Prediction of Response and Inbreeding under Selection Based on Best Linear Unbiased Prediction in Closed Broiler Lines

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(Received March 31, 1999 ; Accepted June 16, 1999)

Abstract A theory for predicting the response and inbreeding under selection with best linear unbiased prediction (BLUP selection) was developed. The derivation was based on the combination of the approximation of BLUP selection by index selection (pseudo-BLUP) and the prediction theory of inbreeding under selection. The derived theory was checked by stochastic simulation. The structure of simulated population was attempted to resemble an actual closed broiler line. Based on the results, the effects on response and inbreeding when using BLUP or phenotypic selection were also examined. On the whole, the derived method gave a good prediction of selection response. Although the rate of inbreeding was seriously under-predicted when the heritability was low, the method was found to be applicable to the trait with moderate to high heritability. With the heritability 0.34, which was the estimation in the actual broiler line, alternation of selection method from phenotypic to BLUP selection was expected to increase the cumulative response over 10 generations by 10%, while producing threefold inbreeding. To use BLUP selection in this broiler line, optimization of selection programme in terms of the number of selected birds and the selection intensity should be required.

Animal Science Journal 70 (5) : 273-281, 1999

Key words : BLUP selection, Selection response, Inbreeding, Broiler breeding

Various selection methods are available to breeders for combining phenotypic records in estimating breeding values in poultry breeding programmes. Traditionally, breeding values have been estimated using selection indices with information from relatives^{9,11,12}. The theory of selection index has been developed to enable simultaneous prediction of an individual's breeding value and fixed effects, such as year and hatch effects, using information from all the available relatives. This is known as best linear unbiased prediction (BLUP) of breeding values with an animal model⁷.

Selection based on BLUP (BLUP selection) maximizes the response after one generation. However, since all genetic relationships are accounted for, more related animals are likely to be selected, leading to higher inbreeding rate and loss of genetic variance, as

verified by simulation studies^{1,13,17}. As mid- or long-term selection response is highly dependent on the rate of inbreeding^{14,16}, BLUP selection applied to mid- or long-term selection programmes may be less efficient than simple selection based on individual's phenotypic value (phenotypic selection).

Since breeding of poultry is typically carried out in closed lines with intense and repeated selection, implementation of BLUP selection should be carefully examined. The use of BLUP selection has been investigated by simulating layer poultry⁸ and by utilizing real broiler data¹⁰. Although more general and less computationally demanding methods are required for studying the optimization of breeding programmes, the problem of predicting inbreeding in selected populations has not been solved until recently. Now, accurate expressions for the rate of inbreeding

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under phenotypic^{15,19)} and index selection²²⁾ are available. A method for predicting rate of response to BLUP selection has been also proposed²⁰⁾.

In this paper, these methods are applied to prediction of the response and inbreeding under BLUP selection. The precisions of predicted values are checked in simulated broiler lines. The effects on response and rate of inbreeding when using BLUP or phenotypic selection are also examined in a typical broiler line.

Materials and Methods

Prediction theory

The trait under selection is assumed to be determined by an infinite number of additive loci, each with infinitesimal effect (the infinitesimal model²⁾). A population with discrete generations is supposed, in which N_m males are randomly mated with N_f females. The number of females mated with one male is an integer number of $d = N_f/N_m$. Subscripts s and u ($= m$ or f) are used to specify sex. Each female produces n_f progeny of each sex ($n = 2n_f$). Each male has $n_m = dn_f$ progeny of each sex. Among the progeny, the best N_m males and N_f females are selected on the basis of their predicted breeding values (PBVs) from BLUP with an animal model. The proportion selected for sex s is $p_s = 1/n_s$, and the selection intensity is $i_s = z_s/p_s$, where z_s is the normal ordinate corresponding to the truncation point of selection (x_s). The variance reduction factor due to Bulmer effect²⁾ is $k_s = i_s (i_s - x_s)$.

PBVs from BLUP were approximated by the pseudo-BLUP²⁰⁾. The selection index assumed in the pseudo-BLUP was

$$I = \beta_{1(t)} (P - \bar{P}_D) + \beta_{2(t)} (\bar{P}_D - \bar{P}_H - \hat{A}_f/2 + \hat{\bar{A}}_f/2) + \beta_{3(t)} (\bar{P}_H - \hat{A}_m/2 - \hat{\bar{A}}_f/2) + \beta_{4(t)} (\hat{A}_m/2 + \hat{A}_f/2), \quad (1)$$

where P is the individual's record, $\bar{P}_D$ is the mean of records of n (including the individual) full-sib records, $\bar{P}_H$ is the mean of nd (including the n full-sibs) half-sib records, $\hat{A}_m$ and $\hat{A}_f$ are PBVs of the sire and dam, respectively, and $\hat{\bar{A}}_f$ is the mean of PBVs of all dams mated to the sire. The selection index

weights were updated and optimized each generation with the algorithm given by Wray and Hill²⁰⁾. In most selection programmes of broiler, information from relatives are not available for the selection of the first generation, because relationships among individuals in the first generation are usually unknown. In our prediction, however, the pseudo-BLUP index was applied to the first selection to simplify the computational procedure.

The asymptotic genetic parameters, which are required for the prediction of asymptotic rate of inbreeding, were obtained in the following way. The total phenotypic variance at generation t is

$$\sigma_{P(t)}^2 = \sigma_{A(t)}^2 + \sigma_E^2,$$

where $\sigma_{A(t)}^2$ is the additive genetic variance, and σ_E^2 is the environmental variance. The additive genetic variance is further decomposed into between-sire family (σ_{Am}^2), between-dam family (σ_{Af}^2) and within-full-sib family (σ_{Aw}^2) components :

$$\sigma_{A(t)}^2 = \sigma_{Am(t)}^2 + \sigma_{Af(t)}^2 + \sigma_{Aw}^2.$$

Following Bulmer²⁾, these components are obtained from

$$\left. \begin{aligned} \sigma_{Am(t)}^2 &= \frac{1}{4} (1 - k_m r_{(t-1)}^2) \sigma_{A(t-1)}^2 \\ \sigma_{Af(t)}^2 &= \frac{1}{4} (1 - k_f r_{(t-1)}^2) \sigma_{A(t-1)}^2 \\ \sigma_{Aw}^2 &= \frac{1}{2} \sigma_{A(0)}^2 \end{aligned} \right\} \quad (2)$$

where $r_{(t-1)}$ is the accuracy of selection in generation $t - 1$. The accuracy of selection is computed as $r_{(t)} = \sigma_{I(t)}/\sigma_{A(t)}$, where $\sigma_{I(t)}$ is the standard deviation of the selection index (1). The genetic parameters are computed each generation by using recurrently equations (2). Preliminary analysis showed that all the genetic parameters reach essentially steady values after several generations. Thus, the value after 5 generations were used as the asymptotic values (asterisks will denote asymptotic values).

The asymptotic effective population size of sex s was

Table 1. Outline and results from REML analysis of an actual broiler line. The analyzed trait is weight (g) at 6 weeks

	Male	Female
Average number of selected birds per generation	40.4	283.4
Average number of scored birds per generation	1,377.4	1,350.1
Total number of birds with record	23,574	
Estimated additive genetic variance	11,648.4	
Estimated environmental variance	22,611.6	
Estimated heritability	0.34	

Data from 1989 to 1998 (in Hyogo National Livestock Breeding Center).

predicted by the equation of Santiago and Caballero¹⁵⁾

$$N_{es} = 4N_s \left[\frac{1}{\mu_{sm}} + \frac{1}{\mu_{sf}} + \frac{S_{sm}^2}{\mu_{sm}^2} + \frac{S_{sf}^2}{\mu_{sf}^2} + 4\rho_s^* i^2 + 4\rho_{as}^* i^2 (Q^2 - 1) \right] \quad (3)$$

where $\mu_{su} (= N_u/N_s)$ is the mean of offspring of sex u from parents of sex s , S_{su}^2 is the variance of offspring of sex u from parents of sex s in the absence of selection, ρ_s^* is the asymptotic intraclass correlation of families from parents of sex s , ρ_{as}^* is the component of ρ_s^* due to the breeding values of parents, $i [(i_m + i_f)/2]$ is the unweighted mean of selection intensities for the two sexes, and Q is the coefficient accounting for the cumulative effect of selection on the effective size. The correlations ρ_s^* and ρ_{as}^* were computed by extending the equations given by Wray *et al.*²²⁾. Following Santiago and Caballero¹⁵⁾, the variance of family size S_{su}^2 and the coefficient Q were approximated by

$$S_{su}^2 = \frac{N_u}{N_s} \left[1 - \frac{1}{n_s} \left(\frac{N_u}{N_s} \right) \right]$$

and

$$Q = \frac{2}{1 + 2kr^{*2}},$$

where r^* is the asymptotic accuracy of selection and $k = (k_m + k_f)/2$.

The asymptotic rate of inbreeding was obtained by

$$\Delta F = \frac{1}{8N_{em}} + \frac{1}{8N_{ef}}.$$

The inbreeding coefficient at generation t was predicted by using the formula of Wright²³⁾

$$F_t = F_{t-1} + \Delta F (1 - 2F_{t-1} + F_{t-2}).$$

In the calculation of the selection response, the reduction of the additive genetic variance due to inbreeding and selection was taken into account by using the equation suggested by Wray and Goddard²¹⁾,

$$\sigma_{A(t)}^2 = \frac{1}{4} \left[(1 - k_m r_{(t-1)}^2) + (1 - k_f r_{(t-1)}^2) \right] \sigma_{A(t-1)}^2 \times \frac{1 + F_{t-1} - 2F_t}{1 - F_{t-1}} + \frac{1}{2} \sigma_{A(0)}^2 (1 - F_{t-1}).$$

The response to selection in generation t was computed from $R_{(t)} = i r_{(t)} \sigma_{A(t)}$. Then the cumulative response over t generations was obtained by

$$CR_{(t)} = \sum_{j=1}^t R_{(j)} = \sum_{j=1}^t i r_{(j)} \sigma_{A(j)}.$$

Data analysis and simulation

To check the precision of predicted response and inbreeding, stochastic simulation was carried out. The structure of simulated population was attempted to resemble an actual broiler line (line 53), which was developed in Hyogo National Livestock Breeding Center. This line has been selected mainly on the weight at 6 weeks. The data from 1989 to 1998 was analyzed by the restricted maximum likelihood (REML) procedure. The results are summarized in Table 1.

Table 2. Simulated selection schemes

Scheme	N_m	N_f	n_f
A	40	280	5
B	70	280	5
C	40	280	3

N_m =number of male parents.

N_f =number of female parents.

n_f =number of scored progeny of each sex from a female parent.

Three selection schemes were considered (Table 2). Scheme A has the same structure as the actual line. In scheme B, the number of sire was increased to 70, giving a lower selection intensity for males than scheme A. Scheme C has the same numbers of parents as scheme A, but the number of tested progeny is reduced. In each scheme, the initial additive genetic variance ($\sigma_{A(0)}^2$) and the environmental variance (σ_E^2) were set to the estimated values 11,648.4 and 22,611.6 (Table 1), respectively, giving the initial heritability $h_0^2=0.34$. Additional runs with $h_0^2=0.1$ and 0.6 were also carried out for each scheme, where the environmental variances were chosen to be 104,835.6 and 7,765.6, respectively.

In the simulated population, breeding values of candidates for the initial selection were randomly sampled from an $N(0, \sigma_{A(0)}^2)$ distribution. Based on the infinitesimal model of gene effect²⁾, the breeding value (A_i) of an individual in the following generation was generated as

$$A_i = \frac{A_m + A_f}{2} + \phi_i \sqrt{\frac{1}{2} \sigma_{A(0)}^2 \left(1 - \frac{F_m + F_f}{2}\right)},$$

where A_m and A_f are the breeding values of the sire and dam, respectively, F_m and F_f are the inbreeding coefficients of the sire and dam, respectively, and ϕ_i is a random number taken from an $N(0, 1)$ distribution. The phenotypic value (P_i) was obtained as

$$P_i = A_i + \phi_i \sigma_E,$$

where ϕ_i is a random number taken from an $N(0, 1)$ distribution.

Fig. 1. Simulated and predicted cumulative selection responses under BLUP (B) and phenotypic (P) selection for scheme A. h_0^2 =initial heritability.

The number of simulated generations were 10 and the number of replicated runs were 100. Selection was based on BLUP with an animal model. For comparison, simple phenotypic selection was also simulated. The predictions for phenotypic selection were made by putting $\beta_{1(t)} = \beta_{2(t)} = \beta_{3(t)} = \beta_{4(t)} = h^2$ in equation (1).

Results

Response to selection

Figure 1 shows the simulated and predicted cumulative selection responses for scheme A. In the simulation, a consistent advantage of BLUP selection was observed. The superiority of BLUP selection was larger for lower heritability, agreeing with the previous simulation studies^{1,8)}. The increases of cumulative response over 10 generations of BLUP selection, relative to phenotypic selection, were 41.7, 10.8 and 2.5%, for $h_0^2=0.1$, 0.34 and 0.6, respectively. The predicted cumulative responses were, on the whole, in good agreements with the simulated values, though slight over-predictions were observed under BLUP selection. The relative discrepancies of the prediction of cumulative response over 10 generations of BLUP selection were 5.1, 2.1 and 0.6% for $h_0^2=0.1$, 0.34 and 0.6, respectively, while the corresponding values under phenotypic selection were 1.2, 1.1 and

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Table 3. Simulated (sim) and predicted (pre) genetic gains at each generation under phenotypic and BLUP selection

Scheme ^{a)}	h_0^2	Selection		Generation				
				2	3	4	5	6-10 ^{b)}
A	0.1	Phenotypic	sim	63.0	59.4	58.0	57.7	56.6
			pre	62.8	60.4	59.1	58.4	57.4
		BLUP	sim	63.0	98.1	89.8	86.2	80.4
			pre	110.0	92.1	85.9	84.3	80.9
	0.34	Phenotypic	sim	117.0	100.3	97.0	94.4	93.4
			pre	115.8	102.1	97.8	96.3	94.6
		BLUP	sim	117.0	119.6	108.0	106.3	103.8
			pre	144.7	113.0	107.7	106.6	103.8
	0.6	Phenotypic	sim	154.5	124.1	119.6	118.9	116.9
			pre	153.8	125.6	120.2	118.8	117.4
		BLUP	sim	154.5	130.6	124.0	122.3	119.5
			pre	165.5	127.4	122.7	121.7	119.7
B	0.1	Phenotypic	sim	58.7	56.3	55.6	54.4	53.2
			pre	59.1	56.8	55.7	55.1	54.4
		BLUP	sim	58.8	91.4	84.6	79.2	75.9
			pre	100.3	84.5	79.6	78.4	76.5
	0.34	Phenotypic	sim	109.0	94.9	90.9	90.4	89.0
			pre	108.8	96.0	92.1	90.8	89.7
		BLUP	sim	109.0	113.7	102.4	101.3	98.2
			pre	135.3	106.0	101.4	100.6	99.0
	0.6	Phenotypic	sim	144.8	116.7	112.3	111.8	110.9
			pre	144.6	118.2	113.2	112.1	111.1
		BLUP	sim	144.8	123.5	115.8	115.5	113.5
			pre	155.4	119.9	115.6	114.9	113.7
C	0.1	Phenotypic	sim	55.4	52.2	51.3	50.3	49.5
			pre	54.1	52.0	51.0	50.4	49.6
		BLUP	sim	55.4	79.3	72.3	70.8	67.9
			pre	88.3	76.0	71.4	70.0	67.7
	0.34	Phenotypic	sim	100.0	88.2	85.0	84.8	82.0
			pre	99.7	88.4	84.8	83.5	82.2
		BLUP	sim	100.0	104.9	93.0	91.7	89.9
			pre	122.1	97.5	92.7	91.7	89.7
	0.6	Phenotypic	sim	133.0	107.9	104.7	102.9	101.9
			pre	132.4	109.3	104.5	103.3	102.1
		BLUP	sim	133.0	113.7	107.3	106.5	104.1
			pre	141.8	111.0	106.6	105.7	104.1

^{a)} See Table 2.

^{b)} Average between 6 and 10 generations.

h_0^2 =initial heritability.

Fig. 2. Simulated and predicted inbreeding coefficients under BLUP (B) and phenotypic (P) selection for scheme A.
 h_0^2 = initial heritability.

0.3%, respectively.

Table 3 compares the simulated and predicted genetic gains at each generation for the three schemes. Under phenotypic selection, the presented method gave a good prediction over all stages of generation, irrespective of the selection scheme and the initial heritability. Under BLUP selection, the genetic gain in the first generation was seriously over-predicted. However, the amount of the over-prediction was reduced by the accumulation of information from relatives with the advance of generation, and the relative discrepancy of the prediction after generation 6 was smaller than 1%. The over-prediction of cumulative response over 10 generations of BLUP selection (Fig. 1) resulted mainly from the over-prediction of genetic gain in the first generation.

Inbreeding

The simulated and predicted inbreeding coefficients for scheme A are shown in Fig. 2. In the simulation, the inbreeding coefficient under BLUP selection was much higher than under phenotypic selection, especially when the selected trait had lower heritability. In contrast to phenotypic selection, where the inbreeding tended to be reduced as the heritability became low, the inbreeding under BLUP selection increased with a decrease of heritability. Although the presented method could predict this behaviour of in-

breeding at least qualitatively, the inbreeding under BLUP selection with the low heritability was under-predicted. The relative discrepancies of prediction in generation 10 under BLUP selection were -22.0, -4.2 and 2.0%, respectively, while the corresponding values under phenotypic selection were 2.9, 3.6 and -2.9%, respectively.

Table 4 gives the simulated rate of inbreeding at each generation and the predicted asymptotic rate of inbreeding. In all the cases studied, the predicted asymptotic rate was larger than the simulated rate in generation 3 (when the first inbred birds appeared), because the inbreeding in generation 3 was caused only by matings between full- or half-sibs. However, after generation 5, the asymptotic rate gave a good prediction, except for BLUP selection with the low heritability, where the rate of inbreeding was seriously under-predicted.

Discussion

The first objective of the present study was to develop a theory for predicting the response and inbreeding under BLUP selection, which is applicable to breeding of broiler lines. The derivation of prediction theory was based on the combination of the pseudo-BLUP²⁰⁾ and the equation for predicting the inbreeding under selection¹⁵⁾. For the response to selection, the derived method gave a good prediction, except for the initial generation of BLUP selection, where the responses were over-predicted. In our simulation, candidate birds for selection in the first generation are not related, so that BLUP selection is expected to give the selection response equivalent to phenotypic selection, as verified in Table 3. In the pseudo-BLUP index (equation 1), however, information from sibs and parents are used for the prediction of first response. This is the reason for the over-prediction of response in the first generation of BLUP selection. The quality of prediction may be simply improved by predicting the first response with phenotypic selection and switching to the prediction with the pseudo-BLUP after the second generation.

The inbreeding under BLUP selection was seriously inflated, particularly for a lower heritability (Fig. 1 and Table 3). This is because for a trait with low

Table 4. Simulated rates of inbreeding at generation t (ΔF_t) and the predicted asymptotic rates (pre) of inbreeding under phenotypic and BLUP selection

Scheme ^{a)}	h_0^2	Selection	Simulated ΔF_t ($\times 100$)				pre ($\times 100$)
			$t=3$	4	5	6-10 ^{b)}	
A	0.1	Phenotypic	0.39	0.43	0.46	0.45	0.46
		BLUP	1.45	2.67	2.68	2.83	2.00
	0.34	Phenotypic	0.45	0.54	0.53	0.56	0.56
		BLUP	1.08	1.64	1.54	1.50	1.43
	0.6	Phenotypic	0.45	0.53	0.63	0.60	0.56
		BLUP	0.80	1.05	0.93	0.90	0.93
B	0.1	Phenotypic	0.25	0.24	0.29	0.28	0.28
		BLUP	0.90	1.77	1.92	1.74	1.10
	0.34	Phenotypic	0.29	0.31	0.36	0.36	0.35
		BLUP	0.70	1.01	0.98	0.99	0.84
	0.6	Phenotypic	0.29	0.34	0.41	0.39	0.35
		BLUP	0.51	0.66	0.66	0.61	0.57
C	0.1	Phenotypic	0.36	0.43	0.39	0.42	0.42
		BLUP	0.95	1.80	1.87	1.91	1.48
	0.34	Phenotypic	0.42	0.50	0.49	0.51	0.51
		BLUP	0.79	1.17	1.07	1.15	1.12
	0.6	Phenotypic	0.44	0.53	0.56	0.53	0.51
		BLUP	0.66	0.77	0.78	0.77	0.78

^{a)} See Table 2.

^{b)} Average between 6 and 10 generations.

h_0^2 = initial heritability.

heritability, BLUP places larger weights on family information and, then, the probability of co-selection of close relatives increases. The presented method can describe this behaviour of inbreeding, but seriously under-predicts the observed inbreeding. There are two major sources of the discrepancy between the simulated and predicted inbreeding under BLUP selection with a low heritability. First, in the prediction equation of effective population size (equation 3), the distribution of family size was approximated by a binomial sampling process¹⁵⁾. But for BLUP selection, a low heritability would imply mostly selection on the best families. Then, in this situation, whole families tend to be either selected or rejected, inducing a serious error in the approximation of family size distribution. Second, in the pseudo-BLUP index (equation 1), the information from relatives are limit-

ed to sibs and parents, while all available information are used in the actual calculation of BLUP. The neglect of information in the pseudo-BLUP may under-predict the concentration of genetic contributions on superior ancestors. This would be specially important in the advanced generations for a low heritability. Contrary to the serious error in the prediction of inbreeding, the error in the prediction of response to BLUP selection with a low heritability was relatively small, except for the response to the first selection. This may suggest that the response to selection is less sensitive for the two sources of error in the prediction of inbreeding. To verify this view, the prediction theory involving the correction for the two sources of error should be developed. Although there are theoretical interests in the development of the prediction theory, selection for a low heritable trait is not the

case of practical broiler breeding, where most of the selected traits such as growth rate and body weight have generally moderate to high heritabilities⁴⁻⁶⁾. The presented method may not be likely to result in a serious error in the prediction for these traits.

The second objective of the present study was to evaluate the effects of BLUP selection in a typical broiler line. In practice of broiler breeding in Japan, phenotypic selection has been carried out. The results for $h_o^2=0.34$ in Fig. 1 show that about 10% of increase is expected in the cumulative selection response by switching to BLUP selection but remaining other conditions unchanged. Implementation of BLUP selection may have additional benefits by automatically monitoring genetic trends and inbreeding. However, as seen from the results in Fig. 2, BLUP selection produces about threefold inbreeding compared to phenotypic selection. It has been generally recommended that the rate of inbreeding in broiler lines should be kept at the level lower than 1%¹⁰⁾. Both the simulated and predicted rates of inbreeding are beyond this critical value (Table 4).

In recent years, different methods have been proposed to reduce rates of inbreeding in selection programmes while keeping genetic gains at the same level (for a review, see Caballero *et al.*³⁾). In addition to these methods, finding the optimum numbers of individuals to be selected for giving maximum gains will be important when designing selection programmes. For example, Villanueva *et al.*¹⁸⁾ have described a procedure for obtaining the optimum numbers of sires and dams for maximizing genetic gain over a specified time period when specific constraints on the rate of inbreeding are imposed. Application of the theory presented in this study to the optimization of broiler breeding will be considered in succeeding reports.

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