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Original article

Selection responses for the number of fertile eggs of the Brown Tsaiya duck (Anas platyrhynchos) after a single artificial insemination with pooled Muscovy (Cairina moschata) semen

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Abstract - A seven-generation selection experiment comprising a selected (S) and a control (C) line was conducted with the objective of increasing the number of fertile eggs (F) of the Brown Tsaiya duck after a single artificial insemination (AI) with pooled Muscovy semen. Both lines consisted of about 20 males and 60 females since parents in each generation and each female duck was tested 3 times, at 26, 29 and 32 weeks of age. The fertile eggs were measured by candling at day 7 of incubation. The selection criterion in the S line was the BLUP animal model value for F. On average, 24.7% of the females and 15% of the males were selected. The direct responses to the selection for F, and correlated responses for the number of eggs set (Ie), the number of total dead embryos (M), the maximum duration of fertility (Dm) and the number of hatched mule ducklings (H) were measured by studying the differences across the generations of selection between the phenotypic value averages in the S and C lines. The predicted genetic responses were calculated by studying the differences between the S and C lines in averaged values of five traits of the BLUP animal model. The selection responses and the predicted responses showed similar trends. There was no genetic change for Ie. After seven generations

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of selection, the average selection responses per generation were 0.40, 0.33, 0.42, 0.41 genetic standard deviation units for F, M, Dm, and H respectively. Embryo viability was not impaired by this selection. For days 2–8 after AI, the fertility rates (F/Ie) were 89.2% and 63.8%, the hatchability rates (H/F) were 72.5% and 70.6%, and (H/Ie) were 64.7% and 45.1% in the S and C lines respectively. It was concluded that upward selection on the number of fertile eggs after a single AI with pooled Muscovy semen may be effective in ducks to increase the duration of the fertile period and the fertility and hatchability rates with AI once a week instead of twice a week.

selection response / fertile egg / Brown Tsaiya / Muscovy / duck

1. INTRODUCTION

Mule duck production for meat (roasted duck) is traditionally important in Taiwan. In the last ten years, it has increased tremendously in France, where male mule ducks are force-fed to produce "foie gras" (fatty liver) and the female can be used for meat production. The efficiency of production depends greatly on artificial insemination (AI) to overcome the behavioral barriers in reproduction between the two parents of the hybrid mule ducklings, which are the Muscovy (Cairina Moschata) drake and the Common duck (Anas Platyrhynchos) dam [14,35]. These two genera do not have the same chromosome complement [10,21]. So, in the last few decades, it has become common to use AI as a production technique, both in France and Taiwan [28, 29, 32]. Unfortunately, owing to the short duration of fertility in this intergeneric crossbreeding, AI has to be practised twice a week in order to maintain the fertility rate [16,19,27]. It would be economically beneficial to inseminate the female duck once a week instead of twice a week, without decreasing the fertility rate. So our question was to study the value of selection for an increased duration of the fertile period in order to reduce the frequency of the required AI. Previous results in domestic fowl have shown that selection for a longer fertile period is feasible [2,23,24]. Because of the possible negative consequences due to the genetic correlation between the duration of the fertile period and embryo death [2], an alternative model of selection for the duration of the fertile period was preferred, based on the number of hatched chicks after a single AI [3,5]. Nevertheless, the optimum selection criterion and the selection responses to selection for an increased duration of the fertile period could be different in the intergeneric crossbreeding of ducks from domestic fowl and breeding within the species. On the contrary, the mean maximum duration of the fertile period has been found to be much shorter in intergeneric crossbreeding (5.5 days, [33]) than in domestic fowl breeding (12 days, quoted in Lake [17]). It is also shorter in the intergeneric crossbreeding compared to pure breeding in the common duck (4.2 d. vs. 7.1 d.) [6]. So it seemed helpful to determine a selection criterion, and to conduct a selection experiment in order to study what genetic progress could be achieved in increasing the duration of the fertile period in the intergeneric crossbreeding of ducks.

Tai *et al.* [33] found that the best selection criterion for the duration of fertility seems to be the number of fertile eggs laid from the 2nd to the 15th day after a single AI with pooled Muscovy semen. So, in 1992, the Taiwan Livestock Research Institute (TLRI), Hsinhua, Tainan [7] initiated a selection experiment for an increased number of fertile eggs (F) (measured by candling on the 7th day after egg set) in the Brown Tsaiya female duck after a single AI with pooled Muscovy semen, using a selected and a control (unselected) line. In order to increase the efficiency of the selection method, the best linear unbiased predictors (BLUP) using an animal model were preferred to the conventional selection index, to evaluate the breeding values of the male and female ducks.

The purpose of this study was to analyze the direct and correlated responses to selection for an increased number of fertile eggs after a single AI with pooled Muscovy semen.

2. MATERIALS AND METHODS

2.1. Animals and experimental procedures

The number of ducks involved in each generation, the number of hatches, the percentage of selected animals, and the selection differentials on breeding values of F in the C line are shown in Table I. The first hatch in G1 was on February 16, 1992 and the last one in G8 was on June 14, 1999. One hundred and six Brown Tsaiya females and 28 Brown Tsaiya males of Line 105, assumed unrelated, were used as the founder stock (G0). Line 105 was studied at TLRI, Ilan Station, for laying traits [8,9]. For the first generation (G1), 165 females and 117 males, progeny of the founder animals, were produced, and the data of the females were recorded. 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 or unselected line (C). Both lines were maintained at the same time under standardized conditions at the TLRI experimental farm in Hsinhua, Tainan. Their management is described in Poivey *et al.* [26].

In the S line, male and female ducks in each generation were selected by truncation on superior values of the BLUP animal model for the number of fertile eggs from the 2nd to the 15th day after AI (3 replications). The model for the prediction of additive genetic values of the selected trait was the following, as described in Cheng [7]:

$$y = Xb + Z_1a + Z_2p + e$$

Table I. The experimental population for the selection on the number of fertile eggs.

	Line	Batch of hatch	Ducks	Parents	% of selection	S.D
G0			M = 28			
			F = 106			
G1		1	M = 117	M = 23(S)	19.7	
			F = 165	F = 48	29.1	
				M = 20(C)		-0.036
				F = 46		
G2	S	2	M = 170	M = 20	11.8	
			F = 214	F = 51	23.8	
	C	1	M = 97	M = 20		-0.160
			F = 151	F = 53		
G3	S	1	M = 96	M = 20	20.8	
			F = 213	F = 58	27.2	
	C	1	M = 60	M = 20		+0.196
			F = 228	F = 56		
G4	S	2	M = 133	M = 20	15.0	
			F = 232	F = 58	25.0	
	C	2	M = 67	M = 19		-0.052
			F = 135	F = 53		
G5	S	1	M = 184	M = 20	10.9	
			F = 248	F = 50	20.2	
	C	1	M = 120	M = 20		-0.044
			F = 193	F = 54		
G6	S	1	M = 105	M = 20	19.0	
			F = 175	F = 55	31.4	
	C	1	M = 126	M = 20		+0.011
			F = 173	F = 53		·
G7	S	2	M = 126	M = 20	16.0	
			F = 296	F = 61	20.6	
	C	2	M = 158	M = 20		-0.019
			F = 290	F = 61		
G8	S	1	M = 114			
			F = 204			
	C	1	M = 94			
		-	F = 157			
Total	S		M = 1045			
	-		F = 1747			
G1-G8	С		M = 839			-0.104
21 23	~		F = 1492			0.101

M: male; F: female; S: selected line; C: control line; S.D: Selection differential in the C line.

- \mathbf{v} = the vector of observations;
- \mathbf{b} = the vector of fixed effects of hatching date;
- ${\bf a}=$ the vector of random genetic effects with ${\bf E}({\bf a})=0$, ${\bf Var}({\bf a})={\bf A}\sigma_a^2$, where ${\bf A}$ is the additive genetic relationship matrix of the animals, $\sigma_a^2=$ the additive genetic (co)-variances;
- \mathbf{p} = the vector of random repeat effects with $E(\mathbf{p}) = 0$, $Var(\mathbf{p}) = \mathbf{I}\sigma_p^2$, where \mathbf{I} is the identity matrix, σ_p^2 = the (co)-variances of repeat effects;
- \mathbf{e} = the vector of random residual effects with $\mathbf{E}(\mathbf{e}) = 0$, $\mathbf{Var}(\mathbf{e}) = \mathbf{I}\sigma_e^2$, where σ_e^2 = the (co)-variances of random residual effects;
- X, Z_1 and Z_2 = the matrices relating the elements of b, a and p to the observations.

In each generation, all the ancestors of the selection candidates back to the founder animals were taken into account to establish the additive genetic relationship matrix. The performance of ducks in all generations (from G1) was also taken into account.

The genetic parameters used were $h^2 = 0.34$ [33] and repeatability r = 0.47 (estimated from G1 data), for G1 up to G3. From G4 they were $h^2 = 0.29$ and r = 0.40 (estimated from the data of the first 3 generations, in Cheng [7]). The predicted additive genetic values of the candidate to be selected were computed using a program by Poivey [25] for G1 to G3, and with the PEST program [12] thereafter. It was scheduled to select 20 males and 60 females in each generation, in order to mate one male with three females to produce the offspring to be measured in the following generation.

Theoretically, the control line was bred from 20 sires and 60 dams (three dams per sire). One son of each sire was randomly chosen to replace his father and one daughter of each dam was randomly chosen to replace her mother, for mating according to a rotational scheme [20].

Starting from the progeny of the founder stock, this selection experiment was conducted over 8 generations from 1992 to 1999 (G1 to G8). The generations were kept separate and the generation interval was one year. In total, from G1 to G8, 2792 and 2331 ducks in the S and C line respectively were recorded. In the S line, the percentage selected was between 20.2% and 31.4% in females and between 10.9% and 19.7% in males.

2.2. Measurements

Pedigree hatching was carried out in each generation, and an individual recording system was used to collect the performance of each duck and to register the pedigree (PALMI system, [1]). The ducks at 26, 29, and 32 weeks of age were artificially inseminated (vaginal folds everted method) with 0.05 mL of pooled semen from 10 to 15 Muscovy drakes from line 302 of TLRI, Ilan Station [34]. After a single AI, the eggs were collected from day 2 to 15 for G1

to G6, and from day 2 to 18 for G7 and G8. They were incubated for 7 days and 9 days respectively. Fertility was estimated by candling the eggs after 7 days of incubation, and the number of live hatched ducklings was recorded. Data regarding the number of eggs set (Ie), the number of fertile eggs at candling (F), the number of total dead embryos (M), the maximum duration of fertility from the 2nd day after AI up to the day of the last fertile egg (Dm), and the number of hatched mule ducklings (H) were analyzed.

2.3. Statistical analysis

The elementary statistical parameters (means and variances) of phenotypic values were obtained using the SAS® procedure [30]. The selection differentials on breeding values of F in the C line were calculated in each generation, as differences between the averages of animals randomly chosen as parents and of all animals measured in that generation. They were calculated in order to detect an unintentional selection. The inbreeding coefficients were calculated in each generation for the females and the males of each line. The cumulated generation direct and correlated selection responses were measured as the differences in the averages of phenotypic performance of animals in the S and C lines. Their variances were calculated taking into account the variance of error measurements and the genetic drift variance [11].

The predicted genetic responses to selection on F was estimated from the within generation line difference (S-C) for average predicted breeding values for each of the five traits in female ducks. These predicted additive genetic values were calculated in a 5-trait analysis using BLUP methodology applied to an individual animal model previously described for one trait. These multiple-trait BLUP animal model values were calculated using the records of all five traits together for the selected and control lines from G1 to G8, using the PEST 3.1 package [12,13], with a performance file of 7890 records and a pedigree file of 4985 animals. The heritabilities, repeatabilities, genetic and phenotypic correlations for the five traits were taken from Poivey *et al.* [26] for these computations of breeding values. For simplification, the approximate standard errors for the generation S-C differences were calculated for each trait with the estimated parameters, considering that the predicted additive genetic values were computed in univariate analyses [31], as in [18].

3. RESULTS

3.1. Percentage of selection

Table I shows the number of females measured and selected as parents, the number of males raised and selected as parents in each generation in the S line, as well as the percentage of selected animals. In the C line, it shows

Generation	S line	C line
G1	0	0
G2	0	0
G3	0.017 ± 0.024	0.0067 ± 0.017
G4	0.041 ± 0.029	0.022 ± 0.025
G5	0.053 ± 0.034	0.034 ± 0.022
G6	0.067 ± 0.024	0.040 ± 0.028
G7	0.082 ± 0.022	0.047 ± 0.027
G8	0.106 ± 0.028	0.060 ± 0.024

Table II. Mean \pm standard deviation of inbreeding coefficients in females of the S and C lines.

the number of measured females and of raised males, as well as the number of randomly chosen parents and the realized selection differential, in each generation. In total, from G1 up to G8, 1045 males, 1747 females, and 839 males, 1492 females, in the S and C line respectively were controlled. In the S line, the selection was effective from G1. Over the seven generations of selection, the average percentage of selected females was 24.7% and the average percentage of selected males was 15%. The unintended selection differential which occurred in the C line was very small (-0.104) over the seven generations of selection and could be neglected. It should be pointed out that the animals of the S and C lines were born in the same hatches in all the generations, except in G2. In G1 some parents were used in the constitution of both the S and C lines; in G2, the animals of the S line were born on 02/10/1993 and on 03/09/1993, while the animals of the C line were born on 04/07/1993. Although the AIs were performed partly at the same period, this could lead to some inaccuracy in the measurement of selection response in G2.

3.2. Inbreeding coefficients

Table II shows the mean and standard deviation of inbreeding coefficients in females of the S and C lines, for each generation. The results for the males were similar. The founder animals were not supposed to be related nor inbred. So, the average inbreeding coefficient in G1 was 0. The same was found in G2, due to the mating plan, which was rotational in the C line and which avoided sib mating in the S line. Thereafter, it increased more quickly in the S line than in the C line, as could be expected, but it remained moderate, the mean in G8 being 0.106 and 0.060 in the S and C line respectively.

Dm

Η

inic from 62 up to 66.								
Generation	G2	G3	G4	G5	G6	G7	G8	
Ie	12.77	13.02	12.73	12.85	12.90	12.34	15.16	
	± 1.90	± 1.90	± 2.33	± 2.16	± 2.22	± 2.64	± 2.96	
F	3.67	4.56	4.37	4.19	4.30	3.18	4.39	
	± 1.78	± 1.81	± 1.82	± 1.78	± 1.77	± 1.63	± 1.77	
M	1.16	1.00	1.06	0.80	1.11	0.85	1.29	
	± 1.11	± 1.09	± 1.23	± 0.93	± 1.08	± 0.93	± 1.16	

5.63

 ± 2.15

3.30

 ± 1.78

5.36

 ± 2.12

3.39

 ± 1.82

5.48

 ± 2.02

3.18

 ± 1.67

4.38

 ± 1.98

2.33

 ± 1.54

5.59

 ± 2.12

3.10

 ± 1.80

Table III. The means and phenotypic standard deviations of the traits in the control line from G2 up to G8.

Ie = number of eggs set; F = number of fertile eggs at candling (7th day of incubation); M = number of total dead embryos; Dm = maximum duration of fertility; H = number of hatched mule ducklings.

3.3. Selection responses and predicted genetic responses

5.63

 ± 2.13

3.56

 ± 1.76

4.90

 ± 2.01

2.51

 ± 1.62

Table III shows the means and phenotypic standard deviations of the traits in the control line from G2 up to G8. Table IV shows the mean selection responses (and standard deviations) and predicted genetic responses (and standard errors) across the seven generations of selection, for the Ie, F, M, Dm, and H traits. Figure 1 shows the trends of selection responses and genetic predicted responses of F, M, H, and Dm. Both were similar, except that the former showed more fluctuations between the generations. The selection responses were highly significant for the selected trait and the correlated ones, except Ie. Selection responses became highly significant at G4 for F, Dm and H, but at G7 for M. At G8, the mean selection response and the mean predicted genetic response were very similar, being 2.61 and 2.52 respectively for F, 0.60 and 0.53 for M, 2.87 and 2.91 for Dm, 2.02 and 1.82 for H. These genetic increases were represented as a percentage of the average traits in G1: 61.7% for F, 32.6% for M, 51% for Dm, and 84.5% for H.

Table V shows the mean (and standard deviation) of fertility and hatchability rates for days 2–15 or days 2–8 after a single AI for the S and C lines in G8. The S and C lines were significantly different for the F/Ie, H/Ie frequencies for days 2–15 and 2–8 after AI. The hatchability rate calculated as the H/F ratio was significantly higher in the S line than in the C line for days 2–15 after AI, and it was also higher but statistically the same for days 2–8 after AI.

Table IV. Mean of the traits in G1, selection response mean \pm standard deviation (1st line), mean of predicted genetic responses \pm standard errors (2nd line) for the five traits.

Generation	G1	G2	G3	G4	G5	G6	G7	G8
Trait ¹	Mean							
Ie	11.83	0.70 ± 0.16	0.20 ± 0.20	0.20 ± 0.26	0.22 ± 0.28	0.17 ± 0.31	0.22 ± 0.33	0.36 ± 0.47
		0.10 ± 0.001	0.17 ± 0.010	0.18 ± 0.030	0.23 ± 0.050	0.28 ± 0.070	0.37 ± 0.090	0.51 ± 0.110
F	4.23	0.94 ± 0.21	0.50 ± 0.27	1.08 ± 0.32	1.40 ± 0.36	1.22 ± 0.41	1.91 ± 0.43	2.61 ± 0.50
		0.16 ± 0.010	0.56 ± 0.030	0.98 ± 0.050	1.30 ± 0.100	1.55 ± 0.140	1.99 ± 0.180	2.52 ± 0.210
M	1.84	0.04 ± 0.08	0.15 ± 0.09	0.15 ± 0.11	0.32 ± 0.11	0.40 ± 0.14	0.79 ± 0.13	0.60 ± 0.15
		0.04 ± 0.001	0.16 ± 0.002	0.25 ± 0.003	0.27 ± 0.007	0.34 ± 0.009	0.48 ± 0.012	0.53 ± 0.013
Dm	5.63	0.53 ± 0.22	0.51 ± 0.28	1.16 ± 0.34	1.56 ± 0.38	1.50 ± 0.43	2.10 ± 0.45	2.87 ± 0.50
		0.17 ± 0.010	0.67 ± 0.030	1.19 ± 0.060	1.52 ± 0.110	1.87 ± 0.150	2.40 ± 0.190	2.91 ± 0.220
Н	2.39	0.90 ± 0.17	0.35 ± 0.21	0.94 ± 0.25	1.08 ± 0.28	0.83 ± 0.31	1.12 ± 0.33	2.02 ± 0.36
		0.12 ± 0.005	0.37 ± 0.010	0.67 ± 0.030	0.97 ± 0.050	1.15 ± 0.070	1.38 ± 0.100	1.82 ± 0.110

¹ Ie = number of eggs set; F = number of fertile eggs at candling (7th day of incubation); M = number of total dead embryos; Dm = maximum duration of fertility; H = number of hatched mule ducklings.

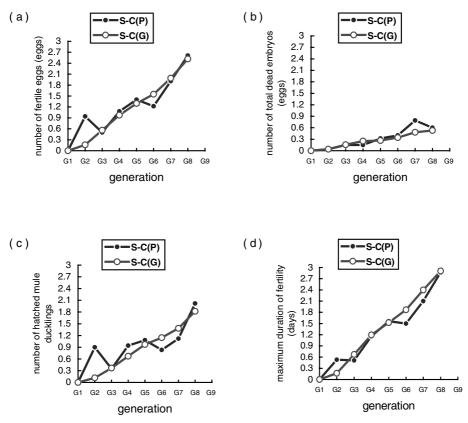


Figure 1. Differences in number of fertile eggs at candling (a), number of total dead embryos (b), number of hatched mule ducklings (c), maximum duration of fertility (d) between selected (S) and control (C) lines for the phenotypic [S-C(P)] and predicted genetic [S-C(G)] values across seven generations of selection.

Table V. Mean \pm standard deviation of fertility and hatchability rates for days 2–15 or days 2–8 after a single AI for S and C lines in G8.

	Days 2	Days 2–8 after AI						
Line	Fertility rate	Hatchability rates		Fertility rate Hatchability rates F		Fertility rate	Hatchabi	lity rates
	F/Ie%	Н/Іе%	H/F%	F/Ie%	Н/Іе%	H/F%		
S	54.40 ^a	39.74 ^a	73.04 ^a	89.18 ^a	64.67 a	72.52 ^a		
	± 0.58	± 0.57	± 0.70	± 0.51	± 0.79	± 0.78		
C	34.39 ^b	24.28 ^b	70.60 ^b	63.79 ^b	45.06 ^b	70.64^{a}		
	± 0.63	± 0.56	± 1.02	± 0.88	±0.91	±1.04		

Ie = number of eggs set; F = number of fertile eggs at candling (7th day of incubation); H = number of hatched mule ducklings.

Two different subscripts (a,b) in a column indicate significant differences (P < 0.05).

4. DISCUSSION

The length of the fertile period in birds depends on the sperm storage in the tubules at the utero-vaginal junction where the spermatozoa are released to be transported upwards towards the infundibulum for ova fertilization [4]. The purpose of this selection experiment was to show to what extent genetic progress could extend the fertile period of the Brown Tsaiya duck, and not to estimate the realized heritability of the selected trait. The selection was thus made with the BLUP of breeding values using an animal model. It is known that mixed model methodology has desirable properties, under certain conditions, when a selection model is involved, to adjust without bias for fixed effects, and to provide best linear unbiased predictors of random effects of the model [15]. Moreover, we expected that the accuracy of the prediction of breeding values could be improved by comparison with the conventional combined selection index. Although the economic target was to increase the number of mule ducklings born after a single AI, we decided to select for an increased F and to study the direct and correlated responses to that selection. Tai et al. [33] found a heritability value of 0.29, estimated from the sire variance component in 348 Brown Tsaiya female ducks for that trait. So it was expected to respond to selection. A control line is useful to adjust for environmental trends, under the assumption of no genotype by environment interaction, when measuring the selection response. The selection responses were calculated, as usual, by taking the differences across the generations of selection between the average phenotypic values of the S and C lines [11,22]. Sorensen and Kennedy [31] have shown that an alternative way of estimating response to selection is to use the mixed model approach, since the phenotypic trend can be partitioned into its genetic and environmental trend.

The results indicated that the measured selection responses and the calculated predicted genetic responses were similar. This could indicate the adequacy of the data representation model and the accuracy of the genetic parameter estimates in the base population. The genetic progress in F measured by the selection response was significant, being 2.77 genetic standard deviation or 39.6% of genetic standard deviation per generation. The correlated responses in Dm and H were also significant, being 2.93 and 2.88 genetic standard deviation respectively. The increase in M was smaller (2.33 genetic standard deviation) and the total embryo mortality rate was not increased by selection. These results are in contrast with those of chicken hens where the duration of the fertile period was correlated with an increased early embryo mortality [2]. They are consistent with the estimated genetic parameters showing high genetic correlations between F and Dm (0.92), H (0.91) and between Dm and H (0.82). According to these results and the fact that the heritability of F is greater than that of H (0.26 versus 0.19), the selection on F might be more effective in increasing H than the direct selection on that trait.

5. CONCLUSION

Selection was effective in increasing the number of ova that could be fertilized after a single AI with pooled Muscovy semen, and consequently the number of eggs able to develop a viable embryo. Such changes had major consequences in increasing the maximum duration of the fertile period, and the physiological effects need to be investigated. Correlatively, selection increased the fertility and hatchability rates according to the eggs set, especially for days 2-8 after AI, showing that selection for one AI per week was possible in this strain of laying ducks. There was not, as was thought in the fowl, an increased rate of embryonic death that could have impaired the benefits of selection. Thus, in the intergeneric crossbreeding of ducks, ova fertilization seems to be a key point. Nevertheless, the total mortality rate in relation to the number of fertile eggs was high (27 to 30%). So it would be useful to continue the selection experiment in order to the study long term effects on fertility and embryo viability. The present results might depend on the strain used (Brown Tsaiya), which is a laying duck. Nonetheless, they open the way to selecting for an extension of the fertile period in meat-type ducks such as the Pekin duck, since this breed is being used effectively as parents for commercial mule ducks. Within species selection was based on a hybrid performance and the number of fertile hybrid eggs was analyzed as a trait of the Brown Tsaiya duck. One might then ask if the response obtained here was not similar in nature from what we would have obtained as a correlated hybrid response from selecting simply within the Tsaiya breed for an increased number of fertile eggs after a single AI. Doing AI with pooled semen from Muscovy male would insure that variations due to the genetic interaction with Muscovy and additive genetic variation between Muscovy were kept at a minimum. This hypothesis seemed to be confirmed because observed selection response was in good agreement with the one expected from BLUP under an animal model. Yet, since the mean maximum duration of fertility was lower in the intergeneric crossbreeding than in the pure breeding lines, some mechanism involved in the fertilization process might be different, which remains to be clarified.

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