Lag of Oviposition Time and Genetic Improvement of Egg Production by Selection Index Method

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Summary

This study aims to use the lag of oviposition time as an additional information in the selection index for further improvement of egg production. The traits used to construct selection indices were partial egg number produced to 150 days of egg production (PEN), annual egg number (AEN), egg weight (EW) and lag of oviposition time (LAG). Four index equations were constructed using different information from individual, full-, half-sibs and dam. Selection objectives were single trait selections for AEN or LAG and multi-trait selection for AEN, EW and LAG predicted by Hazel (1943) (H-index) and Kempthorne and Nordskog (1959) (R-index). Changes in genetic and phenotypic (co) variances of the traits due to selection were calculated by the method of Itoh (1991) and Stranden *et al.* (1993) .

Single trait selection for reduction of LAG is not ideal for improvements of egg number and egg weight indicated by lower increase in annual egg number and higher decrease in egg weight. Single trait selection for AEN gains higher response in egg number but decrease in egg weight, resulting to total genetic merit obtained from this selection objective is not the highest value.

Key words : oviposition time, egg production, selecction index, laying hen

Introduction

Genetic improvement in egg production has been extensively studied since the discovery of quantitative genetics. Breeding values are therefore accurately predicted, and genetic progress in egg production is dramatically increased. The use of conventional traits in selection for improvement of egg production has urged to what is regarded as physiological limit by one egg per day. Breeders have no choices to range birds for selection because of small variation between birds. However, the improvement of egg number is always desired by egg producers to make higher profit of egg production.

For further improvement of egg production several alternative methods have been suggested as follows : 1) Prolong the recording period of

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egg production. This will increase generation interval, consequently genetic progress will be lag behind. 2) Select the birds on the basis of persistency of lay, especially after peak of egg production, predicted by a mathematical model. This is plausible, but the appropriate mathematical model is still lacking for genetic evaluation of this character for individual hens (Miyoshi *et al.*, 1996). 3) Reduce the oviposition interval under different light dark regimes (McClung *et al.*, 1967 ; Forster. 1981 ; Sheldon *et al.*, 1984 and Naito *et al.*, 1989). However, an evident increase in total number of eggs was not reported in these selection experiments.

Recently, Luc *et al.* (1995, 1996) has characterized the laying process by the clutch traits, of which lag of oviposition time was reported to be genetic determination and might be considered in the selection program for improvement of egg production. The present paper is to study the application of the selection index methodology to incorporate lag of oviposition time into the index equation for further improvement of egg production in laying hens.

Materials and Methods

The traits used to construct selection indices were partial egg number (PEN), annual egg number (AEN), egg weight (EW) and lag of oviposition time (LAG). PEN is partial egg number of 150 days of egg production from the first egg. LAG is intra-clutch mean lag of oviposition time which was defined by Luc *et al.* (1995).

Table 1. Phenotypic standard deviations (σ_p), heritabilities (on the diagonal), genetic and phenotypic correlations (above and below diagonal) of the traits[1]

Trait	σ_p	PEN	AEN	EW	LAG
PEN	10	0.33	0.85	−0.43	−0.61
AEN	15	0.73	0.21	−0.31	−0.54
EW	3.5	−0.14	−0.10	0.52	0.38
LAG	0.73	−0.40	−0.34	0.19	0.43

[1] Source : McClung *et al.* (1976), Yoo *et al.* (1988), Natio *et al.* (1989), Fairfull and Gowe (1990), Wei and Van Der Werf (1993), Lillpres and Wilhelmson (1993), Luc *et al.* (1996).

To construct a selection index, genetic and phenotypic parameters of these traits need to be known. These parameters were obtained from the literature and presented in Table 1.

From parameters in Table 1, numerical matrices of phenotypic and genetic (co) variances (V_p and V_g, respectively) were calculated as follows ;

$$V_p = \begin{bmatrix} 100 & 109.5 & -4.900 & -2.920 \\ & 225.0 & -5.250 & -3.723 \\ & & 12.250 & 0.485 \\ & & & 0.533 \end{bmatrix}, \text{ and } V_g = \begin{bmatrix} 33 & 33.564 & -6.234 & -1.677 \\ & 47.250 & -5.378 & -1.776 \\ & & 6.370 & 0.460 \\ & & & 0.229 \end{bmatrix}.$$

The following general index equation containing full information was defined :

$$I = b_1 PEN_I + b_2 PEN_F + b_3 PEN_H + b_4 AEN_D - b_5 EW_I + b_6 LAG_I \cdots [1]$$

where b_i ($i=1, 6$) is weighting factors to be estimated, the subscripts I, F, H and D stand for individual, full sib, half sib and dam, respectively. The PEN_F is mean of n-1 full-sib animals, because the individual was excluded from its full-sibs. The PEN_H is mean of p-1 half-sib groups each has n full-sib animals, because the full-sib group containing individual was excluded from the mean.

To solve this selection index equation, the matrix of phenotypic (co) variances between the measurements in the index (P matrix), and matrix of covariance between additive genetic values of the traits in the selection objective and the information in the index equation (G matrix) must be established. The general P matrix for equation [1] was derived as follows ;

$$P=\begin{bmatrix} \sigma^2_{P_{PEN}} & \frac{1}{2}\sigma^2_{G_{PEN}} & \frac{1}{4}\sigma^2_{G_{PEN}} & \frac{1}{2}\sigma_{G_{PEN,AEN}} & \sigma_{P_{PEN,EW}} & \sigma_{P_{PEN,LAG}} \\ & d1 & \frac{1}{4}\sigma^2_{G_{PEN}} & \frac{1}{2}\sigma_{G_{PEN,AEN}} & \frac{1}{2}\sigma_{G_{PEN,EW}} & \frac{1}{2}\sigma_{G_{PEN,LAG}} \\ & & d2 & 0 & \frac{1}{4}\sigma_{G_{PEN,EW}} & \frac{1}{4}\sigma_{G_{PEN,LAG}} \\ & & & \sigma^2_{P_{AEN}} & \frac{1}{2}\sigma_{G_{AEN,EW}} & \frac{1}{2}\sigma_{G_{AEN,LAG}} \\ & & & & \sigma^2_{P_{EW}} & \sigma_{P_{EW,LAG}} \\ & & & & & \sigma^2_{P_{LAG}} \end{bmatrix}$$

where d_1 is variance of mean of $n-1$ full - sib animals with one record per animal, d_2 is variance of mean of $p-1$ half - sib groups each has n full - sib animals with one record per animal. These variances were derived as follows :

$$d_1=\left(\frac{1+(n-2)a_F h^2}{n-1}\right)\sigma^2_{P_{PEN}} \quad \text{and} \quad d_2=\frac{\left[\frac{1+(n-1)a_F h^2}{n}\right]\sigma^2_{P_{PEN}}+(p-2)a_H h^2\sigma^2_{P_{PEN}}}{p-1}$$

where p is number of females mated with one male, and is assumed to be equal to 8. Each mating was assumed to produce 6 offspring females ($n=6$). The $a_F = \frac{1}{2}$ is additive relationship among full sibs. The $a_H = \frac{1}{4}$ is additive relationship among half sibs. The h^2 is heritability of partial egg number.

The covariance matrix between additive genetic values of the traits in the selection objective and measurements in the index (G matrix) has following general form ;

$$G=\begin{bmatrix} \sigma_{G_{PEN,AEN}} & \sigma_{G_{PEN,EW}} & \sigma_{G_{PEN,LAG}} \\ \frac{1}{2}\sigma_{G_{PEN,AEN}} & \frac{1}{2}\sigma_{G_{PEN,EW}} & \frac{1}{2}\sigma_{G_{PEN,LAG}} \\ \frac{1}{4}\sigma_{G_{PEN,AEN}} & \frac{1}{4}\sigma_{G_{PEN,EW}} & \frac{1}{4}\sigma_{G_{PEN,LAG}} \\ \frac{1}{2}\sigma^2_{G_{AEN}} & \frac{1}{2}\sigma_{G_{AEN,EW}} & \frac{1}{2}\sigma_{G_{AEN,LAG}} \\ \sigma_{G_{EW,AEN}} & \sigma^2_{G_{EW}} & \sigma_{G_{EW,LAG}} \\ \sigma_{G_{LAG,AEN}} & \sigma_{G_{LAG,EW}} & \sigma^2_{G_{LAG}} \end{bmatrix}$$

Using values in the V_p and V_g, the general numerical matrices of P and G can be obtained easily. From the general P and G matrices, the specific P and G matrices were generated for four index equations in Table 2.

Table 2. Assignation of index equations using different information

Equation	Information					
	PEN_I	PEN_F	PEN_H	AEN_D	EW_I	LAG_I
I_1	x	x	x	x	x	x
I_2	x	x	x	x	x	
I_3	x	x	x		x	x
I_4	x	x	x		x	

Selection objectives were single trait selection for AEN or LAG and multi-trait selection for a combination of AEN, EW and LAG. The vector of weighting factors was obtained from $b=P^{-1}Gv$ for Hazel index (H-index) (Hazel, 1943), and $b=[I-P^{-1}GC'(CG'P^{-1}GC')^{-1}CG']P^{-1}Gv$ for restricted index (R index) (Kempthorne and Nordskog, 1959), where v is a vector of relative economic values of the traits in G. This vector was obtained by solving a retrospective index (VanVleck, 1993). If phenotypic selection differentials (Δ_p) were pre-specified as 40 eggs, 5grams and-1honr, respectively for AEN, EW and LAG, the corresponding relative economic values obtained from $(V^*_g)^{-1}\Delta_p$ were 1.1, 1.6 and -0.5, where V^*_g is genetic (co) variances matrix between AEN, EW and LAG. In the R-index, I is the identity matrix, C is an $k{\times}n$ matrix with ones on the diagonal and all other elements zero, in the present case $n=3$ is number of traits in G and $k=3$ is number of trait to be restricted (i.e. EW).

Vector of selection responses for the traits of interest were calculated by formula $\Delta_G=\frac{i}{\sigma_I}G'b$ (Lynch and Walsh, 1994), where i is selection intensity assumed to be equal to 1, $\sigma_I=\sqrt{b'Pb}$ is standard deviation of the index.

Changes in genetic and phenotypic (co) variances of the traits due to selection over generations were calculated by the method of analytical formulae described by Itoh (1991) and Strandén *et al.* (1993). The calculation formula is as follows :

$$V_{g(i)} = V_{g(i-1)} + \frac{k}{b'_{i-1}V_{p(i-1)}b_{i-1}} V_{g(i-1)}b_{i-1}b'_{i-1}V_{g(i-1)}$$

where $V_{g(i)}$ is a genetic (co) variances matrix of the traits at generation i, that is changed by selection at the previous generation $i-1$. The b_{i-1} is a vector of index weights used for selection at generation $i-1$. The $k=-i\ (i-x)$; i is the selection intensity and x is the abscissa at the truncation point. The values of k for various selection proportions were calculated and tabulated by Itoh (1991). The change of V_p matrix at generation i due to selection was calculated as $V_{p(i)} = V_{g(i)} + V_e$, where V_e is environment (co) variances matrix that was assumed to be unchanged over generations.

Results

Cumulative responses in annual egg number, egg weight and total genetic merit over ten generations to single trait selection for LAG are presented in Fig. 1. Cumulative response in annual egg number from the I_1 was estimated to be lowest among four equations. The values at the tenth generation were 18.8, 25.9, 20.5 and 27.1 eggs, respectively for the I_1, I_2, I_3 and I_4. The I_1 did not show superior than I_3 in improvement of egg weight over ten generations. The estimated values at the tenth generation were −4.6 and −4.7 grams for the I_1 and I_3, respectively. The I_2 was estimated to give the highest decrease in egg weight with the value of −6.2 grams at generation ten. Total genetic merit at generation ten was estimated to be different among

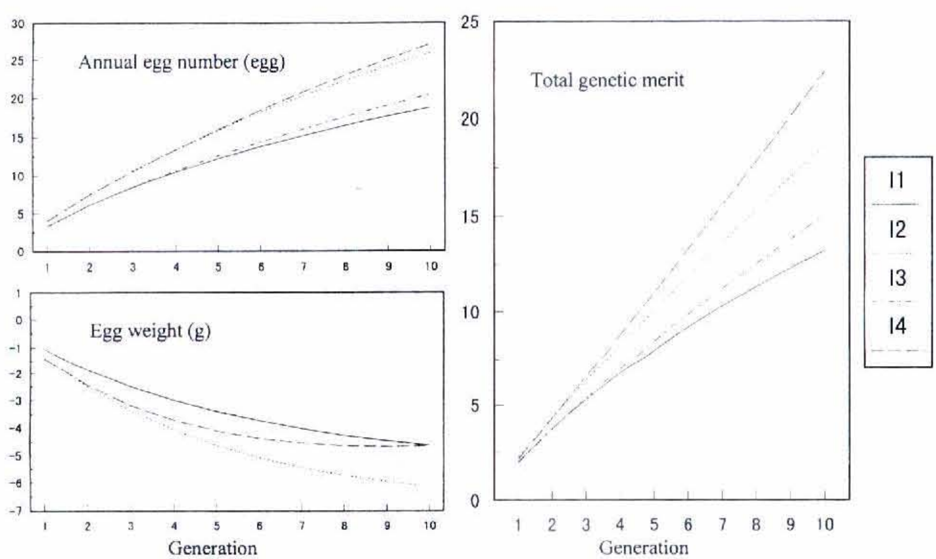

Figure 1. Cumulative responses in annual egg number, egg weight and total genetic merit over ten generations to single trait selection for LAG in four index equations (I_1 - I_4). (Selection intensity=1).

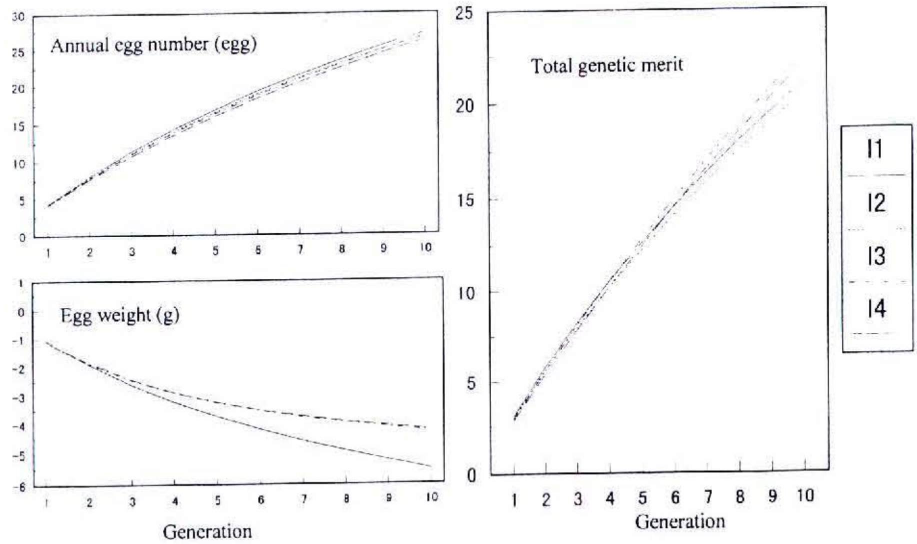

Figure 2. Cumulative responses in annual egg number, egg weight and total genetic merit over ten generations to single trait selection for AEN in four index equations (I_1~I_4), (Selection intensity= 1).

four equations, of which the highest value was 22.4 for the I_4 and the lowest value was 13.2 for the I_1.

Fig. 2 presents cumulative responses in annual egg number, egg weight and total genetic merit to single trait selection for AEN. The I_1 is expected to give the highest response in annual egg number over ten generations among four

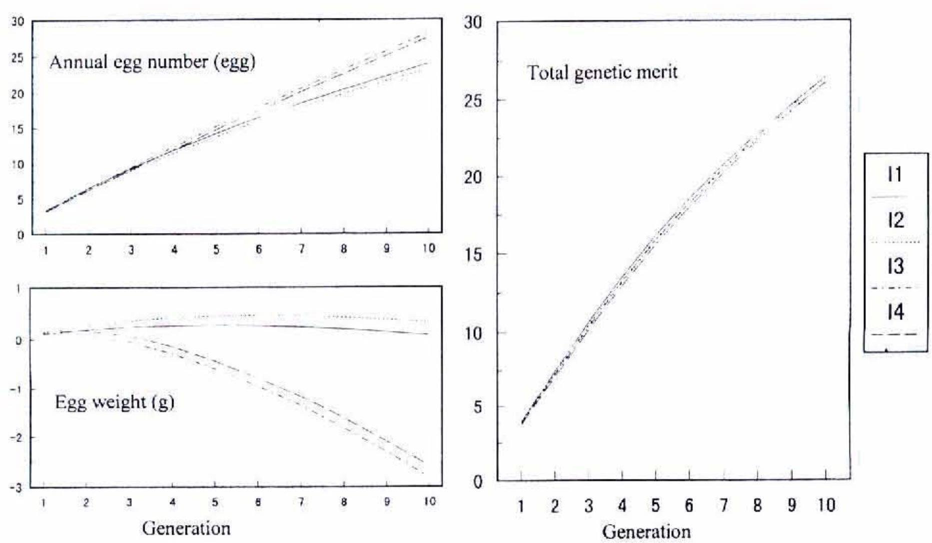

Figure 3. Cumulative responses in annual egg number, egg weight and total genetic merit over ten generations to multiple trait selection Predicted by the H-index in four index equations (I_1~I_4), (Selection intensity= 1).

equations used. However, the highest decrease in egg weight was also estimated from the I_1, resulting to total genetic merit estimated from the I_1 was not the highest value compared to other three equations. Accordingly, the cumulative response in annual egg number at the tenth generation was estimated to be 27.2, 26.6, 26.7 and 26.2 eggs for the I_1, I_2, I_3 and I_4, respectively. The corresponding values for cumulative response in egg weight at the tenth generation estimated from these equations were −5.5, −5.5, −4.3 and −4.2, grams. Total genetic merit were 21.1, 20.4, 22.6 and 22.0 for the I_1, I_2, I_3 and I_4, respectively.

Fig. 3 shows cumulative responses in annual egg number, egg weight and total genetic merit to multi trait selection predicted by the H index. Cumulative response in annual egg number at the tenth generation estimated from the I_1 was higher than that from the I_2 with corresponding values of 23.9 and 23.2 eggs. Similarly, the I_3 showed superior than I_4 in response in annual egg number. Cumulative responses estimated from the I_3 and I_4 were 28.2 and 27.5 eggs, respectively, being higher than those from the I_1 and I_2. However, the I_1 and I_2 showed superior than I_3 and I_4 in improvement of egg weight. Amount of decrease in egg weight at the tenth generation was estimated to be higher in the I_3 and I_4 than in the I_1 and I_2. The difference between the I_1 and I_2 in cumulative response in egg weight at the tenth generation was 0.24 grams in front of the I_2. However, cumulative response in total genetic merit was the highest for the I_1 over ten generations.

When zero response in egg weight was restricted by the R index, the estimated response in annual egg number was presented in Fig. 4. The I_1 showed relatively the highest response in annual egg number among four equations used. Therefore, the highest response in total genetic merit could be expected from this equation. The I_4 was estimated to give the lowest response in annual egg number among four equations.

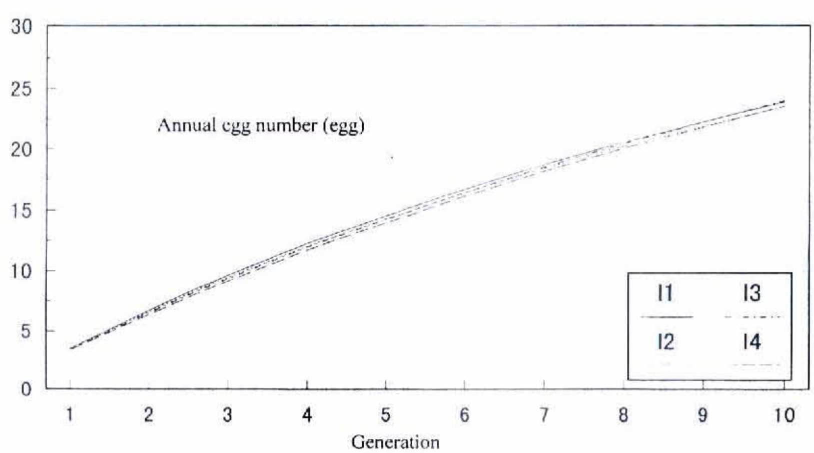

Figure 4. Cumulative responses in annual egg number over ten generations to multiple trait selection for predicted by the R-index in four index equations ($I_1 \sim I_4$). (Selection intensity = 1).

Discussion

In the modern layer, hens are capable to lay eggs almost every day. This implies that there is no genetic difference between hens for further improvement of egg production. The remain character of egg laying is time interval between ovipositions. The LAG is defined as mean difference of time intervals between ovipositions within a clutch from the circadian rhythm. Selection for reduction of LAG is therefore theoretically expected to improve egg production. However, results of this study show that single trait selection for reduction of LAG is not ideal for improvement of egg production as indicated by lower response in annual egg number and higher decrease in egg weight compared to other selection objectives. McClung *et al.* (1976) and Sheldon *et al.* (1984) succeeded in decrease of oviposition interval by selection, but the improvement of total number of eggs was not apparently reported. This indicates that the reduction in oviposition interval is not simply associated with the increase in total number of eggs. McClung *et al.* (1976) showed that the number of pause days and abnormal eggs were increased as a result of the decrease in oviposition interval. Moreover, selection for reduction of oviposition interval is often accompanied the decrease in egg weight because the time for albumen accumulation in the oviduct is reduced. These facts suggest that although lag of oviposition time can be estimated from a very short period in the early production stage, the selection for reduction of oviposition interval should be coincidentally considered with other egg production traits.

Single trait selection for annual egg number is expected to give the highest response for this trait among selection objectives. However, negative response in egg weight as a result of intensive selection for increase of egg number is counteracted owing to negative genetic correlation between these two traits. As an inferior property of single trait selection, the highest response in annual number of eggs can be expected from the equation I_1, the highest decrease in egg weight must be faced from this equation. This resulted to the equation I_1 is not expected to give the highest total genetic merit, except for some first generations (Fig. 2).

Single trait selection for annual number of eggs or lag of oviposition time both result to increase in egg number but decrease in egg weight. The economic benefit obtained from single trait selection is therefore trivial. Multi-trait selection predicted by the H index showed that the equation I_1 is not superior than equations I_3 and I_4 in improvement of annual egg number, but it is superior than those two equations in improvement of egg weight. The comparison between the I_1 and I_2 shows that the I_1 is inferior to I_2 in improvement of egg weight, but superior than I_2 in improvement of annual egg number. This property of adjustment ability of the H-index gave the highest response in total genetic merit for the equation I_1. The equations I_3 and I_4 fail to improve egg weight even fail to maintain the initial egg weight in the H-index. The superiority of the I_1 over other equations is also reflected in the R-index that the gain in annual egg number from the I_1 is expected to be higher than that from other three equations (Fig. 4).

In conclusion, the use of lag of oviposition time as a selection objective in single trait selection program is not ideal for improvement of total number of eggs, even higher decrease in egg weight may occur. However, the incorporation of lag of oviposition time into selection index as an additional information would be expected to give higher selection response in total number of eggs as the result of larger reduction of oviposition interval, but slightly higher decrease in egg weight is also counteracted. However, the compensative adjustment between the gain in egg number and the loose in egg weight gives higher response in total genetic merit of these two traits for the index equation in which lag of oviposition time is incorporated.

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放卵時刻のずれ（LAG）を用いた選抜指数による年間産卵数の遺伝的改良

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本研究ではLAGを選抜指数に組み込んだ場合の産卵性に対する選抜反応を検討した。選抜指数を構成するために用いた形質は，初産から150日間の産卵数（PEN），年間総産卵数（AEN），卵重（EW）及び放卵時刻のずれ（LAG）である。これらの形質に対して異なる情報（個体，全兄弟，半兄弟及びdam）を用い，４つの選抜指数方程式が推定された。単形質選抜はAENあるいはLAGに対し，多形質選抜はAEN，EW及びLAGの相対的経済価値に基ずき指数で行われた。多形質選抜からの選抜反応はHazel（1943）(H-index)及びKempthorne and Nordskog（1959）(R-index）の方法を用いた。また，選抜による各形質の遺伝及び表型分散共分散の変化はItoh（1991）及びStranden et al.（1993）の方法を用いた。

LAGに対する単形質選抜では，年間総産卵数がより低い改良量であり卵重がより大きく減少すると推定された。AENに対する単形質選抜における年間総産卵数はより高い改良量が推定されたが，卵重の減少も大きく推定された。すなわち，総合的な遺伝メリットは，この選抜目標で必ずしも高いものではなかった。

AEN，EW及びLAGに対する多形質選抜において，両予測法におけるLAGを含んだ方程式（I_2及びI_3）での年間産卵数の選抜反応はLAGを含まない方程式（I_2及びI_4）によるものより高く推定された。H-indexでの卵重の増加量は，I_2及びI_3方程式が劣るものであった。しかし，総合的な遺伝メリットは，I_2及びI_3でI_2及びI_4より高い反応が期待された。

キーワード：放卵時刻，産卵，選抜指数，産卵鶏

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