

GENETIC ANALYSIS OF FEMALE WEIGHTS VIA RANDOM REGRESSION AND MULTIPLE TRAIT MODELS IN A MULTIBREED BEEF CATTLE POPULATION



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SUMMARY

The objective of this research was to obtain REML estimates of covariance functions, and variance ratios for weights taken during the productive life of beef cows from a multibreed Angus-Brahman population using random regression models. The dataset contained 40,009 weights from 1,792 cows. Genetic analyses were performed using random regression models (RRM) with Legendre polynomials (LP). Reference heritabilities at birth, weaning, and 1, 2, 3, 4 and 5 years of age were estimated using 2-trait mixed models (MTM). Fixed effects for RRM were contemporary group subclass (year-period of measurement), and cubic LP covariates for age of female, interactions between age of female and expected Brahman fractions of female and her dam, and direct and maternal heterozygosity. Random effects were cubic LP age covariates for direct and maternal additive genetic and direct permanent environment, and residual. Two-trait models for weights up to one year of age had contemporary group (year-period of measurement subclass), age of female, expected Brahman fractions of female and her dam, direct and maternal heterozygosity as fixed effects. Random effects were direct and maternal additive genetic, maternal permanent environment, and residual effects. Two-trait models for weights taken after one year of age ignored maternal effects. Legendre polynomials behaved badly at extreme ages and variance-ratio functions were very sensitive to polynomial order. *The MTM direct heritability estimates were similar to RRM estimates, except for birth weight (0.3 ± 0.06 for MTM and 0.02 ± 0.02 for RRM). The RRM direct heritability values increased from near zero at birth to 0.59 ± 0.05 at 764 d and then decreased to 0.39 ± 0.09 at 2,500 d of age. Maternal heritability reached its maximum value at 222 d (0.09 ± 0.02) and decreased towards 2,500 d (0.02 ± 0.05). Direct permanent environment variance ratios increased from 0.04 ± 0.02 at birth to 0.57 ± 0.08 at 2,500 d of age. Results here suggested that this dataset would need to be reanalyzed using functions less sensitive at the extremes (e.g., splines) to obtain reasonable estimates of variance ratios over the complete range of ages.*

INTRODUCTION

The Southeastern region of the US has 20% of the country's total population of beef cattle and 26% of beef cattle farms (USDA-NASS, 2007). Producers commonly use Angus and crosses of Angus and Brahman in Florida and the Gulf Coast region. The University of Florida developed an Angus-Brahman multibreed population to carry out genetic analyses in a population representative of this region. Mature body weight in beef cows affects the profitability of beef herds. Heavier cows are less efficient at reproductive, physiological and economical levels (Morris *et al.*, 1977). Random regression models are used for analyses of traits that follow a trajectory (Meyer, 1998). These models do not require adjustment of data unlike multiple-trait models, thus they utilize all available data. In addition, because continuous functions of time are used to model the trajectory, covariance components, genetic parameters and breeding values can be computed at any age between the minimum and maximum ages at which data were collected (Kirkpatrick *et al.*, 1990). Legendre polynomials are functions commonly used in random regression models because they are orthogonal, flexible and easy to implement (Kirkpatrick *et al.* 1990; Meyer, 1998). However, RRM with LP are susceptible to numerical problems. Thus, multiple-trait models, which are less susceptible to numerical problems, could be used to obtain estimates of (co)variance components and genetic parameters to have reference values for estimates from RRM at specific ages (Nobre *et al.*, 2003). *The objective was to obtain REML estimates of covariance functions and variance ratios of live weights taken during the productive life of beef cows from a multibreed Angus-Brahman population using random regression models. Reference values of variance ratios for comparison purposes were estimated for weights at birth, weaning, and 1, 2, 3, 4, and 5 years of age using 2-trait mixed models.*

MATERIAL AND METHODS

Animals and Data
Animals were females from the Angus-Brahman multibreed herd of the University of Florida. They were born from 1986 to 2009. Breed groups were defined as follows: Angus, ¼ Angus ¾ Brahman, Brangus, ½ Angus ½ Brahman, ¼ Angus ¾ Brahman, and Brahman. Sires from each one of these breed groups were mated to dams of all breed groups using diallel mating system. The dataset contained live weight records collected at various ages during the productive life of females. Ages at which weights were recorded ranged from birth to 2500 days. The total number of animals was 1,792, the total number of live weight records was 40,009, and the average number of live weight records per animal was 22.33. The minimum number of records by animal was 4 and the maximum was 48. **Table 1** shows the number of cows included in this study according to the breed group of their sire and dam.

Table 1. Number of cows by breed group of sire x breed group of dam combination							
Breed group of dam	Breed group of sire						
	Angus	¼ A ¾ B	Brangus	½ A ½ B	¼ A ¾ B	Brahman	All
Angus	137	24	57	32	54	48	352
¼ A ¾ B	56	36	53	34	41	52	272
Brangus	20	12	135	16	27	20	230
½ A ½ B	84	39	76	41	73	70	383
¼ A ¾ B	41	22	19	25	32	42	181
Brahman	24	14	24	20	24	268	374
All	362	147	364	168	251	500	1,792

Feeding and Management
Cows and calves were kept on pastures of *Paspalum notatum* with free access to mineral supplementation (Lakeland Animal Nutrition, Lakeland, FL). Calves were weaned at approximately seven months of age. Cows and calves received supplementation of Bermuda grass (*Cynodon dactylon*) hay, cottonseed meal, urea and molasses during winter.
Genetic Analysis
Data were edited for erroneous and incomplete information using SAS (SAS Inst. Inc., Cary, NC, 2011). Random regression models with Legendre polynomials were used to obtain restricted maximum likelihood (REML) estimates of covariance functions and direct genetic, maternal genetic, and direct permanent environment ratios. The matrices of coefficients of covariance functions (Kirkpatrick *et al.*, 1990) were computed as the matrices of covariances between random regression coefficients of the RRM (Meyer and Hill, 1997).

The RRM model had contemporary group (year-period of measurement subclass), and cubic LP for age of animal, interactions between animal expected Brahman fraction by animal age, dam expected Brahman fraction by animal age, direct animal heterozygosity by animal age and maternal heterozygosity by animal age as fixed effects. Random effects were cubic LP age covariates for direct additive genetic, maternal genetic, and direct permanent environmental, and residual. Preliminary analysis compared models with different orders of LP and homogeneous or heterogeneous residual variances. *These analyses revealed a strong negative correlation between maternal additive genetic and environmental effects indicating that they could not be disentangled. Thus, only maternal additive genetic effects were considered.* Models were compared via Akaike's and Schwarz's Bayesian criteria and by considering the behavior of covariance components and variance ratios over time. The RRM with LP have been found to be susceptible to artifacts (Nobre *et al.*, 2003; Bohmanova *et al.*, 2005) and to be numerically unstable (Arango *et al.*, 2004). Thus, it has been suggested that multiple-trait models, which are less susceptible to numerical problems, should be used to obtain estimates of (co)variance components and genetic parameters in order to have reference values for estimates from RRM (Nobre *et al.*, 2003). Thus, 2-trait animal models were used to obtain REML estimates of (co)variance components and variance ratios for weights at 7 specific ages. The 2-trait mixed models included contemporary group (year-period subclass), individual and dam expected Brahman fractions, direct and maternal heterozygosity as fixed effects, and direct and maternal additive genetic, and maternal permanent environment as random effects for following traits: birth weight (BW), weaning weight (WW) and weight at 1 year of age (Y1W). For weights after 1 year of age maternal effects were ignored. These weights were weight at 2 (Y2W), three (Y3W), four (Y4W) and five years (Y5W). All 2-trait models included WW, i.e., BW-WW, Y1W-WW, Y2W-WW, Y3W-WW, Y4W-WW, and Y5W-WW).



RESULTS AND DISCUSSION

The selected RRM model based on preliminary analyses of the data was the one that explained fixed age effects, additive genetic, and permanent environment random effects using cubic LP and assumed homogeneous residual variances. Estimated covariance functions were:

$$\text{DAGC}(a_1, a_2) = \begin{bmatrix} \Phi_0(a_1) & \Phi_1(a_1) & \Phi_2(a_1) & \Phi_3(a_1) \end{bmatrix} \begin{bmatrix} 13112.0 & 4980.8 & -309.6 & 1515.4 \\ 4980.8 & 2751.5 & 322.5 & 355.7 \\ -309.6 & 322.5 & 746.3 & 286.4 \\ 1515.4 & 355.7 & 286.4 & 610.5 \end{bmatrix} \begin{bmatrix} \Phi_0(a_2) \\ \Phi_1(a_2) \\ \Phi_2(a_2) \\ \Phi_3(a_2) \end{bmatrix}$$

$$\text{MAGC}(a_1, a_2) = \begin{bmatrix} \Phi_0(a_1) & \Phi_1(a_1) & \Phi_2(a_1) & \Phi_3(a_1) \end{bmatrix} \begin{bmatrix} 739.2 & 58.1 & 67.1 & 158.6 \\ 58.1 & 73.9 & -20.7 & -68.4 \\ 67.1 & -20.7 & 16.1 & 45.1 \\ 158.6 & -68.4 & 45.1 & 128.8 \end{bmatrix} \begin{bmatrix} \Phi_0(a_2) \\ \Phi_1(a_2) \\ \Phi_2(a_2) \\ \Phi_3(a_2) \end{bmatrix}$$

$$\text{DPEC}(a_1, a_2) = \begin{bmatrix} \Phi_0(a_1) & \Phi_1(a_1) & \Phi_2(a_1) & \Phi_3(a_1) \end{bmatrix} \begin{bmatrix} 5596.0 & 3557.8 & 504.8 & -114.4 \\ 3557.8 & 4303.1 & 2439.2 & 400.6 \\ 504.8 & 2439.2 & 3236.4 & 1274.6 \\ -114.4 & 400.6 & 1274.6 & 746.87 \end{bmatrix} \begin{bmatrix} \Phi_0(a_2) \\ \Phi_1(a_2) \\ \Phi_2(a_2) \\ \Phi_3(a_2) \end{bmatrix}$$

Figure 1 shows the values of direct and maternal additive genetic and direct permanent environment covariance functions from birth to 2,500 days of age. Variance components increased with age (Figure 2). The direct heritability (DH) estimate for birth weight from RRM was considerably lower than heritability estimate obtained with MTM (Table2, Figure 3). Conversely, MTM and RRM DH estimates for other ages were similar (Table2, Figure 2). Maternal heritabilities (MH) estimates from RRM were similar to MTM estimates for BW and WW (Figure 4). The DH increased until 0.59 at 764 d and then decreased, maternal heritability reached its maximum value (0.093) at 222 d and then decreased, and direct permanent environment variance ratio increased as animals grew (Figure 4). Legendre polynomials are known to be ill-behaved at the extremes. This may occur regardless of the number of data at extreme points (Mantilla, 2004). This seems to be the case here because birth was the point of growth trajectory with the largest number of records.

FINAL REMARKS

The ill-behavior of LP here suggested that this dataset should be reanalyzed using functions less sensitive at the extremes, such as splines, to obtain reasonable estimates of variance ratios over the complete range of ages. The DH and MH estimates from RRM and MTM indicated that selection for direct effects in this multibreed population from birth to 2500 days of age was feasible, and that the response to selection for maternal additive genetic effects would be slower than for direct genetic effects.

Figure 1. Direct additive genetic (DAGC), maternal additive genetic (MAGC) and direct permanent environment (DPEC) covariance functions

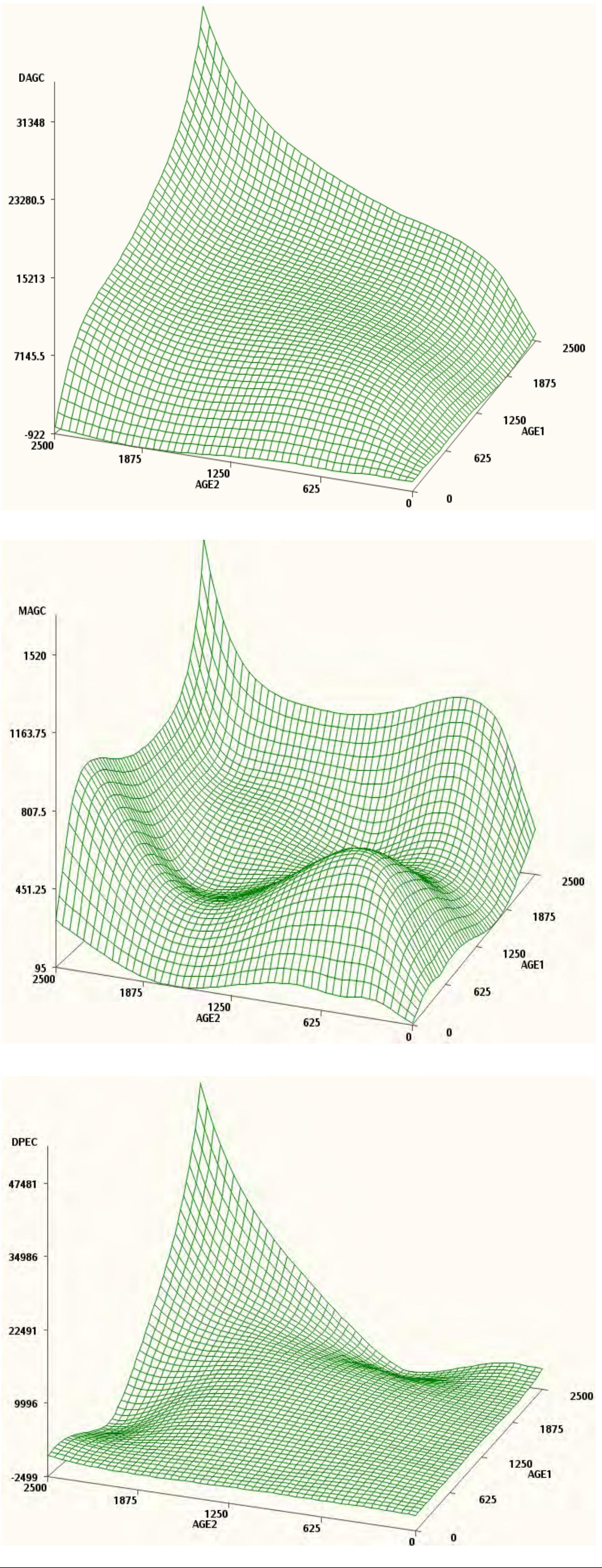


Figure 2. Direct additive genetic (σ²a), maternal additive genetic (σ²m), direct permanent environment (σ²p) and phenotypic (σ²ph) variances

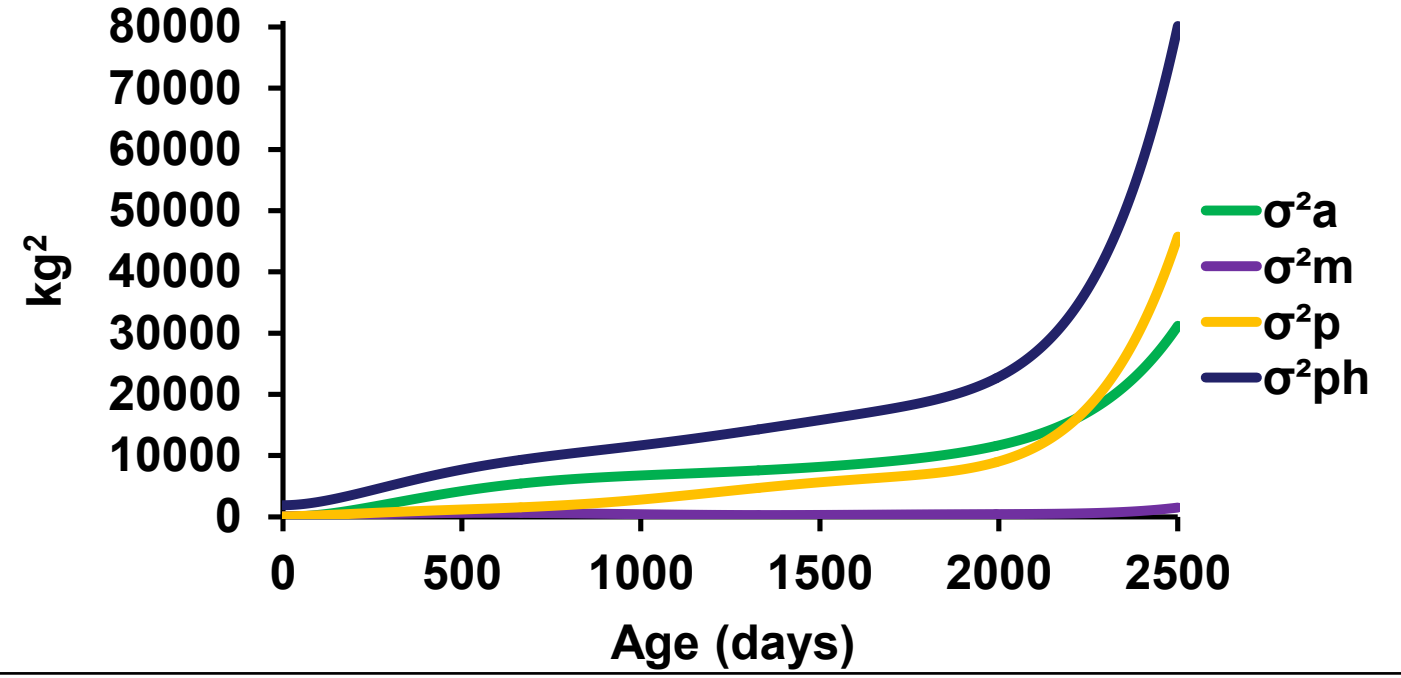


Figure 3. Direct heritabilities using random regression (RRM) and 2-trait (MTM) models

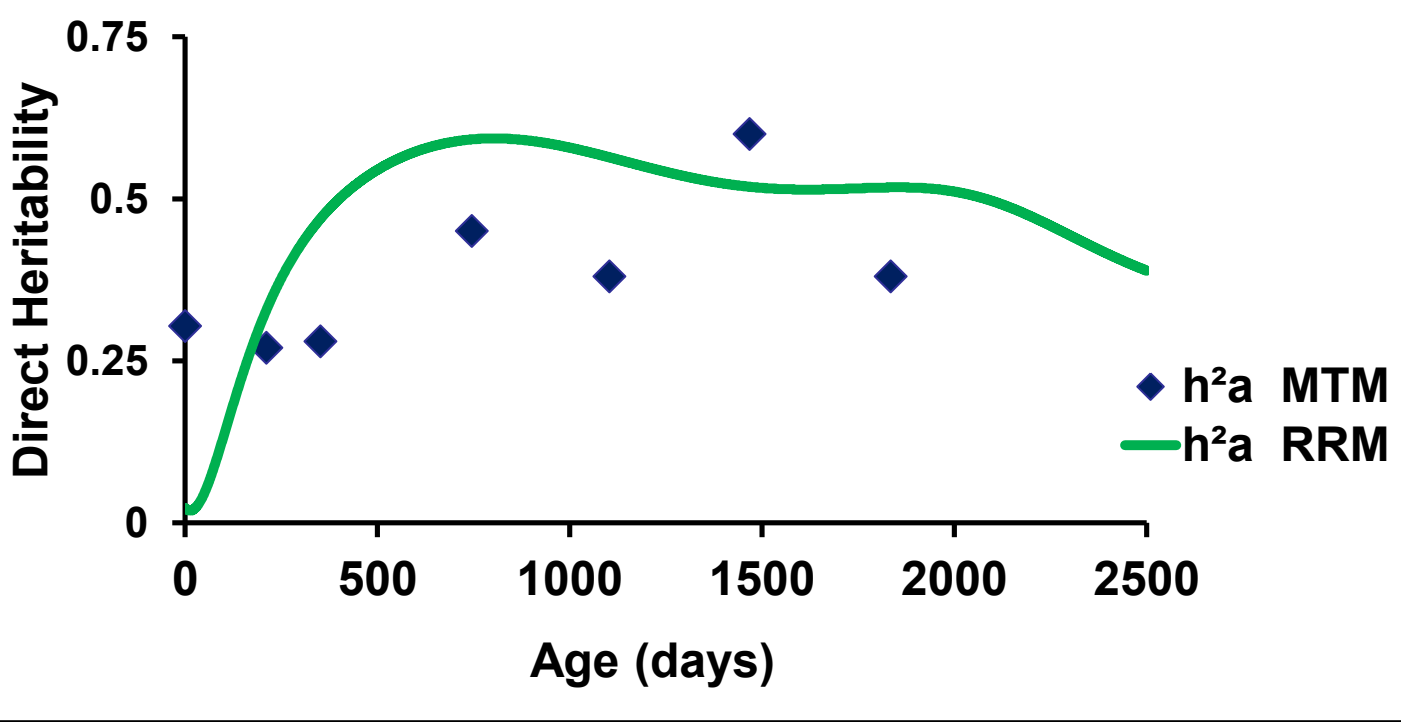


Figure 4. Maternal heritabilities with RRM and MTM, and (σ²p/σ²ph) ratios obtained with RRM

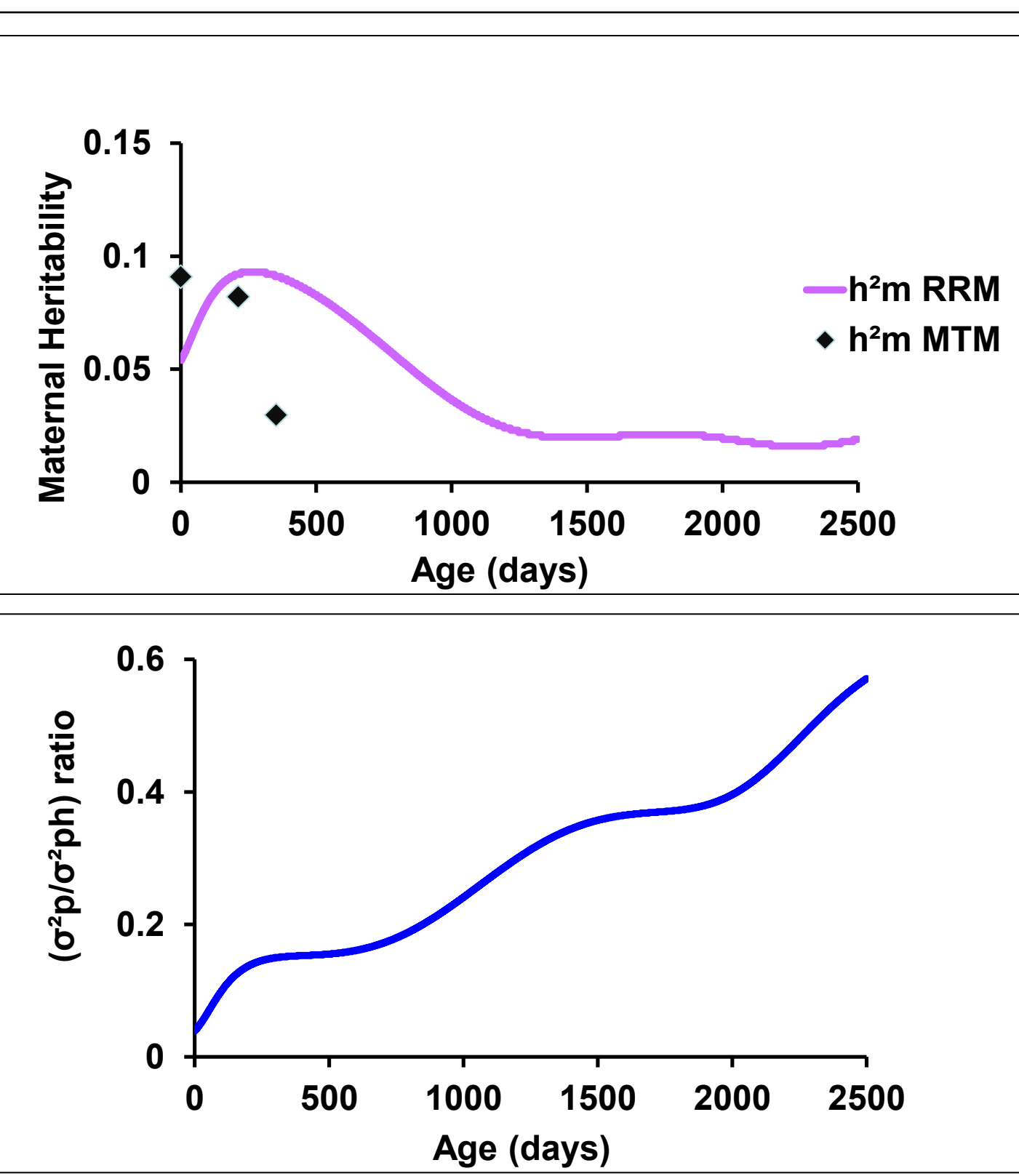


Table 2. Estimates of direct and maternal heritability and direct and maternal variances with RRM and MTM

Trait	h²a RRM	h²a MTM	h²m RRM	h²m MTM	σ²a RRM	σ²a MTM	σ²m RRM	σ²m MTM
BW	0.02 ± 0.02	0.3 ± 0.06	0.05 ± 0.01	0.09 ± 0.05	43.8 ± 32.5	35.6 ± 7.2	101.6 ± 28.3	10.7 ± 5.5
WW	0.33 ± 0.03	0.27 ± 0.05	0.09 ± 0.02	0.08 ± 0.04	1258.6 ± 155.8	808.8 ± 166.2	352.4 ± 84.3	240.6 ± 121.5
Y1W	0.47 ± 0.04	0.28 ± 0.07	0.09 ± 0.02	0.03 ± 0.05	2739.3 ± 302.6	1636.9 ± 412.9	532.8 ± 150.8	175.0 ± 283.3
Y2W	0.59 ± 0.04	0.45 ± 0.06	0.06 ± 0.03	-----	5879.6 ± 594.7	3224.3 ± 526.4	601.3 ± 261.0	-----
Y3W	0.56 ± 0.04	0.38 ± 0.06	0.03± 0.02	-----	7013.3 ± 768.5	5357.7 ± 958.6	361.6 ± 316.4	-----
Y4W	0.52 ± 0.05	0.60 ± 0.07	0.02 ± 0.03	-----	8043.9 ± 1026.8	9479.3 ± 1445.7	304.3 ± 440.9	-----
Y5W	0.52 ± 0.06	0.38 ± 0.09	0.02 ± 0.04	-----	9997.9 ± 1473.9	8980.0 ± 2333.6	411.1 ± 700.3	-----
W2500d	0.39 ± 0.08	-----	0.02 ± 0.05	-----	31203.4 ± 7542.5	-----	1515 ± 4174	-----

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