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Research article

Genetic analysis of service cock effects on reproductive traits of Betong chickens (KU line) using threshold models

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Abstract

The importance of service cock effects was determined on the reproductive traits of Betong chickens (KU line). The traits, namely fertility, early embryonic viability, middle embryonic viability, hatchability of fertile eggs and hatchability of eggs set, were all classified as binary data and were analyzed using a repeatability threshold model. Variance components were estimated using a Bayesian method with Gibbs sampling. Six repeatability threshold models were fitted and the best model for each trait was chosen based on the deviance information criterion. All models consisted of direct additive genetic and animal permanent environmental effects, and different combinations of service cock genetic, service cock permanent environmental and direct additive-service cock genetic covariance effects. For all traits, the best model was the model with all combinations. The estimates of direct heritability were in the range 0.032–0.084 with the estimates of service cock heritability in the range 0.039–0.067, estimates of proportion of animal permanent environmental variance to phenotypic variance in the range 0.092–0.244 and estimates of proportion of service cock permanent environmental variance to phenotypic variance in the range 0.035–0.111. The estimates of direct additive-service cock genetic correlation were positive in all cases. The low heritabilities indicated that improving environmental conditions would have a large impact on phenotypic reproductive performance in this population of Betong chicken.

Introduction

Betong chicken is a famous native chicken breed in the southern part of Thailand and is characterized by golden brown plumage, yellow skin, a single comb and slow-feathering rate (Putsakul et al., 2010). Betong chickens have been raised on the Suwanwajokkasikit Chicken Farm, Department of Animal Science, Faculty of Agriculture, Kasetsart University, Thailand for several years. The preliminary selection program for this flock was based on general appearances to maintain some breed characteristics and emphasis on growth. Betong chickens from the closed KU line have light-to-dark golden-brown plumage, yellow skin, a single comb and slow-feathering. The breed can be grown with a short raising period under controlled feeding management (Putsakul et al., 2010). Feathering phenotype has been observed in these chickens (Chanjula and Pattamarakha, 2002) and this breed typically shows either a very slow-feathering phenotype (VF) or a slow-feathering phenotype (SF).

Beaumont (1996) and Lariviere et al. (2009) have reported details on the most important reproductive traits, especially in parent stock, are fertility and hatchability. The fertility of an egg is influenced by a combination of the hen and her mate (the service cock) and can usually be classified by candling at day 7 of incubation. Embryonic viability is a function of genotype and embryo environment provided by the egg and can be classified into three stages (early, middle

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and late) and the early and middle embryonic viabilities determine whether the embryo is alive or dead, being usually classified by candling at days 7 and 18 of incubation. Late embryonic viability or hatchability determines whether the embryo hatches, and is usually classified at day 22 of incubation. Causes of embryonic death at the three stages were different; early embryonic mortality depended on the age of breeder, egg storage and pre-heat procedures, middle embryonic mortality depended on the proper use of incubators and late embryonic mortality depended on following the appropriate incubation conditions or nutrition deficiency in the breeder diet (Etches, 1996). Genetic factors such as lethal gene and chromosome abnormalities also influence embryonic viability (Mauldin, 2001). Hatchability is defined as fertile eggs that succeed development and produce a viable chick, though in practice, fertility is expressed as a percentage of eggs set and hatchability is expressed as a percentage of fertile eggs and eggs set (Etches, 1996). All these reproductive traits have a binomial distribution, thus genetic parameter for each of them could be estimated using a repeatability threshold model that assumes an underling continuous variable have been applied for binomially distributed traits (Skotarczak et al., 2008).

The reproductive performance of animals is attributed to the influence of genetic and non-genetic factors (Falconer and Mackey, 1996). Hen reproductive traits have been analyzed using animal or repeatability models. Both the hen and service cock have been found to highly influence reproductive traits; several studies eliminated the influence of service cock by using pooled semen artificial insemination (Beaumont, 1996; Bennewitz et al., 2007; Cavero et al., 2011). However, the genotype of the embryo is transmitted from both parents. Moreover, the age of breeders, egg quality, semen quality and the efficiency of the sperm storage tubule all affect reproductive traits (Wilson, 1997). Hence, adding service cock including genetic and non-genetic service cock effects could improve the predictive ability of the repeatability model. The objectives of this study were to determine the importance of both genetic and non-genetic service cock effects on reproductive traits and to estimate genetic parameters using univariate repeatability threshold models.

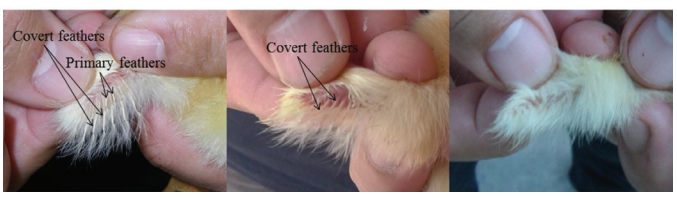

Fig. 1 Feathering phenotypes in one-day-old Betong chickens (KU line): (A) slow-feathering phenotype (showing primary feathers shorter than covert feathers); (B) slow-feathering phenotype (showing covert feathers only); (C) very slow-feathering phenotype (not showing primary and covert feathers)

Materials and Methods

Animals, management and data

The approval ID# ACKU60-AGR-006 was issued by the Institutional Animal Care and Use Committee, Kasetsart University, Bangkok, Thailand and the animal use protocol was in accordance with the guidelines for animal care under the Ethical Review Board of the Office of National Research Council of Thailand for conducting scientific research. Betong chickens (KU line) were obtained from the Suwanwajokkasikit Chicken Farm, Department of Animal Science, Faculty of Agriculture, Kasetsart University. The feathering phenotypes of one-day-old chicks were classified as either VF or SF (Fig. 1). Chickens were reared in a floor pen until aged 18 wk. Feed and water were provided *ad libitum*. At age 18 wk, the pullets were transported to individual battery cages in an evaporative cooling system house and received 16 hr light and 8 hr darkness. The hens were given a commercial feed ration (16% crude protein, 2,850 kcal metalizable energy) throughout the period. All service cocks were reared in individual cages and exposed to a photoperiod of 16 hr light and 8 hr darkness.

The sample consisted of 12,957 hatching eggs which were produced from 813 hens and 259 service cocks collected from nine hatching batches. Pedigree information included five successive generations. The age of hens at laying was 30–66 wk. Hens were randomly artificially inseminated once a week with 3–5 hens per cock and mating was avoided within a full sibling family. Each hen was inseminated with 0.10 mL of diluted semen (semen 1: extender 1) for hatching batches 1–8 and 0.10 mL of undiluted semen for hatching batch 9. The age of the service cocks at insemination was 27–75 wk. Hatching eggs were collected in the cold room at 15°C and 75–80% relative humidity (RH) and pre-heated for 8 hr before loading in to setters. The conditions for incubation periods during the first 18 d were 37.5°C and 60% RH, with the last 3 d at 37.5°C and 75% RH. Pedigree information is shown in Table 1.

Table 1 Pedigree information for reproductive hen traits in Betong chickens (KU line)

Item	Number of animals
Number of animals	1,160
Without records	284
With records	812
Without offspring	523
With offspring	573
With offspring and records	289
Number of sires	173
With progeny in the data	144
With records and progeny in the data	0
Number of dams	400
With progeny in the data	348
With records and progeny in the data	273

Individual egg hatching information was recorded as hen number, service cock number, date eggs laid, number of days between egg laid and insemination, and number of days between eggs set and eggs laid. Continuous fixed effects were considered for age of hen at eggs laid (AH), age of service cock at artificial insemination (AC), egg collection duration (CD) and egg storage duration (SD); categorical fixed effects were feathering phenotype of hen (FH), feathering phenotype of service cock (FC) and hatching batch (HB). CD was defined as number of days between egg laid and date of artificial insemination (AI). The date of AI and first day after AI were assumed to be the effect of the previous insemination (Etches, 1996) and the first egg of the first AI of an individual hen was discarded. Eggs laid after 2–9 d of insemination were coded CD as 1–7 days, respectively. SD was the number of days between eggs set and eggs laid which was in the range 0–28 d. FH and FC were coded as VF and SF, and HB was coded using nine categories (1 to 9).

Traits

Data collection for hen reproductive performance was performed at days 7, 18 and 22 of incubation. At day 7, an egg was classified as "infertile" (coded as 0) if clear or "fertile" (coded as 1) if there was an embryo present for fertility (FE) and an egg was described as "early embryonic death" (coded as 0) if a dead embryo was present or "living" (coded as 1) if there was a living embryo for early embryonic viability (EV). At day 18, an egg was classified as "middle embryonic death" (coded as 0) if there was a dead embryo or as "living" (coded as 1) if there was a living embryo for middle embryonic viability (MV). At day 22, an egg was classified as "late embryonic death" (coded as 0) if unhatched or as "hatched" (coded as 1) if it had hatched for late embryonic viability (LV), commonly called the hatchability of fertile eggs (HF). For hatchability of eggs set (HS), an egg was classified as "unhatched" (coded as 0) if the egg was infertile or had a dead embryo or as "hatched" (coded as 1) if it had hatched. The reproductive performance of hens is shown in Table 2.

Statistical analysis

Multiple univariate logistic regression analyses were used to determine the significance of the fixed effects using SAS PROC GENMOD (SAS, 2017). Fixed factors were analyzed for reproductive traits as shown in Equation 1:

$$ln\frac{P}{(1-p)} = b_0 + b_1AH + b_2AC + b_3CD + b_4SD + b_5FH + b_6FC + b_{7j}HB_j \quad (1)$$

where: $ln\frac{P}{(1-p)}$ = the log odds, p is the probability of liability (y = 1) for FE, EV, MV, HF and HS, AH is the continuous variable of age of hen, AC is the continuous variable of age of service cock, CD is the continuous variable of egg collection duration, SD is the continuous variable of egg storage duration, FH is the category variable of feathering phenotypes of hen, FC is the category variable of feathering phenotypes of service cock, HB is the category variable of hatching batch, b_0 is the intercept, b_1, b_2, b_3 and b_4 are the regression coefficients of AH, AC, CD and SD, respectively, b_5 is the regression coefficient of FH_{VF} vs FH_{SF}, b_6 is the regression coefficient of FC_{VF} vs FC_{SF} and b_{7j} is the regression coefficient of HB_j vs HB_9 when j = 1, 2, …, 8.

Table 2 Percentages of fertility, early embryonic viability, middle embryonic viability, hatchability of fertile eggs and hatchability of egg set in Betong chickens (KU line)

Item	FE	EV	MV	HF	HS
FH					
VF	51.85	93.89	95.37	83.60	38.82
SF	48.58	93.46	96.06	84.65	36.92
FC					
VF	52.07	93.75	95.33	83.00	38.63
SF	48.32	93.71	96.10	85.62	37.26
HB					
1	41.92	97.25	99.53	91.47	37.12
2	45.14	93.60	98.56	93.80	39.06
3	56.07	95.22	94.13	77.78	39.09
4	56.27	94.76	96.62	83.09	42.81
5	56.55	94.37	92.27	74.05	36.46
6	38.32	89.47	97.57	93.97	31.43
7	45.68	90.09	98.00	92.18	37.17
8	36.99	97.56	94.28	90.32	30.73
9	70.36	90.71	97.99	86.38	54.03
Average	49.70	93.67	96.55	87.00	38.65

FH = feathering phenotypes of hen; FC = feathering phenotypes of service cock; VF = very slow-feathering; SF = slow-feathering; HB = hatching batch; FE = fertility = [fertile egg 100 / egg set]; EV = early embryonic viability = [living eggs at 7 d × 100 / fertile egg]; MV = middle embryonic viability = [living egg at 18 d ×100 / living egg at 7 d]; HF = hatchability of fertile eggs = [hatched eggs at 22 d ×100 / living eggs at 18 d]; HS = hatchability of eggs set = [hatched egg at 22 d ×100 / egg set].

Estimates of variance components were obtained using the Bayesian method with Gibbs sampling (BAGS) with THRGIBBS1F90 (Misztal, 2008). Variance components were estimated by means of Gibbs sampling, with 300,000 samples generated, the first 50,000 of which were discarded and every 100th sample was stored. Thus, 2,500 samples were kept for computing posterior means and standard deviations. POSTGIBBS1F90 (Misztal, 2008) was used to determine the number of samples being initially rejected. Convergence was determined by trace plots. The deviance information criterion (DIC) obtained from THRGIBBS1F90 was used for Bayesian model comparison. The model with the lowest DIC value was considered as the most suitable (Sorensen and Gianola, 2002).

Due to different additional random effects in the analysis, six univariate repeatability threshold models were applied:

Model 1: $y = Xb + Z_1a + W_1pe + e$

Model 2: $y = Xb + Z_1a + W_1pe + W_2pc + e$

Model 3: $y = Xb + Z_1a + Z_2c + W_1pe + e$, $COV_{ac} = 0$

Model 4: $y = Xb + Z_1a + Z_2c + W_1pe + e$, $COV_{ac} \neq 0$

Model 5: $y = Xb + Z_1a + Z_2c + W_1pe + W_2pe + e$, $COV_{ac} = 0$

Model 6: $y = Xb + Z_1a + Z_2c + W_1pe + W_2pe + e$, $COV_{ac} \neq 0$

where: y is the vector of underlying continuous variables (liability), b is the vector of fixed effects of AH, AC, CD, SD, FH, FC and HB, a is the vector of direct additive genetic effect, c is the vector of service cock genetic effect, pe is the vector of animal permanent environmental effect, pc is the vector of service cock permanent environmental effect, e is the vector of residual effect and X, Z_1, Z_2, W_1 are W_2 the incidence matrices related records to b, a, c, pe and pc, respectively.

The (co) variance structures for the most complex model (Model 6) were assumed as:

$$V\begin{bmatrix} a \\ c \\ pe \\ pc \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{ac} & 0 & 0 & 0 \\ A\sigma_{ac} & A\sigma_c^2 & 0 & 0 & 0 \\ 0 & 0 & I\sigma_{pe}^2 & 0 & 0 \\ 0 & 0 & 0 & I\sigma_{pc}^2 & 0 \\ 0 & 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

where σ^2_a is the direct additive genetic variance, σ^2_c is the service cock genetic variance, σ_{ac} is the direct additive-service cock genetic covariance, σ^2_{pe} is the animal permanent environmental variance, σ^2_{pc} is the service cock permanent environmental variance, σ^2_e is the residual variance and fixed to 1, A is the numerator relationship matrix and I is the identity matrix. The distributions for random effects a, c, pe, pc and e were assumed as: $a \sim N(0,A\sigma^2_a)$, $c \sim N(0,A\sigma^2_c)$, $pe \sim N(0,I\sigma^2_{pe})$, $pc \sim N(0,I\sigma^2_{pc})$ and $e \sim N(0,I\sigma^2_e)$, respectively.

Results and Discussion

Factors affecting reproductive performances

Factors affecting reproductive performances were determined using multiple univariate logistic regression analyses and the results are shown in Table 3. The effect of AH was significant for FE and HS ($p < 0.01$). The regression coefficients of those traits were negative, representing the probability of an event for FE and HS decreased when AH increased. The odd of an event is the probability of the event divided by the probability of the nonevent. The odds ratio (OR) confirmed the significance of the regression coefficient. OR is the change in odds of the event as the x variable increases by 1 unit (Abraham and Ledolter, 2006). Then, OR of AH was 0.97 and 0.97 for FE and HS, respectively, indicating that if the age of the hen increased by 1 wk, the odds of fertility and hatchability would change by multiplicative factors of 0.97 and 0.97, respectively (the odds of FE and HS were reduced by 3%). On the other hand, AC did not affect reproductive traits ($p > 0.05$). Hocking and Bernard (2000) reported that the age of the hen had a greater effect on the reduction of fertility than the age of the service cock.

The VF and SF phenotypes were observed in Betong chickens (KU line). VF is likely controlled by an extremely slow-feathering gene (K^n) and SF is likely controlled by a slow-feathering gene (K^s) with dominance over the delayed feathering gene (K) and fast-feathering gene (k^+), respectively. The feathering rate is controlled by the K locus on the Z chromosome called the "sex-linked feathering gene" (Somes, 1969; McGibbon, 1977). The category of feathering phenotype of the hen was not significant ($p > 0.05$) on reproductive traits (Table 3). On the other hand, the category of the feathering phenotype of the service cock was significant ($p < 0.05$) for FE and HF. The VF service cock odds ratio was 1.12 times better than for SF service cocks ($p < 0.05$) for FE, but the VF service cock odds ratio was 0.85 times lower than for SF service cocks ($p < 0.05$) for HF. The effects of the feathering rate on reproductive performances in chicken varied in different flocks. Durmus et al. (2010) reported that fertility, early and late embryonic mortalities of the delayed-feathering genotype in brown layers were significantly higher than those with the fast-feathering genotype. On the other hand, Mincheva et al. (2012) reported that the fertility of delayed-feathering hens was lower ($p < 0.05$) than that of fast-feathering hens in White Plymouth Rock. However, hatchability was higher in fast-feathering than delayed-feathering chickens (Durmus et al., 2010; Mincheva et al., 2012).

The effect of CD was significant ($p < 0.05$) for FE, EV and HS (Table 3), and the odds of FE, EV and HS were 0.89, 0.94 and 0.91 times, respectively, when CD increased by 1 d. Egg fertility decreased when CD increased because the fertilizing ability of sperm in the oviduct decreased (Etches, 1996). Fertility could be improved by AI twice a week (Etches, 1996). Additionally, the effect of SD was significant ($p < 0.01$) for all traits; the odds of FE, EV, MV, HF and HS were 0.98, 0.93, 0.91, 0.93 and 0.95 times, respectively, when SD was increased by 1 d. These results indicated that prolonged storage caused a reduction in embryonic viability at the three stages. Prolonged storage of hatching eggs in this study was performed to increase the number of progeny within the family. The negative effect of long storage could be reduced by optimal egg storage conditions and a pre-heat procedure before loading into setters (Cavero et al., 2011).

Table 3 Multiple logistic regression analysis for fertility (FE), early embryonic viability (EV), middle embryonic viability (MV), hatchability of fertile eggs (HF) and hatchability of egg set (HS)

Parameter	FE			EV			MV			HF			HS		
	b±SE	OR	*p*	b±SE	OR	*P*	b±SE	OR	*p*	b±SE	OR	*p*	b±SE	OR	*p*
Intercept	2.54±0.19	-	<.0001	3.22±0.53	-	<.0001	6.21±0.72	-	<.0001	3.61±0.37	-	<.0001	2.15±0.19	-	<.0001
AH	-0.03±0.00	0.97	<.0001	-0.01±0.01	0.99	0.4671	-0.01±0.01	0.99	0.3367	-0.01±0.01	0.99	0.1988	-0.03±0.00	0.97	<.0001
AC	0.00±0.00	1.00	0.3325	0.01±0.01	1.01	0.1615	-0.01±0.01	0.99	0.5269	-0.01±0.01	0.99	0.0571	0.00±0.00	1.00	0.4736
CD	-0.11±0.01	0.89	<.0001	-0.07±0.03	0.94	0.0157	-0.05±0.03	0.95	0.1233	0.01±0.02	1.01	0.4831	-0.10±0.01	0.91	<.0001
SD	-0.03±0.00	0.98	<.0001	-0.07±0.01	0.93	<.0001	-0.09±0.01	0.91	<.0001	-0.07±0.01	0.93	<.0001	-0.05±0.00	0.95	<.0001
FH															
VF vs SF	0.06±0.04	1.06	0.1263	0.20±0.11	1.23	0.0719	-0.06±0.14	0.94	0.6464	-0.01±0.08	0.99	0.8857	0.06±0.04	1.06	0.1878
FC															
VF vs SF	0.11±0.04	1.12	0.0032	-0.02±0.11	0.98	0.8719	-0.12±0.14	0.89	0.4020	-0.17±0.08	0.85	0.0405	0.04±0.04	1.04	0.3204
HB															
1 vs 9	-1.51±0.13	0.22	<.0001	0.93±0.47	2.54	0.0453	0.49±1.07	1.63	0.6492	-0.20±0.30	0.82	0.5065	-1.21±0.13	0.30	<.0001
2 vs 9	-1.21±0.12	0.30	<.0001	0.13±0.30	1.14	0.6737	-0.35±0.61	0.70	0.5597	0.41±0.29	1.50	0.1644	-0.94±0.11	0.39	<.0001
3 vs 9	-0.33±0.13	0.72	0.0089	0.65±0.33	1.91	0.0470	-0.67±0.47	0.51	0.1528	-0.10±0.24	0.90	0.6662	-0.36±0.12	0.70	0.0039
4 vs 9	-0.77±0.09	0.47	<.0001	0.76±0.20	2.14	0.0002	-0.48±0.37	0.62	0.1879	-0.25±0.16	0.78	0.1274	-0.59±0.09	0.55	<.0001
5 vs 9	-0.62±0.09	0.54	<.0001	0.71±0.19	2.02	0.0002	-1.30±0.33	0.27	<.0001	-0.78±0.15	0.46	<.0001	-0.74±0.08	0.48	<.0001
6 vs 9	-1.52±0.09	0.22	<.0001	-0.54±0.21	0.58	0.0083	-0.68±0.43	0.51	0.1150	0.64±0.23	1.89	0.0064	-1.23±0.09	0.29	<.0001
7 vs 9	-0.67±0.11	0.51	<.0001	-0.24±0.26	0.79	0.3466	-0.04±0.46	0.96	0.9253	0.70±0.23	2.02	0.0018	-0.40±0.10	0.67	0.0001
8 vs 9	-0.59±0.14	0.56	<.0001	1.35±0.46	3.88	0.0030	-0.67±0.51	0.51	0.1931	0.91±0.29	2.48	0.0019	-0.17±0.14	0.84	0.2302

b = regression coefficient; OR=odds ratio (e^b); *p* = *p*-value; AH = age of hen; AC = age of service cock; CD = egg collection duration; SD = egg storage duration; FH = feathering phenotype of hen; FC = feathering phenotype of service cock; VF = very slow-feathering; SF = slow-feathering; HB = hatching batch.

The effect of hatching batch was significant for all traits. Percentages of FE were low with high variation between hatching batches (in the range 36.99–70.36%; Table 2). This result suggested that the management or environment for each hatching batch varied (Table 3). The percentage of EV was in the range 89.47–97.56% and confirmed that the egg storage procedures were suitable (Mauldin, 2001). However, infertile eggs at 7 d of incubation were not cracked to determine the true numbers of infertile egg or embryos that had died during the first day of incubation. This may have resulted in an underestimate of fertility. Mauldin (2001) suggested that most infertile eggs in the early stage are caused by infertility, with few recorded as dead embryos within 24 hr of incubation. The MV percentage was in the range 92.27–99.53%, indicating optimal conditions during the incubation period (Mauldin, 2001). Additionally, the percentages of HF were higher than 83% in several HBs, except for HB 3 and 5. Thus, the incubation during 18–21 d approached optimal conditions. Unfortunately, the percentages of HS were low because of the low FE. These results indicated that environment was important with regard to reproductive performances. Hence, improvement of the reproductive performance in Betong chicken (KU line) would be achieved by reducing the CD and SD periods; furthermore, artificial insemination techniques and management must be considered to increase the percentage of FE.

Estimates of genetic parameters

The estimated (co) variance components computed using univariate analyses of reproductive traits with THRGIBBS1F90 are presented in Table 4. The estimates of the direct additive genetic variance from Model 1 were 0.149, 0.088, 0.028, 0.025 and 0.148 for FE, EV, MV, HF and HS, respectively. The estimates of animal permanent environmental variance from Model 1 were 0.577, 0.266, 0.181, 0.229 and 0.442 for FE, EV, MV, HF and HS, respectively. Inclusion of the service cock permanent environmental effect (Model 2 vs Model 1) caused small reductions in the animal permanent environmental variance by 3.99, 9.02, 14.92, 9.17 and 7.01% for FE, EV, MV, HF and HS, respectively. Furthermore, ignoring the service cock permanent environmental effect (Model 5 vs Model 3) substantially overestimated the estimates of service cock genetic variance by 93.75, 70.69, 64.86, 81.82 and 88.50% for FE, EV, MV, HF and HS, respectively. These results indicated the confounding of the genetic and permanent environmental service cock effects. Adding the service cock genetic effects (Model 3 vs Model 1) changed the estimates of direct additive genetic variance by -3.36, 9.09, 46.43, -24.00 and -0.68% for FE, EV, MV, HF and HS, respectively. Moreover, adding the service cock genetic effects (Model 5 vs Model 2) caused small changes in the estimates of the direct additive genetic variance by -0.70, 1.32, 12.50, -22.73 and 0.00% for those traits.

Table 4 Estimates of (co)variance components for fertility (FE), early embryonic viability (EV), middle embryonic viability (MV), hatchability of fertile eggs (HF) and hatchability of eggs set (HS)

Item	σ^2_a	σ^2_c	σ_{ac}	σ^2_{pe}	σ^2_{pc}	σ^2_p	DIC
FE							
Model 1	0.149±0.074	-	-	0.577±0.071	-	1.726±0.059	36,517
Model 2	0.142±0.078	-	-	0.554±0.074	0.342±0.050	2.038±0.080	36,466
Model 3	0.144±04.078	0.560±0.088	-	0.560±0.075	-	2.120±0.120	36,727
Model 4	0.172±0.083	0.589±0.091	0.171±0.114	0.550±0.074	-	2.482±0.193	36,579
Model 5	0.141±0.076	0.035±0.040	-	0.556±0.074	0.319±0.054	2.051±0.083	36,620
Model 6	0.159±0.085	0.071±0.061	0.055±0.073	0.547±0.078	0.303±0.059	2.134±0.131	36,429
EV							
Model 1	0.088±0.056	-	-	0.266±0.073	-	1.354±0.070	17,582
Model 2	0.076±0.056	-	-	0.242±0.073	0.080±0.032	1.398±0.076	17,546
Model 3	0.096±0.064	0.058±0.036	-	0.257±0.076	-	1.315±0.084	17,740
Model 4	0.078±0.059	0.079±0.041	0.030±0.046	0.267±0.076	-	1.454±0.098	17,761
Model 5	0.077±0.057	0.017±0.020	-	0.246±0.073	0.068±0.032	1.408±0.075	17,623
Model 6	0.049±0.057	0.049±0.036	0.013±0.035	0.273±0.078	0.056±0.034	1.440±0.092	16,601
MV							
Model 1	0.028±0.037	-	-	0.181±0.060	-	1.209±0.056	16,651
Model 2	0.040±0.039	-	-	0.154±0.058	0.063±0.036	1.257±0.064	16,862
Model 3	0.041±0.039	0.074±0.049	-	0.155±0.056	-	1.229±0.071	16,677
Model 4	0.027±0.031	0.108±0.059	0.008±0.045	0.166±0.058	-	1.309±0.101	16,828
Model 5	0.045±0.043	0.026±0.035	-	0.153±0.060	0.055±0.037	1.282±0.073	16,297
Model 6	0.042±0.042	0.083±0.054	0.023±0.035	0.150±0.057	0.044±0.034	1.342±0.097	16,251
HF							
Model 1	0.025±0.024	-	-	0.229±0.041	-	1.254±0.040	16,340
Model 2	0.022±0.025	-	-	0.208±0.042	0.097±0.030	1.326±0.050	16,297
Model 3	0.019±0.024	0.110±0.040	-	0.214±0.042	-	1.324±0.057	16,038
Model 4	0.022±0.023	0.131±0.044	0.030±0.040	0.211±0.042	-	1.394±0.079	16,227
Model 5	0.017±0.023	0.020±0.023	-	0.210±0.042	0.082±0.031	1.329±0.051	16,283
Model 6	0.037±0.033	0.048±0.034	0.024±0.035	0.199±0.044	0.069±0.032	1.377±0.071	15,939
HS							
Model 1	0.148±0.067	-	-	0.442±0.060	-	1.590±0.050	36,576
Model 2	0.141±0.070	-	-	0.411±0.062	0.244±0.039	1.796±0.064	36,723
Model 3	0.147±0.071	0.374±0.066	-	0.409±0.064	-	1.783±0.094	36,902
Model 4	0.166±0.071	0.396±0.068	0.151±0.088	0.402±0.060	-	2.116±0.148	36,559
Model 5	0.141±0.069	0.043±0.044	-	0.410±0.062	0.211±0.045	1.805±0.067	36,750
Model 6	0.152±0.072	0.088±0.062	0.076±0.058	0.405±0.063	0.189±0.050	1.911±0.110	36,474

σ^2_a = direct additive genetic variance; σ^2_c = service cock genetic variance; σ_{ac} = direct additive-service cock genetic covariance; σ^2_{pe} = animal permanent environmental variance; σ^2_{pc} = service cock permanent environmental variance; σ^2_p = phenotypic variance; residual variance fixed to 1; DIC = deviance information criterion. Values are shown as mean ± SD.

Adding the direct additive-service cock genetic covariance (Model 4 vs Model 3) changed the estimates of direct additive variance by 19.44, -18.75, -34.15, 15.79 and 12.93% for FE, EV, MV, HF and HS, respectively, as well as increasing the estimates of service cock genetic variance by 5.18, 36.21, 45.95, 10.09 and 5.88%. Furthermore, adding the direct additive-service cock genetic covariance (Model 6 vs Model 5) considerably increased the estimates of service cock genetic variance by 102.86, 188.24, 219.23, 140.00 and 104.65% for FE, EV, MV, HF and HS, respectively. The estimates of direct additive-service cock genetic covariance were positive with high standard deviations. However, Model 6 was the best model because it had the lowest DIC values for all traits.

The genetic parameters obtained from the univariate analyses of all traits are shown in Table 5. Based on Model 6, the parameter estimates were low and were in the ranges 0.026–0.079 for direct heritability (h^2), 0.033–0.060 for service cock heritability (c^2), 0.454–0.701 for direct

additive-service cock genetic correlation (r_{ac}), 0.111–0.257 for the proportion of animal permanent environmental variance to phenotypic variance (pe^2) and 0.033–0.142 for the proportion of service cock permanent environmental variance to phenotypic variance (pc^2). Positive direct additive-service cock genetic correlations showed that selection effort to improve the reproductive performance in hens would help improve the reproductive performance of male progeny. However, the high standard error of the direct additive-service genetic correlation indicated low accuracy of estimated correlation or no correlation between these effects (Rozempolska-Rucińska et al., 2010).

The h^2 estimates of embryonic viability were lower than those of fertility and decreased as the incubation process progressed. Hartmann et al. (2002) reported that environmental conditions during incubation had more effect on hatchability and egg composition than fertility. The h^2 value decreased from the early to the late embryonic viabilities, caused by environmental variation during incubation more than by genetic variation (Dobek et al., 2003).

Table 5 Estimates of genetic parameters for fertility (FE), early embryonic viability (EV), middle embryonic viability (MV), hatchability of fertile eggs (HF) and hatchability of eggs set (HS)

Item	h^2	c^2	r_{ac}	pe^2	pc^2	e^2
FE						
Model 1	0.086±0.041	-	-	0.334±0.038	-	0.580±0.020
Model 2	0.070±0.037	-	-	0.272±0.035	0.167±0.020	0.491±0.019
Model 3	0.069±0.040	0.263±0.031	-	0.264±0.028	-	0.473±0.027
Model 4	0.068±0.031	0.237±0.028	0.533±0.332	0.223±0.035	-	0.405±0.031
Model 5	0.068±0.036	0.017±0.019	-	0.271±0.034	0.155±0.024	0.488±0.020
Model 6	0.074±0.037	0.033±0.027	0.454±0.747	0.257±0.039	0.142±0.028	0.470±0.028
EV						
Model 1	0.064±0.040	-	-	0.195±0.047	-	0.741±0.038
Model 2	0.054±0.038	-	-	0.172±0.046	0.057±0.022	0.717±0.038
Model 3	0.075±0.053	0.044±0.026	-	0.193±0.047	-	0.763±0.048
Model 4	0.053±0.039	0.054±0.026	0.370±0.610	0.183±0.048	-	0.691±0.045
Model 5	0.054±0.039	0.012±0.014	-	0.174±0.046	0.048±0.022	0.712±0.037
Model 6	0.033±0.038	0.033±0.023	0.468±0.726	0.188±0.047	0.039±0.023	0.697±0.044
MV						
Model 1	0.023±0.030	-	-	0.148±0.043	-	0.829±0.038
Model 2	0.032±0.030	-	-	0.121±0.042	0.050±0.027	0.797±0.040
Model 3	0.034±0.033	0.059±0.036	-	0.124±0.040	-	0.816±0.046
Model 4	0.020±0.022	0.081±0.040	-0.013±0.827	0.126±0.041	-	0.769±0.056
Model 5	0.032±0.032	0.018±0.029	-	0.123±0.040	0.044±0.028	0.783±0.043
Model 6	0.031±0.029	0.060±0.036	0.438±0.556	0.111±0.040	0.033±0.025	0.749±0.052
HF						
Model 1	0.020±0.019	-	-	0.182±0.028	-	0.798±0.025
Model 2	0.016±0.019	-	-	0.156±0.028	0.072±0.021	0.755±0.028
Model 3	0.015±0.019	0.083±0.027	-	0.161±0.027	-	0.757±0.032
Model 4	0.015±0.016	0.093±0.028	0.615±0.647	0.151±0.029	-	0.719±0.040
Model 5	0.013±0.017	0.015±0.017	-	0.157±0.028	0.062±0.022	0.754±0.028
Model 6	0.026±0.022	0.034±0.024	0.503±0.760	0.144±0.031	0.050±0.023	0.728±0.036
HS						
Model 1	0.093±0.040	-	-	0.278±0.036	-	0.630±0.020
Model 2	0.078±0.038	-	-	0.229±0.033	0.136±0.019	0.557±0.020
Model 3	0.084±0.043	0.209±0.029	-	0.229±0.028	-	0.563±0.030
Model 4	0.078±0.031	0.187±0.026	0.597±0.304	0.191±0.032	-	0.475±0.033
Model 5	0.078±0.037	0.023±0.024	-	0.227±0.034	0.117±0.024	0.555±0.020
Model 6	0.079±0.035	0.045±0.030	0.701±0.440	0.213±0.036	0.099±0.027	0.525±0.030

† h^2 = direct heritability; c^2= service cock heritability; r_{ac} = direct additive-service cock genetic correlation; pe^2 = proportion of animal permanent environmental variance to phenotypic variance; pc^2 = proportion of service cock permanent environmental variance to phenotypic variance; e^2 = proportion of residual variance to phenotypic variance. Values are shown as mean ± SD.

The estimates of h^2 in the current study were lower than those in previous reports. Bennewitz et al. (2007) reported h^2 values of 0.067, 0.126 and 0.136 for FE, HF and HS, respectively, with pe^2 values of 0.199, 0.206 and 0.260 for FE, HF and HS, respectively, in laying hens, using a repeatability threshold model. Additionally, Rozempolska-Rucińska et al. (2010) reported h^2 values of 0.12 to 0.17, 0.07 to 0.22 and 0.13 to 0.22, with c^2 values of 0.01 to 0.03, 0.01 to 0.02 and 0.01 to 0.03 for FE, HF and HS, respectively, using a repeatability model and a restricted maximum likelihood method in laying hens.

The estimates of the proportion of permanent environmental variance to phenotypic variance (pe^2 and pc^2) were higher than the genetic parameters (h^2 and c^2) for all traits, indicating that reproductive traits were more influenced by permanent environmental effects than by genetic effects. Furthermore, the permanent environment of the hens highly influenced reproductive performance more than the permanent environment of the service cocks, probably because the hen contributed with a substantially larger fraction of the environment provided by the egg components of yolk, albumin and egg shell (Hartmann et al., 2002; Wolc et al., 2010). Unfortunately, the magnitudes of genetic parameters decreased but the magnitudes of residual parameters increased as the incubation process progressed, indicating that the environmental improvements would have a larger effect on reproductive phenotypes than genetic changes.

In conclusion, adding the service cock effects did not affect the estimates of direct heritability but service cock heritability may be overestimated if the service cock permanent environment effect is not included in the repeatability threshold model. However, the estimates of direct heritability and service cock heritability were low for all traits while the correlations between the direct additive and service cock genetic effects were all positive. The low heritabilities indicated that improving environmental conditions would have a large impact on phenotypic reproductive performance in this population of Betong chicken.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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