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Estimation of genetic parameters for mature weight in Angus cattle¹

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ABSTRACT: The aim of this study was to estimate genetic parameters for body weight of Angus cattle up to 5 yr of age and to discuss options for including mature weight (MW) in their genetic evaluation. Data were obtained from the American Angus Association. Only records from herds with at least 500 animals and with > 10% of animals with weights at ≥ 2 yr of age were considered. Traits were weaning weight (WW, $n = 81,525$), yearling weight (YW, $n = 62,721$), and weights measured from 2 to 5 yr of age (MW2, $n = 15,927$, MW3, $n = 12,404$, MW4, $n = 9,805$, MW5, $n = 7,546$). Genetic parameters were estimated using an AIREML algorithm with a multiple-trait animal model. Fixed effects were contemporary group and departure of the actual age from standard age (205, 365, 730, 1095, 1460, and 1825 d of age for WW, YW, MW2, MW3, MW4, and MW5, respectively). Random effects were animal direct additive genetic, maternal additive genetic, maternal permanent environment, and residual. Estimates of direct genetic variances (kg^2) were 298 ± 71.8 , 563 ± 15.1 , 925 ± 52.1 , 1221 ± 65.8 , 1406 ± 80.4 , and 1402 ± 66.9 ; maternal genetic variances were 167 ± 4.8 , 153 ± 6.1 , 123 ± 9.1 , 136 ± 12.25 , 167 ± 18.0 , and 110 ± 14.0 ; maternal permanent environment variances were 124 ± 2.9 , 120 ± 4.3 , 61 ± 7.5 , 69 ± 11.9 , 103 ± 15.9 , and 134 ± 35.2 ; and residual variances were 258 ± 3.8 , 608 ± 8.6 , 829 ± 34.2 , 1016 ± 38.8 , 1017 ± 52.1 , and 1202 ± 63.22 for WW, YW, MW2, MW3, MW4, and MW5, respectively. The direct genetic correlation between WW and YW was 0.84 ± 0.14 and between WW and MW ranged from 0.66 ± 0.06 (WW and MW4) to 0.72 ± 0.11 (WW and MW2). Direct genetic correlations ranged from 0.77 ± 0.08 (YW and MW5) to 0.85 ± 0.07 (YW and MW2) between YW and MW, and they were ≥ 0.95 among MW2, MW3, MW4, and MW5. Maternal genetic correlations between WW and YW and mature weights ranged from 0.52 ± 0.05 (WW and MW4) to 0.95 ± 0.07 (WW and YW), and among mature weights they ranged from 0.54 ± 0.14 (MW4 and MW5) to 0.94 ± 0.07 (MW2 and

MW3). Genetic correlations suggest that a genetic evaluation for mature weight may be MW2-based, and that including weights from older ages could be accomplished by adjusting records to the scale of MW2.

Key words: beef cattle, genetic parameters, growth, mature weight, multiple-trait

INTRODUCTION

Mature weight (MW) has been considered an important trait in genetic improvement programs because it affects economic traits like maintenance requirements, reproduction, and other physiological traits (Montaño-Bermudez et al., 1990; Owens et al., 1993; Koots et al., 1994; Meyer, 1999; Bolignon et al., 2008). Although the importance of mature weight has already been well described, only a few breeding programs include this trait in the net aggregate breeding value. To obtain accurate genetic values for mature weight, good estimates of variances and covariances are required (Rumph et al., 2002).

Several models to estimate genetic parameters for mature weight have been proposed. Applying a repeatability model seems to be the simplest way to obtain estimates for repeated measures (Bolignon et al., 2008). However, with this model the genetic correlation between successive weights is assumed to be one, whereas several authors observed that it did not happen with real data (Arango et al., 2000; Albuquerque and Meyer, 2001). Random regression models could be used (Meyer, 2001), but estimation artifacts may occur due to data structure (Misztal, 2006) reducing the accuracy of estimation of genetic parameters. Multiple-trait models seem to be a good alternative because of their robustness and ability to account for differences in the (co)variance and correlation structure along the growth curve. An important aspect of mature weight genetic analyses is that maternal effects are usually disregarded in the model, although

they still exert some influence on older body weights (Rumph et al., 2002). Thus, the objectives of this study were to use a multiple-trait approach to model repeated growth records accounting for direct additive genetic, maternal additive genetic and maternal permanent environmental effects, in order to estimate genetic parameters for weights from weaning to 5 yr of age in Angus, and to explore options to include mature weight in the overall breeding goal of national beef cattle genetic evaluations.

MATERIAL AND METHODS

Animals and Data

Data were obtained from the American Angus Association (AAA). Animal Care and Use Committee approval was not obtained because data were acquired from an existing database. The AAA generates mature size EPD using cow weights and heights of breeding females, as well as their yearling measurements. Cow weights, heights and body condition scores are taken at or near the time of weaning of the cow's calf. Measurements of body condition score and hip height need to be taken within ± 45 d of the calf's intended weaning date. Cow weights are influenced by body condition score, thus all AAA cow weights were pre-adjusted for body condition score of the cow using adjustment factors reported by Northcutt et al. (1992).

The original data set contained information on 4,955,707 animals. Edits included retaining female records from herds with at least 500 animals and where at least 10% of the animals had weights taken at 2 yr of age or older. Contemporary groups with less than 3 animals were deleted, as well as animals with both parents unknown. Furthermore, only animals born after 1970 were considered in the analyses. Traits included in the analysis were weaning weight

(WW), yearling weight (YW), and cow weights measured from 2 to 5 yr of age (MW2, MW3, MW4, and MW5). Weight at 2 yr of age was used here as an early indicator of mature weight. Although there is no consensus regarding age at maturity in Nelore cattle, several studies have reported that Nelore reaches maturity at about 3-5 yr of age (Rosa, 1999; Mercadante, 2001; Schwengber, 2001).

Animals with MW observations were required to have a WW observation to remain in the edited dataset. Contemporary groups were formed based on criteria used by AAA. Weaning weight contemporary groups were defined using herd, processing date, lot identification, type of management and sex. Yearling weight contemporary groups were defined using all the criteria for WW contemporary groups plus yearling herd, in case animals changed herds after weaning. Contemporary groups for MW2, MW3, MW4, and MW5 contained herd, and birth year. Numbers of observations, means, and SD for WW, YW, and mature weights in the final data set are presented in Table 1.

Statistical model

A multiple-trait animal model was applied to the dataset. The following model, in scalar form, explains the record for weight trait t , of the i^{th} animal, offspring of the d^{th} dam, in the j^{th} contemporary group (y_{tjid}):

$$y_{tjid} = \text{fixed}_{tjid} + \mathbf{d}_{ti} + \mathbf{m}_{td} + \mathbf{mpe}_{td} + \mathbf{e}_{tjid},$$

where $\text{fixed}_{tjid} = \text{CG}_{tj} + \beta(\text{age}_{ti} - \text{age}_0)$, \mathbf{d}_{ti} = random additive genetic effect of animal \mathbf{i} for trait \mathbf{t} , \mathbf{m}_{td} = maternal additive genetic effect of dam \mathbf{d} for trait \mathbf{t} , \mathbf{mpe}_{td} = maternal permanent environment effect of dam \mathbf{d} for trait \mathbf{t} , and \mathbf{e}_{tjid} = random residual effect for trait \mathbf{t} of animal \mathbf{i} . Fixed effects in the model were contemporary group (CG) \mathbf{j} for trait \mathbf{t} and the linear effect of $(\text{age} - \text{age}_0)$, where age_{ti} was the actual age of the animal \mathbf{i} for trait \mathbf{t} , and age_0 was the standard

age for trait t (205, 365, 730, 1,095, 1,460, and 1,825 for WW, YW, MW2, MW3, MW4, and MW5, respectively), and β was the linear regression coefficient. Variances of and covariances between random effects in the model were:

$$\text{var} \begin{bmatrix} d \\ m \\ \text{mpe} \\ e \end{bmatrix} = \begin{bmatrix} G \otimes A & \text{Cov}(d, m) \otimes A & 0 & 0 \\ \text{Cov}(m, d) \otimes A & M \otimes A & 0 & 0 \\ 0 & 0 & \text{MPE} \otimes I & 0 \\ 0 & 0 & 0 & R \otimes I \end{bmatrix},$$

where G is the covariance matrix of direct additive genetic effects; \otimes = direct product; A is the relationship matrix among all animals in the pedigree file, M is the covariance matrix of maternal additive genetic effects; MPE is the matrix of maternal permanent environmental effects; I is the identity matrix; and R is the covariance matrix of residual effects.

Variance components were obtained with the AIREMLF90 program, which uses second derivative REML with extra heuristics (Miszta et al., 2002; Miszta, 2008).

RESULTS AND DISCUSSION

Estimates of variance components and correlations for direct additive genetic effects are shown in Table 2. Estimates increased from weaning to mature ages, tending to stabilize at around 4 yr of age. Faster rates of increase were observed from weaning up to 3 yr of age. After that age the increase was lower and became stable at 4 and 5 yr of age. Changes in additive genetic variances are shown graphically in Figure 1. This increasing pattern of additive genetic variability has also been observed in other breeds, at least for growth up to 2 yr of age. Albuquerque and Meyer (2001) and Nobre et al. (2003) reported similar changes in direct additive variance for body weight in growing Nelore cattle up to 2 yr of age, using random regression models. Although estimates for direct additive genetic variances found here were in agreement with those obtained in some studies using random regression models with Legendre

polynomials (Albuquerque and Meyer, 2001; Nobre et al., 2003; Arango et al., 2004), they differed in magnitude from estimates found in earlier investigations also with random regression models (Meyer and Hill, 1997; Meyer, 1999; Arango et al., 2002). The largest differences occurred at the extremes of the growth curve, and they could be associated with differences among models or sampling (Meyer, 1992). The results of this paper are relevant to Angus and similarly growing breeds but not to tropical breeds with slow growth.

Estimates of direct heritabilities for WW, YW, MW2, MW3, MW4, and MW5 were 0.44 ± 0.11 , 0.43 ± 0.07 , 0.52 ± 0.01 , 0.54 ± 0.01 , 0.56 ± 0.01 , and 0.50 ± 0.01 respectively (Figure 2). These estimates were in agreement with estimates found in the literature for Angus cattle (Meyer, 1999; Rumph et al., 2002), and they were also close to the estimate used by AAA (0.49) in their genetic evaluation for mature size (AAA, 2000). The direct additive genetic correlation (Table 2) between WW and YW was 0.84 ± 0.14 and between WW and MW ranged from 0.66 ± 0.06 (WW and MW4) to 0.72 ± 0.11 (WW and MW2). Direct additive genetic correlations between YW and MW ranged from 0.77 ± 0.08 (YW and MW5) to 0.85 ± 0.07 (YW and MW2). Direct genetic correlations among MW were all ≥ 0.95 . These results showed that weights measured after 2 yr of age were almost the same trait, and tended to have the same (co)variance structure.

Whereas direct additive genetic and residual variances increased across the entire age range considered here, with an inflection point at around 3 to 4 yr of age, maternal additive genetic and permanent environmental variance components decreased by a large amount from WW to MW2 and then oscillated without a clear pattern at older ages (Figure 2). Estimates of maternal additive genetic variances and covariances (Table 3) also followed a pattern similar to that reported in the literature (Nobre et al., 2003; Rumph et al., 2002; Albuquerque and Meyer,

2001). Variance estimates were higher for the trait measured at the youngest age (WW), then they decreased until 2 yr of age, and tended to increase at older ages. Maternal heritability estimates are illustrated in Figure 2. The largest maternal heritability estimate was for WW (0.25 ± 0.01) and decreased towards mature weights (values ranged from 0.04 ± 0.01 for MW5 to 0.07 ± 0.01 for MW2). The variation among maternal additive genetic ratios at older ages may have been an artifact due to lower number of records and perhaps incomplete account for censoring. Although small, the additive maternal genetic effect remained present after weaning (heritability at 365d = 0.12 ± 0.01 , and about half of this value for MW2, MW3, and MW4, and one third for MW5; Figure 2). When paired with maternal permanent environmental effects (Table 6) the overall maternal influence (maternal additive genetic + maternal permanent environmental effects) explained approximately 10% of the variability for MW2, MW3, MW4, and MW5. There are, however, contradictory opinions as to whether this effect should be considered when computing EBV for MW or not (Meyer, 1999; Rumph et al., 2002). However, according to Thompson (1976), if a trait is affected by maternal effects even to a small degree, and maternal effects are not accounted for in the model, then estimates of direct heritability will be biased and inflated. Further, because modern genetic evaluation of post-weaning weight traits tend to not consider maternal effects in the estimation of genetic parameters, estimates of direct genetic effects and direct heritabilities might be inflated (Meyer, 1992b). Thus, failing to account for maternal effects may result in somewhat (but not greatly) biased estimates of MW genetic predictions and genetic parameters. The bias of EBV may be very small or even not noticeable if the maternal effects at MW have very low accuracy because of low number of dams at high ages. Correlations between maternal effects at different ages (Tables 3, 6) were high at young ages, but decreased at mature ones. This suggested that covariances among maternal additive genetic and

between permanent environmental effects varied with age, and that these differences should be accounted for when modeling mature weight.

Estimates of correlations between direct and maternal additive effects resulting from covariances presented in Table 4 are shown in Table 5. All estimates were negative and relatively high. Higher correlation estimates were observed at younger ages (WW and YW), and decreased as animals grew older. Also, as expected, except for MW5, direct-maternal correlations between adjacent ages tended to be higher, and they tended to decrease as the time span between ages increased.

Estimates of maternal permanent environmental variances, covariances, and correlations are presented in Table 6. These estimates followed the same pattern observed for variance components and correlations due to maternal additive genetic effects. Estimates were higher at younger ages and decreased towards MW5. When compared to other genetic parameters, estimates of maternal permanent environmental effects were small. However, there was an influence of this effect even after weaning, indicating that maternal permanent environmental effects should be included in analysis of yearling and mature weights. Maternal permanent environmental correlations among all ages were very high. In particular, maternal permanent environmental correlations among mature ages ranged from 0.75 ± 0.08 between MW2 and MW5 to 0.93 ± 0.01 between MW2 and MW3, indicating that the covariance structure for this effect at different ages was very similar.

Residual variances, covariances, and correlations are shown in Table 7. Residual variances increased with age. Variation among estimates was probably largely due to the reduction of data available for older ages. Even with this level of variation, estimates of residual

variance components seemed to stabilize at around 3 yr of age. Residual correlations were low to moderate, and similar among mature ages.

Inclusion of Mature Weight in the Overall Breeding Goal

Inclusion of mature weight as part of the overall breeding goal could be accomplished by obtaining genetic predictions for all mature weights using multiple-trait or random regression approaches. However, estimates of additive genetic variance components in this population suggest an approximation that would drastically decrease computing costs. Estimates of direct additive genetic correlations between weights at 2, 3, 4, and 5 yr of age were all over 0.95 suggesting that MW2 could be a good substitute for mature weight. Maternal additive genetic correlations among mature weights ranged from moderate to high, but their corresponding variance estimates were small. Thus, a genetic evaluation system for growth traits that incorporates mature weight in Angus could be implemented by adding one additional knot (i.e., weight at 2 yr of age) to a random regression model with splines such as that described by Sanchez et al. (2008). The resulting random regression model with splines would have four knots (1d, 205d, 365d, and 730d). Mature weights taken at ages older than 2 yr would be adjusted to 2 yr of age by modifying the covariates for random regressions and by using heterogeneous residual variances. Implementation of this approach will be the subject of a future research study.

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Table 1. Number of observations, means and standard deviations for body weights at different ages

Trait ¹	n	Mean (kg)	SD (kg)
WW	81,525	251	45
YW	62,721	410	85
MW2	15,927	531	58
MW3	12,404	571	63
MW4	9,805	598	67
MW5	7,546	614	70

¹WW = weaning weight; YW = yearling weight; MW2, MW3, MW4, MW5 = body weights taken at 2, 3, 4, and 5 yr of age respectively.

Table 2. Estimates of direct additive genetic variances (diagonal; kg²), covariances (below diagonal; kg²), and correlations (above diagonal) for body weights at different ages

Trait ¹	WWd	YWd	MW2d	MW3d	MW4d	MW5d
WWd	298 ± 7.18	0.84 ± 0.14	0.72 ± 0.11	0.67 ± 0.08	0.66 ± 0.06	0.67 ± 0.09
YWd	349 ± 9.14	563 ± 15.1	0.85 ± 0.12	0.81 ± 0.09	0.78 ± 0.11	0.77 ± 0.08
MW2d	383 ± 15.0	622 ± 23.4	925 ± 52.1	0.97 ± 0.06	0.96 ± 0.13	0.95 ± 0.12
MW3d	441 ± 18.5	717 ± 29.8	1029 ± 49.4	1221 ± 65.8	0.98 ± 0.13	0.97 ± 0.10
MW4d	428 ± 18.5	696 ± 31.4	1094 ± 61.7	1230 ± 63.3	1406 ± 80.4	0.96 ± 0.14
MW5d	435 ± 19.2	710 ± 32.1	1073 ± 47.9	1270 ± 64.0	1320 ± 66.3	1403 ± 66.9

¹WW = weaning weight; YW = yearling weight; MW2, MW3, MW4, MW5 = body weight at 2, 3, 4, and 5 yr of age; d = direct additive genetic.

Table 3. Estimates of maternal additive genetic variances (diagonal; kg²), covariances (below diagonal; kg²), and correlations (above diagonal) for body weights at different ages

Trait ¹	WWm	YWm	MW2m	MW3m	MW4m	MW5m
WWm	168 ± 4.8	0.95 ± 0.07	0.76 ± 0.10	0.81 ± 0.04	0.52 ± 0.05	0.69 ± 0.08
YWm	152 ± 4.8	154 ± 6.1	0.81 ± 0.06	0.93 ± 0.08	0.59 ± 0.09	0.76 ± 0.05
MW2m	110 ± 8.3	112 ± 7.1	124 ± 9.1	0.94 ± 0.07	0.88 ± 0.11	0.68 ± 0.11
MW3m	110 ± 6.4	121 ± 7.8	110 ± 8.9	136 ± 12.2	0.58 ± 0.08	0.87 ± 0.07
MW4m	88 ± 8.0	94 ± 7.8	101 ± 14.7	79 ± 13.5	168 ± 18.0	0.54 ± 0.14
MW5m	94 ± 7.5	99 ± 7.8	80 ± 8.1	96 ± 13.1	73 ± 19.1	110 ± 14.0

¹WW = weaning weight; YW = yearling weight; MW2, MW3, MW4, MW5 = body weight at 2, 3, 4, and 5 yr of age; m = maternal additive genetic.

Table 4. Estimates of covariances between direct and maternal additive genetic effects for body weights at different ages

Trait ¹	WWd	YWd	MW2d	MW3d	MW4d	MW5d
WWm	-165 ± 4.8	-151 ± 6.1	-165 ± 10.9	-183 ± 12.5	-159 ± 12.8	-170 ± 13.5
YWm	-144 ± 5.3	-146 ± 7.4	-161 ± 13.1	-182 ± 16.1	-156 ± 15.9	-161 ± 16.9
MW2m	-116 ± 10.5	-129 ± 14.4	-153 ± 21.2	-155 ± 24.2	-144 ± 24.6	-116 ± 28.4
MW3m	-129 ± 9.5	-134 ± 13.3	-120 ± 19.7	-152 ± 27.4	-95 ± 22.8	-114 ± 26.8
MW4m	-87 ± 9.1	-72 ± 19.1	-132 ± 38.3	-91 ± 39.3	-169 ± 31.8	-76 ± 41.8
MW5m	-85 ± 8.9	-52 ± 13.2	-57 ± 19.4	-71 ± 28.5	-29 ± 16.9	-28 ± 24.0

¹WW = weaning weight; YW = yearling weight; MW2, MW3, MW4, MW5 = body weight at 2, 3, 4, and 5 yr of age; d = direct additive genetic; m = maternal additive genetic.

Table 5. Estimates of correlations between direct and maternal additive genetic effects for body weights at different ages

Trait ¹	WWd	YWd	MW2d	MW3d	MW4d	MW5d
WWm	-0.74 ± 0.07	-0.49 ± 0.03	-0.42 ± 0.04	-0.40 ± 0.06	-0.33 ± 0.05	-0.35 ± 0.04
YWm	-0.67 ± 0.05	-0.68 ± 0.03	-0.43 ± 0.03	-0.42 ± 0.04	-0.33 ± 0.07	-0.34 ± 0.05
MW2m	-0.60 ± 0.05	-0.49 ± 0.06	-0.45 ± 0.09	-0.40 ± 0.06	-0.34 ± 0.04	-0.29 ± 0.03
MW3m	-0.71 ± 0.11	-0.54 ± 0.04	-0.38 ± 0.04	-0.41 ± 0.08	-0.24 ± 0.04	-0.29 ± 0.05
MW4m	-0.39 ± 0.09	-0.23 ± 0.03	-0.33 ± 0.03	-0.20 ± 0.02	-0.35 ± 0.06	-0.16 ± 0.04
MW5m	-0.47 ± 0.03	-0.21 ± 0.04	-0.18 ± 0.05	-0.19 ± 0.05	-0.07 ± 0.02	-0.07 ± 0.02

¹WW = weaning weight; YW = yearling weight; MW2, MW3, MW4, MW5 = body weight at 2, 3, 4, and 5 yr of age; d = direct additive genetic; m = maternal additive genetic.

Table 6. Estimates of maternal permanent environmental variances (diagonal; kg²), covariances (below diagonal; kg²), and correlations (above diagonal) for body weights at different ages

Trait ¹	WWmpe	YWmpe	MW2mpe	MW3mpe	MW4mpe	MW5mpe
WWmpe	124 ± 2.9	0.98 ± 0.01	0.91 ± 0.01	0.85 ± 0.05	0.77 ± 0.07	0.64 ± 0.09
YWmpe	120 ± 3.3	120 ± 4.3	0.90 ± 0.02	0.88 ± 0.04	0.77 ± 0.07	0.69 ± 0.07
MW2mpe	80 ± 3.8	77 ± 3.4	62 ± 7.5	0.93 ± 0.01	0.87 ± 0.05	0.75 ± 0.08
MW3mpe	79 ± 5.6	80 ± 5.0	61 ± 9.7	69 ± 11.9	0.82 ± 0.05	0.80 ± 0.07
MW4mpe	87 ± 8.2	86 ± 10.9	69 ± 6.2	70 ± 6.6	104 ± 15.9	0.88 ± 0.09
MW5mpe	83 ± 8.1	88 ± 10.1	68 ± 7.8	78 ± 9.4	103 ± 20.8	134 ± 35.2

¹WW = weaning weight; YW = yearling weight; MW2, MW3, MW4, MW5 = body weight maternal additive at 2, 3, 4, and 5 yr of age; mpe = maternal permanent environmental.

Table 7. Estimates of residual variances (diagonal; kg^2), covariances (below diagonal; kg^2), and correlations (above diagonal) for body weights at different ages

Trait ¹	WWe	YWe	MW2e	MW3e	MW4e	MW5e
WWe	258 ± 3.8	0.60 ± 0.01	0.34 ± 0.01	0.29 ± 0.03	0.30 ± 0.02	0.31 ± 0.03
YWe	240 ± 5.0	609 ± 8.6	0.46 ± 0.03	0.35 ± 0.03	0.39 ± 0.01	0.37 ± 0.06
MW2e	160 ± 9.9	324 ± 16.2	830 ± 34.2	0.35 ± 0.01	0.32 ± 0.01	0.38 ± 0.02
MW3e	148 ± 11.5	275 ± 20.7	326 ± 30.7	1016 ± 38.8	0.41 ± 0.02	0.41 ± 0.04
MW4e	153 ± 13.0	310 ± 23.85	294 ± 37.6	417 ± 39.76	1018 ± 52.1	0.48 ± 0.04
MW5e	174 ± 14.3	321 ± 27.05	382 ± 33.9	453 ± 40.7	537 ± 45.7	1203 ± 63.2

¹WW = weaning weight; YW = yearling weight; MW2, MW3, MW4, MW5 = body weight maternal additive at 2, 3, 4, and 5 yr of age; e = residual.

Figure Captions

Figure 1. Estimates of variances for direct additive genetic, maternal additive genetic ($\times 10$), maternal permanent environmental ($\times 10$), and residual effects for seven weights from 205 d (weaning) to 1825 d (MW5) of age

Figure 2. Estimates of direct and maternal heritabilities for seven weights from 205 d (weaning) to 1825 d (MW5) of age

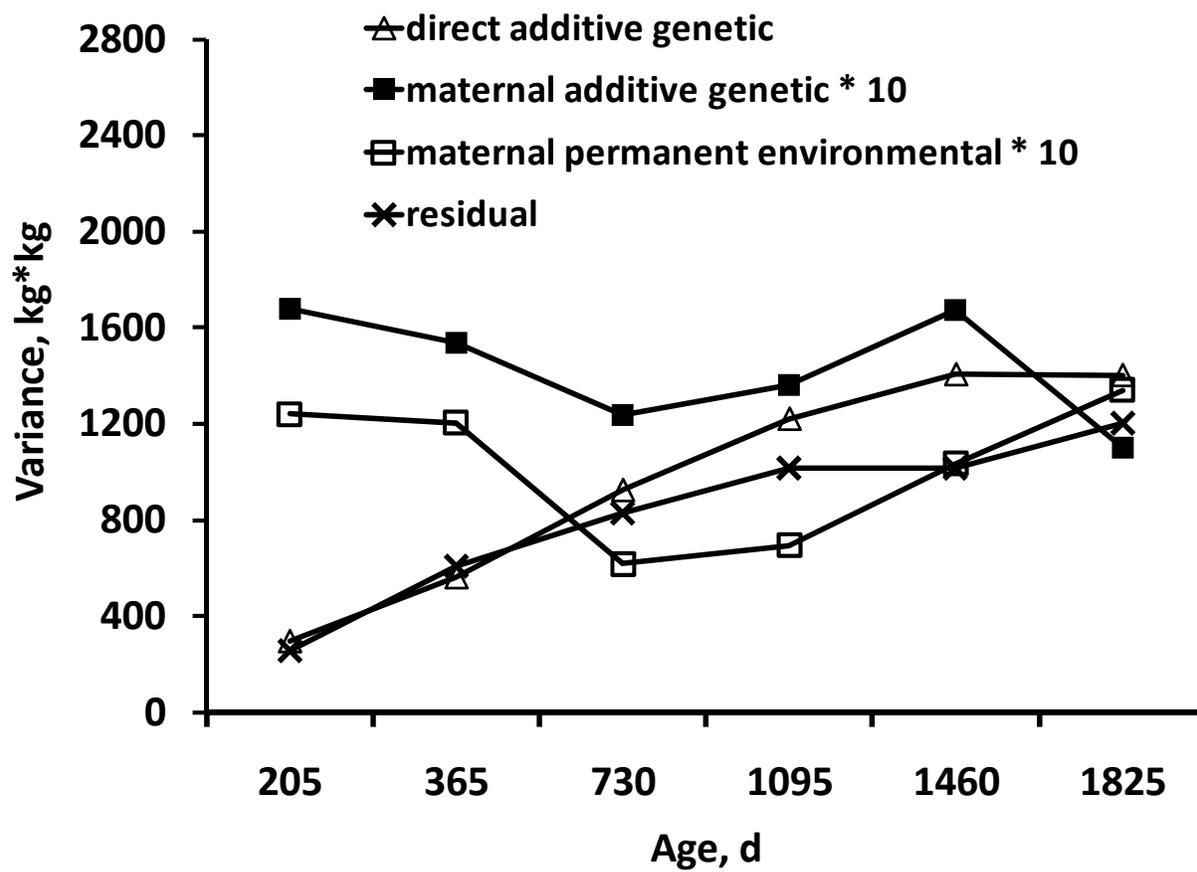


Figure 1

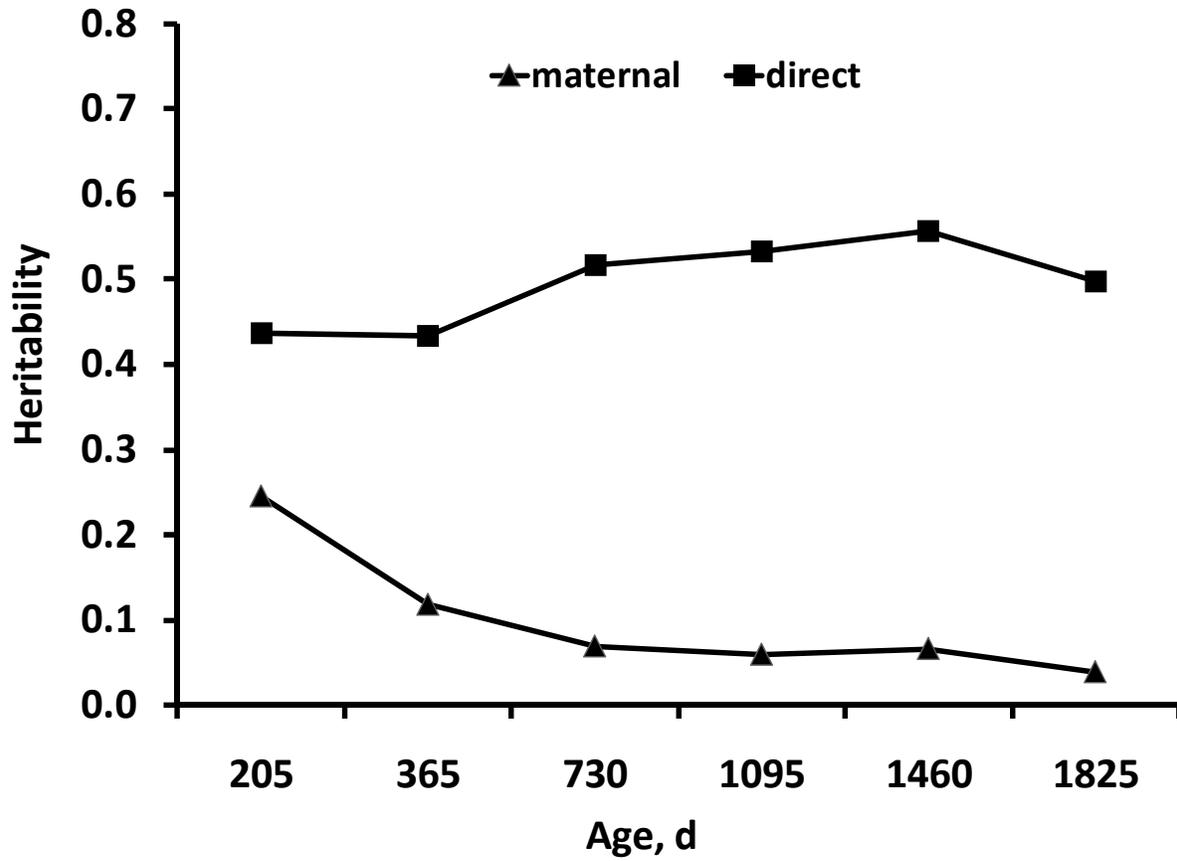


Figure 2