Genetic Trends for Laying Traits in the Brown Tsaiya (*Anas platyrhynchos*) Selected with Restricted Genetic Selection Index

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ABSTRACT : A small body size of Brown Tsaiya laying duck is desirable to reduce maintenance requirements, so the body weight at 40 weeks of age (BW40) has to be maintained at its current level. Egg weight has to be maintained at around 65 g to meet market requirements. Eggshell strength at 40 weeks of age (ES40) must to be increased in order to maintain a low incidence of broken eggs. Thus, number of eggs laid up to 52 weeks of age (EN52) has to be increased without negative correlated response on ES40. A new linear genetic selection index was used: $I_g=a_0\times GEW40$ (g)+$a_1\times GBW40$ (g)+$a_2\times GES40$ (kg/cm^2)+$a_3\times GEN52$ (eggs) where GEW40, GBW40, GES40 and GEN52 were the multitrait best linear unbiased prediction (MT-BLUP) animal model predictors of the breeding values respectively of egg weight and body weight at 40 weeks of age (EW40, BW40), ES40 and EN52. The coefficients a_0, a_1, a_2 and a_3 were calculated with constraints of 0.0 g, 0.0 g and 0.013 kg/cm^2 for expected genetic gains in EW40, BW40 and ES40 respectively and maximum gain in EN52. Since 1997, the drakes and the ducks were selected according to their own indexes, with this new genetic selection index. From G0 to G4, the average per generation predicted genetic responses in female duck were +0.05 g for EW40, +0.92 g for BW40, +0.035 kg/cm^2 for ES40 and +2.13 eggs for EN52. Which represented respectively 0.07%, 0.06%, 0.67% and 1.0% of the means of the EW40, BW40, ES40 and EN52. For ES40 and EN52, it represented also respectively 16.1% and 21.6% of the additive genetic standard deviation of these traits. These results indicated that selection of laying Brown Tsaiya by a restricted genetic selection index and with MT-BLUP animal model could be an efficient tool for improving the efficiency of egg production, increasing egg shell strength and egg number while holding egg weight and body weight constants. ***(Asian-Aust. J. Anim. Sci. 2003. Vol 16, No. 12 : 1705-1710)***

Key Words : Genetic Trends, Restricted Genetic Selection Index, Laying Ducks

INTRODUCTION

The native breed Brown Tsaiya (*Anas platyrhynchos*) is a major breed of laying duck in Taiwan and it is one of the highest laying duck breeds in the world (Tai et al., 1989; Lee et al., 1992). Mean performances were reported in last decade (Tai, 1985; Tai et al., 1989; Cheng et al., 1995). A selection of Brown Tsaiya for the four traits of egg weight and body weight at 40 weeks of age (EW40 and BW40), number of eggs laid up to 52 weeks of age (EN52), eggshell strength at 30 or 40 weeks of age (ES30 or ES40) has been conducted at the Ilan Branch Institute of the Taiwan Livestock Research Institute (Duck Research Center, DRC) since 1984 up to 1996. The purpose was to obtain maximum gain for egg laid (EN52), to increase ES30 or ES40, to keep constants EW40 and BW40. A two stage selection was carried out, as described in Cheng et al. (1995). First, 50% of the female ducks were selected on a linear phenotypic selection index of EW40, BW40 and EN52 with restrictions (Tai et al., 1994). As the heritabilities of ES30 and ES40, and their genetic correlations with the three previous traits were unknown, among these 50%, the top 50% of the best female ducks was selected for ES30 in the first and second generations (1985-1987) and for ES40 from the third generation (1988-1996) by independent culling levels selection. Cheng et al. (1995) estimated the genetic parameters in the base population by restricted maximum likelihood (REML) applied to a multiple trait animal model based on data of the first five generations of selection. Heritabilities were found to be low (0.09 and 0.12) for ES40 and EN52, to medium (0.33 and 0.50) for EW40 and BW40. The pattern of the genetic correlations for the traits to be selected showed that EN52 was uncorrelated with the body weight and was negatively correlated with egg weights and egg shell strength traits. Egg weight, body weight and eggshell strength traits were positively genetically correlated among themselves.

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With these estimated genetic parameters, the genetic trends of the selected traits for five generations were obtained. Selection by a multitrait selection index is theoretically more efficient than selection for several traits by independent culling level. A new linear genetic selection index with restrictions and for desired gains for EW40, BW40, ES40 and EN52 was established as a linear combination of the predicted breeding values of the 4 traits got by a multitrait best linear unbiased prediction (MT-BLUP) animal model (Cheng et al., 1996). It has been conducted at the Ilan Branch Institute of the Taiwan Livestock Research Institute for four generations of selection since 1997.

The purpose of this study is to discuss the results of application of this new restricted genetic selection index with objectives to increase the genetic levels of EN52 and ES40, and to maintain constants the ones of BW40 and EW40.

MATERIALS AND METHODS

Genetic parameters

The estimates of heritabilities, phenotypic and genetic correlations in an animal model with a multivariate multimodel restricted maximum likelihood method (MM-REML) for four traits were taken from Cheng et al. (1995) (Table 1). They were used to calculate predictors of breeding values of each of four traits by a multitrait BLUP animal model.

Animal

The ducks were selected by new restricted genetic selection index for a linear combination of the predicted breeding values of the 4 traits of EW40, BW40, ES40 and EN52. The same management system was applied throughout the 4 generations of selection in this experiment (Tai et al., 1989; Lee et al., 1992). The performance data were individually measured and recorded for male and female ducks in each generation from 1997 (G0) to 2002 (G4). A total of 2,475 females and 998 males was raised and evaluated. The structure of the selection experiment, the means and standard deviation of inbreeding coefficients of male and female duck in each generation are given in Table 2. Theoretically 20 males and 60 females with the highest values of the genetic selection index of the 4 traits were selected in each generation. Each selected male was mated with 3 selected females in order to produce the offspring for the next generation. Mating of close related ducks (full or half brother-sister) was avoided. On average 18.2% of the drakes and 20.1% of the female ducks were selected.

Table 1. Heritabilities and phenotypic and genetic correlations estimated by animal model with MM-REML method for four traits (Cheng et al., 1995)

Trait	EW40	BW40	ES40	EN52
EW40	0.329	0.424	0.132	0.060
BW40	0.617	0.499	0.064	0.063
ES40	0.483	0.231	0.094	-0.043
EN52	-0.323	0.006	-0.203	0.118

EW40: egg weight at 40 weeks of age. BW40: body weight at 40 weeks of age. ES40: eggshell strength at 40 weeks of age. EN52: number of eggs laid up to 52 weeks of age. Phenotypic correlations: above the diagonal. Genetic correlations: below the diagonal.
Heritabilities: the diagonal.

Restricted genetic selection index taking into account the information from relatives

The classical genetic selection index for multiple trait can be written (Rouvier, 1969, 1977; Mallard, 1972): Ig $=\mathbf{a'\hat{g}}$ where **a** is a vector of coefficients of breeding values, $\mathbf{\hat{g}}$ is the vector of predictors of breeding values for each of the n traits, calculated as the multiple regression of **g** above all the phenotypic predictors, E ($\mathbf{\hat{g}}$)=0. The multiple correlation between Ig and H=**a'g** is maximum. H is the aggregate genotype, **g** is the vector of breeding values with E (**g**)=0. When selecting by truncation for Ig with intensity of selection i, the expected genetic gain in each trait is given by

$$E\Delta\mathbf{g}_n=\frac{i}{\sigma_{Ig}}\ \mathbf{Ba} \qquad [1]$$

where $E\Delta\mathbf{g}_n$ is the expected genetic gain in each trait and the matrix E ($\mathbf{\hat{g}\hat{g}'}$)=**B**; σ_{Ig} is the standard deviation of Ig. With the classical selection index (the means are supposed to be known), the matrix **B** can be calculated, if the matrix G=E (**gg'**) is assumed to be known. The correlation between H and Ig is calculated by

$$R^2_{HIg}=\mathbf{a'Ba/a'Ga}.$$

According to Lin (1990) followed by Cheng et al. (1996), **B** can be approximated by $\mathbf{\hat{B}}$ which is the matrix

Table 2. Structure of the selection experiment and inbreeding coefficients of Brown Tsaiya ducks for five generations (means±SD)

Generation	Number of offspring	Number of parents	Inbreeding coefficient
G0	M=212	M=60	0.115±0.061
	F=830	F=150	
G1	M=346	M=60	0.111±0.031
	F=599	F=156	
G2	M=233	M=18	0.137±0.030
	F=553	F=45	
G3	M=103	M=20	0.029±0.056
	F=193	F=54	
G4	M=104	M=20	0.059±0.036
	F=300	F=60	
Total	M=998		
	F=2475		

M=number of males; F=number of females.

Table 3. Restricted genetic selection indices used in male and female Brown Tsaiya for G0-G3 generations of selection: coefficient values of the MT-BLUP animal model predictors of the breeding values and expected genetic gains in each trait with selection intensity i=1

Index		Coefficients				Expected genetic gains			
		a_0	a_1	a_2	a_3	EW40	BW40	ES40	EN52
G0	Male	0.0787423	-0.001238	1.5646306	0.0900138	0	0	0.013	2.490
	Female	0.037249	-0.00064	0.8614897	0.0462978	0	0	0.013	3.508
G1	Male	0.0261623	-0.000773	1.7467403	0.070637	0	0	0.013	2.780
	Female	0.0373417	-0.001001	0.7543072	0.0335516	0	0	0.013	4.117
G2	Male	0.2321607	-0.00802	2.341494	0.1209006	0	0	0.013	2.122
	Female	0.1091774	-0.003055	0.808794	0.0050992	0	0	0.013	3.354
G3	Male	0.4668392	-0.001137	0.9458406	0.1581483	0	0	0.013	1.924
	Female	0.261027	-0.005143	0.4659732	0.0988885	0	0	0.013	2.451

EW40, BW40, ES40 and EN52: same the Table 1. Expected genetic gains of EW40=0, BW40=0, ES40=0.013 kg/cm^2 and EN52=maximum.

of the variances and covariances of the predicted breeding values in an animal model, separately for male and female ducks. Since i/σ_{Ig} is a constant, it can be dropped without affecting the proportionality of **a**. Then, restricted genetic selection index coefficients **a**, or coefficients for desired gains can be obtained from [1] by

$$\mathbf{a} = \mathbf{B}^{-1}\mathbf{w} \qquad [2]$$

where **w** is a vector of proportional values for the desired gains of the restricted traits.

Selection method

A new linear restricted genetic selection index suggested by Cheng et al. (1996) was used: Ig=a_0×GEW40 (g)+a_1×GBW40 (g)+a_2×GES40 (kg/cm^2)+a_3×GEN52 (eggs) where GEW40, GBW40, GES40 and GEN52 were the multitrait best linear unbiased prediction (MT-BLUP) animal model predictors of the breeding values of EW40, BW40, ES40 and EN52, respectively. The coefficients a_0, a_1, a_2 and a_3 were calculated with constraints of 0.0 g, 0.0 g and 0.013 kg/cm^2 for expected genetic gains in EW40, BW40 and ES40 respectively and maximum gain in EN52 (with a selection intensity i=1). Since 1997, taken as a new G0, the drakes and the ducks were selected according to their own indexes in each generation from G0 up to G4.

Genetic trends

The data for the four traits (EW40, BW40, ES40 and EN52) and the same models as described in Cheng et al. (1995) were used for computation of predicted breeding values of each of four traits by an MT-BLUP animal model that accounts for inbreeding using the PEST program (Groeneveld, 1990; Groeneveld et al., 1992). The pedigree information was traced back to the founder animals which were assumed to be unrelated and not inbred for calculating the inbreeding coefficients and additive relationship coefficients. The genetic trends for each trait were estimated by averaging the MT-BLUP predicted breeding values of male and female ducks across the generations. The average predicted genetic responses per generation were calculated in the female ducks as the differences of these values between G4 and G0 divided by 4 which was the number of generations of selection. The phenotypic selection differentials and the selection differentials on predicted breeding values for each trait were calculated in female ducks.

RESULTS

Multitrait genetic selection indices

The means and standard deviations of inbreeding coefficients are shown in Table 2. The matrix E $(\hat{\mathbf{g}}\hat{\mathbf{g}}')=\mathbf{B}$ was approximated by $\hat{\mathbf{B}}$ matrix of (co)variances of the predicted breeding values by MT-BLUP for EW40, BW40, ES40 and EN52 which was calculated for males and females in each generation. From formula [2] giving vector **a**, the restricted genetic selection indices Ig were calculated for male and female ducks of each generation with the following constraints (vector **w**): EΔgEW40=0, EΔgBW40= 0, EΔgES40=0.013 kg/cm^2 and EΔgEN52= maximum. The expected genetic gains in each trait by a truncation selection with selection intensity i=1 where calculated from formula [1] (Table 3).

Genetic trends

Table 4 presents the average phenotypic values and selection differential in Brown Tsaiya female ducks for EW40, BW40, ES40 and EN52 for the five selected generations (G0 to G4). It gives the phenotypic values of the selected animal, the realized selection differentials on phenotypic values and on predicted breeding values, the numbers of selected ducks. The average predicted breeding values and the average predicted genetic responses in female ducks for MT-BLUP animal model are shown in Table 5. The average predicted genetic responses per generation in the females were +0.05 g for EW40, +0.92 g for BW40, +0.035 kg/cm^2 for ES40 and +2.13 eggs for EN52. They represented 0.07%, 0.06%, 0.67% and 1.0% of the means of the phenotypic values for the four traits

Table 4. The average phenotypic values and selection differential for EW40, BW40, ES40 and EN52 of Brown Tsaiya female ducks for five generations

Items	Generations	Phenotypic value of individuals	Phenotypic value of selected individuals	Selection differential on phenotypic values	Selection differential on breeding values
EW40 (g)	G0	66.4±4.4 (n=773)	66.5±4.1 (n=150)	+0.1	-0.066
	G1	63.2±4.1 (n=542)	63.3±4.1 (n=156)	+0.1	+0.087
	G2	66.1±4.2 (n=531)	67.0±4.3 (n=45)	+0.9	+0.007
	G3	68.7±4.0 (n=193)	69.7±3.4 (n=54)	+1.0	+0.117
	G4	67.1±4.5 (n=299)	68.8±4.6 (n=60)	+1.7	+0.360
BW40 (g)	G0	1,349±132 (n=828)	1,378±130 (n=150)	+29	+13.40
	G1	1,415±104 (n=582)	1,429±102 (n=156)	+14	+5.54
	G2	1,360±110 (n=552)	1,330±95 (n=45)	-30	-12.29
	G3	1,382±122 (n=193)	1,349±97 (n=54)	-33	-8.37
	G4	1,354±136 (n=300)	1,384±142 (n=60)	+30	+10.22
ES40 (kg/cm^2)	G0	4.72±0.88 (n=758)	5.09±0.87 (n=150)	+0.37	+0.032
	G1	5.22±0.86 (n=542)	5.48±0.69 (n=156)	+0.26	+0.024
	G2	5.54±0.84 (n=529)	5.98±0.68 (n=45)	+0.44	+0.046
	G3	5.26±0.74 (n=193)	5.37±0.71 (n=54)	+0.11	+0.046
	G4	5.30±0.81 (n=298)	5.43±0.71 (n=60)	+0.13	+0.016
EN52 (eggs)	G0	219.3±27.2 (n=790)	229.7±14.1 (n=150)	+10.4	+3.63
	G1	207.4±29.0 (n=549)	224.1±14.9 (n=156)	+16.7	+2.68
	G2	211.2±35.1 (n=546)	223.4±28.6 (n=45)	+12.2	+2.71
	G3	211.1±23.7 (n=193)	224.1±11.2 (n=54)	+13.0	+1.62
	G4	216.8±29.8 (n=299)	234.3±9.1 (n=60)	+17.5	+3.87

EW40, BW40, ES40 and EN52 :same the Table 1. Phenotypic value: means±SD, n=number of measured female ducks.

respectively. It also represented 16.1% and 21.6% of the additive genetic standard deviation of ES40 and EN52 respectively.

DISCUSSION

As far as we know, there is no published data from a selection experiment for such laying traits in laying female ducks by applications of restricted genetic selection index. Ducrocq (1994) reviewed the benefits from multitrait evaluations using a BLUP animal model. One of its most interesting properties is the fact that the additive relationship matrix can account for changes in mean and variances due to selection, as long as the information on which selection decisions are based is included in the analysis (Kennedy et al., 1988). Lin (1990) derived a simple procedure to compute a restricted BLUP by modifying the economic weighing factor rather than imposing restrictions on the multitrait mixed-model equations (MME). A simple computation procedure was derived to calculate a genetic multitrait selection index $Ig=\mathbf{a}'\hat{\mathbf{g}}$ using the multitrait BLUP animal model of breeding values and the formula [2]. The matrix $E(\hat{\mathbf{g}}\hat{\mathbf{g}}')=\mathbf{B}$ is approximated by $\hat{\mathbf{B}}$. It was constructed by calculating the matrix $\hat{\mathbf{B}}$ of variances and covariances of the predicted breeding values of all the animals in each last generation, separately for males and females with the approximation $E(\hat{\mathbf{B}})=\mathbf{B}$ (Cheng et al., 1996). The application of this method would lead to variance-covariance matrix of the MT-BLUP animal model predictors of breeding values calculated separately for males and females in each generation. Because, as from one generation to the following, the predicted breeding values change, the $\hat{\mathbf{B}}$ matrix change also.

The increase in inbreeding coefficient is rather small from G0 (0.115) to G2 (0.137). Since 1984 the ducks were selected with the same objectives in four lines defined according to the sire origins of founder animals which were from 4 breed farms, as described in Cheng et al. (1995). According to the results of a diallel crossbreeding between these lines no significant heterosis was found (unpublished results). One line was culled in 1995 and the three other lines were pooled in 1999 (G2). Due to combining 3 lines in G2, the mean of inbreeding coefficients dropped to 0.029 in G3 and to 0.059 in G4.

Economically speaking in Taiwanese egg markets, a small body size of female duck is desirable to reduce maintenance requirement and egg weight has to be maintained at the current level (around 65 grams) to meet market requirement (Shen and Chen, 2003). ES40 must not be decreased in order to maintain a low incidence of broken eggs. Thus, EN52 has to be increased without negative correlated response on ES40.

The average genetic response per generation for the number of eggs laid up to 52 weeks of age (EN52) represents 21.6% of the additive genetic standard deviation. The phenotypic trend on EN52 seemed not to confirm the genetic trend between G0 and G1. From G1 (207.4 eggs) up

Table 5. The average predicted breeding values (APBV) in male and female ducks in each generation and the average predicted genetic responses per generation in female duck

Items		APBV		Female ducks		
		Male	Female	APGR	APGRPV%	APGRSD%
EW40	G0	-0.225±1.287	-0.067±1.753			
(g)	G1	-0.163±1.255	0.080±1.512			
	G2	0.060±1.188	0.231±1.567	+0.05	0.07%	1.7%
	G3	0.281±1.190	0.334±1.348			
	G4	0.495±1.378	0.150±1.632			
BW40	G0	15.728±34.685	16.287±63.946			
(g)	G1	25.007±35.263	33.026±47.321			
	G2	40.023±33.334	41.630±48.215	+0.92	0.06%	0.99%
	G3	35.262±43.023	38.041±45.172			
	G4	40.167±52.325	19.947±60.389			
ES40	G0	-0.0091±0.0904	0.0027±0.1104			
(kg/cm²)	G1	0.0254±0.0906	0.0366±0.0997			
	G2	0.0422±0.0975	0.0477±0.1090	+0.035	0.67%	16.1%
	G3	0.1179±0.1027	0.1216±0.1091			
	G4	0.1385±0.1063	0.1432±0.1172			
EN52	G0	5.261±3.987	4.730±4.553			
(eggs)	G1	7.316±3.821	7.296±4.359			
	G2	9.841±3.484	9.476±4.670	+2.13	1.0%	21.6%
	G3	12.192±3.411	12.061±4.238			
	G4	13.106±3.393	13.239±4.264			

EW40, BW40, ES40 and EN52: same the Table 1. APGR: average predicted genetic response per generation in actual unit.
APGRPV%: average predicted genetic response per generation in percentage of average of phenotypic values.
APGRSD%: average predicted genetic response per generation in percentage of the genetic standard deviation.

to G4 (216.8 eggs) the phenotypic trend confirmed the genetic one. The egg production up to 52 weeks of age is at a high phenotypic level, and could reach a plateau with the current management system. One hypothesis might be that the environmental effects were more favorable in G0, than later where the genetic level was higher. Moreover the environment might be a limiting factor for the full expression of the genetic progress. On the other hand, as the age at first egg is about 17 weeks of age, 52 weeks is a relatively young age for birds which are laying up to 64 or 68 weeks of age. So an increase in the test period length could be a solution to enhance the genetic progress on egg number, but it would increase the generation interval length.

The per generation genetic response on EW40 represents 1.7% of the additive genetic standard deviation of the trait. This slight increase may be due to the selection for ES40, which is quite correlated to EW40 (rg=0.483). The realized selection differentials on the predicted breeding values for BW40 were +13.40, +5.54, -12.29 and -8.37 from G0 to G3 respectively. The genetic response on BW40 (0.99% of the additive genetic standard deviation) was small and close to the expected genetic gain. When selecting for ES40, there was a correlated positive response on BW40 which counteracted the effects of that selection. This could explain a fluctuant genetic response for this trait. The eggshell strength depended on the age of the duck and the measurement at 40 weeks of age was preferred than at 30 weeks of age (Cheng et al., 1996). The average per generation predicted genetic response of ES40 (0.035 kg/cm^2 and 16.1% of the genetic standard deviation) was larger than in the previous selection by independent culling level (0.014 kg/cm^2 and 6.3% respectively). The genetic response is confirmed by the phenotypic trend (from 4.72 kg/cm^2 in G0 up to 5.30 kg/cm^2 in G4).

The restricted genetic selection index based on MT-BLUP animal model of breeding values was more efficient than the previous selection on phenotypic values by independent culling level, to increase the genetic levels of EN52 (+2.13 eggs per generation versus +0.935 eggs) and of ES40, while maintaining at about constant genetic levels EW40 (+0.05 g per generation versus +0.177 g) and BW40 (+0.92 g per generation versus 8.029 g). The selection intensities in female ducks were similar (i=1.4 versus i=1.25). The selection intensity was calculated from the mean percentage of selected ducks, supposing a normal distribution of the selection index values. Moreover, the predicted genetic responses did not fit the expected ones (Table 3, for i=1), being a little smaller for EN52 and larger for ES40. That could be due to a lack of multiple co-linearity of relationship between the predicted breeding values of the 4 traits or to small inaccuracies in the genetic parameters values, specially the genetic correlations. Moreover the assumptions of the infinitesimal model which allow to ascertain that the genetic parameters are estimated in the base population without bias due to the selection could be not completely fulfilled if some genes with large effect were segregating, specially for ES40. So it would be useful for the future to re-estimate the genetic parameters of the 4 traits. After estimating the new genetic parameters (including age at first egg), it would be possible to optimize a breeding program for continuing genetic improvement of laying traits. In addition, it would be interesting to study the persistence of egg production up to 72 weeks of age which is an important economical trait and to do a genetic analysis of laying curves.

CONCLUSIONS

In a four generations selection of the Brown Tsaiya line, the average genetic responses per generation were 0.05g (EW40), 0.92 g (BW40), 0.035 kg/cm^2 (ES40), 2.13 eggs (EN52), by application of the new multitrait restricted genetic selection index. They were 0.177, 8.029, 0.017 and 0.935, respectively, with the selection by independent culling level (Cheng et al., 1996), with similar selection intensity in female ducks (i=1.4 vs. i=1.271). The application of multitrait restricted genetic selection index fitted better the desired gains than the selection by independent culling level. It was efficient to increase the genetic levels of both the moderately antagonistic traits ES40 and EN52, and to maintain about constants EW40 and BW40, although the positive genetic correlation between EW40 and ES40. It was well known that linear phenotypic selection index was more efficient than selection by independent culling level to improve several traits simultaneously. These new results confirm that restricted genetic selection index for several traits is more efficient than independent culling level and also the superiority of BLUP compared to selection on individual phenotypic values.

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