

Selection for High and Low Yolk-Albumen Ratio in Chickens

V. Effects of Selection and Relaxation on Egg Component Traits

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For the primary objective of changing egg components, a divergent selection for high and low yolk-albumen ratio was carried out over 12 generations. The selection was also relaxed for next 12 generations to confirm the establishment of the lines. This paper examined the responses to selection for yolk-albumen ratio as the changes of yolk weight and albumen weight. A random-bred population of White Leghorn chickens used in this experiment was hatched in 1969. Egg traits were measured from 8 to 9 months of age in every generation and then hens were selected for high and low yolk-albumen ratio. Proportions of selection were 1/3~1/4 for females. The selection was relaxed from the 12th generation by constraining selection differentials close to zero for yolk-albumen ratio, yolk weight and albumen weight, provided that at least one female per family was randomly chosen. About 16 males were mated to females sampled from the same line with avoiding full-sibs and half-sibs matings. Amount of responses over 12 selected generations compared with foundation population for yolk-albumen ratio was estimated to increase to 10.17% (0.94% per generation) in the high line and to decrease to 9.81% (0.80% per generation) in the low line. Realized heritabilities that were estimated by regression on cumulative selection differentials were almost the same in both lines with the values of 0.226 ± 0.019 and 0.230 ± 0.021 , respectively for the high and low lines, and 0.228 ± 0.006 for the estimation by the differences between lines. The differences between lines for yolk weight increased to about 2.5g at the generation 9 and then stagnated. Those for albumen weight continuously increased after generation 2 (0.818 g/generation). These changes suggested that selection responses for yolk-albumen ratio depended on the changes in yolk weight and albumen weight in the early generations, and the increases of albumen weight in the late generations. When selection was relaxed, significant increases in yolk-albumen ratio (0.41% per generation) were observed only in the low line. In the high line, the changes were in the range of 55~60%. The changes in yolk weight and albumen weight were not significant in the high line. The low line showed the increases in yolk weight and significant decreases in albumen weight (0.26 per generation). The differences between lines for these traits were significantly decreased, indicating the phenomenon of regression to foundation population. However, these changes were caused by the changes in the low line. These results suggested that selection response has approached the limitation in increasing yolk-albumen ratio. The reduction in yolk-albumen ratio would relate to a necessity that yolk weight could not be decreased beyond the under biological limit.

(*Jpn. Poult. Sci.*, 33 : 329-338, 1996)

Key words : yolk-albumen ratio, egg components, divergent selection, relaxed selection.

Received Jan. 11, 1996

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Introduction

The improvement of egg number and egg size is now still one of the important problems in laying chickens. CLAYTON (1968) discussed the efficiencies of selection for egg production in the commercial laying strains. KINNEY *et al.* (1974) also compared egg production efficiencies by using various selection systems. HUNTON (1984) reviewed the plateaus of selection responses in egg production, and reported that efficiency of egg production in the commercial layers has been approached the physiological limitation. SHELDON (1980) quoted the review of NORDSKOG (1977) in genetic statistics for animal breeding and pointed out that it is difficult to improve dramatically egg production by the usual practical methods of artificial selection in the commercial laying chickens.

On the other hand, even when hens lay the same amount of eggs, the egg components e.g. yolk weight and albumen weight that mainly determine the size of an egg are not always the same. MIYOSHI *et al.* (1975) and MIYOSHI and MITSUMOTO (1994) proposed that the different breeding goals on the egg components may be applied in the commercial chickens because a large variation exists for egg component traits. Moreover, HUSSEIN *et al.* (1993) pointed out that if the demand of broken-out eggs increases, the egg components especially yolk-albumen ratio will become an important factor. From this point, in the case of consideration to eggs for food or as raw materials for food processing, the development of chicken breeds suitable for various purposes on egg components or egg quality has been desired (HILL *et al.*, 1966; SINGH, 1972 and ARAFA *et al.*, 1982).

The primary objective of this experiment was to change the egg components. Hence, a divergent selection for yolk-albumen ratio that has not received much attention in the selection programs was implemented. Results of the first two generations showed a possibility for changing this trait (MIYOSHI and MITSUMOTO, 1974). The experiments were continuously extended for seven generations and reported by MIYOSHI and MITSUMOTO (1980 a, b). However, the trends of hatchability over selected generations showed a counteraction with physiological state from changing egg components (MIYOSHI and MITSUMOTO, 1981). This paper presents the effects of selection and relaxation each in 12 generations on the changes of yolk weight and albumen weight, and discusses the plateau of selection for egg component traits.

Materials and Methods

In 1964 a base population was obtained from White Leghorn chickens of five poultry farms, then random mating in four times resulted in the foundation population (F0) of this experiment in 1969. Only in the generation 0, the hens were classified into four groups according to the egg weights (S, MS, ML and L). In each group, two lines were selected for large and small yolk weights, corresponding to high and low yolk-albumen ratio. In the followed generations, divergent selection for high and low yolk-albumen ratio was carried out. Consequently, a total of eight lines were continuously maintained (SS, SL, MSS, MSL, MLS, MLL, LS and LL). However, because the

Table 1. Number of tested females per generation in the high (H) and low (L) yolk-albumen lines.

Selected			Relaxed		
Generation	H-line	L-line	Generation	H-line	L-line
0	353	353	12	163	173
1	174	171	13	151	236
2	205	161	14	116	120
3	195	214	15	113	118
4	205	207	16	44	61
5	201	194	17	84	81
6	171	157	18	62	88
7	197	201	19	77	106
8	186	186	20	66	101
9	201	206	21	89	91
10	234	204	22	94	100
11	187	192	23	131	119
12	163	173	24	81	88

inbreeding was increased owing to the size of population, at the generation 9 the crosses within selection direction were performed (SS×MSS and SL×MSL in the smaller egg size group, and MLS×LS and MLL×LL in the larger egg size group). The crosses of (SS×MSS)×(MLS×LS) and (SL×MSL)×(MLL×LL) were carried out at the generation 14 to establish the two present lines of high and low yolk-albumen ratios, respectively. Total numbers of hens in each generation used in this experiment are presented in Table 1. The proportions of selection in each generation were from 1/3 to 1/4 for females, while 4~16 males per line were randomly mated to selected females to produce next generation with avoiding the matings between full-sibs and half-sibs as much as possible (MIYOSHI and MITSUMOTO, 1980a). From the 12th generation the selection was relaxed by constraining selection differentials close to zero not only for yolk-albumen ratio as a trait of direct selection criterion but also for yolk weight and albumen weight. Furthermore, to avoid the decrease of the number of female families, at least one female per family was randomly chosen. Throughout this experiment, mating and hatching were carried out from June to July in every year. Feeding and management were uniform for all the generations as far as possible. Egg component traits were measured in spring when hens reached to 8~9 months of age in every year. Five consecutively laid eggs per hen were collected, weights of an egg, yolk and albumen were measured. Yolk-albumen ratio for each egg was calculated as percentage of yolk weight over albumen weight. Mean of five eggs was calculated for each trait as a value of each hen (MIYOSHI and MITSUMOTO, 1980a).

Results and Discussion

Effects of the selection :

Throughout the 12 generations, direct response trends for yolk-albumen ratio evaluated as population mean were observed to increase in the high line (10.17%) and

to decrease in the low line (9.81%) in comparison with foundation population. Amounts of changes per generation estimated by regression of population means on generation numbers were 0.94% and 0.80% for the high and low lines, respectively. The changes of population means for yolk-albumen ratio by the cumulative selection differentials are shown in Figure 1. Cumulative selection differential in the high line over 12 generations was about 10% larger than that in the low line, though realized selection differentials of the high line in each generation slightly differ from those of the low lines. Regressions of population means on the cumulative selection differentials were significant ($p < 0.01$) for both lines. The regression coefficients were almost the same for the high and low lines ($0.226 \pm 0.019\%$ for the high line and $0.230 \pm 0.021\%$ for the low line). Hence, the changes of population means for yolk-albumen ratio in the two lines showed a symmetrical trend over 12 generations. However, the changes were observed to increase in the early generations of the high line and to decrease in the late generations of the low line (Fig. 1).

Although a small difference between lines in selection differentials in each generation was applied, the changes in population mean in each generation for yolk-albumen ratio showed differences between the high and low lines. Moreover, the fluctuation of population means for yolk-albumen ratio in some generations was similar for both lines. Therefore, selection responses were also evaluated as the difference between lines in population means of the high and low lines. Figure 2 showed the changes of differences between lines in yolk-albumen ratio by differences between lines in cumulative selection differential. The regression was significant with a coefficient of 0.228 ± 0.006 . This suggested the existence of additive genetic variance for yolk-albumen ratio in the foundation population, and that there is no plateau in genetic responses after 12 selected generations. The value also refer to realized heritability for yolk-albumen ratio. However, it was smaller than in the high

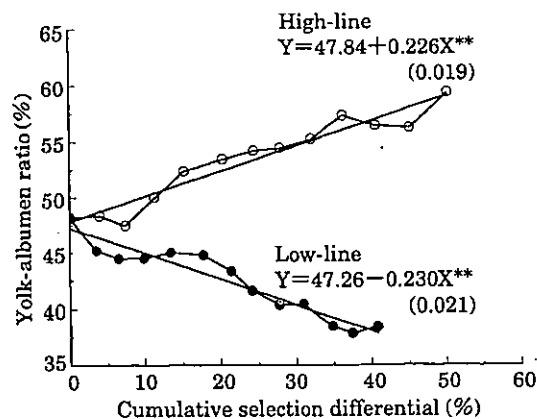


Fig. 1. Changes in mean of yolk-albumen ratio by cumulative selection differentials over 12 selected generations.

** : Significant differences from 0 at $p < 0.01$ for the regression coefficients.

The numbers in the parentheses are standard errors.

line of 0.36 with a range of 0.16~0.50 and larger than in the low line of 0.05 with a range of 0.01~0.15 reported by MIYOSHI and MITSUMOTO (1980 a) for the data over 7 generations, and was also smaller than the values estimated by analysis of variance of 0.41~0.45 (SINGH *et al.*, 1972), and 0.15~0.50 with average of 0.33 (MIYOSHI and MITSUMOTO, 1980 a).

The differences between the two lines in selection responses evaluated the changes in yolk weight and albumen weight that were used as basis for calculation of yolk-albumen ratio. Thus yolk-albumen ratio may be a kind of simple selection index for yolk weight and albumen weight. Hence, when the actual selection intensity is applied for either yolk weight or albumen weight or both of them, the antagonistic responses to selection for these traits can be expected. Genetic correlations among the egg weight, albumen weight and yolk weight were known to be mutually positive (HILL *et al.*, 1966 ; KUMAR and KAPRI, 1968 and TANABE, 1971). On the other hand, because the foundation population of this experiment had a relatively small egg weight, its proportion of yolk weight and albumen weight was smaller than that of other populations (MIYOSHI *et al.*, 1975). These facts suggested that it is a possible difficulty to decrease the yolk weight and albumen weight.

Figure 3 showed the changes in mean of yolk weight, albumen weight and their differences between lines by generations. Means of yolk weight in the high line increased to the F7, except for a decrease at the F2 and then stagnated. The decreases in yolk weight after the F7 were observed in the low line. The changes in means of albumen weight followed the selection direction as expected in each line. Moreover, changes in egg components also accompanied changes in egg weight with a similar pattern of changing in albumen weight in both lines.

The differences between lines in yolk and albumen weights were significantly increased (0.185 g/generation and 0.818 g/generation, respectively). However, a

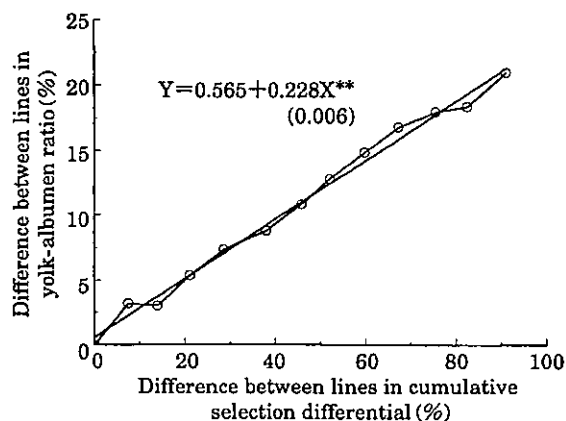


Fig. 2. Changes of differences between lines in yolk-albumen ratio by differences between lines in cumulative selection differentials over 12 selected generations.

** : Significant differences from 0 at $p < 0.01$ for the regression coefficients.

The numbers in the parentheses is standard error.

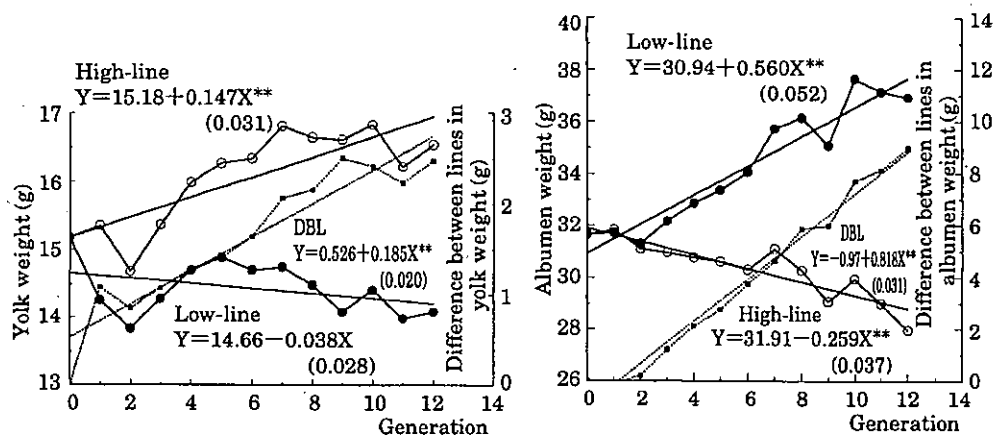


Fig. 3. Changes in mean of yolk weight and albumen weight and their differences between lines (DBL, in dot lines) over 12 selected generations.

** : Significant differences from 0 at $p < 0.01$ for the regression coefficients.

The numbers in the parentheses are standard errors.

stagnation for differences between lines in yolk weight was observed after generation 8, while albumen weight showed continuous increases after generation 2. These facts suggested that genetic responses evaluated as differences between lines for yolk-albumen ratio were caused by the changes in yolk and albumen weights over first 8 generations, the responses in followed generations were depended on the changes only in albumen weight. SCHEINGBERG *et al.* (1953) reported that the correlated response for albumen weight was more than that for yolk weight when selection for egg weight. MIYOSHI *et al.* (1975, 1993) also studied the egg components in the commercial chickens using the method of analysis of correlation matrices among egg components by varimax rotation of principal composites and showed that yolk weight possibly did not belong to the closely associated group of egg weight and albumen weight. In general, the above facts maybe related to the difficulties of decrease in yolk weight and remarkable increase in albumen weight in this selection experiment. Because it is expected that the selection responses for yolk-albumen ratio has achieved a physiological constant for egg components.

Influences of the relaxation :

To examine the efficiencies of selection on the direct selection trait of yolk-albumen ratio and correlated traits of egg components, the selection was relaxed by constraining selection differentials to zero in each generation. The plots between population means of yolk-albumen ratio and its differences between lines by generations are presented in Figure 4. Regression of the responses to relaxed selection in population mean over 12 generations was estimated. The difference between lines was significantly decreased ($-0.528\% \pm 0.094$ per generation). However, this change may be contributed by the increases in the low line. Amounts of 2.85% decrease and 4.23% increase for the high and low lines, respectively, were observed in the relaxed generations from the F12 to the F24. Change per generation estimated by regression coefficient for the high line was 0.11% but was not significant. The population means

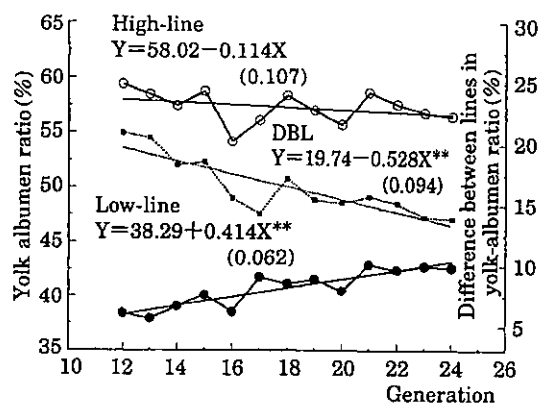


Fig. 4. Changes in mean of yolk-albumen ratio and its differences between lines (DBL, in dot lines) over 12 relaxed generations.

** : Significant differences from 0 at $p < 0.01$ for the regression coefficients.

The numbers in the parentheses are standard errors.

were in the range from 55% to 60%. In the low line, significant regression coefficient ($p < 0.01$) was estimated with the value of 0.41% as amount of changes per generation, indicating that the selection responses in this line over 12 generations have not reached to the limitation.

The changes of population means for yolk weight and albumen weight and their differences between lines after the F12 are presented in Figure 5. Yolk weight in the high line fluctuated within the value of about 1g except for a clear decrease at the F16. Yolk weight in the low line increased from the F15 to the F19 and closed to the value of 15.18g in the F0. Moreover, the decreases at the F16 for other traits (e.g. egg weight and shell weight) were possibly caused by the measurements which were carried out at an earlier age because the incubation of this generation was delayed about one month due to experiment facilities (FLETCHER *et al.*, 1983; MIYOSHI *et al.*, 1996). Albumen weight in the high line oscillated within the value of 1.5g, and that in the low line was significantly decreased ($p < 0.01$) with amount of 0.26g per generation. Moreover, significant decreases in differences between lines for yolk weight and albumen weight were observed (yolk weight : 0.078g/generation and albumen weight : 0.253g/generation). However, the difference between lines for yolk weight was observed to have a trend of stagnation from the generation 15. Thus, the regressional phenomenon to foundation population for yolk-albumen ratio was indicated by the decreases in difference between lines for yolk weight in the early relaxed generations and albumen weight in the late generations. Moreover, these changes possibly caused mainly by the changes of these traits in the low line.

As mentioned above, since yolk weight and albumen weight had a positive genetic correlation, simultaneously antagonistic changes in both traits under the divergent selection for yolk-albumen ratio can be expected. The objective of selection was attained over the 12 generations of selection in the high line as indicated by large yolk

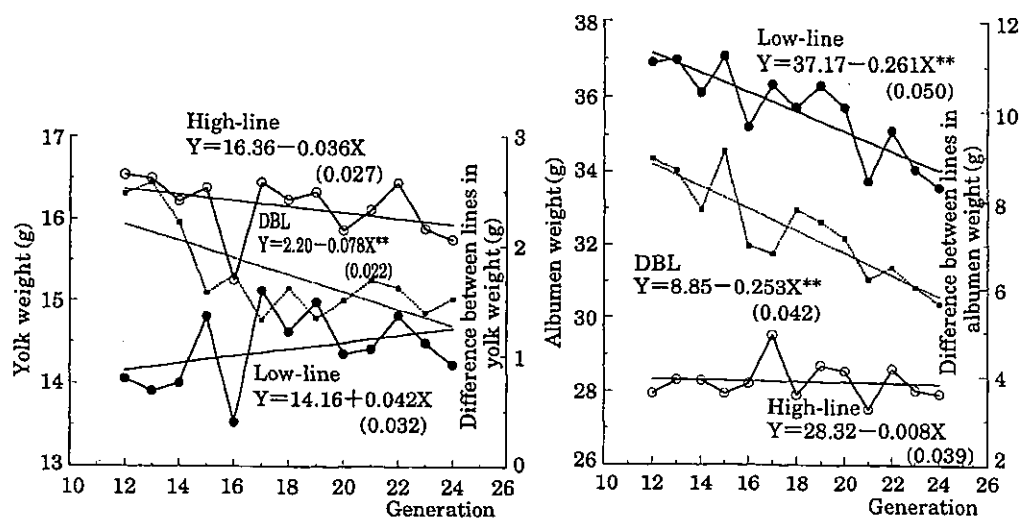


Fig. 5. Changes in mean of yolk weight and albumen weight and their differences between lines (DBL, in dot lines) over 12 relaxed generations.

** : Significant differences from 0 at $p < 0.01$ for the regression coefficients.

The numbers in the parentheses are standard errors.

weight and small albumen weight, hence the line that produced the eggs with high yolk-albumen ratio was established. This line had 10~20% yolk-albumen ratio higher than the commercial lines reported by MIYOSHI and MITSUMOTO (1994). However, the changes of population means in the low line suggested that it is difficult to develop a line that can produce the eggs with small yolk and large albumen as compared to some commercial lines that had even lower yolk-albumen ratio than the low line in this study (MIYOSHI and MITSUMOTO, 1994). Moreover, because egg has biological homeostasis, especially yolk weight can not be decreased beyond the under limit. The increases of egg weight and albumen weight often accompany the decreases in hatchability as reported by MIYOSHI and MITSUMOTO (1981). Therefore, the consideration should be paid for the relation between egg components and development of embryo (MURAMATSU *et al.*, 1990), body composition of chicks (MIYOSHI and MITSUMOTO, 1995) and factors of egg formation (MIYOSHI *et al.*, 1996).

Acknowledgements

The authors wish to thank Dr. M. SUZUKI of our Laboratory of Animal Genetics and Reproduction (Animal Breeding) for his statistical assistance, and undergraduate and graduated students for their assistance in taking care of the chicks and collection of the data.

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鶏卵における高および低卵黄・卵白比の選抜について

V. 卵構成に対する選抜の効果および選抜緩和の影響

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鶏卵構成を変化させる目的で卵黄・卵白比に対し、高および低の2方向への選抜を12世代にわたり実施した。系統の造成を確認することも含め、その後さらに12世代、選抜を緩和した。本報では、卵黄・卵白比に対する選抜反応を卵黄重および卵白重の変化から検討した。

1969年に孵化した白色レグホーン種を用い、毎世代8～9カ月齢に測定した卵形質によって、卵黄・卵白比の高低で選抜した。雌に対する選抜割合は、1/4～1/3であった。12世代以降では卵黄・卵白比、卵黄重および卵白重に対する選抜差がゼロに近似するように雌家系から1羽以上を抽出した。雄は同一方向の選抜系統から各世代、16羽を抽出し、急激な近交係数の上昇がない組み合わせで次代を得た。

12世代にわたる卵黄・卵白比の基礎集団平均に対する反応量は高系統で10.17%の増加(0.94%/世代)、低系統で9.81%の減少(0.80%/世代)が推定された。累積選抜差に対する回帰から推定した実現遺伝率は両系統で近似した(高系統; 0.226 ± 0.019 , 低系統; 0.230 ± 0.021)。また、高低系統間の差に基づく実現遺伝率は 0.228 ± 0.006 が推定された。

卵黄重における両系統間の差は9世代で約2.5gとな

り、その増加は停滞する傾向を示したが、卵白重では2世代以降に有意な増加(0.818g/世代)が認められた。これらのことより、卵黄・卵白比における選抜反応は早い世代では卵黄重および卵白重の変化に起因し、その後の世代では卵白重の増加によるものと推察した。

選抜を緩和した場合、卵黄・卵白比は低系統においてのみ有意な増加(0.41%/世代)が認められた。高系統では55～60%の範囲で推移した。また、高系統の卵黄重および卵白重にも有意な変化が認められなかった。低系統では卵黄重の増加および卵白重の有意な減少(0.26g/世代)が推定された。高低系統間の差はいずれの形質も有意に減少し基礎集団平均への回帰が認められたが、いずれも低系統における変化に起因した現象であると推察した。これらのことは卵黄・卵白比を高める方向への選抜反応が限界に漸近したことを示唆したが、卵黄・卵白比を低めることは、特に、卵黄重を減少させ得ない必然性に関連するものであると推察した。

(家禽会誌, 33: 329-338, 1996)

キーワード: 卵黄・卵白比, 鶏卵構成, 分枝選抜, 選抜緩和

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