

Genetic Parameters of Reproductive Traits in Brown Tsaiya Ducks Artificially Inseminated with Semen from Muscovy Drakes

J. P. Poivey,*† Y. S. Cheng,‡¹ R. Rouvier,* C. Tai,§ C. T. Wang,‡ and H. L. Liu‡

*Institut National de la Recherche Agronomique, Station d'Amélioration Génétique des Animaux, BP 27, 31326 Castanet-Tolosan, France; †Taiwan Livestock Research Institute, Heng Chun Station, Kenting, Ping Tung 94606 Taiwan R.O.C.; ‡Taiwan Livestock Research Institute, Hsinhua, Tainan 712 Taiwan R.O.C.; and §Institute of Biotechnology, Cheng Kung University, Tainan 712 Taiwan R.O.C.

ABSTRACT A selection experiment on maximum duration of fertility of Brown Tsaiya ducks after artificial insemination (AI) with pooled Muscovy semen has been conducted since 1992. The Brown Tsaiya ducks were divided into two lines: a control line (T) with no selection and a selected line (S). The traits measured were the number of eggs set that were laid from Days 2 to 15 after one AI (NES), the number of fertile eggs at candling (NEF), the total number of dead embryos (NED), the maximum duration of fertility (MD), and the number of hatched mule ducklings (NEH). The selected trait was NEF. Six generations with a total of 2,127 females were measured. The variance components were estimated for each line in a multiple-trait animal model, using the restricted maxi-

imum likelihood (REML) methodology, which yields estimates free of bias caused by selection and inbreeding.

Estimates of the heritability and genetic correlation from the two lines were very similar. Heritabilities in the S and T lines, respectively, were 0.14 and 0.10 for NES, 0.30 and 0.26 for NEF, 0.06 and 0.09 for NED, 0.28 and 0.21 for MD, and 0.18 and 0.19 for NEH. High and favorable genetic correlations existed between NEF and MD (0.96 and 0.92), between NEF and NEH (0.86 and 0.91), and between MD and NEH (0.90 and 0.82). The results suggested that selection for NEF could improve the maximum duration of fertility, but it could be useful to check the estimates of genetic parameters in a meat-type female duck.

(Key words: reproduction, genetic parameter, Brown Tsaiya duck)

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INTRODUCTION

Mule ducklings are the progeny from intergeneric crossing between Muscovy (*Cairina moschata*) drakes and common duck females (*Anas platyrhynchos*). Application of artificial insemination (AI) has successfully improved the reproductive efficiency of ducks bred to produce mules in the last decade (Tai, 1985; Rouvier et al., 1987, 1988). Unfortunately, in order to maintain fertility in the intergeneric cross, it is necessary to inseminate ducks twice a week. It would be useful to know whether genetic selection for duration of fertility would be possible in order to reduce the number of AI required. Selection efficiency depends on the genetic parameters of the target traits. Tai et al. (1994) estimated heritabilities for duration of fertility traits in the Brown Tsaiya dam mule ducks and found that the best selection criterion for duration of fertility seemed to be the number of fertile eggs from

the second up to the fifteenth day after AI. Nevertheless, the genetic correlations between reproductive traits were not known nor were the genetic parameters of the number of ducklings hatched.

The length of fertile period in birds has been defined by Lake (1975) as the interval of time between AI and the last fertile egg laid. The length of this interval depends on the sperm storage in the tubules at the utero-vaginal junction where the spermatozoa are released for movement toward the infundibulum for ova fertilization (Brillard, 1993; Brillard et al., 1998). In hens, Pingel (1990a) found that the duration of the fertile period responded to genetic selection, and Beaumont (1992) estimated the genetic parameters of the duration of fertility traits. In the case of intergeneric crosses, genetic mechanisms are complex and give generally low results for fertility. Some of these difficulties have been studied in mule ducks, and results show that the two genera, parents of mule duck,

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¹To whom correspondence should be addressed: yushin@mail.tlri.gov.tw.

Abbreviation Key: AI = artificial insemination; BLUP = best linear unbiased predictors; MD = maximum duration of fertility; NED = number of dead embryos; NEF = number of fertile eggs; NEH = number of hatched ducklings; NES = number of eggs set laid; REML = restricted maximum likelihood; S = selection line; T = control line.

have different chromosomal complements (Mott et al., 1968; Denjean et al., 1997). Therefore, poor duration of the fertile period and hatchability could be attributed to many factors such as physiological incompatibility of gametes and differences in karyotypes (Pingel, 1990b).

A selection experiment, using as the selection trait the number of fertile eggs (NEF) (at candling at 7 d after egg set) after one AI with pooled Muscovy semen, began in 1992. The experiment was conducted with a Brown Tsaiya duck strain and a selected and a control line (Cheng, 1995) in Hsinhua, Taiwan Livestock Research Institute. The number of eggs set laid from Days 2 to 15 after one AI (NES), the total number of dead embryos (NED), the maximum duration of fertility (MD) and the number of hatched mule ducklings (NEH) were recorded. The estimation of genetic parameters for economically related traits had two main objectives: better understanding of the nature of the genetic variation of these traits and optimization of selection methods for their improvement (Tai et al., 1989).

The goal of the current study was to estimate and discuss the heritabilities and genetic correlations of the reported trait (NEF) and the four correlated traits (NES, NED, MD, and NEH) calculated from data collected on the first six generations of the selected and control lines.

MATERIALS AND METHODS

Ducks and Experimental Design

One hundred six female Brown Tsaiya ducks and 28 male Brown Tsaiya ducks of Line 105 were used as the foundation stock (G0). The foundation stock was derived from a Brown Tsaiya strain studied for laying traits (Cheng et al., 1995, 1996). Foundation birds were assumed to be unrelated and not inbred. In the first generation (G1), 165 females and 117 males were produced, and the data for the ducks were recorded. According to the best linear unbiased predictors (BLUP) of breeding values (Henderson, 1988), calculated by the BLUP animal model (Poivey, 1986; Cheng, 1995) for NEF, these ducks were divided into two groups in order to constitute the G1 of the parents of the selected line (S) and of the control (unselected) line (T). In the S line, 48 dams and 23 sires with the highest predictors of breeding values were mated to produce ducklings of the next generation (G2). The same procedure of selection was used for the following generations. In order to represent the distribution of the G1, 60 dams and 20 sires of the control, with average breeding values similar to the mean of G1, were sampled. In the T line, 46 dams and 20 sires were mated to produce 151 females and 97 male G2 ducks. Thereafter, the control line was bred with 20 sires and theoretically 60 dams (three dams per sire). One son was randomly chosen to replace his father, and one daughter was randomly chosen to replace her mother, for mating according to the rotational scheme described by Matheron and Chevalet (1977). Table 1 shows the structure of the selection experiment from G1 up to G6. A total of 2,127 females and

1,275 males was raised and evaluated. The males were evaluated on the performances (NEF) of relatives. In G6, the means \pm SD of the inbreeding coefficients were 0.066 ± 0.023 in the S line and 0.039 ± 0.029 in the T line.

The ducklings were raised in floor pens and fed a diet containing 19% CP and 2,925 kcal/kg ME from 0 to 4 wk followed by a diet containing 13% CP and 2,830 kcal/kg ME from 5 to 15 wk. From the age of first egg, they were raised in individual cages. During the laying period, ducks were fed a diet containing 20% CP and 2,810 kcal/kg ME. Drinking water and feed were provided ad libitum throughout the experimental period.

Data

Pedigree hatching was conducted in each generation, and an individual recording system was used. In order to separate the unknown direct genetic effects of the Muscovy drakes on the duration of fertility traits, AI was done with pooled Muscovy semen. The ducks at 26, 29, and 32 wk of age were AI with 0.05 mL of pooled semen from 10 to 15 Muscovy drakes from Line 302 (Tai Liu and Tai, 1991). After a single AI, eggs were collected for a period of 14 d (from Days 2 to 15) and incubated 7 d each. Fertility was estimated by candling the eggs after 7 d of incubation, and NEH was recorded. We analyzed data for NES, NEF, NEH, NED, and maximum duration of fertility from 2 d after AI up to the day of the last fertile eggs (MD). At the sixth generation, the second repetition of individual performances (29 wk) was discarded, because of problems in data recording due to a change of personnel during this period.

Statistical Analysis

In S, ducks were selected according to the BLUP animal model for the NEF, with repetition, as described in Cheng (1995). It has been shown that when the method of restricted maximum likelihood (REML) (Patterson and Thompson, 1971) is applied to an animal model, when all information contributing to the selection is included in the analysis, and when a large number of additive loci is assumed (infinite model), it can provide unbiased estimates of the genetic parameters (heritabilities and genetic correlations) even in selected populations (Im et al., 1989; Kennedy, 1990). Furthermore, accounting for inbreeding in the relationship matrix prevents underestimation of genetic variances (Tixier-Boichard et al., 1995). Also, the use of a relationship matrix in the animal model accounts for genetic drift variance (Sorensen and Kennedy, 1983). Thus, a multitrait REML with an animal model was used with the VCE 4.2 package developed by Groeneveld (1996).

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1 \mathbf{a} + \mathbf{Z}_2 \mathbf{p} + \mathbf{e}$$

where \mathbf{y} is the vector of duck performance for the five traits measured; $\boldsymbol{\beta}$ is the vector of fixed effects (date of hatch); \mathbf{a} is the vector of random genetic effect with $E(\mathbf{a})$

TABLE 1. Experimental population for selection on duration of fertility¹

Generation	Line	Number of hatch	Date of hatch	Number of ducks ²	Number of parents	Percentage of selection
G1		1	02/16/1992	M = 117 F = 165	M = 23 (S)	19.7
					F = 48 (S) M = 20 (T) F = 46 (T)	
G2	S	2	02/10/1993	M = 170	M = 20	11.8
	T	1	03/09/1993 04/07/1993	F = 214 M = 97 F = 151	F = 51 M = 20 F = 53	23.8
G3	S	1	03/14/1994	M = 96	M = 20	20.8
	T	1	03/14/1994	F = 213 M = 60 F = 228	F = 58 M = 20 F = 56	27.2
G4	S	2	02/23/1995	M = 133	M = 20	15.0
	T	2	05/30/1995 02/23/1995 05/30/1995	F = 232 M = 67 F = 135	F = 58 M = 19 F = 53	25.0
G5	S	1	05/13/1996	M = 184	M = 20	10.9
	T	1	05/13/1996	F = 248 M = 120 F = 193	F = 50 M = 20 F = 54	20.2
G6	S	1	05/02/1997	M = 105	M = 20	19.0
	T	1	05/02/1997	F = 175 M = 126 F = 173	F = 55 M = 20 F = 53	31.4

¹S = selected line; T = control line; M = male; F = female.

²Total M = 1,275; F = 2,127.

= 0; the variance of \mathbf{a} is $\mathbf{A}\sigma_a^2$; \mathbf{A} is the matrix of coefficients of relationship between the animals, and σ_a^2 is the additive genetic (co)variances; \mathbf{p} is the vector of random effects for repetition at the three ages, with $E(\mathbf{p}) = 0$, and $\text{Var}(\mathbf{p}) = \mathbf{I}\sigma_p^2$, where \mathbf{I} is the identity matrix; \mathbf{e} is the random residual with $E(\mathbf{e}) = 0$, $\text{Var}(\mathbf{e}) = \mathbf{I}\sigma_e^2$; and \mathbf{X} , \mathbf{Z}_1 , and \mathbf{Z}_2 are known incidence matrices connecting the performances and the effects.

The pooled data for each of S and T were analyzed separately from G1 to G6. The distributions of the random effects and performances were assumed to be normal. Tai et al. (1994) and Cheng (1995) found that the discrepancies from normality were small according to the kurtosis and skewness coefficients for NEF, NEH, and MD; slightly larger for NED; and larger yet for NES with a distribution of the number of eggs per batch between 13 and 14. Theoretically, the estimates of the genetic parameters in the base population are expected to be similar when calculated from the data of S and T. In order to obtain two estimates of the same genetic parameters, they were analyzed separately.

Variance components derived from sires and dams within sires were estimated, using the same model for fixed effects, with the Henderson III method by using the GLM procedure and with REML by using the VARCOMP procedure for univariate analysis (SAS Institute, 1994). The model also included an individual effect nested within the dam and sire effects in order to account for the repetitions of performances. These procedures do not take into account the relationships between sires and dams. The heritabilities were calculated from the sire

component (h_s^2), dam component (h_d^2), and sire + dam components (h_{s+d}^2). For REML estimations, the obtained asymptotic covariances of estimations were used to calculate the standard errors of heritability estimates according to the method of Kendall and Stuart method (1961) for the variance of a ratio.

RESULTS

Table 2 shows the means and SD for NES, NEF, NED, MD, and NEH in each of the two lines. They referred to all records obtained from G1 to G6. The skewness and kurtosis coefficients were calculated, and according to the values of these coefficients the distributions of NEF, NEH, and MD showed small discrepancies from normality; these discrepancies were significant for NES. Because the NES is recorded every 14 d in each repetition, the NES means demonstrate the high laying ability of the Brown Tsaiya. It also explains the skewness and kurtosis of NES.

Phenotypic correlations and repeatabilities, computed among the estimated variance components, are given in Table 3. The values were similar for the two lines. The five traits have relatively high repeatabilities (between 0.26 and 0.43). Heritabilities and genetic correlations with their standard errors estimated by REML animal model from data of S and T are given in Table 4. As expected, the heritabilities were similar in both lines, with the largest difference being for MD. The differences were not significant for NEF, according to the standard errors of the estimates. The heritabilities were medium for NEF (0.30 and 0.26) and MD (0.28 and 0.21), lower for NEH (0.18

TABLE 2. Means, phenotypic SD, skewness, and kurtosis of the five traits for selected (S) and control (T) lines from records (n)¹ of Generations 1 to 6

Line	Trait ³	Means	SD	Skewness	Kurtosis
S	NES	13.15	1.76	-3.48	15.70
	NEF	5.23	2.00	-0.05	-0.36
	NED	1.21	1.21	1.26	2.15
	MD	6.42	2.25	0.19	-0.09
	NEH	4.03	2.01	0.12	-0.49
T	NES	12.74	2.21	-2.61	8.06
	NEF	4.25	1.83	0.17	-0.34
	NED	1.11	1.18	1.30	2.36
	MD	5.44	2.12	0.40	0.19
	NEH	3.13	1.82	0.28	-0.33

¹n = 2,862 for the selected line and 2,522 for the control line.

²NES = number of eggs set; NEF = number of fertile eggs at candling (7 d of incubation); NED = total number of dead embryos; MD = maximum duration of fertility; NEH = number of hatched mule ducklings.

TABLE 3. Repeatabilities (on diagonal) and phenotypic correlations (above diagonal) for the five traits, estimated from the selected line (S) and control line (T)

Trait ¹	NES	NEF	NED	MD	NEH
NES					
S	0.43	0.40	0.11	0.16	0.26
T	0.29	0.38	0.12	0.13	0.27
NEF					
S		0.41	0.30	0.76	0.75
T		0.36	0.33	0.73	0.76
NED					
S			0.27	0.26	-0.22
T			0.26	0.29	-0.17
MD					
S				0.33	0.57
T				0.28	0.54
NEH					
S					0.33
T					0.28

¹NES = number of eggs set; NEF = number of fertile eggs at candling (7 d of incubation); NED = total number of dead embryos; MD = maximum duration of fertility; NEH = number of hatched mule ducklings.

TABLE 4. Heritabilities (on diagonal) and genetic correlations (above the diagonal) ± standard errors of estimates for the five traits, estimated from the selected (S) and control (T) lines

Trait ¹	NES	NEF	NED	MD	NEH
NES					
S	0.14 ± 0.04	0.48 ± 0.10	0.62 ± 0.13	0.25 ± 0.12	0.09 ± 0.14
T	0.10 ± 0.01	0.53 ± 0.04	0.39 ± 0.09	0.25 ± 0.05	0.37 ± 0.08
NEF					
S		0.30 ± 0.03	0.68 ± 0.08	0.96 ± 0.01	0.86 ± 0.03
T		0.26 ± 0.01	0.61 ± 0.07	0.92 ± 0.01	0.91 ± 0.01
NED					
S			0.06 ± 0.01	0.59 ± 0.08	0.27 ± 0.12
T			0.09 ± 0.02	0.72 ± 0.04	0.26 ± 0.08
MD					
S				0.28 ± 0.03	0.90 ± 0.03
T				0.21 ± 0.02	0.82 ± 0.03
NEH					
S					0.18 ± 0.02
T					0.19 ± 0.01

¹NES = number of eggs set; NEF = number of fertile eggs at candling (7 d of incubation); NED = total number of dead embryos; MD = maximum duration of fertility; NEH = number of hatched mule ducklings.

TABLE 5. Estimation of heritabilities by sire and dam variance components^{1,2}

Item	S			T		
	h_S^2	h_D^2	h_{S+D}^2	h_S^2	h_D^2	h_{S+D}^2
NES	0.05 0.01 ± 0.09	0.46 0.36 ± 0.15	0.25 0.19 ± 0.12	0.14 0.19 ± 0.10	0.37 0.05 ± 0.14	0.26 0.12 ± 0.12
NEF	0.19 0.25 ± 0.10	0.35 0.43 ± 0.11	0.27 0.34 ± 0.10	0.19 0.25 ± 0.10	0.46 0.41 ± 0.13	0.32 0.33 ± 0.12
NED	0.01 0.01 ± 0.04	0.00 0.05 ± 0.05	0.00 0.03 ± 0.04	0.05 0.01 ± 0.04	0.00 0.05 ± 0.05	0.002 0.03 ± 0.04
MD	0.26 0.30 ± 0.10	0.32 0.36 ± 0.10	0.29 0.33 ± 0.10	0.22 0.24 ± 0.08	0.22 0.16 ± 0.10	0.22 0.20 ± 0.09
NEH	0.21 0.27 ± 0.10	0.24 0.31 ± 0.11	0.23 0.29 ± 0.10	0.22 0.28 ± 0.11	0.41 0.35 ± 0.14	0.31 0.32 ± 0.13

¹Henderson III on the first line, restricted maximum likelihood on the second line with SE.

²NES = number of eggs set; NEF = number of fertile eggs at candling (7 d of incubation); NED = total number of dead embryos; MD = maximum duration of fertility; NEH = number of hatched mule ducklings; S = selected line; T = control line.

and 0.19), low for NES (0.14 and 0.10) and NED (0.06 and 0.09) in S and T, respectively. Genetic correlation estimates were also similar in both lines. Correlations between NES, NED, and NEH were positive and small. The high and favorable genetic correlations between NEF and MD, between NEF and NEH, and between MD and NEH should be noted. Those correlations were higher than those between NEF and NED.

The heritability values, using the methods for Henderson III and REML sire and dam component estimation, are presented in Table 5. Within the REML animal model estimations, the sire component heritability estimates of NEF, MD, NEH were similar, although somewhat lower for NEF and higher for NEH. The estimated values of NES were greatly variable and NED were extremely low. For NEF, the dam component seemed to be higher than the sire component.

DISCUSSION

When the aim of the study is to analyze fertility rates. Kirby and Froman (1990) have shown that logit, log-odds, and logistic analysis of rates may be more advantageous than traditional methods of evaluation. However, because the aim of this selection experiment was to increase NEF and to study the correlated response on NEH and MD, analysis of the number of eggs, dead embryos, and hatched ducklings was preferred over analysis of ratios. On the other hand, the distributions of the traits of main interest (NEF, NEH, and MD) can be considered as approximately normal.

This study is the first to estimate (and to do so with sufficient accuracy) the genetic parameters for additive genetic variation of these five traits related to reproductive ability in a common female duck bred for the production of the mule hybrid. The Brown Tsaiya is small sized (1.4 kg adult body weight) and is one of the most prolific laying duck breeds in the world (Lee et al., 1992). It was used in this experiment to improve our understanding of the nature of genetic variation of reproductive traits

with economic interest. In Brown Tsaiya ducks, the maximum duration of fertility with an average of 4.25 d and 5.13 d in T and S, respectively, is much shorter than in chicken hens (12 d) and turkeys (3 wk) (Lorenz, 1950; Brillard et al., 1998). In this study, we used the Lake's definition (1975) of maximum duration of fertile period as days minus 1, because the first fertile egg is laid 2 d after AI. The economic aim is to increase the number of live ducklings hatched. Tai et al. (1994) estimated heritabilities from sire (h_S^2) and dam within sire (h_D^2) variance components for 348 Brown Tsaiya ducks at 50 wk of age. They concluded that the best selection criterion for duration of fertility seemed to be the number of fertile eggs from the second to the fifteenth day after AI, with heritability estimates of $h_S^2 = 0.29 \pm 0.18$ and $h_D^2 = 0.38 \pm 0.22$. But the number of mule ducklings hatched was not measured, and the genetic correlations could not be estimated. In the Tai et al. (1994) results, $h_D^2 > h_S^2$ could be explained by dominance, maternal, and common environment effects. Our data confirmed that these effects could be suspected for NEF in the Brown Tsaiya, because REML estimates gave $h_D^2 > h_S^2$ (Table 5). In laying hens, Pingel (1990a) found a realized heritability $h^2 = 0.24$ for the maximum duration of fertility. Beaumont (1992) obtained multivariate REML estimates at 33 and 44 wk of age from 2,375 layer hens, for fertile eggs ($h^2 = 0.23$ and 0.22), hatched eggs ($h^2 = 0.23$ and 0.21), and maximum duration of fertility ($h^2 = 0.20$ and 0.22). The genetic correlations between maximum duration of fertility and fertile eggs, and hatched eggs, were high $r_g = 0.99$ and 0.93, respectively. According to a study of the Box-Cox transformation of data, which increased normality, Beaumont (1992) found that REML is robust against non-normality of these traits. The author concluded that the best criterion of selection for duration of fertility in hens seems to be the number of chickens hatched after AI, and the best procedure for estimating the genetic parameters is multivariate REML.

Our results showed that the heritabilities of NEF and MD were a little higher than those found in chicken hens

and confirm the previous results from Tai et al. (1994) showing that there was a genetic variation for these traits. The heritability of NEH was lower than that of NEF, which seems here the most interesting trait to select for. The heritabilities of NES and NED were low, showing little additive genetic variability. The low h^2 of NES could be due to the little total variability because of the high laying rate of these birds and the short holding time of the eggs (14 d). For NED, the sire and dam heritability estimates were not able to show that other genetic factors could play a role in embryo mortality such as dominance and maternal effects. Repeatability values were the lowest for NED. The random environmental influences might be important.

The NEF, MD, and NEH traits are highly positively correlated with each other (only a little less than in the hens), revealing common genes acting additively. As indicated by Beaumont (1992), more fertile eggs will be laid by females with greater abilities to store spermatozoa to fertilize the ova for a longer time. Thus, more embryos will achieve complete development, and more ducklings will be hatched. The genetic correlations between NEF, MD, and NED, even if positive, are smaller. The choice of the selection criterion (NEF) seems to be sound but should be implemented by the analysis of the selection experiment (estimates of genetic progress). The acquired knowledge of the genetic parameters of the duration of fertility traits in the mule duck dam population is limited to that of the Brown Tsaiya duck breed, which is a layer type duck. It has been shown in hens (quoted by Beaumont, 1992) that the strain (i.e., egg-type or meat-type) has a significant effect on the number of utero-vaginal glands filled by spermatozoa, which might result in a difference for the duration of fertility, although this theory has not yet been demonstrated. Nevertheless, it would be useful to estimate genetic parameters for the duration of fertility traits for meat-type ducks, such as the Pekin duck, as this breed is being used effectively as the dam for commercial mule ducks.

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