A Comparison of Actual and Expected Selection Responses from Selection Indices for Desired Gains in Layer Chicken Lines

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(Received May 27, 1996)

Abstract In Okazaki station of National Livestock Improvement Center, selection index for desired gains based on the assumed parameters has been used to improve layer chicken. The same indices were applied on three lines from 1989 to 1994. Pre-specified restrictions as objective were no change on egg weight at 252 days of age (EW) and body weight at 256 days of age (BW), 5% increase of egg production efficiency from first egg to 280 days of age in all lines, and more five days reduction of age at first egg (SM) was aimed in one line. The EW, BW, SM and egg production efficiency between 169-280 days were included in the index as selection criteria. In this study, expected theoretical responses from the index were compared with actual responses obtained by the regression of average predicted breeding values by birth year multiplied by number of generation selected. Breeding values of five traits were predicted with multiple-trait BLUP under animal models using (co) variances estimated with REML. Directions of the actual responses for the traits except BW agreed well with those of expected theoretical responses in all lines. Disagreement found in BW was caused by the difference between assumed genetic correlations and REML ones. The amount of responses was less than theoretically expected and differed across lines reflecting the discrepancy between genetic parameters assumed and REML estimates in each line. The results indicate that more reliable genetic parameters for a line under question, the so-called REML estimates, should be used in order to attain pre-specified objectives.

Anim. Sci. Technol. (Jpn.) 67 (11) : 941-948, 1996

Key words : Desired gain index, Breeding objective, Selection responses, Breeding value, Layer lines

In animal breeding, multiple traits are often aimed to be improvement. Since Hazel²⁾ has proposed the selection index method for use in animal populations in 1943, various types of selection indices have been developed towards the achievement of different objectives^{4-6, 8, 10, 15, 16)}. Generally, for constructing the

index, economic weights are required on the objective traits. However, in practice, their estimation may be difficult because they fluctuate depending on demand and genetic level of a population. On the other hand, selection index for desired gains by Yamada *et al.*¹⁶⁾, proposed as the index with restriction for pre-

determined genetic changes in individual traits, requires no economic weights. In Okazaki station of the National Livestock Improvement Center, the desired gain index has been used to improve layer chicken lines for the last decade. However there is no reports on efficiency of the desired gain index because of some difficulties assessing genetic trends for the traits in practical layer selection without control line. A recent development of Best Linear Unbiased Prediction (BLUP)³⁾ under an animal model makes it possible to trace the genetic and environmental changes due to selection without control line¹³⁾. In addition, genetic parameters used for constructing the index in Okazaki station were referred from literature. A discrepancy of assumed parameters from true ones for a line under question must decrease selection response expected by the index.

The objective of this study was to predict genetic trends with BLUP under multiple-trait animal model using genetic parameters estimated with Restricted Maximum Likelihood (REML)⁹⁾ procedure in each layer line and compare them with expected selection responses from the desired gain index derived by genetic parameters assumed at the station.

Materials and Methods

Data from National Livestock Improvement Center, Okazaki station were used in this study. They consisted of White Leghorn line (E1), recessive White Rock line (L17) and Rhode Island Red line (Y8) which were selected between 1989 and 1994. The traits measured were egg weight at 252 days of age (EW, g), body weight at 256 days of age (BW, kg), age at first egg (SM, days), and egg production efficiencies A (EPA, %) and B (EPB, %) recorded between 169–280 days and from first egg to 280 days, respectively. Basic statistics for the traits were reported by Danbaro *et al.*¹⁾.

Number of fully pedigreed chickens with records, effective population size, selected fractions and standardized selection differential for females in three lines are shown in Table 1. Selection for females was on an index for desired gains. Desired gains (*q*) to each line are given in Table 5. In all lines, no genetic changes on BW and EW, no weight on EPA, and 5% increase of EPB were pre-determined as restriction. A reduction of five days in SM was aimed only in Y8. Selection was continued for five generations. Selected fractions fluctuated from generation to generation with average of 26% to 19%, corresponding to the

Table 1. Number of chickens with records (No.), effective population size (N_e)^a, selected fraction (*p*) and standardized selection intensity (*i*)^b in layer lines

Year	Line E1				Line L17				Line Y8			
	No.	N_e	<i>p</i> (%)	<i>i</i>	No.	N_e	<i>p</i> (%)	<i>i</i>	No.	N_e	<i>p</i> (%)	<i>i</i>
1989	405	43	21	0.69	421	42	5	-0.30	318	34	33	0.09
1990	405	75	31	0.57	431	65	3	0.20	354	67	27	0.70
1991	564	76	24	0.55	466	104	41	0.39	632	63	20	0.59
1992	373	96	37	0.57	907	98	15	0.51	329	93	31	0.54
1993	628	96	19	0.66	618	140	27	0.48	742	117	21	0.64
1994	465	—	—	—	592	—	—	—	620	—	—	—
Mean	473	71*	26	0.61*	573	73*	19	0.26*	499	66*	25	0.51*

^a $N_e = 4 N_m N_f / (N_m + N_f)$, N_m : Number of sires, N_f : Number of dams.

^b Calculating by standardized selection difference between average index scores of selected and all chickens.

* Harmonic mean.

intensity of 1.25 to 1.43. The average standardized selection intensities measured from the index score differentials in females were considerably less than those expected from selected fractions since for practical reasons the color and quality of shell were also considered in final selection in addition to the loss due to diseases and inevitable accidents. For replacement males, two males were chosen from each selected full-sib family and one male was finally selected based on phenotype related to physical soundness. However numbers of candidate families and of males in each family were not clear. Therefore exact selection intensity on the score was unknown. One sire was mated with between 5 and 8 dams with full attention to the avoidance of inbreeding.

REML gives more reliable estimates of variance and covariance components in the base population if all records used in selection and pedigree information from the start of selection are available¹⁴. In this study, variance and covariance components were cited from a paper by Danbaro *et al.*¹ in which the multiple-trait REML under animal models was applied on each selected line.

Breeding values of the traits were predicted with BLUP under multiple-trait animal models³. In the linear mixed models, year and

house were considered as fixed effects, and inbreeding coefficient of individual was included as a covariate. Random effects were animals (breeding values) and residuals. Genetic changes, namely trends, were expressed as regression coefficients of average predicted breeding values (PBV) by birth year on generation.

The desired gain indices actually used in the station (I_A) were derived from an usual simple manner¹⁶ as $\mathbf{b}_A = \mathbf{G}_A^{-1}\mathbf{q}$, based on assumed genetic parameters given in Tables 2 and 3. To accomplish objective $\mathbf{q}$, EW, BW, SM and EPA were used as selection criteria. Another indices (I_R) were examined by using REML estimates; $\mathbf{b}_R = \mathbf{G}_R^{-1}\mathbf{q}$. The $\mathbf{b}_A$ and $\mathbf{b}_R$ stand for weighting coefficient vectors of the indices, and $\mathbf{G}_A$ and $\mathbf{G}_R$ for genetic variance and covariance matrices between the traits of selection criteria and objective where subscripts A and R represent $\mathbf{b}$ and $\mathbf{G}$ are derived from assumed parameters in the station and REML estimates, respectively.

It must be noticed that $\mathbf{q}$ expresses the gains attained after σ_{I_A}/i_A generations only when parameters used are true and selection succeeds according to plan. The σ_{I_A} stands for standard deviation of I_A and i_A for the actual selection intensity calculated by selection differential of the index scores (Table 1). However actual

Table 2. Comparison of heritabilities, and genetic and residual variance components between assumed at the station and estimated by REML

Traits	Heritabilities				Genetic variances				Residual variances			
	Assumed	REML			Assumed	REML			Assumed	REML		
		E 1	L 17	Y 8		E 1	L 17	Y 8		E 1	L 17	Y 8
EW(g)	0.50	0.51	0.53	0.59	8.00	8.58	8.88	10.98	8.00	8.24	7.74	7.60
BW(kg)	0.50	0.56	0.51	0.52	0.013	0.010	0.016	0.017	0.013	0.008	0.015	0.015
SM(days)	0.40	0.45	0.41	0.35	67.60	68.86	59.19	94.75	101.40	83.15	84.41	174.80
EPA(%)	0.15	0.13	0.19	0.15	25.35	11.70	13.49	18.24	143.65	74.42	58.79	103.80
EPB(%)	0.10	0.20	0.22	0.27	10.00	18.49	16.62	38.04	90.00	75.15	59.78	103.22

EW=Egg weight measured at 252 days, BW=Body weight at 256 days, SM=Age at first egg.

EPA=Egg production efficiency recorded between 169-280 days, EPB=Egg production efficiency recorded from first egg to 280 days.

and expected responses may deviate from $\mathbf{q}$ due to the bias of genetic parameters and selection process from intended ones. Selection responses in five traits were examined as following methods. Expected responses ($\mathbf{g}_e$) based on $\mathbf{I}_A$ were estimated as $\mathbf{g}_e = \mathbf{G}_R \mathbf{b}_A$. The $\mathbf{g}_e$ is correlated response, which may be expected after σ_{I_A}/i_A generations if selection pressure based on $\mathbf{I}_A$ acts on the variance and covariance structure estimated by REML in the ideal condition, because $\mathbf{G}_R$ reflects the real genetic structure of the base in each line well rather than $\mathbf{G}_A$. The actual responses obtained from index selection ($\mathbf{g}_a$) were calculated by regression coefficients of average PBV on generation multiplied by number of generations selected (NG=5). Theoretical responses ($\mathbf{g}_t$) were estimated as follows; $\mathbf{g}_t = \mathbf{g}_e \times \frac{\text{NG}}{\sqrt{\mathbf{b}'_A \mathbf{P}_R \mathbf{b}_A / i_A}}$ in

which $\mathbf{P}_R$ stands for phenotypic variance and covariance matrix by REML. The $\mathbf{g}_t$ means the response expected under the actual selection intensity within five generation in the planned condition.

Results and Discussion

Assumed heritabilities of EW, BW, SM and EPA did not differ largely from those by REML, although assumed heritabilities of EPB were relatively smaller than those by REML, considering their sizes as given in Table 2. On the other hand, large differences between variance components were found. Especially both genetic and residual components in EPA were assumed larger than those by REML. The over assumption may result in smaller responses in EPA and other correlated traits than expected.

As the genetic correlations shown in Table 3, different correlations (-0.15 vs. -0.6) were assumed between EW and egg production efficiencies (EPA and EPB). However, for REML estimates, large difference was not found within each line, but considerable differences existed across lines. Also no genetic relationships were assumed between BW and EPA or EPB, but low correlations were suggested. Degree of discrepancy was depending on the combination of the traits and lines. Especially, large differences were found

Table 3. Comparison of genetic correlations between assumed at the station and estimated by REML

Combination of traits	Assumed	REML		
		E 1	L 17	Y 8
EW :				
BW	0.30	0.33	0.28	0.30
SM	0.10	0.13	0.03	0.50
EPA	-0.15	-0.31	-0.16	-0.46
EPB	-0.60	-0.18	-0.13	-0.52
BW :				
SM	0.10	-0.01	0.06	0.35
EPA	0.00	-0.05	-0.15	-0.15
EPB	0.00	0.04	-0.10	0.10
SM :				
EPA	-0.30	-0.47	-0.23	-0.81
EPB	-0.50	-0.70	-0.33	-0.80
EPA :				
EPB	0.85	0.80	0.89	0.93

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in genetic correlations between SM and egg production efficiencies in Y 8.

The weighting coefficients, $\mathbf{b}_A$ and $\mathbf{b}_R$ of desired gain indices derived from two parameter sets are shown in Table 4. The discrepancy may affect correlated selection responses not only in amount but also in direction, as compared with pre-specified objective because the index scores of individuals and their ranking must change according to the weighting coefficients. The coefficients of BW in L17 and of SM in Y8 have reverse signs, when comparing both indices. Therefore the actual indices would result in more decrease changes in BW in L17 and SM in Y8 rather than pre-specified. The index I_R in L17 derived from REML estimates indicates that in order to maintain BW constant, chickens with heavier BW must be scored somewhat higher, provided that REML estimates reflect well the genetic variance and covariance structure of the base in L17. However, I_A used in the station has small but negative weight on BW so that negative pressure acts on BW and as a result, chickens with smaller BW would be selected for. Therefore, the discrepancy of weighting coefficients on BW must result in decrease change regardless of restriction to no genetic change. The same phenomena will be expected to happen in SM of Y8.

A comparison of some kinds of selection responses is shown in Table 5. In lines E1 and L17 the same breeding objectives ($\mathbf{q}$) were pre-specified. However, the $\mathbf{q}$ and $\mathbf{g}_e$ in two lines

differed each other according to the difference between $\mathbf{G}_A$ and $\mathbf{G}_R$ in both lines. Increasing trend in EPA and decreasing trend in SM due to selection on I_A at the center were favorable in practical layer breeding and rational because no restriction on SM and EPA as objectives. Large amount of expected decrease in BW, especially in L17, was caused by the discrepancy between weighting coefficients of I_A and I_R . As the actual responses ($\mathbf{g}_a$), genetic trends of the traits except EW in E1 and EW and SM in L17 showed significant changes ($P < 0.05$). From a qualitative view point, these trends except BW are consistent with the objective and theoretical responses ($\mathbf{g}_t$). The amount of responses obtained in EPA and EPB in L17 was comparable with those of theoretical ones, but not enough in E1.

In line Y8, the index for reduction of five days in SM may change EW and BW downward rather than expected, because positive large correlations of SM with EW and BW were existed in addition to negative large correlation between EW and EPA. All actual responses except EW were consistent in direction with theoretical responses. However, responses attained in SM and EPB were about one half of theoretical ones. Change of BW was not significant but somewhat large. This change may be explained in part by the existence of genetic correlation of 0.35 between SM and BW.

In all lines, selection responses attained in the station except those of body weight were

Table 4. Comparison of weighting coefficients of selection indices for desired gains derived from assumed parameters and REML estimates

Line	Parameters (Index)	EW	BW	SM	EPA
E1	Assumed (I_A)	0.1227	-0.0009	—	0.4181
	REML (I_R)	0.1814	-0.0010	—	0.4632
L17	Assumed (I_A)	0.1227	-0.0009	—	0.4181
	REML (I_R)	0.0575	0.0012	—	0.3731
Y8	Assumed (I_A)	0.1227	-0.0009	-0.0001	0.4180
	REML (I_R)	0.1424	-0.0008	0.0528	0.3535

Table 5. Comparison of actual and expected selection responses for the traits in layer lines

Lines/Traits	Objective (q)	Expected (g_e)	Actual (g_a)	Theoretical (g_t)
E 1				
EW(g)	0.0	-0.355	-0.002	-0.276
BW(g)	0.0	-4.272	-12.015*	-3.328
SM(days)	—	-5.121	-1.917*	-3.990
EPA(%)	—	4.519	0.665*	3.521
EPB(%)	5.0	4.604	0.952*	3.587
L 17				
EW(g)	0.0	0.274	-0.112	0.099
BW(g)	0.0	-29.899	-32.079*	-10.817
SM(days)	—	-2.640	0.412	-0.955
EPA(%)	—	5.494	2.519*	1.988
EPB(%)	5.0	5.632	1.806*	2.038
Y 8				
EW(g)	0.0	-1.519	0.125	-0.848
BW(g)	0.0	-33.486	-10.637	-18.698
SM(days)	-5.0	-12.583	-3.107*	-7.026
EPA(%)	—	6.895	1.825*	3.850
EPB(%)	5.0	8.752	1.760*	4.887

See the text for meanings of q , g_e , g_a , and g_t .

* $P < 0.05$.

consistent in direction with the objective. However, the amount of responses was less than theoretically expected and varied across lines because the degree of discrepancy in genetic parameters depended on lines. In this study, although assumed heritabilities agreed with REML estimates to a certain degree, but genetic and residual variance components were considerably different each other, especially in egg production efficiency. In addition, the disagreement found in genetic correlations affected on selection responses unfavorably not only in direction but also in amount. Of course, other important causes cannot be disregarded. For example, although the genetic variance and covariance structure is assumed to be kept constant, which means the same index can be applied during selection, genetic variances and covariances would change due to selection so that the optimum weighting coefficients of the index may change

inevitably^{7,12}. It may affect adversely on the amount of responses attained. It is not clear how the deviation of changes found in one or more objective traits from pre-specified affects on an achievement of the other objective traits.

These results indicate that in order to attain pre-specified breeding objective more reliable variance and covariance estimates for a line under question should be used for constructing the index. In poultry breeding, analysis of variance under hierarchical family structure has been used to estimate variance components, however REML under an animal model has good properties in estimation and nowadays can be easily applied on such a very large mixed model equations constructed in poultry population. It is well known, however, that reliability of REML estimates depends on data structure of a given population and possible analytical model applied. Especially, in REML, pedigree information is essential so

that REML is applicable at least after second generation. Robertson¹¹⁾ suggested that selecting 50% resulted in a maximum total response but not rate of progress. Accordingly, at the beginning of selection, in case of no reliable genetic parameters the selection should not be intense. Further study is necessary to evaluate the effect of discrepancy of estimated parameters from true on selection responses attained by selection index for desired gains.

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卵用鶏における改良目標に基づく選抜指数式による実現ならびに 期待選抜反応の比較

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家畜改良センター岡崎牧場において改良量に基づく選抜指数式により 1989 年から 1994 年にかけて選抜が実施されてきた卵用鶏 3 系統を用いて, 期待される選抜反応と実際に達成された選抜反応との比較検討を行った. 3 系統とも, 252 日齢での卵重 (EW) と 256 日齢の体重 (BW) を変化させず, 初産から 280 日齢までの産卵率 (EPB) を 5% 上昇させ, さらに 1 系統では初産日齢 (SM) を 5 日短縮する改良目標が設定された. 選抜指標としては, EW, BW, SM および 169 日齢から 280 日齢の産卵率 (EPA) が用いられた. 選抜指数式の作成には 3 系統ともに同一の遺伝的パラメーターが仮定され, 同一の指数により 5 世代にわたる選抜が実施された. 達成された選抜反応は, 多形質 REML 法により推定した遺伝的パラメーターをもとに, 多形質アニマルモデル BLUP 法を用いて育種価を予測し, 生年ごとの育種価予測値平均の世代への回帰係数より算出した. 3 系統ともに, BW を除き, 選抜反応の方向は設定した改良目標と一致していた. しかし, 体重の選抜反応は 2 系統では有意な減少傾向を示し, これは BW と EPA あるいは EPB 間には遺伝的関連がないと仮定した指数を用いているのに対して, REML では小さいながらも負の遺伝相関が存在したことに起因すると考えられた. EPB の改良量に関しては, 仮定したパラメーターと各系統の REML 推定値の差異を反映して, ほぼ理論値に一致する系統から 30% 程度の系統までと異なる反応量を示した. したがって, REML 法による各系統固有の遺伝的パラメーター推定値を用いた選抜指数式による選抜が改良の方向性や改良量に関して確実な効果をもたらすものと考えられた.

日畜会報, 67 (11): 941-948, 1996