or \mathbf{K}_τ are the coefficients of the covariance functions defining covariances between any two ages in the data for the corresponding random effect (Meyer and Hill, 1997). Thus, the estimated covariance for the r th random regression (r represents α , γ , δ , or τ) for animal i at ages t_{ij} and t_{ij}' was as follows:

$$\Psi_r = \sum_{m=0}^{N_Q-1} \sum_{n=0}^{N_Q-1} \phi_m(t_{ij})\phi_n(t_{ij}')\kappa_{rnm}$$

where κ_{rnm} is the m nth element of \mathbf{K}_r (Kirkpatrick, et al. 1990). According to Kirkpatrick and Heckman (1989), fewer dimensions of \mathbf{K}_r often produce a good approximation of Ψ_r , and eigenvalues and eigenvectors of \mathbf{K}_r can be used as approximations of eigenvalues and eigenfunctions of Ψ_r .

Statistical Analyses

Covariances between random regression coefficients of \mathbf{K}_α , \mathbf{K}_δ , \mathbf{K}_γ , or \mathbf{K}_τ were estimated by Bayesian procedures. Gibbs sampler was used to obtain marginal posterior distributions for all parameters of the model.

Estimates were obtained by RRGIBBS program (Meyer, 2002). This program generates a Markov chain for the parameters in the model, sampling from conditional posterior distributions as described by Jamrozik and Schaeffer (1997) and Rekaya et al. (1999). It allows the Bayesian estimation of (co)variance components for random regression models using Gibbs sampling. Convergence of the Gibbs chain was monitored by visual inspection of plots of samples for selected components. Flat priors were assumed for fixed location parameters. Prior inverted Wishart distributions were assumed for G, M, P, and C effects, and prior independent scaled inverted χ^2 distributions were assumed for residual variances. The hyperparameters of the inverted Wishart distributions (ν and \mathbf{S}) were -5 and 0 for G and P, and -4 and 0 for M and C effects, whereas those of the scaled inverted χ^2 distributions (ν and s^2) were equal to -2 and 0 , making the distributions flat (i.e., uninformative). After a burn-in period of 20,000 samples, 270,000 samples were used to estimate means for all (co)variances of the RRM. From the estimates of the random regression parameters, variance and covariance components and genetic and phenotypic parameters were calculated for the ages of interest (i.e., at birth, 90, 120, 150, 180, 210, 240, 270, 300, 330, and 356 d). These ages were chosen because they almost

Table 2. Estimated coefficient matrices (K_r) of the covariance function and the corresponding eigenvalues with their percent contribution to the total variation and the correlation between them (above diagonal) for additive genetic (G), maternal genetic (M), animal permanent environment (P), and maternal permanent environment (C) effects

Effect	Coefficient of K_r^a				Eigenvalue	Contribution %
	L_0	L_1	L_2	L_3		
G						
L_0	737.43	0.89	-0.59	-0.04	835.89	92.91
L_1	245.67	103.93	-0.31	-0.09	43.73	4.86
L_2	-105.37	-20.83	43.41	-0.60	19.65	2.18
L_3	-3.92	-3.59	15.25	14.96	0.45	0.05
M						
L_0	93.65	0.78	-0.56		107.29	90.80
L_1	32.63	18.67	0.07		10.75	9.10
L_2	-13.10	0.71	5.84		0.12	0.10
P						
L_0	437.05	0.95	-0.39	-0.62	595.93	94.88
L_1	253.29	161.33	-0.31	-0.75	17.14	2.73
L_2	-32.33	-15.80	15.97	0.63	14.65	2.33
L_3	-48.00	-35.11	9.38	13.76	0.40	0.06
C						
L_0	45.30	0.74	-0.30		53.52	86.03
L_1	18.05	13.19	0.40		8.60	13.82
L_2	-3.96	2.82	3.73		0.09	0.15

^a L_0 is the intercept, L_1 is the linear term, L_2 is the quadratic, and L_3 is the cubic term.

cover the age trajectory. Heritability estimate at age i was calculated as follows:

$$h_i^2 = \sigma_a^2 / \sigma_p^2$$

where σ_a^2 is the additive genetic variance and σ_p^2 is the phenotypic variance, which is the sum of additive genetic, maternal genetic, direct permanent environmental, maternal permanent environmental, and error variances at age i . Ratios of maternal genetic, direct permanent environmental, and maternal permanent environmental variances to phenotypic variances were expressed in similar fashion. Posterior standard deviations of the estimated genetic and phenotypic parameters were estimated by the Delta method as described by Lynch and Walsh (1997).

Results and Discussion

Covariance Functions

Table 2 presents the estimated coefficient matrices (K_a , K_m , K_p , and K_c) of the covariance functions, their respective eigenvalues, their proportions out of the total variation and the correlations between the coefficients for G, P, M, and C effects. There were strong positive correlations between the intercept and the linear coefficients of the different effects. The correlations between the intercept and the linear coefficients of G and P were higher than those of M and C. The correlations between the intercept and the quadratic regression coefficients of all effects were negative, ranging from low (P and C) to moderate (G and M). Albuquerque and Meyer (2001a)

described similar results. They reported moderate to high positive correlations between intercept and linear coefficients and low negative correlations between intercept and quadratic regression coefficients, when fitting random regression for the growth curve from birth to 630 d of age in Nelore cattle.

Strong correlations between random regression coefficients caused one eigenvalue of the estimated covariance matrices for G, P, M, or C to be essentially zero. Eigenfunctions, estimated from the eigenvectors of the genetic covariance matrix provide an insight into the effects of selection across the growth trajectory (Kirkpatrick et al., 1990). A large eigenvalue indicates that a rapid change corresponding to that eigenfunction will take place, whereas a small or zero eigenvalue indicates that the change will be slow. The first three eigenvalues of G and P and the first two eigenvalues of M and C explained a large fraction of the total variation. The fourth-order polynomial for G and P and the third-order polynomial for M and C explained a very small fraction of the total variation. Albuquerque and Meyer (2001a) reported similar results for the decomposition of the covariance function. In their study, the first three eigenfunctions explained most of the variation in G, M, P, and C effects (100, 100, 97, and 100%, respectively). Here, the first three eigenvalues and the first two eigenvalues explained 100% of the total variation in G and P, and M and C effects, which is in close agreement with the corresponding results of Albuquerque and Meyer (2001a). Similarly, the results of Schenkel et al. (2002) on weight gain of station-tested beef bulls indicated that the first three eigenvalues explained 100% of the total variations of G and P effects; however, the orders

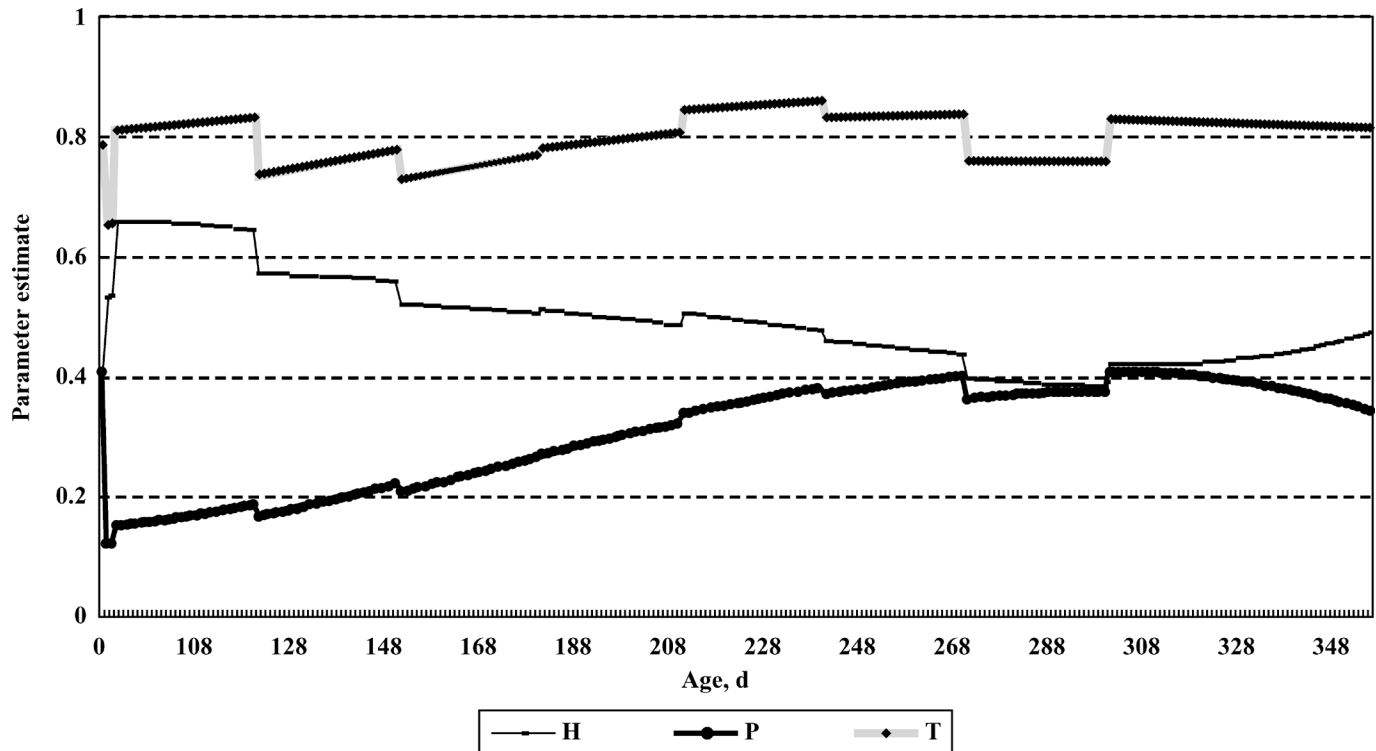


Figure 3. Estimates of direct heritability (H), direct permanent environment ratio (P), and repeatability (T) of weights of Japanese Black calves measured from birth to 356 d of age.

of Legendre polynomials used in both studies are different from those applied here. When fitting different orders of Legendre polynomials for analyzing growth of Nelore cattle, Nobre et al. (2003) also found similar results to those reported here, indicating that the first three eigenvalues explained 93, 100, and 100% of the total variation in the additive genetic, direct permanent environmental, and maternal effects, respectively. In their study, the orders of Legendre polynomials fitted to G, M, and P effects were 8, 3, and 3, respectively. They further stated that small eigenvalues indicated that parameters from random regression models could be poorly conditioned and suggested the need for reducing the number of effects in the model.

Animal Parameters

Estimates of heritability (h^2), ratio of animal permanent environmental variance to phenotypic variance (p^2), and repeatability ($t = h^2 + p^2$) for the whole period are shown in Figure 3. Estimates of h^2 , genetic (r_G) and phenotypic (r_{PH}) correlations for weights at 0, 90, 120, 150, 180, 210, 240, 270, 300, 330, and 356 d of age are presented in Table 3. Estimates of h^2 increased from 0.38 at birth up to 0.66 at 96 d, fluctuated slightly around this value up to 120 d, then decreased to 0.38 at 300 d and increased again up to 0.47 at 356 d. The estimates of h^2 were consistently higher due to higher estimates of σ_A^2 (data not shown). Residual variances for weights at all calf ages are shown at the bottom of

Table 3. Residual variances were heterogeneous across ages. Their contributions to the total variation for weight ranged from 4 to 24%.

Estimates of p^2 and direct permanent environmental correlations (r_P) for the chosen ages are shown in Table 4. The direct permanent environmental ratio (p^2) decreased from 0.41 at birth to 0.12 at 90 d, and then increased gradually up to 0.40 at 270 d, where it oscillated around this value up to the end. The observed patterns of h^2 and p^2 across the age trajectory here are different from those reported by Meyer (2001), who found that h^2 estimates decreased after birth, with a minimum at about 100 d of age, whereas p^2 estimates increased with age. Estimates of repeatability (t) exhibited less change with age than h^2 or p^2 (Figure 3). This indicates a negative sampling correlation between additive genetic and direct permanent environmental effects ($r = -0.90$).

The repeatability estimate of birth weight was 0.79. After birth, the values fluctuated across the age trajectory with a minimum of 0.65 at 90 d and a maximum of 0.86 at 240 d. Meyer (2001) gave approximately similar t values for BW of Australian beef cattle. She reported an increase up to 0.82 at approximately 1 mo of age, followed by a decrease to a minimum of 0.57 at approximately 4 mo of age and an increase again up to 0.80 at 240 d of age. Meyer (2001) described a similar pattern for estimates of t to that observed here (i.e., changes in t with age were smaller than those for h^2 or p^2). Also using a Bayesian procedure with Gibbs

Table 3. Estimates of heritability (diagonal), and genetic (above diagonal) and phenotypic (below diagonal) correlations for weights at 0, 90, 120, 150, 180, 210, 240, 270, 300, 330, and 356 d of age

Age, d	0	90	120	150	180	210	240	270	300	330	356
0	0.38 ± 0.06	0.70 ± 0.07	0.72 ± 0.07	0.74 ± 0.07	0.75 ± 0.08	0.76 ± 0.08	0.77 ± 0.08	0.77 ± 0.07	0.76 ± 0.07	0.69 ± 0.07	0.57 ± 0.07
90	0.47 ± 0.12	0.53 ± 0.07	0.99 ± 0.09	0.97 ± 0.09	0.94 ± 0.09	0.92 ± 0.09	0.90 ± 0.09	0.89 ± 0.09	0.88 ± 0.09	0.85 ± 0.09	0.76 ± 0.08
120	0.54 ± 0.12	0.84 ± 0.13	0.65 ± 0.07	0.99 ± 0.10	0.98 ± 0.10	0.96 ± 0.10	0.94 ± 0.10	0.93 ± 0.10	0.91 ± 0.09	0.86 ± 0.09	0.74 ± 0.09
150	0.53 ± 0.12	0.78 ± 0.13	0.91 ± 0.12	0.56 ± 0.08	0.99 ± 0.10	0.98 ± 0.10	0.97 ± 0.10	0.96 ± 0.10	0.93 ± 0.10	0.85 ± 0.10	0.71 ± 0.09
180	0.53 ± 0.12	0.73 ± 0.14	0.87 ± 0.12	0.87 ± 0.13	0.51 ± 0.08	1.00 ± 0.11	0.99 ± 0.11	0.98 ± 0.11	0.94 ± 0.10	0.85 ± 0.10	0.69 ± 0.10
210	0.55 ± 0.13	0.70 ± 0.14	0.86 ± 0.12	0.87 ± 0.13	0.89 ± 0.13	0.49 ± 0.08	1.00 ± 0.11	0.99 ± 0.10	0.95 ± 0.10	0.86 ± 0.10	0.69 ± 0.09
240	0.57 ± 0.12	0.69 ± 0.14	0.85 ± 0.12	0.87 ± 0.13	0.87 ± 0.12	0.92 ± 0.12	0.48 ± 0.08	1.00 ± 0.10	0.97 ± 0.10	0.88 ± 0.09	0.71 ± 0.09
270	0.58 ± 0.12	0.66 ± 0.13	0.82 ± 0.12	0.84 ± 0.13	0.86 ± 0.12	0.89 ± 0.12	0.93 ± 0.10	0.44 ± 0.07	0.99 ± 0.08	0.92 ± 0.08	0.77 ± 0.07
300	0.56 ± 0.12	0.62 ± 0.13	0.76 ± 0.12	0.77 ± 0.12	0.79 ± 0.12	0.83 ± 0.12	0.87 ± 0.10	0.87 ± 0.09	0.38 ± 0.07	0.97 ± 0.05	0.86 ± 0.05
330	0.59 ± 0.12	0.63 ± 0.13	0.75 ± 0.12	0.76 ± 0.12	0.80 ± 0.12	0.80 ± 0.11	0.85 ± 0.10	0.87 ± 0.09	0.86 ± 0.07	0.43 ± 0.07	0.96 ± 0.03
356	0.55 ± 0.11	0.59 ± 0.12	0.67 ± 0.11	0.66 ± 0.11	0.66 ± 0.11	0.68 ± 0.11	0.73 ± 0.09	0.76 ± 0.08	0.79 ± 0.06	0.90 ± 0.03	0.47 ± 0.07
σ_e^2 , kg ² a	3.3 (11)	103.0 (24)	21.5 (4)	87.4 (12)	141.2 (13)	130.4 (11)	76.6 (6)	121.5 (8)	280.7 (16)	128.4 (8)	128.4 (7)

^a σ_e^2 are the error variance components for weights at the given ages (percentage of the total variance).

Table 4. Estimates of animal permanent environment ratios (p^2 , diagonal) and correlations (above diagonal) for weights at 0, 90, 120, 150, 180, 210, 240, 270, 300, 330, and 356 d of age

Age, d	0	90	120	150	180	210	240	270	300	330	356
0	0.41 ± 0.07	0.64 ± 0.07	0.63 ± 0.07	0.62 ± 0.07	0.61 ± 0.07	0.60 ± 0.07	0.59 ± 0.07	0.56 ± 0.07	0.52 ± 0.06	0.47 ± 0.06	0.40 ± 0.06
90	0.12 ± 0.08	0.12 ± 0.08	1.00 ± 0.15	0.99 ± 0.16	0.98 ± 0.16	0.96 ± 0.16	0.92 ± 0.16	0.86 ± 0.15	0.77 ± 0.15	0.65 ± 0.15	0.53 ± 0.14
120			0.19 ± 0.08	1.00 ± 0.15	0.99 ± 0.15	0.97 ± 0.15	0.94 ± 0.16	0.89 ± 0.15	0.80 ± 0.15	0.69 ± 0.14	0.57 ± 0.14
150				0.22 ± 0.09	1.00 ± 0.15	0.99 ± 0.15	0.96 ± 0.15	0.91 ± 0.15	0.84 ± 0.14	0.74 ± 0.14	0.62 ± 0.13
180					0.27 ± 0.09	1.00 ± 0.14	0.98 ± 0.14	0.94 ± 0.14	0.88 ± 0.14	0.79 ± 0.13	0.68 ± 0.13
210						0.32 ± 0.09	0.99 ± 0.13	0.97 ± 0.13	0.92 ± 0.12	0.84 ± 0.12	0.75 ± 0.12
240							0.38 ± 0.09	0.99 ± 0.11	0.96 ± 0.10	0.90 ± 0.10	0.82 ± 0.10
270								0.40 ± 0.09	0.99 ± 0.08	0.95 ± 0.08	0.89 ± 0.08
300									0.37 ± 0.08	0.99 ± 0.05	0.95 ± 0.05
330										0.39 ± 0.08	0.99 ± 0.02
356											0.34 ± 0.08

sampler, Schenkel et al. (2002) reported h^2 estimates of 0.37, 0.39, and 0.40 for BW at 84, 112, and 140 d of age, whereas their p^2 estimates were 0.39, 0.40, and 0.41, respectively. They indicated that h^2 and p^2 increased with time. The trend for changes of h^2 and p^2 with age is different from that reported here. In addition, their h^2 estimates are lower than the corresponding estimates of 0.53, 0.65, and 0.56 reported here at comparable ages (i.e., 90, 120, and 150 d of age), whereas their p^2 estimates are higher than the corresponding estimates presented here (0.12, 0.19, and 0.22, respectively). The differences could be due to the different models used, sizes of data, and/or breed differences.

Information on parameter estimates for growth of Japanese black cattle is scarce. All estimates found in the literature were calculated by methods other than random regression. Estimates were variable, reflecting the different genetic backgrounds of Japanese Black cattle subpopulations. Sasaki et al. (1982) and Kitamura et al. (1999) reported lower h^2 values for BW at 210 and 252 d of age, accounting for 0.20 and 0.22, respectively, compared with the estimates of 0.32 and 0.38 obtained here at comparable ages (210 and 240 d, respectively). Mukai et al. (2000) estimated h^2 values for data collected from three prefectures on BW of Japanese Black calves at birth and 300 d of age. Their estimates ranged between 0.19 and 0.39 and between 0.25 and 0.30 for both traits, respectively. These estimates are in partial agreement with the h^2 value of 0.38 reported here at the same ages (Table 3). On the other hand, Ujiie et al. (1990) reported markedly higher h^2 estimate (0.82) for final BW at 240 d of Japanese Black calves compared with the corresponding estimate of 0.48 obtained here. Treating BW at different ages as different traits, Shimada et al. (1995) reported h^2 estimates accounting for 0.61, 0.29, 0.28, 0.30, and 0.33 for BW of Japanese Black calves at birth, 90, 120, 150, and 180 d of age. Although their h^2 estimate of birth weight is higher than the corresponding value (0.38) reported here, the other h^2 estimates were lower. The discrepancy observed between the estimates reported in the literature, concerning growth of the Japanese Black cattle, and those of the present study could be attributed to the different methods of analyses, different sizes of data, and/or the genetic diversity of the breed among subpopulations.

In general, genetic, phenotypic, and environmental correlations decreased as the interval between ages increased. Genetic correlations between birth weight and other weights were lower than the corresponding values observed between weights at adjacent ages, suggesting that birth weight is not under the same genetic control as weights at older ages. Albuquerque and Meyer (2001a) reported similar findings; correlations of birth weight with weights taken at other ages were lower than those between weights measured at adjacent ages. Our results are also consistent with the results obtained by Meyer (2001), Huisman et al. (2002), and Schenkel et al. (2002), who found that correlations between adja-

cent ages were high and decreased as the interval between ages increased. Genetic correlations between weights at 180 and 210 d, between weights at 210 and 240 d, and between weights at 240 and 270 d approached unity. The genetic correlations were all positive, suggesting that selection for weight at an early age would have a positive effect on weights at later ages. Working on Japanese Black cattle, Mukai et al. (2000) reported genetic correlations between weights at birth and at 300 d of age ranging between 0.40 and 0.87. Our r_G estimate for this trait (0.78) falls within this range.

Phenotypic correlations were lower than those due to additive genetic, with a minimum of 0.47 between weights at birth and at 90 d, and a maximum of 0.93 between weights at 240 d and 270 d of age. Their pattern, however, was similar (i.e., correlations between adjacent ages were high and decreased as the intervals increased).

Animal permanent environmental correlations between weights at birth and other weights were lower than those among weights at other ages. They were slightly lower than those due to additive genetic, but they were higher than the phenotypic ones, with a minimum of 0.40 between weights at birth and 356 d, and a maximum approached unity between weights at 90 d and 120 d, between 120 d and 150 d, between 150 d and 180 d and between 180 d and 210 d of age.

Maternal Parameters

Maternal genetic effects of growth traits are known to be important in beef cattle. Partitioning maternal effects into maternal genetic and maternal permanent environmental effects presents some difficulties, according to Willham (1980), Gerstmayr (1992), and Meyer (1992). There is evidence that most of the maternal variation would be accounted for by including only one of the maternal effects (maternal genetic or maternal permanent environmental), Meyer (1992).

Maternal heritability (m^2) and maternal permanent environmental estimates (c^2) for the whole period are presented in Figure 4. Estimates of m^2 and maternal genetic (r_M) correlations for weights at 0, 90, 120, 150, 180, 210, 240, 270, 300, 330, and 356 d of age are presented in Table 5. Estimates of c^2 and maternal permanent environmental (r_M) correlations for the aforementioned ages are shown in Table 6. Maternal heritabilities increased from 0.04 at birth up to 0.09 at 120 d, and were around 0.06 thereafter. The c^2 estimates were approximately equal over the age ranges, accounting for 0.03 of variance. The results of Meyer et al. (1993) indicated that maternal effect might affect postweaning growth as a carryover effect from weaning weight. If this is the case, maternal effect might have some influence on postweaning growth. Meyer (1992) presented an extensive list of literature estimates of maternal heritability and showed that estimates for postweaning gain and final weight are generally low, ranging be-

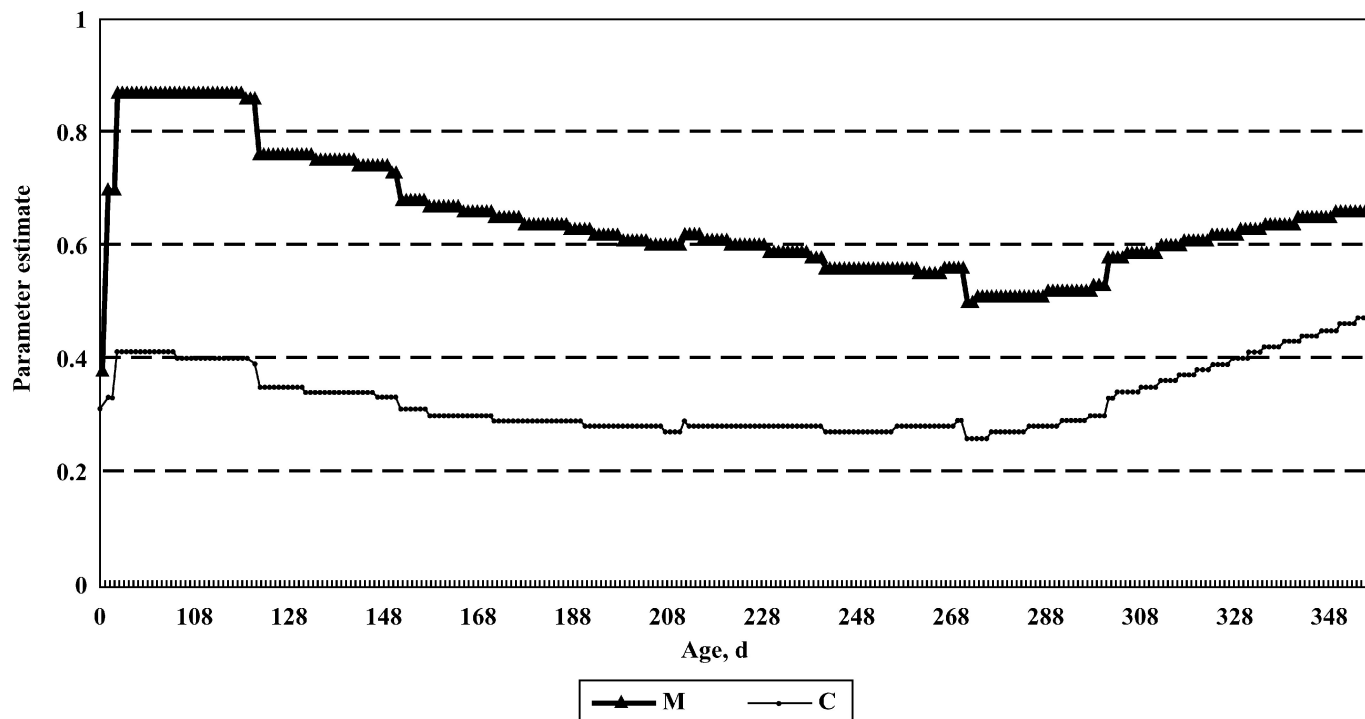


Figure 4. Estimates of maternal heritability (M) and maternal permanent environment ratio (C) for weights of Japanese Black calves measured from birth to 35.

tween 0.01 and 0.09. The m^2 estimates for postweaning growth, reported here, are in agreement with the values reviewed by Meyer (1992). Waldron et al. (1993) estimated m^2 and c^2 for weight traits in one Hereford and two Angus experimental herds in Australia, using a univariate animal model. The m^2 values reported in their study were 0.07, 0.13, 0.04, and 0.04 for weights at birth, weaning, yearling, and 18 mo of age, respectively, and the respective c^2 estimates were 0.05, 0.15, 0.03, and 0.01. The corresponding m^2 and c^2 estimates reported here are in partial agreement with their findings. Furthermore, they concluded that m^2 progressively decreased in importance with time after weaning. Our results indicated that maternal effect decreased from 0.09 at 120 d of age to 0.06 at 180 d of age (weaning age) and remained constant around this value up to the end of the age trajectory. Furthermore, Albuquerque and Meyer (2001b) reported results similar to those obtained here. They indicated that m^2 increased from 0.01 at birth to 0.07 and 0.08 at 180 d and 210 d, after which estimates decreased slowly with age. Conversely, Meyer (2001) reported c^2 estimates higher than those of m^2 , noting that the later estimates varied slightly over the range of ages. In contrast, our m^2 estimates were slightly larger than those of c^2 .

Working with Japanese Black calves, Shimada et al. (1995) reported m^2 values of 0.09, 0.32, 0.35, 0.37, and 0.38 weights at birth, weaning, yearling, and 18 mo of age, whereas their estimates of c^2 were 0.01, 0.03, 0.01, 0, and 0.01, respectively. Their m^2 estimates reported were higher than the corresponding estimates reported

here, whereas the c^2 estimates partially agree with our results. Further, their m^2 estimates were higher than those of c^2 and this is in agreement with the corresponding findings here. Kitamura et al. (1999) reported m^2 and c^2 values of 0.06 and 0.07 for calf market weight at 250 d of age of Japanese Black calves, respectively. Using a REML procedure under an animal model, Mukai et al. (2000) obtained m^2 values ranging between 0.16 and 0.28 and between 0.10 and 0.18 for birth and market (300 d) weights of Japanese Black cattle, respectively. The m^2 estimate reported by Kitamura et al. (1999) is in close agreement with our estimate of 0.06 for 240 d of age, whereas the m^2 estimates reported by Mukai et al. (2000) are higher than the estimates of 0.04 and 0.06 reported here at similar ages. On the other hand, the c^2 estimate given by Kitamura et al. (1999) is higher than that reported here at a comparable age (0.03).

Similar patterns to the estimates of r_G and r_P were also observed for the maternal genetic (r_M) and maternal permanent environment (r_C) correlations (i.e., estimates decreased with increasing time between measurements). Estimates of r_M were lower than those of r_C . Although r_M estimates were lower than those due to additive genetic, r_C estimates were approximately equal to those of r_P . The estimates of r_M and r_C of birth weight with the other weights were lower than those of weights taken at older ages. The lowest estimates of r_M and r_C were between birth weight and weight at 356 d of age, accounting for 0.19 and 0.35, respectively. Estimates of r_M between weights at 210 d and 240 d

and between 240 d and 270 d were the highest (0.98), whereas r_C estimates between weights at 90 d and 120 d and between 120 d and 150 d approached unity. There were positive and strong estimates of r_M and r_C between weights at adjacent ages, starting from 3 mo, indicating that maternal effects were essentially identical.

General Discussion

To improve growth performance of Japanese Black cattle, it is necessary to appropriately model the genetic and environmental factors contributing to the performance over the test period. By using random regression, it is possible to fit a more complete model than with traditional methods. Random regression allows the trajectory of genetic and environmental parameters over the test period to be investigated. Random regression models accommodate time dependent changes in the genetic and environmental factors; however, the key issues in application of RRM to growth traits are the number of times individuals need to be measured, at what times in their lives, and what will be the upper age range. Here, covariance matrices for G, P, M, and C were estimated by Bayesian procedures via Gibbs sampling. As indicated by the eigenvalues, the intercept and the linear coefficients accounted for most of the variance in weights of calves. The quadratic and cubic terms seem to still be relevant for additive genetic and direct permanent environmental effects, as well as the quadratic term for the maternal genetic and maternal permanent environmental effects.

Information obtained here is useful for determining the optimal length of test period, to assess the role of environmental effects along the test period, and to reflect to what extent and how genetic changes in performance over time can be achieved by selection. The random regression model allowed the comparison of different testing ages and the results showed that h^2 and p^2 of weights taken at the different ages were moderate to high, whereas those due to maternal genetic and maternal permanent environment were low, but significant. In beef cattle, maternal effects are important for growth traits until weaning although significant effects remain thereafter.

Direct and maternal heritabilities were highest at 120 d. Direct heritability estimates of weights at all ages were moderate to high, indicating that selection on weight at any age is feasible. Genetic correlations across ages were positive. Consequently, selection for increased weight at any age would tend to increase weights throughout the entire growth period. Another important consequence is that preweaning weights can be used to select for weights at later ages.

Genetic evaluation of growth of Japanese Black cattle often considers three different traits, namely birth weight, starting weight, and final weight at fattening period. Obviously, the last two weights are taken at arbitrary ages and estimating their genetic parameters will have little effect on growth improvement in the

breed. However, random regression models using records taken at different ages would be more appropriate because they would allow the use of more weights and, hence, more accuracy will be achieved.

Differences between estimated genetic parameters reported in the literature on Japanese Black cattle and those estimated here could be attributed to different methods of estimation used and to the use of data sets from different subpopulations of Japanese Black cattle with distinct genetic backgrounds. In particular, inferences from the results of this study cannot be extrapolated to the complete population of Japanese Black cattle because the data used represent a single herd from only one prefecture.

Implications

The present study is the first attempt to model growth of Japanese Black calves using random regression. By using random regression models, it is possible to determine nonlinear changes in genetic and environmental effects. Results indicated that direct heritability estimates of weights taken at different ages were high, whereas those due to maternal effect were low, but significant. The largest direct and maternal heritabilities were for weight at 120 d of age. Genetic and maternal genetic correlations between weights taken at adjacent ages were positive and strong. It is suggested that preweaning growth could be used to select for weights at later ages, which will have a positive effect on weights at later ages. Further studies on mothering ability and milk production of dams are warranted.

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