

Genetic parameters of body weight, egg production and shell quality traits in the Brown Tsaiya laying duck

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Summary – Heritabilities and genetic correlations were estimated for 5 575 laying Brown Tsaiya ducks on performance data from 5 generations of a selection experiment, by means of a multivariate, multimodel, restricted maximum likelihood method (MM-REML) applied to an animal model on the 12 traits: feather length at 20 weeks of age (FL20); body weight at 20 and 40 weeks of age (BW20; BW40); age at first egg (AGE1EGG); number of eggs laid up to 40 and 52 weeks of age (NEGG40; NEGG52); eggshell strength at 30 and 40 weeks of age (ES30; ES40); egg weight at 30 and 40 weeks of age (EW30; EW40); egg yolk weight at 40 weeks of age (EYW40); and the proportion of egg weight to body weight at 40 weeks of age (EW40/BW40). Adult females were heavier than adult males (BW40: 1 391 g vs 1 310 g). ES40 was lower than ES30 (3.5 kg/cm² vs 3.8 kg/cm²). Heritabilities were found to be low (0.094, 0.107, 0.118, 0.160, 0.169, 0.191 and 0.201 for ES40, ES30, NEGG52, NEGG40, FL20, EYW40 and AGE1EGG, respectively), to medium (0.327, 0.329, 0.353, 0.425 and 0.499 for EW40/BW40, EW40, EW30, BW20 and BW40, respectively). Fifty genetic correlations were tabulated. The pattern of the genetic correlations for the traits to be selected showed that NEGG52 was highly positively correlated with NEGG40 ($rg = 0.948$), uncorrelated with the body weight and was negatively correlated with AGE1EGG ($rg = -0.749$), EW40 ($rg = -0.323$), EW30 ($rg = -0.200$), EYW40 ($rg = -0.340$), ES30 ($rg = -0.194$), ES40 ($rg = -0.203$), FL20 ($rg = -0.131$) and EW40/BW40 ($rg = -0.259$). Egg weights, body weights and eggshell strength traits were positively genetically correlated among themselves. The results suggest that a linear selection index for NEGG52 with constraints for EW40, BW40 and ES40 could be an efficient tool for improving the efficiency of egg production with this small body type laying duck.

heritability / genetic correlation / animal model / laying duck

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Résumé – Paramètres génétiques des caractères de poids corporels, de production d'œufs, et de qualité de la coquille chez la cane pondreuse Tsaiya Brune. Les héritabilités et corrélations génétiques ont été estimées pour 5 575 pondreuses Tsaiya Brune, sur la base de performances concernant les 5 premières générations d'une expérience de sélection par la méthode du REML-MM (maximum de vraisemblance restreinte-multivariate multimodèle) appliquée à un modèle animal sur 12 caractères : la longueur de la plume à l'âge de 20 sem (FL20), le poids corporel à 20 et 40 sem (BW20 ; BW40), l'âge au premier œuf (AGE1EGG), les nombres d'œufs à 40 et 52 sem (NEGG40 ; NEGG52), la solidité de la coquille à 30 et 40 sem (ES30 ; ES40), le poids des œufs à 30 et 40 sem (EW30 ; EW40), le poids des jaunes d'œufs à 40 sem (EYW40) et le rapport du poids de l'œuf au poids corporel à 40 sem (EW40/BW40). Les femelles adultes étaient plus lourdes que les mâles (BW40 : 1 391 vs 1 310 g). ES40 était inférieure à ES30 (3,5 vs 3,8 kg/cm²). Les valeurs d'héritabilité d'ES40, ES30, NEGG52, NEGG40, FL20, EYW40 et AGE1EGG étaient faibles : 0,094 ; 0,107 ; 0,118 ; 0,160 ; 0,169 ; 0,191 et 0,201 respectivement. Elles étaient de 0,327 ; 0,329 ; 0,353 ; 0,425 et 0,499 pour EW40/BW40, EW40, EW30, BW20 et BW40. Cinquante corrélations génétiques sont tabulées. NEGG52 était fortement corrélé avec NEGG40 (rg = 0,948), mais n'était pas corrélé avec les poids corporels et était corrélé négativement avec AGE1EGG (rg = -0,749), EW40 (rg = -0,323), EW30 (rg = -0,200), EYW40 (rg = -0,340), ES30 (rg = -0,194), ES40 (rg = -0,203), FL20 (rg = -0,131) et EW40/BW40 (rg = -0,259). Les poids des œufs, les poids corporels et les caractères de la solidité de la coquille étaient positivement corrélés entre eux. Les résultats suggèrent qu'une sélection sur un index linéaire pour NEGG52 avec des contraintes pour EW40, BW40 et ES40 pourrait être efficace pour améliorer les performances de la production d'œuf de la cane Tsaiya Brune.

héritabilité / corrélation génétique / modèle animal / cane pondreuse

INTRODUCTION

Twelve traits relating to feather length, body weights, egg production, egg weights and eggshell quality have been recorded in a selected Brown Tsaiya laying duck strain (L105) at the Duck Research Center, Ilan, Taiwan Livestock Research Institute since 1984 (Tai *et al*, 1994). Not much is known about the genetic parameters and especially the genetic correlations for these traits in ducks. Tai *et al* (1989) estimated heritabilities for 8 of these traits in the first generation. Lee *et al* (1992) estimated genetic parameters in each of the first 4 generations, using variance component estimation method applied to a hierarchical relationship structure. On the other hand, the best linear unbiased prediction (BLUP) (Henderson, 1988) has been increasingly applied to an animal model for predicting the genetic merit of candidates for selection in most species of farm animals. For this purpose estimates of the genetic parameters in the base population are required. Some simulation research has shown that the use of maximum likelihood (ML) or minimum variance quadratic unbiased estimation (MIVQUE) methods on selected data can lead to unbiased estimates of additive genetic variance in the base population (Rothschild *et al*, 1979; Meyer and Thompson, 1984; Sorensen and Kennedy, 1984). It has been shown that when the method of restricted maximum likelihood (REML, Patterson and Thompson, 1971) is applied to an animal model, in particular when

all the information contributing to selection is included in the analysis and a large number of additive loci is assumed, it can provide unbiased estimation in selected populations (Kennedy, 1990; Meyer, 1990, 1991). Consequently, REML has recently been applied in animal breeding for estimating variance and covariance components in selected populations (Hofer *et al*, 1992; Besbes, 1993; Ducos *et al*, 1993; Hagger, 1994; Mielenz *et al*, 1994; Poujardieu *et al*, 1994). As far as we know, it has not yet been used to estimate genetic parameters in laying ducks.

The purpose of this study was to estimate and discuss genetic parameters for the 12 traits recorded for the first 5 generations in a selection experiment for laying Brown Tsaiya ducks.

MATERIALS AND METHODS

Data description

The ducks were collected from 4 different locations around Taiwan. Sires came from 4 breed farms and dams from another 4 egg-production farms. With 4-by-4 mating, each origin of sire was mated to the 4 origins of dams (5 ducks per drake) and then progeny was assigned to mating groups depending on the sire origins. Twelve traits were individually measured and recorded as follows:

FL20: feather length at 20 weeks of age (except in 2nd and 4th generations) in both sexes.

BW20, BW40: body weight at 20 and 40 weeks of age respectively in both sexes.

AGE1EGG: age at first egg.

NEGG40, NEGG52: number of eggs laid up to 40 and 52 weeks of age, respectively.

ES30: eggshell strength at 30 weeks of age (except in 4th and 5th generations).

ES40: eggshell strength at 40 weeks of age (except in 1st and 2nd generations).

EW30, EW40: egg weight at 30 and 40 weeks of age, respectively.

EYW40: egg yolk weight at 40 weeks of age (except in first generation).

EW40/BW40: the ratio of egg weight to body weight at 40 weeks of age.

Eggs laid over 5 consecutive days at 30 and 40 weeks of age were weighed and measured by eggshell strength meters for the average of EW30, EW40, ES30 and ES40.

The structure of the selection experiment (without control strain) is described in table I for the number of ducks (males and females) and the hatching date of each generation. Population size was increased from the third generation mainly in order to maintain an optimal population size for long-term selection (Lee *et al*, 1992). A 2-stage selection was carried out. First, 50% of the female ducks were selected on a linear phenotypic selection index:

$$I = 0.099 \cdot EW40(g) - 0.277 \cdot BW40(100 g) + 0.026 \cdot NEGG52(\text{eggs})$$

Among these selected females, the top 50% were selected for ES30 (first and second generations) or ES40 (third to fifth generations). The drakes were similarly chosen taking into account the performances of their full and half sisters.

Table I. Structure of the selection experiment.

<i>Generation</i>	<i>Origin</i> ^a	<i>Number of hatch</i>	<i>Hatch period</i>	<i>Offspring</i>	<i>Parents</i> ^b
G0	4 origins of sire	—	—	—	<i>M</i> = 40 <i>F</i> = 156
	4 origins of dam				
G1	1 051	5	24/12/84–21/01/85	<i>M</i> = 111 <i>F</i> = 537	<i>M</i> = 18 <i>F</i> = 121
	1 052				
	1 053				
	1 054				
G2	1 051	4	08/12/86–30/12/86	<i>M</i> = 161 <i>F</i> = 450	<i>M</i> = 34 <i>F</i> = 113
	1 052				
	1 053				
	1 054				
G3	1 051	5	21/03/88–19/04/88	<i>M</i> = 40 <i>F</i> = 449	<i>M</i> = 30 <i>F</i> = 117
	1 052				
	1 053				
	1 054				
G4	1 051	6	15/11/89–19/12/89	<i>M</i> = 797 <i>F</i> = 934	<i>M</i> = 30 <i>F</i> = 108
	1 052				
	1 053				
	1 054				
G5	1 051	6	20/05/91–24/06/91	<i>M</i> = 624 <i>F</i> = 1 112	<i>M</i> = 31 <i>F</i> = 130
	1 052				
	1 053				
	1 054				
Total		26		<i>M</i> = 2 093 <i>F</i> = 3 482	

^a Four origins: 1 051, 1 052, 1 053, 1 054; ^b parents of the next generation offspring: *M* = number of males, *F* = number of females.

Statistical analysis

All records were analysed by an SAS univariate procedure to test normal distribution, and some extreme and abnormal data were discarded (less than 3 depending on the trait). Skewed distributions were observed for the AGE1EGG, NEGG40 and NEGG52 variables. They were thus transformed using a power distribution (Box and Cox, 1964; Besbes *et al*, 1993) in order to satisfy the classical hypotheses for normally distributed traits. This transformation relies on a single parameter *t* as shown previously for laying hens (Ibe and Hill, 1988; Besbes *et al*, 1992). The following formula was used:

$$g_t(y) = \begin{cases} \frac{y^t - 1}{t\bar{y}^{(t-1)}} & \text{if } t \neq 0 \\ \log y & \text{if } t = 0 \end{cases}$$

where \bar{y} is the geometric mean of the original observations. The parameter t was empirically chosen in such a way that skewness became close to zero and there was a low residual sum of squares in the genetic model used to describe the data. The t values were 3.8, 3.0 and -1.2 , respectively, for NEGG52, NEGG40 and AGE1EGG.

Analysis of FL20, BW20 and BW40 was based on the following linear model:

$$y_{ijkl} = \mu + H_i + S_j + a_{ijk} + e_{ijkl}$$

where for AGE1EGG, NEGG40, NEGG52, ES30, ES40, EW30, EW40, EYW40 and EW40/BW40 the following model was used:

$$y_{ikl} = \mu + H_i + a_{ik} + e_{ikl}$$

where y_{ijkl} and y_{ikl} are the $ijkl$ th and ikl th observations respectively, μ is the population mean, H is the fixed effect for the i th hatch, S is the fixed effect for the j th sex, a_{ijk} and a_{ik} are the random additive genetic effects of the ijk th and ik th animals respectively, and e_{ijkl} and e_{ikl} are the residual effects.

Sires from the 4 origins were considered to belong to the same population. The data for the 4 lines were pooled. Heritabilities and genetic correlations were estimated by the restricted maximum likelihood method (REML) applied to an animal model. A derivative-free REML algorithm (Graser *et al.*, 1987) from the DF-REML program of Groeneveld and Kovac (1990a,b) as adapted by Boichard (1994) and the VCE multivariate multimodel REML (co)variance component estimation (MM-REML) program of Groeneveld (1994a) were used for all trait analyses.

Computing strategy

The general linear model is as follows:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

With $E[\mathbf{y}] = \mathbf{X}\boldsymbol{\beta}$, $E[\mathbf{u}] = 0$ and $E[\mathbf{e}] = 0$

$$\text{Var} \begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{Z}\mathbf{G}\mathbf{Z}' + \mathbf{R} = \mathbf{V} & \mathbf{Z}\mathbf{G} & \mathbf{R} \\ & \mathbf{G}\mathbf{Z}' & \mathbf{G} & \mathbf{0} \\ & \mathbf{R} & \mathbf{0} & \mathbf{R} \end{bmatrix}$$

where

\mathbf{y} = vector of observations for the trait;

$\boldsymbol{\beta}$ = vector of fixed effects;

\mathbf{u} = vector of animal effects;

\mathbf{e} = random vector of residual effects;

\mathbf{X}, \mathbf{Z} are incidence matrices relating observations to the effects in the model, $\mathbf{G} = \mathbf{A} \otimes \mathbf{G}_0$; \mathbf{A} is the numerator relationship matrix; \mathbf{G}_0 is the (co)variance matrix for additive genetic effects among traits; $\mathbf{R} = \mathbf{I}_e \otimes \mathbf{R}_o$; \mathbf{I}_e is the identity matrix; \mathbf{R}_o is the residual (co)variance among traits; \otimes = the Kronecker product.

The mixed-model equations (MME) are then (Henderson, 1963, 1973):

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \hat{\boldsymbol{\beta}} \\ \hat{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix}$$

The logarithm of the restricted, multivariate, normal likelihood function to be maximized is as follows (Groeneveld, 1994b):

$$LV = \mathbf{y}'\mathbf{R}^{-1}\mathbf{y} - \mathbf{y}'\mathbf{R}^{-1}\mathbf{W}\mathbf{b}^\circ + \log |\mathbf{C}^*| + na \log |\mathbf{G}_0| + n \log |\mathbf{R}_0|$$

where LV is proportional to the logarithm of the likelihood function; $\mathbf{W} = (\mathbf{X}|\mathbf{Z})$; \mathbf{b}° is the solution vector of the MME; \mathbf{C}^* is the inverse of the coefficient matrix of the MME; na = the number of animals; and n = the number of observations. The log likelihood value was maximized by a Downhill-Simplex procedure or a Quasi-Newton algorithm method and MME were solved by Cholesky factorization using a super-nodal block factorization (Groeneveld, 1994a,b).

The number of levels for fixed effects was 26 for hatch and 2 for sex. Heritabilities and genetic correlations were estimated with an animal model, taking all ducks which had at least one observation. The selected traits EW40, BW40, NEGG52, ES30 and ES40 were included together in the MM-REML analysis to obtain heritabilities and genetic correlations for the 5 traits selected. Each of the secondary traits was then added to study correlations between selected traits and 7 secondary traits. Finally the 7 secondary traits were analyzed together for genetic correlations. All relationship coefficients were calculated from the founder stock (G0) and all duck measurements from G1 to G5 were considered.

Management

The same management system described by Tai *et al* (1989) was applied throughout the 5 generations of selection in this study.

RESULTS

Tables II and III give the number of animals, and the means and standard deviations of phenotypic values for the 12 traits over 5 generations. Table IV gives the estimated heritability values (univariate model with DF-REML method) for 8 traits including untransformed and transformed variables. It also compares our values with those found by Tai *et al* (1989) and Lee *et al* (1992) for the first generation of the same population. Heritability values were only increased slightly following the Box-Cox transformation, especially for NEGG52 and NEGG40. So only the untransformed variables will be studied. Previous studies yielded heritabilities from the sire variance component (h_s^2) and the dam variance component (h_d^2). Our estimates are not very different from the h_s^2 estimated values. Table V gives the estimates of heritability and genetic correlation values for the 5 selected traits achieved by MM-REML method analysis. Table VI gives heritabilities for the 7 secondary traits and their genetic correlations with the 5 selected traits. Table VII gives genetic correlations for 7 secondary traits. There was a group of low heritability values, 0.094, 0.107, 0.118, 0.160, 0.169, 0.191 and 0.201 for ES40, ES30, NEGG52, NEGG40, FL20, EYW40 and AGE1EGG, respectively, and a group of medium heritability values, 0.327, 0.329, 0.353, 0.425 and 0.499 for EW40/BW40, EW40, EW30, BW20 and BW40, respectively. FL20 was genetically positively correlated with AGE1EGG, body weight and egg weight traits, and

Table II. Laying performances of Brown Tsaiya over 5 consecutive generations (means \pm standard of phenotypic values, n = number of ducks).

Gene- ration	AGE1EGG (d)	• NEGG40 (eggs)	NEGG52 (eggs)	ES30 (kg/cm ²)	ES40 (kg/cm ²)	EW30 (g)	EW40 (g)	EYW40 (g)	EW40/BW40
G1	125.6 \pm 10.9 (n = 537)	139.2 \pm 15.2 (n = 537)	206.9 \pm 25.6 (n = 537)	3.8 \pm 0.5 (n = 536)	—	64.2 \pm 4.3 (n = 537)	67.8 \pm 4.4 (n = 509)	—	0.048 \pm 0.004 (n = 509)
G2	116.0 \pm 12.6 (n = 446)	147.9 \pm 18.7 (n = 434)	219.2 \pm 25.9 (n = 418)	3.8 \pm 0.5 (n = 436)	—	64.6 \pm 4.5 (n = 436)	67.4 \pm 5.1 (n = 426)	22.9 \pm 2.3 (n = 425)	0.051 \pm 0.004 (n = 422)
G3	118.6 \pm 10.8 (n = 417)	136.1 \pm 22.5 (n = 358)	204.9 \pm 29.0 (n = 358)	3.9 \pm 0.7 (n = 331)	3.6 \pm 0.6 (n = 395)	62.4 \pm 5.0 (n = 336)	68.2 \pm 5.0 (n = 395)	23.8 \pm 2.1 (n = 395)	0.049 \pm 0.004 (n = 392)
G4	116.6 \pm 13.8 (n = 687)	121.9 \pm 26.6 (n = 570)	200.7 \pm 32.8 (n = 570)	—	3.6 \pm 0.6 (n = 553)	64.5 \pm 4.3 (n = 640)	67.7 \pm 4.8 (n = 565)	23.2 \pm 1.8 (n = 565)	0.049 \pm 0.004 (n = 552)
G5	119.8 \pm 14.8 (n = 846)	123.2 \pm 23.4 (n = 678)	197.1 \pm 30.5 (n = 678)	—	3.4 \pm 0.8 (n = 692)	64.9 \pm 5.2 (n = 527)	68.8 \pm 5.7 (n = 696)	23.2 \pm 2.7 (n = 695)	0.047 \pm 0.005 (n = 679)

AGE1EGG: age at first egg; ES30, ES40: egg shell strength at 30, 40 weeks of age; EYW40: egg yolk weight at 40 weeks of age; NEGG40, NEGG52: number of eggs laid up to 40, 52 weeks of age; EW30, EW40: egg weight at 30, 40 weeks of age; EW40/BW40: the proportion of egg weight to body weight at 40 weeks of age.

Table III. Growth performances of male and female Brown Tsaiya over 5 generations.

Gene- ration	FL20 (cm)		BW20 (g)		BW40 (g)	
	Male	Female	Male	Female	Male	Female
G1	15.3 ± 0.4 (n = 84)	15.0 ± 0.5 (n = 344)	1 263 ± 108 (n = 111)	1 403 ± 133 (n = 537)	1 343 ± 111 (n = 111)	1 405 ± 133 (n = 537)
G2	—	—	1 248 ± 103 (n = 161)	1 353 ± 126 (n = 446)	1 272 ± 136 (n = 149)	1 326 ± 125 (n = 431)
G3	15.6 ± 0.6 (n = 116)	15.5 ± 0.7 (n = 224)	1 241 ± 91 (n = 125)	1 317 ± 117 (n = 401)	1 340 ± 108 (n = 113)	1 379 ± 118 (n = 402)
G4	—	—	1 329 ± 111 (n = 223)	1 341 ± 147 (n = 680)	—	1 388 ± 113 (n = 635)
G5	15.3 ± 0.6 (n = 350)	15.1 ± 0.6 (n = 636)	1 319 ± 117 (n = 442)	1 418 ± 150 (n = 827)	1 287 ± 128 (n = 197)	1 459 ± 152 (n = 769)

FL20: feather length at 20 weeks of age; BW20, BW40: body weight at 20, 40 weeks of age.

slightly positively correlated with eggshell strength and EYW40, but slightly negatively correlated with egg production traits and EW40/BW40. Body weight traits were highly genetically correlated between themselves ($rg = 0.988$), and were positively correlated with egg weights, EYW40 and eggshell strength, but were not correlated with AGE1EGG and NEGG52. Age at first egg was negatively correlated with egg production traits, positively correlated with EYW40 and egg weight traits, and slightly positively correlated with ES40 and EW40/BW40. The 2 egg production traits were highly genetically correlated ($rg = 0.948$) between themselves and were negatively correlated with all other traits except BW40. ES30 and ES40 were highly correlated between themselves ($rg = 0.845$) and also EW30 and EW40 ($rg = 0.979$). EYW40 was highly positively correlated with egg weight ($rg = 0.870-0.914$). Egg weight and EYW40 were positive correlated with eggshell strength ($rg = 0.318-0.585$). EW40/BW40 was highly negatively correlated with body weight ($rg = -0.686$ to -0.748) and slightly negatively correlated with egg production traits and ES30, but was not correlated with EW40. It was positively correlated with EW30 and ES40. If computer facilities had not been limited, the MM-REML method could have been applied to take the whole selection process into account simultaneously and related genetic information could thus have been seen more clearly.

DISCUSSION

Unlike for poultry, very little data is available on the genetic parameters of laying duck traits. Pingel (1990) quotes 4 references for the heritability of egg number and egg weight in Pekin ducks. They vary from $h^2 = 0.23$ to 0.32 for egg number and from $h^2 = 0.23$ to 0.47 for egg weight. One value of $h^2 = 0.34$ has been found

Table IV. Comparison of heritabilities for 3 traits before (NT) and after (T) a Box-Cox transformation and comparison of heritabilities of untransformed variables with Tai *et al* (1989) and Lee *et al* (1992) in the Brown Tsaiya (univariate analysis).

Trait	Ducks	h^2 (NT)	h^2 (T)	Tai <i>et al</i> (1989)		Lee <i>et al</i> (1992)	
				h_s^2	h_d^2	h_s^2	h_s^2
NEGG52	$n = 2\ 561$	0.111 ± 0.003	0.134 ± 0.017	0.14 ± 0.12	0.25 ± 0.17	0.13	0.28
NEGG40	$n = 2\ 577$	0.146 ± 0.004	0.194 ± 0.062	0.12 ± 0.12	0.17 ± 0.16	—	—
AGEIEGG	$n = 2933$	0.188 ± 0.004	0.191 ± 0.004	0.18 ± 0.13	0.24 ± 0.17	0.17	0.34
BW20	$n = 3\ 953$	0.394 ± 0.031	—	0.36 ± 0.15	0.30 ± 0.16	—	—
BW40	$n = 3\ 344$	0.479 ± 0.080	—	0.39 ± 0.17	0.55 ± 0.18	0.51	0.44
ES30	$n = 1\ 303$	0.120 ± 0.006	—	0.11 ± 0.12	0.15 ± 0.18	0.08	0.22
EW30	$n = 2\ 476$	0.353 ± 0.003	—	0.32 ± 0.15	0.21 ± 0.17	—	—
EW40	$n = 2\ 591$	0.304 ± 0.004	—	0.24 ± 0.13	0.19 ± 0.18	0.25	0.16

Tai *et al* (1989) and Lee *et al* (1992): results of first generation; h^2 (T): t value = 3.8 for NEGG52, 3.0 for NEGG40 and - 1.2 for AGEIEGG; h_s^2 : heritability from the sire variance component; h_d^2 : heritability from the dam variance component.

Table V. Heritabilities and genetic correlations (rg) among 5 selected traits (5-variance analysis).

Trait	1	2	3	4	5
EW40	0.329				
BW40	0.617	0.499			
NEGG52	-0.323	0.006	0.118		
ES30	0.583	0.472	-0.194	0.107	
ES40	0.483	0.231	-0.203	0.845	0.094

Heritabilities in the main diagonal; rg : below the diagonal.

Table VI. Heritabilities (h^2) and genetic correlations (rg) among 7 secondary traits and 5 selected traits (6-variate analysis for each secondary trait).

	EW40	BW40	NEGG52	ES30	ES40	h^2
FL20	0.488	0.428	-0.131	0.055	0.115	0.169
BW20	0.596	0.988	-0.058	0.394	0.362	0.425
AGE1EGG	0.322	0.065	-0.749	-0.083	0.139	0.201
NEGG40	-0.354	-0.090	0.948	-0.106	-0.333	0.160
EW30	0.979	0.523	-0.200	0.533	0.322	0.353
EYW40	0.914	0.602	-0.340	0.585	0.318	0.191
EW40/BW40	0.054	-0.748	-0.259	-0.130	0.121	0.327

Table VII. Genetic correlations among 7 secondary traits (7-variate analysis).

	FL20	BW20	AGE1EGG	NEGG40	EW30	EYW40
BW20	0.460					
AGE1EGG	0.467	0.058				
NEGG40	-0.167	-0.148	-0.757			
EW30	0.392	0.463	0.220	-0.214		
EYW40	0.184	0.532	0.338	-0.385	0.870	
EW40/BW40	-0.109	-0.686	0.187	-0.135	0.303	0.088

for the age at first egg. Richard *et al* (1983) found $h^2 = 0.16$ and 0.49 for egg number and age at first egg in Muscovy ducks. The conventional hierarchical analysis of variance was used to estimate the sire and dam within-sire variance components. Poujardieu *et al* (1994) presented genetic parameters in common duck for growth and cramming traits of male ducks estimated by an REML animal model. Some REML estimates in laying hens based on an additive animal model were reported recently. Besbes *et al* (1992) gave estimates of heritabilities for egg production traits (numbers of eggs between 19 to 26, 26 to 38 and 26 to 54 weeks of age) which were 0.25, 0.09 and 0.18, respectively. Their heritabilities for egg weight and body weight were 0.47 and 0.50, respectively. Wei and van der Werf (1993) estimated additive and dominance variances in White Leghorn lines and reported high heritability

values for egg numbers. Hagger (1994) found $h^2 = 0.292$ for NEGG40, $h^2 = 0.754$ for EW40, and $h^2 = 0.790$ and 0.732 for male and female BW40. Mielenz *et al* (1994) reported $h^2 = 0.40$ for egg number up to day 270, $h^2 = 0.75$ and 0.62 for egg weight and body weight at day 215. These reports have generally shown higher heritabilities than those of Brown Tsaiya especially for egg number. In poultry, the values from Besbes *et al* (1992) were the closest to our results for Brown Tsaiya.

A sex effect was introduced in the model of analysis for body weight and feather length, because males Brown Tsaiya are significantly lighter than females. This is quite unusual if we compare them with Muscovy ducks where there is a very large sexual dimorphism for body weight in favor of males, but also with Pekin ducks, in which the males are 10% heavier than the females.

Taking all the information from the selected traits enables the best use of MM-REML in an animal model in order to get unbiased estimates of the genetic parameters in the base population. Owing to limited computing facilities, we calculated the genetic parameters for the 5 selected traits included together in the MM-REML analysis. It was assumed that the genetic parameters should be consistent at least for these traits and also the genetic correlations of these 5 selected traits along with the 7 secondary trait ones. The heritability values calculated by univariate or multivariate REML are very close and the maximum difference is only 3%.

The estimates of the heritabilities of the 12 traits and their genetic correlations could provide a basic knowledge of the genetic parameters in the base population of this laying Brown Tsaiya line selected for 5 generations. The main purpose of breeding could be to increase additive genetic value for egg production traits while getting a moderate body weight and keeping egg weight and eggshell quality at optimum levels according to market requirements. ES40 is lower on average than ES30. So it seems better to take ES40 as a selection criterion for eggshell strength. Heritability values of egg production traits in Brown Tsaiya are small but there is some additive genetic variation, and selection for NEGG52 is possible. The same is true for eggshell quality traits. NEGG40 and NEGG52 are slightly negatively correlated with ES30 and negatively correlated with ES40. They are negatively correlated with EW40 and EYW40, and slightly negatively correlated with EW30. EW40 is highly correlated with EYW40 and behaves as if it were the same trait. BW20 and BW40 behave genetically as the same trait, with BW20 being slightly negatively correlated with egg production up to 52 weeks of age, but BW40 showing no genetic correlation with egg number. Thus selection for egg number up to 40 or 52 weeks of age alone should be antagonistic to genetic progress in EW40 and ES40. Constraints for these 2 traits could be introduced into a selection index, the aim of which should be to increase egg number while maintaining EW40, BW40 and ES40 at their current levels.

In fact EW40/BW40 was found to be strongly influenced by body weights, with highly negative genetic correlations. When compared with laying hens, the Brown Tsaiya showed a good ratio of egg weight to body weight at 40 weeks of age (0.0489 vs 0.0316 (Liljedahl *et al*, 1979)). The Brown Tsaiya ducks already have quite a moderate body weight. In order to improve egg production, egg weight/body weight ratio and feed efficiency by limiting maintenance cost, it seems that ducks of small body type should be considered. Besbes *et al* (1992) also showed a genetic

correlation of -0.14 (line A) or -0.22 (line B) between egg number and egg weight, 0.32 (line A) or 0.33 (line B) between egg weight and body weight and 0.25 (line A) or -0.12 (line B) between egg number and body weight. The results indicated that different lines could exhibit different genetic correlations between egg number and body weight. Hagger (1994) estimated that genetic correlations between NEGG40 and EW40 was -0.267 and that between NEGG40 and male and female BW40 were -0.161 and -0.036 , respectively, with the genetic correlations between EW40, male and female BW40 being 0.338 and 0.294 , respectively. Mielenz *et al* (1994) reported genetic correlations among egg number up to day 270, egg weight and body weight at day 215 were -0.11 and 0.07 , respectively, and 0.39 between egg weight and body weight at day 215. Obviously, the genetic correlations between egg number and body weight can vary according to line and sex as found in laying hens, whereas Brown Tsaiya showed no genetic correlations between them. It could be concluded that in laying hens most of the heritabilities estimated by the REML animal model showed higher values for egg number than in Brown Tsaiya, and the genetic correlations reported among traits were also different.

Once the heritabilities and genetic correlations in the base population are known, the breeder can define a selection strategy by selecting for a linear combination of the predicted breeding values of the 4 traits EW40, BW40, NEGG52 and ES40. The optimal linear combination can be chosen according to the expected correlated responses for the several traits.

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