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# 4

## Genetic analysis on body weight at different ages in broiler chicken raised in commercial environment

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### Abstract

A multivariate model was developed and used to estimate genetic parameters of body weight (BW) at 1-6 week of age of broilers raised in a commercial environment. The development of model was based on the predictive ability of breeding values evaluated from a cross-validation procedure that relied on half-sib correlation. The multivariate model accounted for heterogeneous variances between sexes through standardization applied to male and female BW differently. It was found that the direct additive genetic, permanent environmental maternal and residual variances for BW increased drastically as broilers aged. The drastic increase in variances over weeks of age were mainly due to scaling effects. Ratio of the permanent environmental maternal variance to phenotypic variance decreased gradually with increasing age. Heritability of BW traits ranged from 0.28 to 0.33 at different weeks of age. The direct genetic effects on consecutive weekly BWs had high genetic correlations (0.85-0.99), but the genetic correlations between early and late BWs were low (0.32-0.57). The difference in variance components between sexes increased with increasing age. In conclusion, the permanent environmental maternal effect on broiler chicken BW decreased with increasing age from week 1-6. Potential bias of the model that considered identical variances for sexes could be reduced when heterogeneous variances between sexes are accounted for in the model.

### 4.1. Introduction

Optimal modelling plays a key role in improving accuracy of predicted breeding values for traits of interest, and thereby increasing genetic gain in breeding programs. Apart from direct additive genetic effects, other factors including maternal effects, sex by genotype interaction, and heterogeneous residual variances have been accounted for when modelling body weight (BW) in poultry, (Barbieri *et al.*, 2015; Begli *et al.*, 2016; Grosso *et al.*, 2010; Maniatis *et al.*, 2013; Mebratie *et al.*, 2017). However, the method used for including those factors in BW modelling varies across studies. In addition, when analyzing longitudinal data for BW in chicken, it was found that the effects of maternal factors and sex by genotype interaction change with age of the birds (Begli *et al.*, 2016; Mebratie *et al.*, 2017; Norris and Ngambi, 2006; Rovadoscki *et al.*, 2016).

Maternal effects are often ignored for egg production traits that are expressed relatively late in life, but the effects are considered to be important for growth traits in broiler chicken, especially at juvenile stage that broilers are usually selected in breeding programs (Besbes and Ducrocq, 2003). Two commonly modelled maternal effects for BW traits are additive genetic and permanent environmental effects of the

dam (Barbieri *et al.*, 2015; Maniatis *et al.*, 2013; Norris and Ngambi, 2006). The maternal effects reduce as chicken are older (Barbieri *et al.*, 2015; Maniatis *et al.*, 2013; Norris and Ngambi, 2006). Another maternal effect, age of hen, may also affect BW because strong correlations between hen age and egg weight and strong correlations between egg weight and broiler BW especially at an early age were found (Di Masso *et al.*, 1998; Tahir *et al.*, 2011; Whiting and Pesti, 1984). Failing to account for maternal effects results in reduced accuracy of selection, overestimated direct additive genetic effect and thus loss of selection response (Roehe and Kennedy, 1993).

Sex by genotype interaction for BW in commercial broiler chicken has been reported (Mebratie *et al.*, 2017). The authors suggested that modelling BW of males and females as two separate, but correlated traits could improve accuracy of selection compared to the model that assumed an average heritability and a genetic correlation of unity between BW expressed in different sexes. Moreover, the residual variance in males was larger than the variance among females for BW. The authors also found an increasing magnitude of sex by genotype interaction with increasing age. In addition, a drastic increase in residual variances was found for BW traits as chicken aged. The increasing residual variances over different ages of birds were also found in other studies (Begli *et al.*, 2016; Dana *et al.*, 2011; Mebratie *et al.*, 2017).

Different models including univariate, multivariate, and univariate random regression models have been used to analyze longitudinal data to model the development of BW in chicken over ages (Begli *et al.*, 2016; Dana *et al.*, 2011; Niknafs *et al.*, 2012; Rovadoscki *et al.*, 2016). However, in the longitudinal data of these studies, there were relatively low number of birds or few age points recorded for BW. For example, Begli *et al.* (2016) had weekly BW recorded at week 2-10, but there were only 450 birds in the experiment. With such low number of birds, some effects may not be detected by the model. Meanwhile, Mebratie *et al.* (2017) had about 646,000 birds, but BW records were at only 3 different ages of  $t-7$ ,  $t-4$  and  $t$  days for three different groups of birds. With a low number of age points, the development of BW cannot be accurately modelled.

In addition, the production environment where birds are tested may influence BW and thus how it should be modelled. Few studies (Kapell *et al.*, 2012) present genetic parameters for broiler BW in a commercial environment. Most of the studies report the parameter for poultry BW in the breeding environment (Grosso *et al.*, 2010; Koerhuis and Thompson, 1997; Maniatis *et al.*, 2013; Niknafs *et al.*, 2012) or in controlled experimental environment (Begli *et al.*, 2016; Norris and Ngambi, 2006; Rovadoscki *et al.*, 2016). Sib-testing in both the breeding and the commercial environment is a common approach in broiler breeding programs when genotype-by-environment interactions are important. Growth performances of

birds in the commercial environment are often found to be lower than the performances of birds in the breeding environment, whereas standard deviation of BW was higher in the commercial environment (Kapell *et al.*, 2012; N'Dri *et al.*, 2007). In addition, both the absolute and the relative differences in BW between sexes are smaller in the commercial environment compared to the breeding environment (Kapell *et al.*, 2012; N'Dri *et al.*, 2007). Heritability estimates of BW in the commercial environment can be both higher or lower than the heritability of BW in the breeding environment (Kapell *et al.*, 2012; N'Dri *et al.*, 2007). Furthermore, an important difference between modelling BW traits for the breeding and commercial environments is that birds in the commercial environment provide information for selection, but they are not selection candidates because of bio-security restrictions, and thereby dams and sires of those birds do not have BW performances in this commercial environment. Proper account of selection of parents may necessitate the use of multivariate joint modeling of both commercial and breeding environments. Development of a multivariate model for BW of broiler in the commercial environment is one of the steps in building the joint model.

The current study investigated genetic parameters of BW in broilers at different ages raised in a commercial environment. The specific objectives were to (i) develop statistical models to improve accuracy of predicting breeding values, and (ii) estimate parameters for male and female BW at different ages when broilers were reared under commercial conditions.

## 4.2. Materials and methods

### *Data*

Longitudinal data on BW were obtained from Cobb-Vantress who reared broiler chicken in a standard commercial production environment and recorded BW weekly. The broilers were from a purebred line primarily selected for BW in the breeding environment with very stringent regulations for bio-security. The data included 12 broiler flocks sourced from around two generations of breeder flocks. Birds in broiler flocks 1-6 had weekly records of BW from 1-6 weeks of age. Birds in broiler flocks 7-12 has weekly records of BW from 1-5 weeks of age only. Birds with unidentified sex and missing information were removed from the data. Duplicated records on the same week and BW records of 0 were also removed. Only records of BW at each week that were within four standard deviations of the mean were kept. As a result, 2.58% of birds and 0.71% of BW records were removed from the original data.

After data trimming, the number of birds was 17,967 with a total of 91,846 BW records. Birds were offspring from 253 sires and 1,187 dams. The sires and dams did not have phenotypic records in this commercial environment. In each broiler flock, all birds were hatched at the same time, sourced from

#### 4 Broiler body weight at different ages

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multiple breeder flocks in which dams had different ages. The mating system was hierarchical with each sire mated with multiple dams, but each dam mated with a single sire only. The pedigree covered around three generations back from the youngest birds and comprised 20,509 birds.

##### ***Development of statistical models for body weights in broilers***

To develop a statistical model for BW at weeks 1-6, initially univariate models were developed to identify fixed and random factors affecting BW at different weeks of age and different sexes. The longitudinal data were divided by weeks of age and sexes into 12 subsets. For each of the twelve datasets, a univariate model was developed through removal of factors in a hierarchical fashion. A factor or interaction was removed by comparing the model with and without the effect based on criteria of model convergence, log-likelihood ratio test and predictive ability of breeding values from cross-validation as described below. The starting model included fixed effects (flock of birds, source of flocks, hatch of dam within source of flock, and age of dam when offspring were hatched) and all their possible interactions including a fourth order interaction. The random factors of the starting model were the direct additive genetic effect, maternal additive genetic effect and permanent environmental maternal effect. The final model was selected when the removal of a factor from the model significantly reduced the fit of the model or predictive ability of the model in the cross-validation. For the 12 datasets, 7 different models were selected as results of model development process based on sets of model selection criteria:

*Convergence of model:* The REML module (DMUAI) from the DMU software package (Madsen and Jensen, 2013) was used to estimate variance components in all models. Strict criteria for the convergence of a model were set, in which the Frobenius norms of both the update vector and the gradient vector must be lower than  $10^{-5}$  (Madsen and Jensen, 2013).

*Log-likelihood ratio test:* Log-likelihood ratio tests were carried out to identify the significance of a random effect in a model by comparing models with or without the effect (significant difference,  $P < 0.05$ ).

*Cross validation:* Predictive ability of the univariate models was compared using cross validation. The full dataset of BW records at each week for each sex was divided into training and validation datasets based on flocks and full-sib relationships. The training dataset included all bird records from the first half of all flocks and about half of the records from the latter half of all flocks. The validation dataset included records of the other half from the latter half of all flocks. The approximately equal division of records into the training and validation datasets in the latter half of all flocks was carried out within full-sib groups. The full dataset was used to estimate variance components of the model and to compute phenotypes corrected for fixed effects in the validation datasets using the DMUAI procedure of the DMU package. In other words, the corrected phenotype ( $y_c$ ) was equal to the sum of breeding values ( $EBV_f$ ), random

maternal effects and residuals estimated from the full dataset. The training dataset was used to predict breeding values of birds (EBV<sub>v</sub>) in the validation datasets using the variance components estimated from the full dataset.

In the conventional method as used by Christensen *et al.* (2012), validation was based on correlation between  $y_c$  and EBV<sub>v</sub> of the same individuals in the validation dataset. However, in the presence of maternal effects, this correlation might be overestimated because information from full-sibs influences EBV<sub>v</sub>, and thus maternal effects are confounded into EBV<sub>v</sub>. Our validation used the correlation between  $y_c$  and EBV<sub>v</sub> of two different birds that were half-sibs because half-sibs did not share the maternal effects. Random pairs of two half-sibs were sampled for each sire, and all the pairs were used to calculate the correlation between  $y_c$  and EBV<sub>v</sub> of two half-sibs. From the validation dataset, 6000 replicates of the pairing sampling were carried out. The number of replicates of the pairing sampling was to ensure a high probability of all birds in the validation dataset contributed to the calculation of the half-sib correlation. Predictive ability of breeding values for a model was based on the average of correlations between  $y_c$  and EBV<sub>v</sub> ( $Cor(EBV_{vi}, y_{cj})$ ) of two half-sib birds  $i$  and  $j$  in the validation dataset:

$$Predictive\ ability = \frac{Cor(EBV_{vi}, y_{cj})}{\sqrt{h^2 * r_{i,j}}}$$

Where  $h^2$  is heritability calculated from variance components estimated from the full dataset,  $r_{i,j}$  is the additive genetic relationship between half-sibs that is equal to 0.25.

There were seven different univariate models selected from the model development process, and the maternal additive genetic effect was included in the model only for male BW1. However, for simplification and convergence ease, consistent fixed effects across BW at different weeks of age were chosen, namely flock of birds, source of flocks and age of dam when offspring were hatched. The random effects were direct additive genetic effect, permanent environmental maternal effect and a residual.

**Statistical models**

For BW at each week of age, sex by genotype interaction was tested using bivariate models that treated male and female BWs as two different traits. However, it was found that the bivariate models lead to convergence failure because genetic correlations converges towards the edges of the parameter space of 1.0. Male and female BW tended to might have different variances, particularly at the later ages that selection occurs, but their correlations were not significantly different from unity. This refers to scaling effects between male and female BW. If the difference in variances between sexes was not accounted in the model, bias of prediction would increase (Thompson, 2008) and re-ranking of EBVs could occur (van der Heide et al., 2016). It was found that correlations between BW at two consecutive weeks were high,



and multivariate models that used BW1-6 as phenotypic records failed to converge. In preliminary analysis, when Legendre polynomial functions with order of two or more were fitted, the models failed to converge. With the results from univariate models for BW traits, the linear function may not describe well the change of the direct additive genetic effect over weeks of age. In addition, between two model approaches, we preferred the multivariate model to the random regression model because with more parameters, a multivariate model describes better the covariance matrix of the direct additive genetic effect.

To model male and female BW1-6, we used a multivariate model that used BW1-2 and weekly weight gains as phenotypic records, and standardized phenotypic records differently within sex and week. Weekly weight gains were calculated as the difference of BW between week 2 and 3 (WG3), week 3 and 4 (WG4), week 4 and 5 (WG5) and week 5 and 6 (WG6). The use of BW1-2 and WG3-6 in replacement for BW1-6 as phenotypic records aimed to improve the convergence of the multivariate model. The choice of these BW and weight gains was to minimize missing records due to the use of weight gains. Male and female phenotypic records were standardized separately using corresponding phenotypic standard deviations that were estimated from univariate model (4.1) for BW1-2 and WG3-5, and univariate model (4.2) for WG6:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{a} + \mathbf{W}\mathbf{c} + \mathbf{e} \quad (4.1)$$

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{a} + \mathbf{e} \quad (4.2)$$

where  $\mathbf{y}$  is vector of male or female phenotypic records of BW1-2 and WG3-6 at normal scale;  $\mathbf{b}$  is vectors of fixed effects of flock of birds, source of flocks and age of dam. Matrices of  $\mathbf{X}$ ,  $\mathbf{Z}$ , and  $\mathbf{W}$  are incidence matrices. Vectors  $\mathbf{a}$ ,  $\mathbf{c}$  and  $\mathbf{e}$  are the direct additive genetic effect, permanent environmental maternal effect and residual, respectively. These random effects were assumed to be normally distributed:  $\mathbf{a} \sim \mathbf{N}[\mathbf{0}, \mathbf{A}\sigma_a^2]$ ,  $\mathbf{c} \sim \mathbf{N}[\mathbf{0}, \mathbf{I}_d\sigma_c^2]$  and  $\mathbf{e} \sim \mathbf{N}[\mathbf{0}, \mathbf{I}\sigma_e^2]$ , where  $\mathbf{A}$  is the pedigree relationship matrix;  $\mathbf{I}_d$  is the identity matrix for dams;  $\mathbf{I}$  is the identity matrix for individual birds;  $\sigma_a^2$ ,  $\sigma_c^2$  and  $\sigma_e^2$  are variances at normal scale.

Phenotypic records of males and females at each week were standardized by dividing the phenotypic records to the corresponding phenotypic standard deviations that were estimated from models (4.1) and (4.2). In the multivariate model, reduced ranks were applied to male and female traits for additive genetic effects and permanent environmental maternal effects. The standardization of phenotypic records and reduced ranks between sexes were to model the differences in variances between male and female traits and their unity correlation. The permanent environmental maternal effect of WG6 was removed due to

its insignificance. In matrix notation, the multivariate model (4.3) using standardized phenotypic records of BW1-2 and WG3-6 was:

$$\begin{bmatrix} \mathbf{y}_{1-5}^{m0} \\ \mathbf{y}_{1-5}^{f0} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{1-5}^m & 0 \\ 0 & \mathbf{X}_{1-5}^f \end{bmatrix} \begin{bmatrix} \mathbf{b}_{1-5}^m \\ \mathbf{b}_{1-5}^f \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{1-5}^m & 0 \\ 0 & \mathbf{Z}_{1-5}^f \end{bmatrix} \mathbf{a}_{1-5} + \begin{bmatrix} \mathbf{W}_{1-5}^m & 0 \\ 0 & \mathbf{W}_{1-5}^f \end{bmatrix} \mathbf{c}_{1-5} + \begin{bmatrix} \mathbf{e}_{1-5}^m \\ \mathbf{e}_{1-5}^f \end{bmatrix}$$

$$\begin{bmatrix} \mathbf{y}_6^{m0} \\ \mathbf{y}_6^{f0} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_6^m & 0 \\ 0 & \mathbf{X}_6^f \end{bmatrix} \begin{bmatrix} \mathbf{b}_6^m \\ \mathbf{b}_6^f \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_6^m & 0 \\ 0 & \mathbf{Z}_6^f \end{bmatrix} \mathbf{a}_6 + \begin{bmatrix} \mathbf{e}_6^m \\ \mathbf{e}_6^f \end{bmatrix} \quad (4.3)$$

where  $\mathbf{y}_{1-5}^{m0}$  and  $\mathbf{y}_{1-5}^{f0}$  are the vectors of male and female standardized phenotypic records, respectively, for BW1-2 and WG3-5;  $\mathbf{b}_{1-5}^m$  and  $\mathbf{b}_{1-5}^f$  are vectors of fixed effects of bird flock, source of flocks and age of dam for males and females, respectively, of BW1-2 and WG3-5. Similarly,  $\mathbf{y}_6^{m0}$  and  $\mathbf{y}_6^{f0}$  are the vectors of male and female standardized phenotypic records, respectively, for WG6;  $\mathbf{b}_6^m$  and  $\mathbf{b}_6^f$  are vectors of fixed effects for male and female birds, respectively. Matrices of  $\mathbf{X}_{1-5}^m$ ,  $\mathbf{X}_{1-5}^f$ ,  $\mathbf{Z}_{1-5}^m$ ,  $\mathbf{Z}_{1-5}^f$ ,  $\mathbf{W}_{1-5}^m$ ,  $\mathbf{W}_{1-5}^f$ ,  $\mathbf{X}_6^m$ ,  $\mathbf{X}_6^f$ ,  $\mathbf{Z}_6^m$  and  $\mathbf{Z}_6^f$  are incidence matrices. Vectors  $\mathbf{a}_{1-5}$  and  $\mathbf{a}_6$  are direct additive genetic effects of the bird for BW1-2, WG3-6, respectively;  $\mathbf{c}_{1-5}$  are vectors of the permanent environmental maternal effect for BW1-2 and WG3-5. Direct additive genetic and permanent environmental maternal effects were reduced ranks between sexes. Vectors  $\mathbf{e}_{1-5}^m$ ,  $\mathbf{e}_{1-5}^f$ ,  $\mathbf{e}_6^m$  and  $\mathbf{e}_6^f$  are random residuals of male BW1-2 and WG3-5, female BW1-2 and WG3-5, male WG6 and female WG6, respectively. The random vectors of the direct additive genetic effect and permanent environmental maternal effect were assumed to be normally distributed:  $\mathbf{a}_{1-6} \sim \mathbf{N}[\mathbf{0}, \mathbf{A} \otimes \mathbf{V}_a^0]$ ,  $\mathbf{c}_{1-5} \sim \mathbf{N}[\mathbf{0}, \mathbf{I} \otimes \mathbf{V}_c^0]$ , where  $\mathbf{A}$  is the pedigree relationship matrix;  $\mathbf{I}$  is the identity matrix for dams;  $\mathbf{V}_a^0$  is the 6x6 covariance matrix of the direct additive genetic effects;  $\mathbf{V}_c^0$  is the 5x5 covariance matrix of the permanent environmental maternal effects. The residuals were also assumed to be normally distributed:  $\mathbf{e}_{1-5}^m$ ,  $\mathbf{e}_{1-5}^f$ ,  $\mathbf{e}_6^m$  and  $\mathbf{e}_6^f \sim \mathbf{N}[\mathbf{0}, \mathbf{I} \otimes \mathbf{V}_e^0]$ , where  $\mathbf{I}$  is the identity matrix for individual birds; the covariance matrix  $\mathbf{V}_e^0$  is an 12x12 matrix, in which the residual covariances between male and female records for BW1-2 and WG3-5 traits are zero. Covariance matrices  $\mathbf{V}_a^0$ ,  $\mathbf{V}_c^0$  and  $\mathbf{V}_e^0$  are at standardized scale.

#### **Transformation of parameters to body weight scale**

Parameters estimated from the model (4.3) were in standardized scale of BW and weight gains. However, results of parameters were presented in BW at different weeks of age by re-transforming (co)variances of standardized BW1-2 and WG3-6 back to the scale of BW1-6. Transformations from standardized BW1-2 and WG3-6 to normal scale of male and female BW1-6 were carried out for (co)variance matrices and the asymptotic covariance matrix. The asymptotic covariance matrix, which is the inverse of the average of observed and expected information in the REML likelihood (Jensen, 1997) from DMUAI procedures

#### 4 Broiler body weight at different ages

(Madsen and Jensen, 2013), was used to compute approximate standard errors for estimates using the approach by Fischer *et al.* (2004). The transformation formula can be found in Appendix 4.1.

### 4.3. Results

Table 4.1 shows the means, coefficient of variation, standard deviation, and minimum and maximum values for BW at different weeks of age from male and female broilers reared in a commercial environment. The results show that BW of the birds increased drastically with increasing weeks of age. The increase was more than 2.5 times from BW1 to BW2. Similarly, the standard deviation of BW increased quickly at the early ages of birds, but the rate of the increase was lower at the later ages. The CV remained relatively stable over different ages of birds. The results also showed that both the absolute and the relative differences in BW between males and females increased with age. The relative differences between male and female BW was 1.01, 1.03, 1.06, 1.10, 1.12 and 1.15 at week 1-6, respectively.

**Table 4.1:** Descriptive statistics for body weight (BW) records (unit in gram) of males and females from commercial broiler chicken at 1-6 weeks of age.

Week	Male						Female					
	n	$\mu$	CV	SD	Min.	Max.	n	$\mu$	CV	SD	Min.	Max.
1	8039	155	0.14	22	68	236	8388	154	0.14	21	72	224
2	8631	403	0.16	63	152	582	9010	393	0.16	61	150	580
3	8425	810	0.16	131	278	1226	8870	762	0.15	116	302	1102
4	8225	1243	0.18	218	350	1930	8689	1131	0.17	189	336	1732
5	7455	1735	0.17	302	480	2796	7922	1550	0.16	248	506	2274
6	3975	2231	0.16	364	658	3225	4217	1940	0.15	290	685	2752

Note: n is number of records;  $\mu$  is mean; CV is coefficient of variation; SD is standard deviation.

Table 4.2 shows the estimated variance components and their relative weekly increase. All variances increased sharply with increasing weeks of age. The relative increase in variances was larger at early age than later. For example, the relative increase in direct additive genetic variance from BW1 to BW2 was 1028 and 976% for males and females, respectively, whereas the relative increase in the variance from BW5 to BW6 was 51 and 41% for males and females. In addition, the increase of the direct genetic and residual variances was steeper than the increase of the maternal variance. The relative increase in variance of the permanent environmental maternal effect was lower than variances of the direct additive genetic effect at week 1-6. There was no increase in the permanent environmental maternal variance from week 5-6 as the effect was not significant for the weight gain from week 5-6.

#### 4 Broiler body weight at different ages

The direct additive genetic, permanent environmental maternal and phenotypic variances were higher for male than female BW at all weeks of age. The relative increases in variances were also higher for male BW. The difference in variances between male and female BW increased with increasing weeks of age.

**Table 4.2:** Estimated variance components and relative increase in variance for body weight (BW) of broiler chicken over 1-6 weeks. Variance components were direct additive genetic effect (*a*), permanent environmental maternal effect (*c*), and phenotypic effect for male ([effect].M) and female BW ([effect].F). Relative increase in variances at week *t* (2-6) is the difference between variances at week *t* and week *t-1* divided by the variance at week *t-1*.

Week	Variance						Relative increase in variance (%)					
	a.M	a.F	c.M	c.F	p.M	p.F	a.M	a.F	c.M	c.F	p.M	p.F
1	86	83	33	32	306	300						
2	970	893	234	215	3089	2830	1028	976	609	572	909	843
3	3538	2821	786	636	12435	9712	265	216	236	196	303	243
4	10724	7936	1599	1231	34219	24668	203	181	103	94	175	154
5	23904	16733	2591	1911	74742	50852	123	111	62	55	118	106
6	36122	23621	2591	1911	130640	82065	51	41	0	0	75	61

Table 4.3 shows additive genetic, permanent environmental maternal and phenotypic coefficients of variation for male and female BW at different weeks of age. The direct additive genetic coefficients of variation fluctuated around 0.060-0.089 for male BW between week 1-6 and 0.059-0.083 for female BW between week 1-6. The permanent environmental maternal coefficients of variation had a decreasing tendency for both male and female BW as weeks of age increased from 1 to 6. In contrast, the environmental residual and phenotypic coefficients of variation had increasing tendency for male and female BW. The difference between phenotypic coefficients of variation of male and female BW increased with increasing weeks of age.

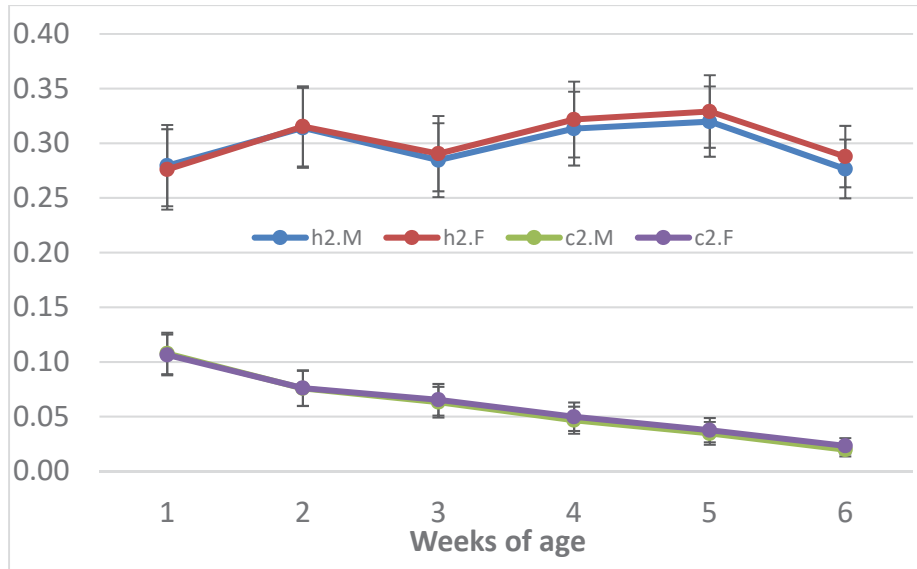
#### 4 Broiler body weight at different ages

**Table 4.3:** Direct additive genetic ( $a$ ), permanent environmental maternal ( $c$ ) and phenotypic ( $p$ ) coefficients of variation (CV) for male and female BW of broiler chicken over 1-6 weeks of age

BW at week	Male			Female		
	$CV_a$	$CV_c$	$CV_p$	$CV_a$	$CV_c$	$CV_p$
1	0.060	0.037	0.113	0.059	0.037	0.113
2	0.077	0.038	0.138	0.076	0.037	0.135
3	0.073	0.035	0.138	0.070	0.033	0.129
4	0.083	0.032	0.149	0.079	0.031	0.139
5	0.089	0.029	0.158	0.083	0.028	0.146
6	0.085	0.023	0.162	0.079	0.023	0.148

Figure 4.1 shows estimates of heritability and ratio of the permanent environmental maternal variance to the total phenotypic variance for BW over different weeks of age. With increasing weeks of age, the heritability had increasing tendency although there were two drops at week 3 and 6 when compared with heritability of BW in the previous week. Heritability of BW at week 1 and 6 were lowest at 0.276-0.288. Heritability of BW at week 5 was highest at 0.320 and 0.329 for male and female BW, respectively. The difference in heritability between male and female BW was negligible at all weeks of age, but the difference tended to increase with increasing weeks of age.

For BW, the ratio of the permanent environmental maternal variance to the total phenotypic variance reduced gradually from week 1-6. The ratio was 0.108 for male and 0.106 for female of BW at week 1, and it declined to 0.020 for male and 0.023 for female of BW at week 6. The difference in the permanent environmental maternal effect between male and female BW was negligible at all weeks of age. The permanent environmental maternal effect for WG6 was not included in the multivariate model because inclusion of the effect in the model led to convergence problems and the effect was not significant. However, the permanent environmental maternal effect of BW6 still existed because BW6 was the sum of BW2 and WG3-6.



**Figure 4.1:** Heritability ( $h^2$ ) ( $\pm$ SE) and ratio of the permanent environmental maternal variance to the total phenotypic variance ( $c^2$ ) ( $\pm$ SE) for male (M) and female (F) BW over 1-6 weeks of age.

**Table 4.4:** Estimated genetic correlations of the direct additive genetic effect for male (above diagonal) and female BW (below diagonal) between BWs at different weeks of age.

Week	1	2	3	4	5	6
1	1	0.846	0.717	0.528	0.402	0.320
2	0.846	1	0.922	0.706	0.547	0.435
3	0.730	0.933	1	0.898	0.769	0.664
4	0.548	0.727	0.901	1	0.963	0.901
5	0.424	0.572	0.776	0.964	1	0.983
6	0.351	0.472	0.683	0.911	0.986	1

Note: Standard errors for the correlations ranged from 0.003-0.079.

Table 4.4 show the estimated genetic correlations of direct additive genetic effects between BWs at different weeks of age. Positive correlations between BWs at different weeks of age were found for the direct additive genetic effects. The direct additive genetic effects on two consecutive weekly BWs were highly correlated with genetic correlations ranging from 0.846-0.986 with standard error of 0.003-0.029. The correlations between two consecutive weekly BWs were lower in the early ages than in the late ages. The correlations between early and late BWs were weaker for the direct additive genetic effect. The genetic correlation between BW1 and BW6 was only 0.320 for male BW and 0.351 for female BW.

Table 4.5 show the phenotypic correlations between BWs at different weeks of age for male and female records. Similar to the genetic correlations between different weeks of age, the phenotypic correlations

#### 4 Broiler body weight at different ages

were higher between two consecutive weekly BWs than the correlations between early and late BWs. The phenotypic correlations between two consecutive weekly BWs were 0.752-0.925 for male records and 0.763-0.941 for female records. The correlations between BWs at week 1-2 and week 5-6 were 0.307-0.546 for male records and 0.350-0.566 for female records. The correlations between BWs at different weeks of age for female BW were slightly higher than the corresponding correlations for male BW.

**Table 4.5:** Estimated phenotypic correlations between BWs at different weeks of age for males (above diagonal) and females (below diagonal)..

Week	1	2	3	4	5	6
1	1	0.752	0.635	0.502	0.395	0.307
2	0.763	1	0.869	0.688	0.546	0.431
3	0.664	0.885	1	0.863	0.724	0.595
4	0.521	0.697	0.864	1	0.915	0.797
5	0.421	0.566	0.732	0.921	1	0.925
6	0.350	0.468	0.625	0.831	0.941	1

Note: Standard errors for the correlations ranged from 0.002-0.013.

#### 4.4. Discussion

A multivariate model was developed and used to estimate variance components for male and female BW at different weeks of age of broiler chicken tested in a commercial production environment. A criterion used in the development of the model was cross-validation procedure that was based on half-sib correlation in order to avoid biases due to maternal effects. The model used BW and weight gains as phenotypic records to overcome convergence problems, and male and female BW were standardized differently to model the heterogeneous variances between sexes.

##### *Statistical model and methodology*

A criterion for the development of statistical models was the predictive ability of breeding values in cross-validation tests that were based on the half-sib correlation (results not shown). Methods of estimating this predictability is different from the conventional method of cross-validation. The conventional method is based on correlation between corrected phenotypes ( $y_c$ ) and EBVs of the same animals in the validation dataset (Christensen *et al.*, 2012). This conventional method can lead to an overestimation of the model predictive ability when maternal effects are present. The estimation of EBVs of birds in the validation dataset is from information of their full-sibs, half-sibs, dam, sire, and other relatives in the pedigree, of which full-sibs provide most information to the prediction. If the maternal effects are not accounted for

appropriately in the model, the effects shared among full-sibs may influence the EBVs of birds in the validation dataset, and the predictability of breeding values for the model would be overestimated.

To avoid this overestimation, we use a different approach to calculate the predictive ability in the cross validation including the division of training and validation datasets and half-sib correlation. The division is to ensure that birds in the validation dataset always have their full-sibs and half-sibs in the training dataset. If the maternal effects are not properly accounted for in the model, the effects will confound into EBVs. The correlation of  $EBV_v$  and  $y_c$  is between birds that are paternal half-sibs in the validation dataset, and due to the mating structure such half sibs will not share potential bias from maternal effects. However, the interference of the maternal additive genetic effect is reduced but not completely removed because the different dams of two half-sib birds might be related in the pedigree. Another limitation of our method is that the cross validation relies on correlation between  $EBV_v$  and  $y_c$  of half-sibs which may have higher standard error than the conventional method using correlation between EBVs and  $y_c$  of the same birds.

It is common that sex by genotype interaction is ignored in genetic evaluations of breeding programs because re-ranking due to sex by genotype interaction is small (van der Heide *et al.*, 2016), and because treating male and female traits as two traits can easily lead to convergence problems in the models. Heterogeneous variance between sexes, therefore, are often also ignored. However, when the heterogeneous variance exists and is not accounted in the model, a serious re-ranking may occur and lead to reduced response to selection (Cardoso *et al.*, 2007). Failure to account for different variances between sexes could also lead bias to variance components and estimated breeding values (Thompson, 2008). A distinct feature of the multivariate model (4.3) was the standardization applied differently to male and female records based on phenotypic standard deviations that were calculated from univariate models (1-2). This relatively simple standardization approach can model the heterogeneous variances between sexes and their unity correlations. This approach can reduce potential bias compared to the model that considered identical variances for sexes. In addition, the use of heterogeneous variances can be very good for multi-trait selection indexes for different sexes. Compared to the bivariate model that treats male and female records as two different traits, our model requires less computation and it is less likely to encounter convergence problems. Another feature of the multivariate model (4.3) was different residual variance for male and female traits. When the standardization of male and female records were not efficient, this would show in the model as a heterogeneous residual variance.

In addition, our model utilized all performances of BW1-6 simultaneously in the multivariate model. Because there were repeated measurement for BW, repeatability and random regression models were



considered. However, repeatability model would have low accuracy because correlations between early and late BW were low. Random regression models would require high order of fitting functions due to the fluctuation of heritability at different weeks of age, particularly at week 2-3. When convergence of the multivariate model was not an issue, the multivariate model had more parameters, and described better the covariance matrix of the direct additive genetic effect over weeks of age than the random regression model. In addition, the covariance matrices from a multivariate model can be fitted with functions, thus the change of an effect over week of ages can be described just like in a random regression model. A Legendre polynomial covariance function that were used to model the covariance of the additive genetic effect can be found in Appendix 4.2. Multivariate model is typically regarded as better prediction to breeding values than univariate model because the multi-trait model capitalize information from correlated traits (Henderson and Quaas, 1976).

Our model used BW1-2 and weight gains to model BW1-6. This is a linear transformation that leads to the same inferences but have much better convergence properties. However, after transformations, variance components of the model (4.3) were not as expected. Although correlations between sexes were assumed to be one, genetic correlations between BWs at different weeks were not identical for males and as females. For examples, correlation between BW1 and BW2 was 0.846 for both male and female, but correlation between male BW1 and male BW6 was different compared to the correlation between female BW1 and female BW6. Although the difference in heritability between sexes is negligible for BW3-6, there was an increasing difference in heritability between male and female with increasing weeks of age.

##### *Variance components*

With increasing age, the direct additive genetic, permanent environmental maternal and residual variances of BW increased sharply. However, the direct additive genetic, permanent environmental maternal and residual coefficients of variation changed relatively little with increasing weeks of ages. The small change in the coefficients of variation, despite of the sharp increase in variances, indicates that the change in variance components over week 1-6 is mainly due to scaling effect as the mean BW also increased considerably with increasing ages. The sharp increase in variances and relatively little changes in coefficients of variation were also found in BW of indigenous chicken from week 0-16 (Dana *et al.*, 2011), BW of crossbred chicken from week 2-10 (Begli *et al.*, 2016) and BW of broiler chicken from day  $t-7$  to  $t$  (Mebratie *et al.*, 2017).

However, the scaling effect was not the only factor responsible for the change of variance components over ages of broilers because the rates of the change were different between weeks of age and for different random effects in the model. The rate of the change in variance components from BW1 to BW2

is much more substantial than the change between later consecutive weeks of age. In addition, the rates of the change are different between different random effects. The permanent environmental maternal variance increased considerably but its proportion of the total phenotypic variance reduced gradually. The phenotypic variances also increased rapidly for both male and female BW, but the increase was at a slower rate for female BW due to the lower growth rate of females.

##### *Maternal effects*

The permanent environmental maternal effect on BW reduced gradually from week 1-6. The effect was still significant on BW at week 6, but the effect was not significant for WG6. Jasouri *et al.* (2017) also found a diminishing trend of the effect on BW in dual-purpose chicken when they aged. They found that the permanent environmental maternal effect was still significant at week 12. Dana *et al.* (2011) found the environmental maternal effect on BW at week 8, but not BW at week 12 in indigenous chicken. Begli *et al.* (2016) showed that the ratio of the permanent environmental maternal variance to the total phenotypic variance for BW of F2 chicken crossed between commercial broilers and native fowls increased slightly from 0.10 at week 2 to 0.12 at week 6, and then reduced to 0.07 at week 10. Maniatis *et al.* (2013) showed that the ratio of the permanent environmental maternal variance to the total phenotypic variance was 0.12 for BW at week 1 and 0.05 for BW at week 5 of commercial broiler chicken. The decrease in the permanent environmental maternal effect with increasing age was also found for meat quail (Barbieri *et al.*, 2015) and local Venda chicken (Norris and Ngambi, 2006). In comparisons, the permanent environmental maternal effect at the corresponding age in our study is lower than other studies (Begli *et al.*, 2016; Dana *et al.*, 2011; Jasouri *et al.*, 2017; Maniatis *et al.*, 2013; Zonuz *et al.*, 2013). This may be due to the raising environment. Birds in our study are raised in commercial production environment while those studies have birds from breeding units (Dana *et al.*, 2011; Jasouri *et al.*, 2017; Maniatis *et al.*, 2013; Zonuz *et al.*, 2013) or controlled experimental environments (Begli *et al.*, 2016; Norris and Ngambi, 2006).

The maternal effect, age of dam, was also included into the multivariate model (4.3), as it was in the study by Koerhuis and Thompson (1997) on juvenile BW of broilers. The influence of dam age on broiler BW may be related to egg weight. Significant effects of dam age and egg weight on broiler BW has been reported (Lapao *et al.*, 1999; Tahir *et al.*, 2011; Tona *et al.*, 2004; Wolanski *et al.*, 2007). The effect of egg weight was significant on BW of broilers at hatching and at 50 days of age, and a linear function of egg weight on hatching BW was found in Tahir *et al.* (2011). Tona *et al.* (2004) found that BWs of broilers at week 0-2 from younger dams were significantly lower than the BWs from older dams.

In our studies, the maternal additive genetic effect was not included in the multivariate model (4.3) as the effect was not significant for all BW traits except male BW1 (Appendix 4.3). Meanwhile, many studies show that the presence of the maternal effects including both additive genetic and permanent environmental effects can increase the fit of the models (Chapuis *et al.*, 1996; Jasouri *et al.*, 2017; Koerhuis and Thompson, 1997; Maniatis *et al.*, 2013; Zonuz *et al.*, 2013). Inclusion of both the maternal effects in the model improved considerably the fit of models for BW traits at week 0, 8 and 12 in dual-purpose chicken compared to the models without or with only one of the maternal effects (Jasouri *et al.*, 2017). A similar conclusion on the inclusion of both the maternal effects in the model was for BW at week 0 and 5 in broilers (Maniatis *et al.*, 2013), BW at week 8 in Iranian native chicken (Zonuz *et al.*, 2013), BW at week 12 and 16 in turkeys (Chapuis *et al.*, 1996), and juvenile BW in broilers (Koerhuis and Thompson, 1997). These five studies used REML for estimation of variance components, and comparison criteria between models was based on log-likelihood, Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC). Jasouri *et al.* (2017) found that breeding values estimated for BW at week 0 and 8 were substantially affected by the maternal effects included in the model whereas breeding values estimated for BW at week 12 were similar for models with and without the maternal effects included.

##### *Heritability*

Heritability estimates in our study were moderate and ranged from 0.276 to 0.320 for male BW and from 0.276 to 0.329 for female BW at week 1-6. Kapell *et al.* (2012), in which broiler chicken were also raised in commercial production environment, obtained a heritability for BW5 of 0.32-0.36. In the same study (Kapell *et al.*, 2012), heritability of BW5 were 0.32-0.40 for broiler chicken that were raised in the breeding environment. Other studies on broiler chicken raised in a breeding environment report heritability of 0.21-0.42 for juvenile male BW, 0.30-0.53 for juvenile female BW (Mebratie *et al.*, 2017), 0.26-0.33 for juvenile male BW, 0.30-0.36 juvenile female BW (Koerhuis and Thompson, 1997) and 0.22 for BW at week 5 (Maniatis *et al.*, 2013). Also raised in the breeding environment, heritability were 0.19-0.23 for BW of Horro indigenous chicken at weeks 2-16 (Dana *et al.*, 2011), 0.31-0.32 for BW of dual-purpose chicken at weeks 8 and 12 (Jasouri *et al.*, 2017), and 0.24 for BW of Iranian native chicken at week 8 (Zonuz *et al.*, 2013). In Begli *et al.* (2016) crossbred chicken were raised in a controlled experimental environment, and heritability estimates varied from 0.32 to 0.34 for BW at week 2-6, and it dropped linearly from 0.34 for BW at week 6 to 0.19 for BW at week 10. In Norris and Ngambi (2006), heritability was 0.36 for BW of local Venda chicken at week 0 and 0.25 at week 4.

Heritability for BW at week 2-3 does not seem to follow the overall change of heritability over ages. It might be due to the change of maternal additive genetic effect at week 2-3 that is not accounted in the

multivariate model (4.3). Even if the maternal additive genetic effect was not significant, failing to account for this effect might cause an overestimation of the direct additive genetic effect. Other possible explanation to the change of heritability for BW at week 2-3 could be diseases. Birds around this age are prone to coccidiosis and other diseases of the digestive tract (Shamim *et al.*, 2015) that affect BW of broilers. Respiratory diseases caused by infectious bronchitis virus, avian metapneumovirus and mycoplasma species may also affect BW of broilers at this age, when level of maternal antibodies declines substantially and birds start to croak (De Boeck *et al.*, 2015). In addition, feed change from starter to growing diets may affect BW of broilers at this age.

##### *Genetic correlations*

The genetic correlation between BWs at consecutive weeks was high, particularly for BWs at weeks 2-6, in which the correlations between BWs at two consecutive weeks were above 0.898. The correlations between BWs at week 4 and 6 were also high at 0.901 for male records and 0.911 for female records. These findings are in agreement with Barbieri *et al.* (2015), Begli *et al.* (2016) and Niknafs *et al.* (2012), which estimated the genetic correlations between BWs at two consecutive weeks ranging from 0.90 to 0.99 for BWs from week 2 onwards. Begli *et al.* (2016) found high correlations (>0.91) between BWs at week 4-7. In Mebratie *et al.* (2017), the genetic correlation between juvenile BWs at  $t$  and  $t+4$  days of age were 0.94 for male records and 0.92 for female records. The genetic correlations were 0.97 between BWs at week 6 and 8, 0.86 between BWs at week 8 and 12, and 0.99 between BWs at week 12 and 16 in Dana *et al.* (2011). These high correlations imply that the age of selection for broilers can be reduced compared to the age of target BW in breeding program with relatively low loss in accuracy of selection. In our study, the correlations between early and late BWs were relatively low, ranging from 0.320 to 0.572 for BWs between week 1-2 and 5-6. Maniatis *et al.* (2013) found a genetic correlation of 0.17 between BWs at week 1 and 5. The genetic correlations for BWs were 0.66 between week 2 and 6, 0.46 between week 2 and 8, and 0.26 between week 2 and 10 (Begli *et al.*, 2016). Other studies found genetic correlations of BW to be 0.36-0.37 between week 1 and 8-12 (Niknafs *et al.*, 2012), 0.25-0.46 between week 0 and 6-16 (Dana *et al.*, 2011), and 0.20-0.38 between week 1 and 5-6 (Barbieri *et al.*, 2015). These findings suggest that early BW has a relatively low influence on target BW of selection.

##### *Sex by genotype interaction*

Sex by genotype interaction refers to the same genotype expressed differently in male and female BWs. This can be modelled by regarding BW in males and females as two different traits. Each bird, either male or female, would have two breeding values for male BW and for female BW. Indications of sex by genotype interaction can be heterogeneous variances, different heritability and correlation of less than one

between male and female BWs. Sex by genotype interaction for BW has been demonstrated in broilers (Mebratie *et al.*, 2017; van der Heide *et al.*, 2016) and other poultry species (Chapuis *et al.*, 1996; Mignon-Grasteau *et al.*, 1998). These studies show that variances between sexes could differ by a factor of 2 or more. These studies also found different heritability between sexes and correlations of 0.83-0.94 between male and female BW. However, these high correlations imply relatively small re-ranking between sexes. In addition, van der Heide *et al.* (2016) shows that correlations between estimated breeding values from sex-joined (univariate) and sex-specific (bivariate) models were 0.94-0.97 for broiler chicken BW at week 6.

In our study, the genetic variances for male and female BWs tended to be different, but the genetic correlation was not significantly different from one. Treating male and female BWs as two different traits led to convergence problems in the model, due to parameters at the edge of the parameter space. The unity correlation between sexes implies no re-ranking between male and female performances. The difference in heritability between sexes was also negligible even when different residuals for sexes were assumed in the multivariate model (4.3). Despite of unity correlation and similar heritability, the difference in genetic variances between male and female BW increased with increasing weeks of age.

#### 4.5. Conclusion

A model was developed and used to estimate genetic parameters of BW at 1-6 weeks of age of broilers raised in a commercial environment. To improve accuracy of predicting EBVs, we have used several different approaches including model cross-validation based on half-sib correlation, scaling applied separately to male and female records and the use of weight gains to model BW. Half-sib correlation was used to reduce the interference of maternal effects on the cross-validation when maternal effects might be present. Scaling was to account for heterogeneous variance between sexes to reduce potential bias of the model that considered identical variances for sexes. All performances of BW1-6 were utilized simultaneously in a multivariate model using weight gains. Parameter estimates from the multivariate model show that the direct additive genetic, permanent environmental maternal and residual variances for BW increased sharply as age of broilers increased. The sharp increase in variances over weeks of age were mainly due to scaling effect. However, rate of the increase was also different e.g. ratio of the permanent environmental maternal variance to phenotypic variance reduced gradually with increasing age.

**Appendix 4.1:**

Transformations from standardized BW1-2 and WG3-6 to normal scale of male and female BW1-6 were carried out for (co)variance matrices and the asymptotic covariance matrices using formula (4.4-4.7):

$$\mathbf{V}_a = \mathbf{T}_3 [\mathbf{T}_2 (\mathbf{T}_1 \mathbf{V}_a^0 \mathbf{T}'_1) \mathbf{T}'_2] \mathbf{T}'_3 \quad (4.4)$$

$$\mathbf{V}_c = \mathbf{T}_{c3} [\mathbf{T}_{c2} (\mathbf{T}_{c1} \mathbf{V}_c^0 \mathbf{T}'_{c1}) \mathbf{T}'_{c2}] \mathbf{T}'_{c3} \quad (4.5)$$

$$\mathbf{V}_e = \mathbf{T}_3 [\mathbf{T}_2 (\mathbf{T}_1 \mathbf{V}_e^0 \mathbf{T}'_1) \mathbf{T}'_2] \mathbf{T}'_3 \quad (4.6)$$

$$\mathbf{V}_I = \mathbf{T}_{VI3} [\mathbf{T}_{VI2} (\mathbf{T}_{VI1} \mathbf{V}_I^0 \mathbf{T}'_{VI1}) \mathbf{T}'_{VI2}] \mathbf{T}'_{VI3} \quad (4.7)$$

where matrices of direct additive genetic, permanent environmental maternal, residual and asymptotic covariances were  $\mathbf{V}_a$ ,  $\mathbf{V}_c$ ,  $\mathbf{V}_e$  and  $\mathbf{V}_I$ , respectively, at normal BW scale, and  $\mathbf{V}_a^0$ ,  $\mathbf{V}_c^0$ ,  $\mathbf{V}_e^0$  and  $\mathbf{V}_I^0$ , respectively, at standardized weight gain scale. Transforming matrices for formula (4-7) were:

$$\mathbf{T}_1 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}, \mathbf{T}_3 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 \end{bmatrix}$$

$$\mathbf{T}_{c1} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}, \mathbf{T}_{c3} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 \\ 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 \end{bmatrix}$$

#### 4 Broiler body weight at different ages

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$$\mathbf{T}_{VI1} = \begin{bmatrix} \mathbf{T}_1 \otimes \mathbf{T}_1 & 0 & 0 \\ 0 & \mathbf{T}_{c1} \otimes \mathbf{T}_{c1} & 0 \\ 0 & 0 & \mathbf{T}_1 \otimes \mathbf{T}_1 \end{bmatrix}$$

$$\mathbf{T}_{VI2} = \begin{bmatrix} \mathbf{T}_2 \otimes \mathbf{T}_2 & 0 & 0 \\ 0 & \mathbf{T}_{c2} \otimes \mathbf{T}_{c2} & 0 \\ 0 & 0 & \mathbf{T}_2 \otimes \mathbf{T}_2 \end{bmatrix}, \mathbf{T}_{VI3} = \begin{bmatrix} \mathbf{T}_3 \otimes \mathbf{T}_3 & 0 & 0 \\ 0 & \mathbf{T}_{c3} \otimes \mathbf{T}_{c3} & 0 \\ 0 & 0 & \mathbf{T}_3 \otimes \mathbf{T}_3 \end{bmatrix}$$

Matrix  $\mathbf{T}_2$  is a 12x12 matrix, of which off-diagonal elements are zero, the diagonal is vector of phenotypic standard deviations with trait orders: male BW1, female BW1, male BW2, female BW2, male WG3, female WG3, male WG4, female WG4, male WG5, female WG5, male WG6 and female WG6. Matrix  $\mathbf{T}_{c2}$  is a 10x10 matrix that is sub-matrix of  $\mathbf{T}_2$  for traits of male and female BW1-2 and WG3-5. The phenotypic standard deviations of diagonals from matrices  $\mathbf{T}_2$  and  $\mathbf{T}_{c2}$  were computed from variance estimates of univariate models (4.1) and (4.2).

#### Appendix 4.2:

The covariance of a Legendre polynomial function that was fitted to model the additive genetic variances and covariances of BW traits over 1-6 week of ages was computed:

$$\widehat{\mathbf{V}}_a^L = \boldsymbol{\Phi}^{-1} \widehat{\mathbf{V}}_a \boldsymbol{\Phi}^{-T} \quad (4.8)$$

where  $\widehat{\mathbf{V}}_a^L$  is the covariance matrix of the Legendre polynomial coefficients for the additive genetic effect of BW traits over weeks of age;  $\boldsymbol{\Phi}$  is a matrix of the Legendre polynomial coefficients with order of five that were computed using standardized weeks of age;  $\boldsymbol{\Phi}^{-1}$  is the inverse of  $\boldsymbol{\Phi}$ ;  $\boldsymbol{\Phi}^{-T}$  is the transpose of the inverse of  $\boldsymbol{\Phi}$ ; and  $\widehat{\mathbf{V}}_a$  is the covariance matrix of the additive genetic effect for BW1-6 estimated from the multivariate model (4.3).

Variances and covariances of the Legendre polynomial coefficients on weeks were computed separately for male and female BW (Table 4.6).

**Table 4.6:** Variances and covariances of Legendre polynomial coefficients on weeks for additive genetic effects of male and female body weights

	Male						Female					
	a <sub>0</sub>	a <sub>1</sub>	a <sub>2</sub>	a <sub>3</sub>	a <sub>4</sub>	a <sub>5</sub>	a <sub>0</sub>	a <sub>1</sub>	a <sub>2</sub>	a <sub>3</sub>	a <sub>4</sub>	a <sub>5</sub>
a <sub>0</sub>	14143						10369					
a <sub>1</sub>	9677	7630					6664	5063				
a <sub>2</sub>	945	1347	639				464	790	394			
a <sub>3</sub>	-1008	-815	-112	145			-726	-595	-87	109		
a <sub>4</sub>	-284	-286	-106	26	25		-215	-207	-71	21	18	
a <sub>5</sub>	147	140	29	-42	-5	21	124	110	19	-32	-4	15

Notes: a<sub>0</sub> is a coefficient on intercept; a<sub>1</sub>, a<sub>2</sub>, a<sub>3</sub>, a<sub>4</sub> and a<sub>5</sub> are a coefficient on weeks to the first, second, third, fourth and fifth power, respectively.

**Appendix 4.3:**

Log-likelihood ratio tests (significant difference, P<0.05) were carried out to identify the significance of maternal additive genetic effect for BW traits by week and sex. Three univariate models (4.9-4.11) were used for the log-likelihood ratio tests:

$$y = Xb + Za + Mm + Wc + e \quad (4.9)$$

$$y = Xb + Za + Mm + Wc + e \quad (4.10)$$

$$y = Xb + Za + Wc + e \quad (4.11)$$

where **y** is vector of male or female phenotypic records of BW1-6 at normal scale; **b** is vectors of fixed effects of flock of birds, source of flocks and age of dam. Matrices of **X**, **Z**, **M**, and **W** are incidence matrices. Vectors **a**, **m**, **c** and **e** are the direct additive genetic effect, maternal additive genetic effect, permanent environmental maternal effect and residual, respectively. In model (4.9), these random effects were assumed to be normally distributed:

$$\begin{bmatrix} \mathbf{a} \\ \mathbf{m} \end{bmatrix} \sim N[\mathbf{0}, \mathbf{A} \otimes \begin{bmatrix} \sigma_a^2 & \sigma_{a,m} \\ \sigma_{a,m} & \sigma_m^2 \end{bmatrix}], \mathbf{c} \sim N[\mathbf{0}, \mathbf{I}_d \sigma_c^2] \text{ and } \mathbf{e} \sim N[\mathbf{0}, \mathbf{I}_e \sigma_e^2],$$

where **A** is the pedigree relationship matrix; **I<sub>d</sub>** is the identity matrix for dams; **I** is the identity matrix for individual birds;  $\sigma_a^2$ ,  $\sigma_m^2$ ,  $\sigma_{a,m}$ ,  $\sigma_c^2$  and  $\sigma_e^2$  are the direct additive genetic variance, maternal additive genetic variance, direct and maternal additive genetic covariance, permanent environmental maternal variance, and residual variance, respectively. The random effects in model (4.10) were assumed to be

normally distributed as in model (4.9), except that  $\begin{bmatrix} \mathbf{a} \\ \mathbf{m} \end{bmatrix} \sim N[\mathbf{0}, \mathbf{A} \otimes \begin{bmatrix} \sigma_a^2 & 0 \\ 0 & \sigma_m^2 \end{bmatrix}]$ . The random effects in



#### 4 Broiler body weight at different ages

model (4.11) were assumed to be normally distributed as in model (9), except that the maternal additive genetic effect is not present.

**Table 4.7:** Estimates ( $\pm$ SE) of variance components<sup>1</sup> from model (4.9) and the significance of maternal additive genetic effects from log-likelihood ratio tests for male (M) and female (F) body weight of broiler chicken over 1-6 weeks of age.

Week	Sex	$\sigma_a^2$	$\sigma_{a,m}$	$\sigma_m^2$	$\sigma_c^2$	$\sigma_e^2$	Significance <sup>2</sup> of $\sigma_{a,m}$	Significance <sup>3</sup> of $\sigma_m^2$
1	M	64 $\pm 14$	-6 $\pm 10$	28 $\pm 10$	18 $\pm 6$	201 $\pm 8$	NS	***
1	F	64 $\pm 14$	0 $\pm 8$	12 $\pm 7$	24 $\pm 5$	198 $\pm 8$	NS	NS
2	M	816 $\pm 154$	13 $\pm 80$	65 $\pm 58$	208 $\pm 48$	1905 $\pm 86$	NS	NS
2	F	789 $\pm 141$	39 $\pm 66$	46 $\pm 47$	155 $\pm 43$	1737 $\pm 79$	NS	NS
3	M	3035 $\pm 578$	-53 $\pm 298$	225 $\pm 224$	773 $\pm 186$	7707 $\pm 329$	NS	NS
3	F	2890 $\pm 491$	-83 $\pm 231$	181 $\pm 165$	395 $\pm 133$	5800 $\pm 274$	NS	NS
4	M	10622 $\pm 1793$	-713 $\pm 872$	695 $\pm 618$	1585 $\pm 472$	19284 $\pm 993$	NS	NS
4	F	7786 $\pm 1279$	-220 $\pm 596$	442 $\pm 414$	892 $\pm 339$	14147 $\pm 709$	NS	NS
5	M	20665 $\pm 3567$	52 $\pm 1628$	836 $\pm 1077$	1986 $\pm 978$	44490 $\pm 2042$	NS	NS
5	F	15786 $\pm 2654$	358 $\pm 1207$	536 $\pm 782$	1817 $\pm 746$	29082 $\pm 1484$	NS	NS
6 <sup>4</sup>	M	25558 $\pm 6187$		1014 $\pm 2510$	2530 $\pm 2399$	87633 $\pm 3968$	NS	NS
6 <sup>4</sup>	F	23450 $\pm 4667$		0 $\pm 1606$	802 $\pm 1413$	46161 $\pm 2718$	NS	NS

Notes:

<sup>1</sup> Variance components estimated from model (4.9) were direct additive genetic variance ( $\sigma_a^2$ ), maternal additive genetic variance ( $\sigma_m^2$ ), covariance between direct and maternal additive genetic effects ( $\sigma_{a,m}$ ), permanent environmental maternal variance ( $\sigma_c^2$ ), and residual variance ( $\sigma_e^2$ ).

<sup>2</sup> Log-likelihood ratio tests (significant difference,  $P < 0.05$ ) were used to test the significance of  $\sigma_{a,m}$  by comparing log-likelihoods of models (4.9) and (4.10).

<sup>3</sup> Log-likelihood ratio tests (significant difference,  $P < 0.05$ ) were used to test the significance of  $\sigma_m^2$  by comparing log-likelihoods of models (4.9) and (4.11).

NS: no significant difference ( $P > 0.05$ ); \*\*\*: significant difference with  $P < 0.001$ .

<sup>4</sup> Because model (4.9) did not converge, variance estimates for BW6 were from model (4.10). There was no estimate for  $\sigma_{a,m}$  in model (4.10).

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#### 4 Broiler body weight at different ages

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