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Economic feasibility of measuring feed consumption
in a poultry breeding operation

by

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INTRODUCTION

About two-thirds of the costs incurred in egg production is by feed consumption. The remaining cost of production apart from chick cost can be considered as fixed. Feed consumption is such an important cost factor of egg production that the criterion for overall performance of commercial and non-commercial stocks entered in the annual random sample tests conducted by the U.S.D.A. is income over feed and chick costs. In spite of this, research and development in poultry breeding have been mostly devoted to the genetic evaluation and selection for traits related to income such as egg production, viability and body weight. Quantitative genetic studies on individual variation in feed consumption has been almost entirely ignored. In fact, in a comprehensive summary of estimates of the phenotypic and genetic parameters of all economic traits on poultry population thus far published in the literature, Kinney (1969) was unable to include data on feed consumption of laying hens. The lack of interest in the quantitative genetics studies of feed consumption and its consequent exclusion from selection indexes in breeding programs is understandable. The measurement and collection of individual feed consumption records in large numbers is expensive. It is also well recognized that the variability in feed consumption is largely accounted for by body weight and

egg mass. Because of this interrelationship, it is expected that selection for these income-related traits (e.g., egg mass and body weight) will result in an improvement in income over feed cost through correlated response.

Harris (1970) pointed out that the decision as to whether or not to include the measurement of a trait (e.g., feed consumption) in a testing program depends on whether the additional amount of economic improvement obtainable from the inclusion of that trait is worth more than the cost of its measurement. In a commercial breeding operation however, where millions of commercial chicks are hatched every year from the same relatively few parental or grandparental breeding stock, the additional cost of measurement of such trait in the breeding stock might very well be a small fraction of the total benefits that could be derived from even a slight improvement in performance of the resulting commercial stock.

In attempting to improve income over feed cost, the commercial poultry breeder is faced with three basic alternative selection criteria for his breeding program: (a) one that includes records only on income-related traits (e.g., egg mass and adult body weight), (b) one that includes records only on income-related traits but uses some information on feed consumption (e.g., regression of feed consumption on egg mass and body weight records), and (c) one that includes records on income-related traits plus actual feed consumption records.

This study was conducted primarily to investigate the conditions under which a selection index, using information on income-related traits, can be made economically more valuable by incorporating actual feed consumption records in the index.

REVIEW OF LITERATURE

Measures of Efficiency in Egg Production

A definition of the efficiency of any production activity requires also definitions of the input and output involved in that activity. When the input and output are both variable, Ackoff (1962) stated that either the difference or the ratio of the two factors can be used as a measure of efficiency.

In poultry production, several measures of efficiency are in current use. For example, the results of the 1968 random sample tests in the U.S. and Canada summarized by the U.S. Department of Agriculture, Agricultural Research Service (1969) measured the efficiency of each stock entered in the tests in terms of income over feed and chick cost and in terms of pounds of feed consumed per pound of egg produced. The ratio of egg mass/feed mass is sometimes used (Arboleda and Campos, 1966; Harris, P., 1969). As a modification of egg mass/feed mass ratio, Morgan and Carlson (1968) suggested a performance efficiency index or PEI which they defined as,

$$PEI = \left(\frac{\text{egg wt.} \times \text{percent egg prod.}}{\text{feed consumed per day}} \right) \left(\frac{30 \times \text{egg wt.}}{\text{body wt.}} \right)$$

The authors claimed that PEI is a better measure of efficiency than the egg mass/feed mass ratio because it favors individuals that lay larger eggs per unit body weight.

For poultry producers whose principal objective is to maximize profit, income over feed and chick cost appears to be the preferable measure of efficiency since it is in itself an expression of profit. Clayton (1968) concluded that income over feed cost is a good measure of economic efficiency. Furthermore, since income over feed cost is a linear combination of income-related traits (e.g., egg mass and body weight) and the cost-related traits (e.g., feed consumption), it is possible to attach relative economic weights to each trait involved. Maximum genetic improvement of income over feed cost can then be examined in terms of a selection index criterion (Hazel, 1943).

Estimation of Genetic Parameters of Feed Consumption Among Layers

To measure egg production efficiency, the cost of feed consumed is the important input factor for production. This is understandable since feed consumption represents 50 to 70 percent of the total cost of production (Winter and Funk, 1960).

To obtain reliable estimate of genetic and phenotypic parameters of feed consumption, a fairly large number of individuals is required. Usually the measurement of feed consumption however, is regarded as very expensive.

Indirect Measurement of Feed Consumption and Efficiency

Because the amount of feed consumed has long been known to be closely related to body weight and egg production. Formulas have been constructed for estimating the amount of feed that will be consumed by a flock of hens with a known average body weight and production rate (Card, 1952; Heuser, 1955). Arboleda and Campos (1966) also found from individually feeding 262 White Leghorn pullets that 52 percent of the variability of feed consumption was accounted for by egg mass output and body weight. Egg production alone is major determinant of net income or production efficiency. For example, Nordskog (1960) found that egg production accounted for 92 percent of the variability in income over feed cost among entries in random sample tests in various states entered up to the year 1957. McNally and Foster (1969) also found that 97 percent of the variability in net income is attributable to total weight of eggs per bird housed among entries in the 4th and 5th Gosford (United Kingdom) random sample tests.

Because of the high determination of income over feed cost by the income-related traits, Nordskog (1967) constructed a performance index (in units of dollars) for inter-line selection which was a function only of egg production, percent eggs larger than 2 ounces, body weight at the end of the test and percent mortality. Other measures of production efficiency

without actually measuring feed consumption have been proposed. Nordskog et al. (1969) proposed an indirect measure of efficiency,

$$E = (.82P + c_1)/(34.57W + c_2)$$

where,

P = gram of egg mass output per day

W = weight of hen (kg)

$c_1 = qa$

a = a slope intercept of the regression plane of feed consumption on body weight and egg mass

q = fraction of feed regressed on P relative to the total feed regressed on P and W

$c_2 = (1-q)a.$

As a measure of feed consumption then it only requires some existing regression equation of feed consumption on body weight and on egg mass. Casey, D. W. (1970) also used production efficiency measures in terms of the ratio egg mass/body weight, and in terms of the ratio egg weight/body weight.

The Importance of Feed Consumption Measurement in Commercial Breeding Operation

In commercial poultry breeding the utilization of any source of genetic variability that will result in the improvement of the desired efficiency criterion is important. Egg production, although very highly correlated with income over

feed cost, has a generally low heritability (Lerner, 1958; Kinney, 1969). This low genetic variability makes genetic improvement by selection in egg production difficult to achieve. Clayton (1968), in reviewing the performance of commercial stocks entered in random sample tests in the U.S. and Canada, found no evidence of improvement in hen-housed egg production over a period of six years. Dickerson (1955) found that the peak of 230 eggs survivor's production to 504 days of age had not been exceeded in a further 20 years of selection. Yamada et al. (1958) also found that improvement of rate of production reached a plateau by the fifth year of selection. They attributed the plateau to the decline in genetic variance. Nordskog et al. (1967) selected for total-year production based on early part record production for eight generations but failed to show any significant improvement in either part-year or total-year egg production record. Morris (1963) reported results of a 12-year continuous selection experiment to improve total-year production using the early part-record and was unable to show significant improvement in total-year record.

The use of an auxiliary trait to increase the heritability of the desired primary trait has been suggested by several workers. Rendel (1954) showed that the genetic improvement ΔG , in a primary trait, say x_1 , by selecting on an index $Y = x_1 - ax_2$ is

$$\Delta G = i h_1^2 \sigma_{p_1} (1-r_G^2) / \sqrt{1-r_p^2}$$

where \underline{a} is the phenotypic regression of x_1 , \underline{i} is the selection intensity, h_1^2 is the heritability of x_1 , σ_{p_1} is the phenotypic standard deviation of x_1 , r_G and r_p are the genotypic and phenotypic correlations between x_1 and x_2 , respectively. Hence, if $\sqrt{1-r_G^2}$ is smaller than $(1-r_G^2)$ selecting on an index Y is more efficient in improving x_1 than selecting on x_1 only.

Purser (1960) presented experimental results where the improvement in cannon length in sheep (x_1) based on selection index $Y = x_1 - .082 x_2$ where x_2 is the body weight of the sheep, was at least 25 percent greater than could be obtained if selection were on the basis of x_1 only. Searle (1965) further showed that combining two traits x_1 and x_2 in a selection index of the form $Y = b_1 x_1 + b_2 x_2$, will improve the efficiency in genetically improving x_1 than by selection on x_1 alone and especially so if for heritabilities that are similar in magnitude, the genetic correlation is close to unity, or if for greatly disparate heritabilities, the genetic correlation is appreciably large.

Selection Index Theory

Efficiency of egg production is a combination of income-related and cost-related traits. The genetic change in these

traits must be such that it will maximize the change in the efficiency criterion instead of just one trait (e.g., egg production). The maximization of genetic improvement of an efficiency criterion such as income over feed cost by a derived selection index had been developed by Smith (1939) and Hazel (1943). The applicability of selection index to animal and plant breeding was extended by Henderson (1963) to individuals with unequal number of records per observation and selection of lines and crosses. Kempthorne and Nordskog (1959) also introduced the concept of restricted selection indexes.

The theory of selection index assumes that:

- (a) the phenotypic value of trait x_i is expressible as $x_i = g_i + e_i$, where g_i is the breeding value or the additive genetic component and e_i is the non-additive genetic and environmental component;
- (b) for trait $i = 1, \dots, t$; the breeding value, H , of an individual is defined as $H = \sum_{i=1}^t a_i g_i$, where a_i is the economic value of a unit of the i th trait;
- (c) the quantities x_i and H are such that the regression of H on any linear function of x_i 's is linear.

If selection is based on a linear function of x_i , i.e.;

$$Y = \sum_{i=1}^t b_i x_i, \text{ then the improvement in } H \text{ is equal to } B_{HY} \Delta Y,$$

where ΔY is the selection differential or the difference in the mean of Y before selection and the mean of Y after selection and B_{HY} is the regression of H on Y . The expected improvement

in H from selection on Y is then

$$\Delta H(Y) = \text{Cov}(H, Y) \Delta Y / \sigma_Y^2 = r_{HY} \sigma_H (\Delta Y / \sigma_Y)$$

where r_{HY} is the correlation between H and Y, and σ_Y^2 is the variance of Y. If Y is normally distributed, if the b's are known without errors and if truncation selection is practiced by selecting the top p percent; the relationship of p to ΔY is $\Delta Y / \sigma_Y = z/p = i$ where z is the ordinate of the standardized normal distribution and i is defined as the selection intensity. The expected gain in H given selection on Y is then $\Delta H(Y) = i \text{Cov}(H, Y) / \sigma_Y$.

Cochran (1951) pointed out that in practice, since only parameter estimates are used in deriving a selection index to maximize H, the b's in the index are subject to sampling errors. Harris (1964) investigated the consequences of using parameter estimates on the predicted gain and the true expected gain in a population with known parameters. He demonstrated that progress from selection for a particular calculated index tended to be over-estimated, but this bias was reduced as the amount of data was increased.

THEORY

A Statistical Model of Feed Consumption

Of several different possible statistical models that could be used to represent feed consumption, a linear model was chosen for this study because it is simpler. The model is

$$x_{3i} = \beta_1 x_{1i} + \beta_2 x_{2i} + u_i \quad (1)$$

where x_{3i} , x_{1i} and x_{2i} are the records of feed consumption, body weight and egg mass, respectively, of the ith layer measured as deviations from the respective population means; β_1 and β_2 are constants that represent, respectively, the amount of feed for maintenance of a unit of body weight and a unit of egg mass. The component u_i is a residual representing the amount of feed wasted in digestion and metabolism and other factors.

The elements in the model can then be transformed to a standardized normal variables,

$$x'_{3i} = p_1 x'_{1i} + p_2 x'_{2i} + p_u u'_i \quad (2)$$

where

$x'_{ki} = x_{ki}/\sigma_k$ = the standardized kth variable,

$$p_k = \beta_k \sigma_k / \sigma_3$$

σ_k = the standard deviation of the kth variable.

The variance of x'_{3i} is then,

$$\begin{aligned} \sigma'^2_{x_3} = & p_1^2 \sigma'^2_1 + p_2^2 \sigma'^2_2 + p_u \sigma'^2_u + 2p_1 p_2 \sigma'_{12} \\ & + 2p_1 p_u \sigma'_{1u} + 2p_2 p_u \sigma'_{2u} \end{aligned} \quad (3)$$

A variable, x_k , can be represented by,

$$x_k = g_k + e_k \quad (4)$$

where g_k is the breeding value or the additive genetic component and e_k is the environmental and non-additive genetic component of x_k . If g_k and e_k are assumed to be independent, the variance of the standardized variable, x'_k , can be written as,

$$\begin{aligned} \sigma'^2_{x_k} &= v \left(\frac{g_k + e_k}{\sigma_k} \right)^2 = \frac{\sigma^2_{g_k}}{\sigma_k^2} + \frac{\sigma^2_{e_k}}{\sigma_k^2} \\ \sigma'^2_{x_k} &= h_k^2 + e_k^{*2} = 1 \end{aligned} \quad (5)$$

where h_k^2 is the heritability of the kth trait and e_k^{*2} is the non-additive and environmental fraction of the phenotypic variance σ_k^2 of the kth trait. Also, the covariance between two standardized variables, x'_j and x'_k is,

$$\sigma'_{jk} = \text{Cov} \left(\frac{x_j}{\sigma_j}, \frac{x_k}{\sigma_k} \right) = \frac{\text{Cov}(x_j, x_k)}{\sigma_j \sigma_k} = r_{p_{jk}} \quad (6)$$

where $r_{P_{jk}}$ is the phenotypic correlation between the traits x_j and x_k . Using relations 4 and 6, $r_{P_{jk}}$ can be represented as,

$$r_{P_{jk}} = \text{Cov} \left(\frac{g_j + e_j}{\sigma_j}, \frac{g_k + e_k}{\sigma_k} \right)$$

$$r_{P_{jk}} = r_{G_{jk}} h_j h_k + r_{E_{jk}} e_j^* e_k^* \quad (7)$$

where

$r_{G_{jk}}$ = the correlation between g_j and g_k

$$h = \sqrt{h^2}$$

$$e^* = \sqrt{e^{*2}}$$

$r_{E_{jk}}$ = the correlation between e_j and e_k .

From Equations 2, 3, 4, 5 and 7 the heritability of feed consumption (h_3^2) and its genetic correlation with body weight ($r_{G_{31}}$) and with egg mass ($r_{G_{32}}$) can be obtained according to the following relationships:

$$h_3^2 = p_1^2 h_1^2 + p_2^2 h_2^2 + p_u^2 h_u^2 + 2p_1 p_2 h_1 h_2 r_{G_{12}}$$

$$+ 2p_1 p_u h_1 h_u r_{G_{1u}} + 2p_2 p_u h_2 h_u r_{G_{2u}} \quad (8)$$

$$r_{G_{31}} = (p_1 h_1^2 + p_2 r_{G_{12}} h_1 h_2 + p_u r_{G_{1u}} h_1 h_u) / h_3 h_1 \quad (9)$$

$$r_{G_{32}} = (p_1 r_{G_{12}} h_1 h_2 + p_2 h_2^2 + p_u r_{G_{2u}} h_2 h_u) / h_3 h_2 \quad (10)$$

If $h_u^2 = 0$ (i.e., no genetic component in the residual), then Equations 6, 7 and 8 simplify to

$$h_3^2 = p_1^2 h_1^2 + p_2^2 h_2^2 + 2p_1 p_2 h_1 h_2 r_{G_{12}} \quad (11)$$

$$r_{G_{31}} = (p_1 h_1^2 + p_2 r_{G_{12}} h_1 h_2) / h_3 h_1 \quad (12)$$

$$r_{G_{32}} = (p_1 r_{G_{12}} h_1 h_2 + p_2 h_2^2) / (h_3 h_2) \quad (13)$$

Equations 11, 12 and 13 show that under the model given in 1, with no additive genetic component in the residual, the genetic parameters of feed consumption can be predicted from the genetic parameters of body weight and egg mass provided that p_1 and p_2 are known.

Selection Indexes for Improving Income Over Feed Cost

Definition of four different selection indexes

Consider the aggregate breeding value of income over feed cost, H defined by a linear combination of the breeding values of body weight (g_1), egg mass (g_2) and feed consumption (g_3),

$$H = a_1g_1 + a_2g_2 - a_3g_3 \quad (14)$$

where a_i is the economic value of a unit of the i th trait.

From selection index theory (Hazel, 1943; Henderson, 1963), we can formulate two selection indexes Y_1 and Y_2 , defined by,

$$Y_1 = b_{11}x_1 + b_{12}x_2 + b_{13}x_3 \quad (15)$$

$$Y_2 = b_{21}x_1 + b_{22}x_2 \quad (16)$$

where the b_{ki} 's are obtained such that the correlation of selection index Y_k and H is maximum.

If we represent the breeding value of feed consumption as a linear regression on the breeding values of body weight and egg mass, i.e.,

$$g_3 = \beta_1g_1 + \beta_2g_2$$

then we can represent Equation 14 as,

$$H^* = a_1g_1 + a_2g_2 - a_3(\beta_1g_1 + \beta_2g_2)$$

$$H^* = (a_1 - a_3\beta_1)g_1 + (a_2 - a_3\beta_2)g_2 \quad (17)$$

With the aggregate value of income over feed cost defined by H^* , we can formulate a third selection index, Y_3 , defined by,

$$Y_3 = b_{31}x_1 + b_{32}x_2 \quad (18)$$

where b_{31} and b_{32} are obtained such that the correlation of Y_3 with H^* is maximum.

Finally, if we define the aggregate breeding value of income, H^{**} , as

$$H^{**} = a_1 g_1 + a_2 g_2 \quad (19)$$

we can formulate a fourth selection index, Y_4 , defined by,

$$Y_4 = b_{41}x_1 + b_{42}x_2 \quad (20)$$

where b_{41} and b_{42} are obtained such that the correlation of Y_4 with H^{**} is maximum.

The relative efficiency of the selection indexes in improving H

If maximum improvement in H is the desired objective in a breeding operation, then the expected gain, $\Delta H(Y_k)$, in H from using selection index Y_k , is given by,

$$\Delta H(Y_k) = \frac{\text{Cov}(H, Y_k)}{\sigma_{Y_k}^2} (\bar{Y}_{k_s} - \mu_{Y_k})$$

$$\Delta H(Y_k) = \frac{i \text{Cov}(H, Y_k)}{\sigma_{Y_k}} \quad (21)$$

where

\bar{Y}_{k_s} = mean of the selected individuals on index Y_k
 μ_{Y_k} = population mean of Y_k

$i = (\bar{Y}_{k_s} - \mu_{Y_k}) / \sigma_{Y_k}$; the standardized selection

differential or the selection intensity.

Using matrix notation, let

$$H = \underline{a}' \underline{g}$$

$$Y_k = \underline{b}_k' \underline{x}_k$$

where \underline{a} and \underline{g} are the column vectors of economic weights and of breeding values of traits in H , respectively; \underline{b}_k is the column vector of coefficients corresponding to the traits in the column vector \underline{x}_k in selection index Y_k . The prime (') means the transpose of the vector (or matrix) defined. The normal equations obtained by maximizing $r_{Y_k H}$ are,

$$\underline{P}_k \underline{b}_k = \underline{G}_k \underline{a} \quad (22)$$

so that

$$\underline{b}_k = \underline{P}_k^{-1} \underline{G}_k \underline{a}$$

where \underline{P}_k^{-1} is the inverse of the variance-covariance matrix \underline{P}_k , of the traits in Y_k ; \underline{G}_k is the genetic variance-covariance matrix generated by the elements in \underline{g} and \underline{x}_k . Using Equation 22, it can be shown that,

$$\text{Cov}(Y_k, H) = \underline{b}_k' \underline{G}_k \underline{a} = \underline{b}_k' \underline{P}_k \underline{b}_k$$

$$\text{Cov}(Y_k, H) = \sigma_{Y_k}^2 \quad (23)$$

From Equations 21 and 23, the expected gain in H using Y_1 and Y_2 are,

$$\Delta H(Y_1) = i \frac{\text{Cov}(Y_1, H_1)}{\sigma_{Y_1}} = \underline{i} \sigma_{Y_1} \quad (24)$$

$$\Delta H(Y_2) = i \frac{\text{Cov}(Y_2, H_1)}{\sigma_{Y_2}} = \underline{i} \sigma_{Y_2} \quad (25)$$

Since the index coefficients of Y_3 and Y_4 are not obtained from relation 22, the identity given by 23 does not hold for these indexes, thus the expected gain in H from these indexes can only be expressed as,

$$\Delta H(Y_3) = \frac{i \text{Cov}(Y_3, H)}{\sigma_{Y_3}} \quad (26)$$

$$\Delta H(Y_4) = \frac{i \text{Cov}(Y_4, H)}{\sigma_{Y_4}} \quad (27)$$

In general, let us denote the efficiency of a selection index Y_k relative to selection index Y_ℓ as,

$$E_{k,\ell} = \frac{\Delta H(Y_k)}{\Delta H(Y_\ell)} \quad .$$

The efficiency of Y_2 relative to Y_1 can then be expressed as,

$$E_{2,1} = \frac{\sum_i \sigma_{Y_2}^2}{\sum_i \sigma_{Y_1}^2} .$$

Cunningham (1969) showed that $\sigma_{Y_2}^2 = \sigma_{Y_1}^2 - b_{1i}^2/W_{ii}$ where W_{ii} is the i th diagonal of the inverse of the P_1 matrix corresponding to the i th trait with the index b_{1i} that is deleted from the selection index Y_1 . Since b_{1i}^2/W_{ii} cannot be negative, the range of values that $\sigma_{Y_2}^2$ takes is $0 \leq \sigma_{Y_2}^2 \leq \sigma_{Y_1}^2$. Consequently, $E_{2,1} \leq 1$. The efficiency of Y_3 relative to Y_2 can be expressed as,

$$E_{3,2} = \frac{\sum_i \text{Cov}(H, Y_3)}{\sum_i \sigma_{Y_2} \sigma_{Y_3}} .$$

In matrix notation,

$$E_{3,2} = \frac{\underline{b}_3' \underline{G}_3 \underline{a}}{[(\underline{b}_3' \underline{P}_3 \underline{b}_3)(\underline{b}_2' \underline{P}_2 \underline{b}_2)]^{1/2}} .$$

But since

$$\underline{G}_3 = \underline{G}_2 = \begin{bmatrix} \sigma_{G_{11}} & \sigma_{G_{12}} & \sigma_{G_{13}} \\ \sigma_{G_{21}} & \sigma_{G_{22}} & \sigma_{G_{23}} \end{bmatrix}$$

and

$$\underline{P}_3 = \underline{P}_2 = \begin{bmatrix} \sigma_{P_{11}} & \sigma_{P_{12}} \\ \sigma_{P_{21}} & \sigma_{P_{22}} \end{bmatrix} = \underline{P} ,$$

where $\sigma_{G_{ij}}$ is the genetic covariance between x_i and x_j and $\sigma_{P_{ij}}$ is the phenotypic covariance between x_i and x_j , then from Equation 22 we can write $E_{3,2}$ as,

$$E_{3,2} = \frac{\underline{b}_3' \underline{P} \underline{b}_2}{[(\underline{b}_3' \underline{P} \underline{b}_3) (\underline{b}_2' \underline{P} \underline{b}_2)]^{1/2}} .$$

$E_{3,2}$ is now reduced to a correlation between the elements of \underline{b}_3 and \underline{b}_2 with products weighted by the corresponding elements of the matrix \underline{P} . Hence, in terms of a correlation, $E_{3,2} \leq 1$. Alternatively, $\Delta H(Y_2) \geq \Delta H(Y_3)$. A similar reasoning can be applied to $E_{4,2}$. Hence it can be shown that $E_{4,2} \leq 1$ or $\Delta H(Y_2) \geq \Delta H(Y_4)$.

The efficiency of Y_4 relative to Y_3 can be expressed as,

$$\begin{aligned} E_{4,3} &= \frac{i \text{Cov}(H, Y_4) \sigma_{Y_3}}{i \text{Cov}(H, Y_3) \sigma_{Y_4}} \\ &= \frac{\text{Cov}(H, Y_4) \sigma_{Y_3} \sigma_H}{\text{Cov}(H, Y_3) \sigma_{Y_4} \sigma_H} \end{aligned}$$

$$E_{4,3} = \frac{r_{HY_4}}{r_{HY_3}} .$$

The efficiency of Y_4 relative to Y_3 is not as determinate as when it is relative to Y_2 . However, between Y_3 and Y_4 , the one whose correlation with H is higher is the more efficient index.

To summarize the above theoretical considerations, the relative expected gain from the different selection indexes is given by

$$\Delta H_1(Y_1) \geq \Delta H(Y_2) \geq [\Delta H(Y_3) \begin{matrix} < \\ > \end{matrix} \Delta H(Y_4)] .$$

MATERIALS AND METHODS

Stocks Used

Two pure lines A and B and their reciprocal crosses, AB and BA of White Leghorn layers were used in this experiment.¹ Underlying both pure lines A and B, was a long history of inbreeding and selection. Lately, however, these have been maintained as closed flocks with selection for economic traits and have been used as parental stocks for some experimental crosses. Lines A and B differed in adult body size, production rate and age at first egg. The same set of sires was used to produce the pure line pullets and the F_1 cross line pullets except for an additional five sires in each line used only for producing pure line pullets. This was necessary because of the relatively low fertility and hatchability among the pure line matings. In all matings, the dams were randomly assigned to the sires. All the cross line progenies were hatched at the same time but again due to low fertility and hatchability, the pure line progenies of both lines A and B were hatched in three periods at two-week intervals.

Only those individuals alive at the end of the feeding test were included in the statistical analyses. The total

¹These stocks were made available for this present study through the courtesy of Dekalb AgResearch, Inc. Dekalb, Illinois 60115.

numbers were:

Line or cross:	<u>A</u>	<u>B</u>	<u>AB</u>	<u>BA</u>
Number:	573	215	471	649

Housing Scheme and Feeding Procedure

At about four months of age, the cross line pullets were transferred to an individual laying cage house and randomly assigned to ten adjoining rows of 150 individual cages per row. Records of individual egg production were kept immediately after housing. Records of egg quality traits were taken from eggs collected within five days of the 35th week of age. Individual body weights were also taken at this age. A ration containing 19 percent protein was fed to the cross line pullets for the entire feeding test.

The pure line pullets in all three hatches, being about two months younger than the cross lines, were transferred to another laying cage house two months after the housing of the cross line pullets. Each dam family of each pure line was equally split and assigned to two groups at the time of housing. One group was fed 14 percent protein diet while the other was fed 19 percent protein diet. The two groups of pullets on different diets were put in two separate banks of cages. Each bank, consisting of four rows of 150 cages each row, were separated only by feed-cart alley. This arrangement facilitated mechanical mass feeding of the separate diets between individual

feeding test periods.

All the layers in pure lines and crosses were fed individually for two 4-week feeding periods at an interval of four weeks. In addition, of the 573 layers in line A, 303 were continuously fed for 24 weeks.

Measurement of Individual Feed Consumption

Only one plan of individual feeding measurement was used during the entire feeding test. The plan was developed from a preliminary experiment. The aim was to make it possible for a single worker to handle the experimental birds with a minimum setup cost. For this purpose a special individual hen feeder was developed to minimize spillage. The individual feeder consisting of two parts, a hopper and a trough, was fashioned from two half-gallon milk cartons (Figure 1). Figure 2 shows the trough and hopper joined as a single feeder ready for use in individual feeding. Figure 3 shows a row of hens being individually fed.

About one week before each feeding test, the required number of feeders were made. At the start of the experiment all feed remaining in the existing permanent metal troughs used in mass feeding was removed. The carton troughs were then fitted quickly into the troughs. Meanwhile the hoppers which had already been filled with 1200 grams of feed each, the day

Figure 1. Feeding trough (left) and hopper (right) of an individual feeder made from two half-gallon milk cartons. Heavy duty stapler, tapes and paper cutter were used to make the trough and hopper. A 1/4" x 3" rubber band around the trough holds the hopper in place when inserted into the trough. A 1-3/4" x 4" cut on the front side of the hopper enables the feed to flow gravitationally into the trough

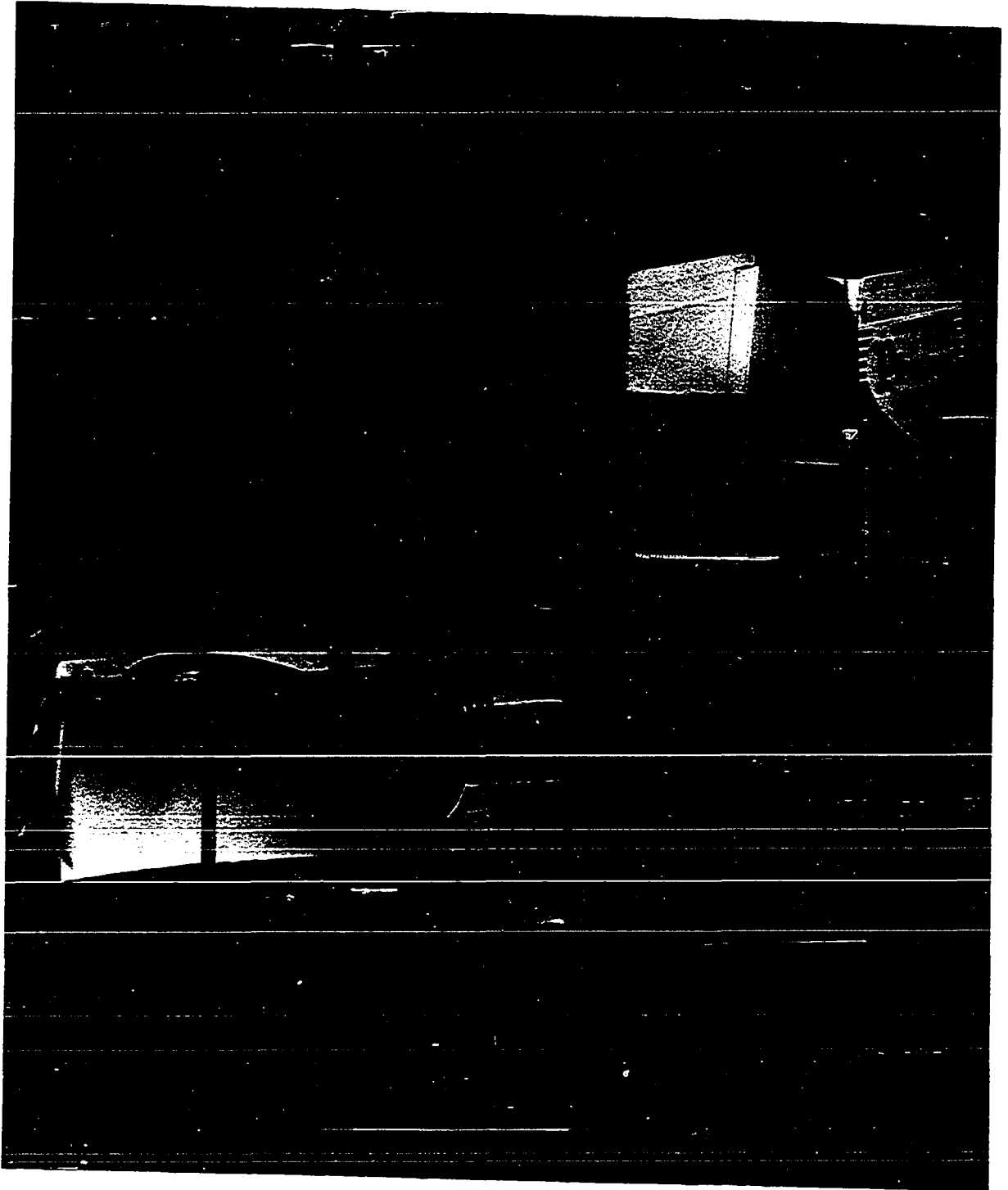


Figure 2. The feed hopper is inserted upside down into the trough for individual feeding

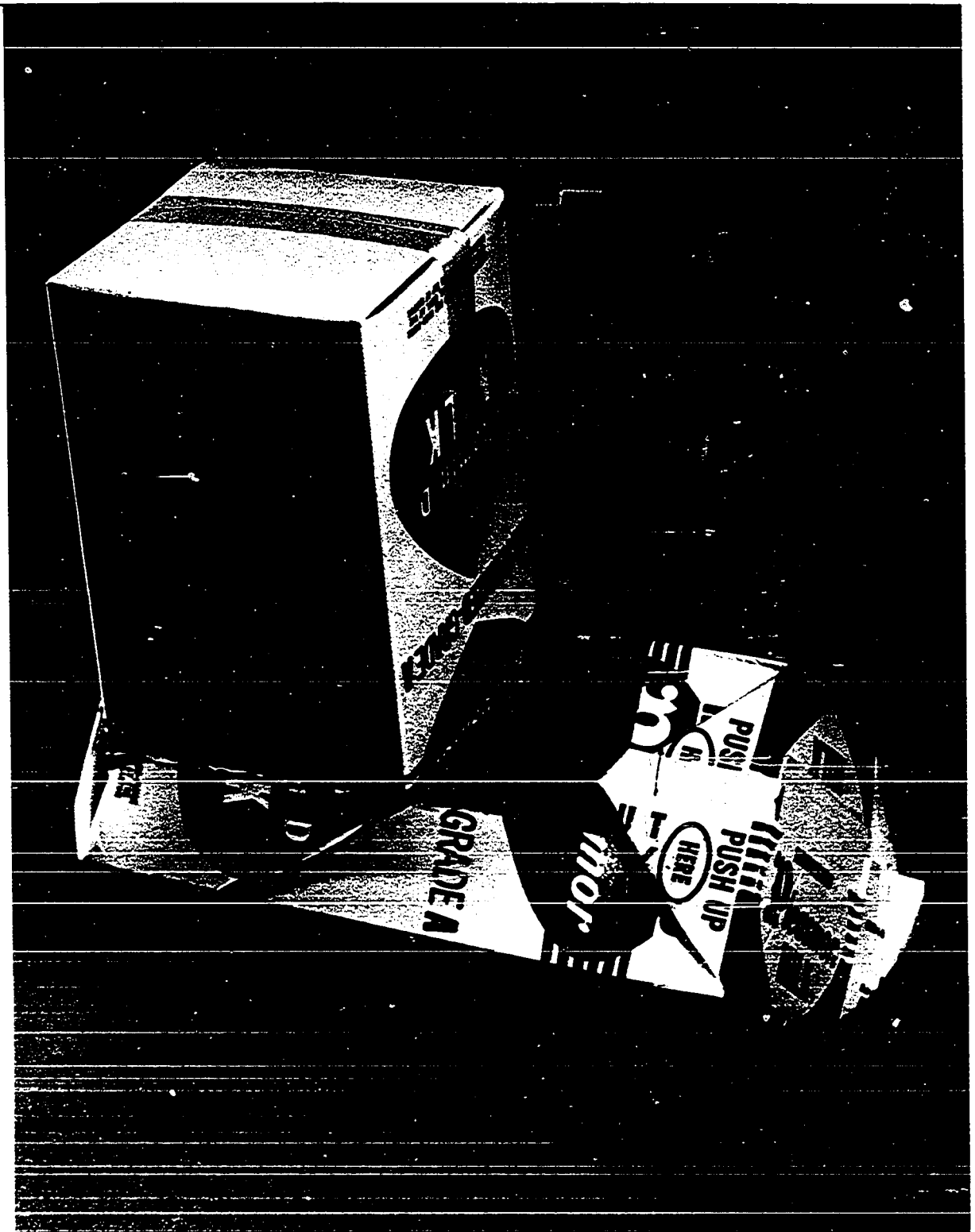
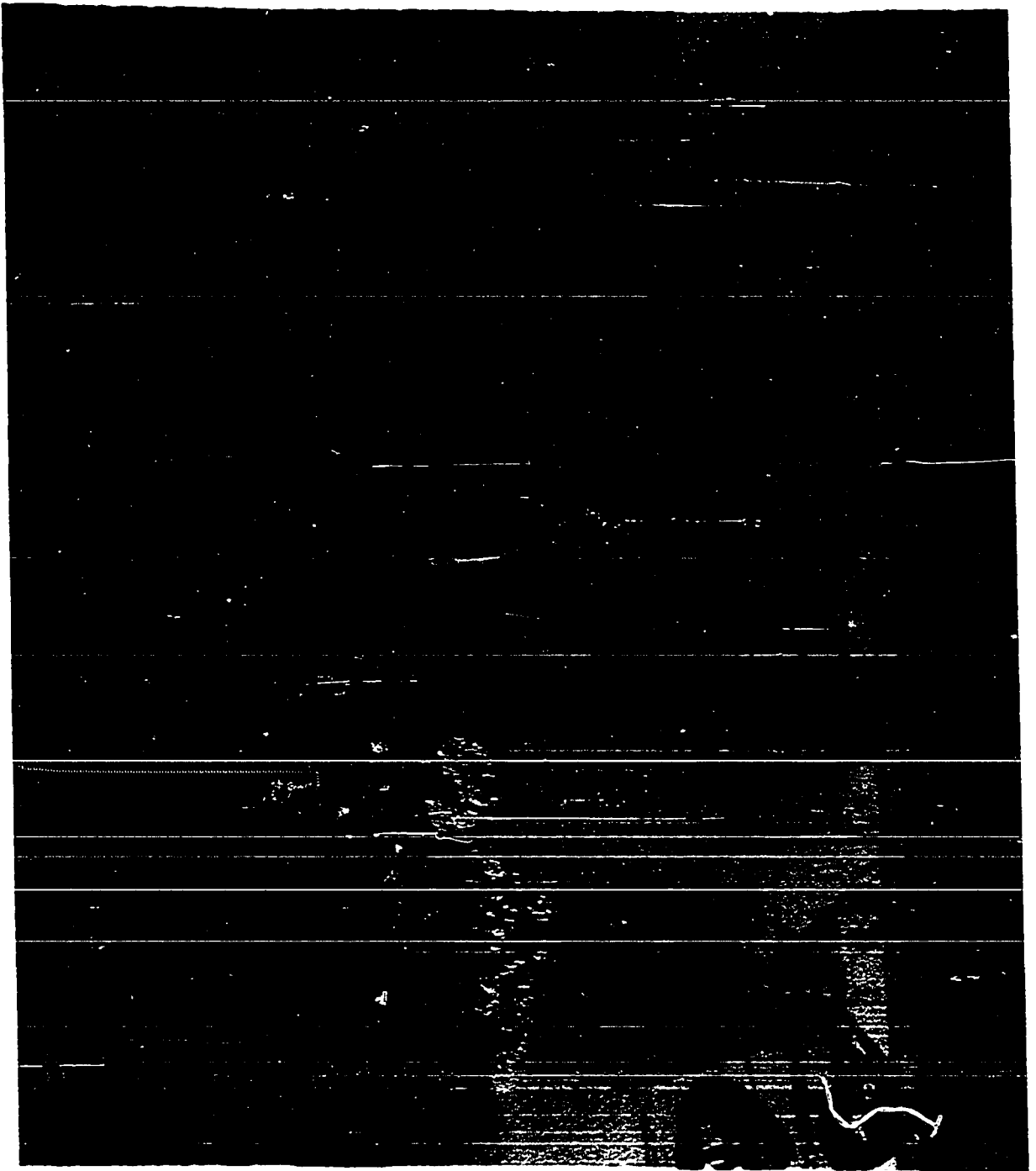


Figure 3. Front view of individually-caged layers with individual feeders. The hoppers prevent the layers from reaching over the other troughs



before, were inserted into the troughs as quickly as possible for each individual bird. In setting up the feeders the help of some additional workers speeded up the operation so that each bird received its feed at about the same time. In all cases the changeover from mass feeding to individual feeding was done in the afternoon to minimize disturbance to the layers and hopefully maintain their normal feeding schedule.

Although the feeders were all made from the same pattern, individual differences in the manner of feeding prevented some feeders from functioning as well as others. This made it necessary to inspect rapidly all the feeders each morning and to adjust the opening of the hoppers showing malfunction. Feeders accumulating too much feed in the trough and leading to possible spillage were also adjusted. However, spillage was mainly controlled because feed beaked out of the carton hopper was caught by the metal trough and therefore could be fed back to the same bird. Fortunately, most of the feeders operated normally and without any special adjustment. About six days after the start of the feeding test, the feeders were inspected daily. Hoppers that were nearly empty were replaced with another containing another full complement of 1200 grams of feed weighed-in a day before. For the final week of the 28-day feeding test, only 400 to 800 grams of feed were added to minimize the feed weighed back. On the 28th day, the feed

remaining in the hopper was emptied into the carton trough which was then inserted back into the hopper. Each feeder was identified by cage number. The leftover feed was then stored in one corner of the laying house until weighed the following day. Meanwhile, the birds were returned to a mass feeding regime after the individual feeders were removed.

The instrument for weighing the feed placed in the carton hoppers was a Net Weigher Model 610N¹. From six to eight 1200-gram feed rations could be weighed per minute with this scale each with a sensitivity of ± 4 grams. The amount of feed desired for filling the hoppers could be pre-set by making a simple mechanical adjustment on the scale. To weigh back the leftover feed, an electric balance was used with readings rounded to the nearest whole gram.

¹Manufactured by the Exact Weight Scale Co., Columbus Ohio.

STATISTICAL PROCEDURES

Regression Analyses of Feed Consumption

Test of significance of the regression of feed consumption on other economic traits

To test the significance of the contribution of the variation of the different economic traits to the variations in feed consumption the following full regression model was used:

$$F_i = \mu + \beta_1 x_{1i} + \beta_2 x_{2i} + \beta_3 x_{3i} + \beta_4 x_{4i} + \beta_5 x_{5i} + u_i$$

where:

F_i = the feed consumption of the i th layer,

μ = the population mean of feed consumption,

β_k = the partial regression of feed consumption on the k th economic trait,

x_{k_i} = the record on the k th economic trait of the i th individual expressed as a deviation from the population mean for the trait,

u_i = the residual feed consumption.

The different economic traits used as independent variables in the above model were: x_1 = body weight, x_2 = egg mass, x_3 = age at sexual maturity, x_4 = albumen height, and x_5 = specific gravity. The significance of the different regression coefficients were tested by sequentially fitting the variables (Kempthorne, 1952).

Test of significance for the homogeneity of regression of feed consumption on body weight and egg mass

To test whether the regression of feed consumption on body weight and on egg mass were the same in two or more groups of layers, the following full regression model was used:

$$F_{li} = \mu + \sum_{l=1}^t \beta_{1l} x_{1li} + \sum_{l=1}^t \beta_{2l} x_{2li} + u_i .$$

where:

F_{li} = feed consumption of the i th bird in the l th group,

μ = over-all mean performance,

β_{1l} = regression of feed consumption on body weight in the l th group,

β_{2l} = regression of feed consumption on egg mass in the l th group,

t = number of groups,

u_{k_i} = residual feed consumption.

The test of significance for the homogeneity of partial regression coefficients of feed consumption on either egg mass or body weight among different groups was performed sequentially by fitting the full model and the reduced model restricted by the hypothesis of homogeneity and testing the significance of the sum of squares of this difference (Brown, 1970).

Estimation of Phenotypic and Genetic Variances and Covariances

The estimates of phenotypic and genetic variances of the traits were derived from the analysis of variance of the records on traits using the following statistical model:

$$Y_{ijk} = \mu + s_i + d_{ij} + e_{ijk} \quad (28)$$

where:

Y_{ijk} = record on the trait of the kth progeny of the jth dam mated to the ith sire,

μ = population mean of the trait,

s_i = effect of the ith sire,

d_{ij} = effect of the jth dam mated to the ith sire,

e_{ijk} = effect of the kth progeny of the jth dam and ith sire.

For the pure lines, the record for the traits was adjusted for the hatch and ration effects before making the analysis of the above model.

From the analysis of variance of the above statistical model, the phenotypic or genetic covariance between two traits, x and y, were computed from the formula (Kempthorne, 1957):

$$\sigma_{xy} = (\sigma_{x+y}^2 - \sigma_x^2 - \sigma_y^2)/2$$

where:

$$\begin{aligned}\sigma_{xy} &= \text{the covariance between } x \text{ and } y, \\ \sigma_{x+y}^2 &= \text{the variance of the sum of } x \text{ and } y, \\ \sigma_x^2 &= \text{the variance of } x, \\ \sigma_y^2 &= \text{the variance of } y.\end{aligned}$$

The heritability of each trait was computed for sire and for dam components of variance. Hence,

$$h_s^2 = 4\sigma_s^2/\sigma_p^2$$

$$h_d^2 = 4\sigma_d^2/\sigma_p^2$$

where:

h^2 = the heritability based on the components given by subscript

σ_s^2 = sire component of variance

σ_d^2 = dam component of variance

σ_p^2 = phenotypic variance of the trait.

The approximate standard errors used for these heritability estimates were,

$$\text{for } h_s^2: s_h = 4\sigma_{ss}/\sigma_p^2$$

$$\text{for } h_d^2: s_h = 4\sigma_{dd}/\sigma_p^2$$

where:

$$\sigma_{ss} = \sqrt{\frac{2}{K_{ss}^2} \left[\frac{(MS)_s^2}{N_s} + \frac{(MS)_d^2}{N_d} \right]}$$

$$\sigma_{dd} = \sqrt{\frac{2}{K_{dd}^2} \left[\frac{(MS)_d^2}{N_d} + \frac{(MS)_e^2}{N_e} \right]} .$$

$(MS)_s$, $(MS)_d$, $(MS)_e$ are the mean squares for sires, dams and progenies, respectively, with degrees of freedom N_s , N_d and N_e . K_{dd} is the coefficient of the dam component in the dams within sire mean square. Likewise, K_{ss} is the coefficient of the sire component in the sire mean square (Dickerson, 1969).

The genetic correlations between traits x and y as computed from sire (r_{G_s}), and from dam (r_{G_d}) components are given by

$$r_{G_s} = \sigma_{s_{xy}} / \sqrt{\sigma_{s_x}^2 \sigma_{s_y}^2}$$

$$r_{G_d} = \sigma_{d_{xy}} / \sqrt{\sigma_{d_x}^2 \sigma_{d_y}^2}$$

where $\sigma_{s_{xy}}$ and $\sigma_{d_{xy}}$ are, respectively, the dam and sire covariance components; $\sigma_{s_x}^2$, $\sigma_{s_y}^2$ are the sire components of variance, $\sigma_{d_x}^2$ and $\sigma_{d_y}^2$ are the dam components of variance for traits x and y.

The phenotypic correlation between traits x and y were computed from simple product moment correlation method.

Genetic Analysis of Residual Feed Consumption

The residual feed consumption (u_i) was obtained by

$$u_i = F_i - \hat{F}_i$$

where:

F_i = feed consumption record of the ith individual,

$\hat{F}_i = \hat{\mu}_F + \hat{\beta}_1(W_i - \bar{w}) + \hat{\beta}_2(M_i - \bar{m})$; the predicted feed consumption of the ith individual from a least square regression equation,

$\hat{\mu}_F$ = estimated mean feed consumption,

$\hat{\beta}_1$ = estimate of the partial regression of feed consumption on body weight (W) with mean \bar{w} ,

$\hat{\beta}_2$ = estimate of the partial regression of feed consumption on egg mass (M) with mean \bar{m} .

To determine whether there is some genetic variation in the residual, analysis of variance was made on the residual using the hierarchal model presented in (28).

RESULTS

Cost of Individual Feed Consumption Records

The approximate number of pullets actually fed per month and the corresponding cost of labor incurred for individual feeding and feeder construction are shown in Table 1.

Table 1. Cost of an individual feed consumption record

Item	Actual	Modified
Approximate number of individuals fed per month	1700	2000
Cost of labor for feeding	\$600	\$600
Assembly cost of individual feeders	\$100	\$ 50
Total cost of individual feed consumption per month	\$700	\$650
Cost of individual feed consumption record per bird per month	\$0.41	\$0.32

It should be pointed out that different techniques of feeding and recording were tried as the feeding tests were in progress. Most of the cost of the individual feeding hoppers was labor since the milk cartons used for constructing were bought at a small price. The cost of the automatic weighing machine, considered as fixed cost, was not included in the study. At the end of the feeding test, it was felt that

slightly more birds than actually tested in the present experiment, could have been included without much difficulty and the cost of assembling the feeders could have been lowered if certain precautions (e.g., debeaking and proper trough placement) were taken before the feeding test. Taking these factors into consideration, the estimated cost of the individual feed consumption record was modified as shown in Table 1.

Means and Standard Deviations of the Economic Traits

The means and standard deviations of the traits measured and the number of survivors in the lines and crosses fed individually for 8 weeks are presented in Table 2. The means of lines A and B differed significantly for all traits observed. Line A was heavier in body weight, produced larger and more eggs and consumed significantly more feed than line B within the 8-week feeding test period. Although each line was represented by three hatches, line A started laying about 18 days earlier than line B. This marked difference in age at first egg had been recognized in previous generations as a consistent line effect. Egg quality, in terms of albumen height and specific gravity, was slightly higher in line B than line A. These differences indicate substantial genetic diversity between the lines.

Table 2. Means and standard deviations of traits and number of pullets under the 8-week feeding test

Traits	Lines and crosses			
	A	B	AB	BA
Body weight (gm)	1551 \pm 176	1441 \pm 167	1570 \pm 163	1590 \pm 168
Egg mass (gm)	1974 \pm 559	1550 \pm 582	2562 \pm 347	2412 \pm 443
Feed consumption (gm)	5986 \pm 720	5330 \pm 632	5838 \pm 645	5667 \pm 676
Age at first egg (days)	152.46 \pm 13.54	170.44 \pm 12.85	153.71 \pm 13.48	160.72 \pm 16.88
Albumen height (mm)	47.16 \pm 6.99	48.73 \pm 6.94	45.02 \pm 5.22	41.42 \pm 4.78
Specific gravity (%)	74.10 \pm 5.09	77.99 \pm 4.83	74.09 \pm 4.76	76.81 \pm 4.38
Number of pullets	573	215	471	649

Crosses AB and BA also differed significantly for the various traits. Cross AB was lighter in body weight, started laying eggs 7 days earlier, produced more egg mass and consumed more feed than cross BA. Cross AB also had higher mean albumen height but lower mean specific gravity of eggs.

Since the pure lines were hatched later and housed separately from the crosses, a strictly valid comparison between their performance was not possible even though the traits were measured at about the same age and over the same period. The crosses exceeded the pure lines by 56 grams in body weight, produced 600 grams more egg mass but consumed only 94 grams more feed than the pure lines. In fact, line A although lighter in weight and producing less egg mass than either crosses, consumed 224 grams more feed than the average of the two crosses. The crosses averaged 0.12 more grams of egg mass per gram of feed consumed than the pure lines. The higher performance of the crosses is undoubtedly a consequence of the hybrid vigor resulting from crossing these two genetically diverse pure lines.

The means and standard deviations of body weight, egg mass and feed consumption of the 303 pullets in line A individually fed for 24 weeks are presented in Table 3.

Table 3. Means and standard deviations of the traits observed in line A pullets under 24-week test

Traits	Mean \pm standard deviation (gm)
Body weight	1520 \pm 168
Egg mass	5704 \pm 1757
Feed consumption	17160 \pm 2385

Regression Analyses of Feed Consumption

Partial regression of feed consumption on various economic traits

The partial regressions of feed consumption on body weight, egg mass and age at first egg, albumen height and specific gravity of eggs in each of the four lines are shown in Table 4.

In all lines and crosses, the regressions of feed consumption on body weight and on egg mass were highly significant. Age at first egg apparently had little, if any, effect on the variation of feed consumption. The regression of feed consumption on albumen height was significant at .01 probability level in cross AB. The regression of feed consumption on specific gravity of eggs was highly significant in both line B and cross AB.

Table 4. Partial regression coefficients of 8-week feed consumption on different traits as independent variables of a multiple regression equation

Variable	Lines and crosses			
	A	B	AB	BA
Body weight (gm)	1.9168**	1.7161**	1.8216**	1.6017**
Egg mass (gm)	0.5070**	0.5293**	0.6996**	0.8082**
Age at first egg (days)	0.9716	-3.4287	0.3870	-0.9186
Albumen height (mm)	-1.5890	1.1505	-12.1598**	-6.9227
Specific gravity (%)	-6.3558	-19.9251*	-17.5489**	-0.3274

** P < .01.

* P < .05.

Table 5 gives the percentage contribution of each trait to the sum of squares of feed consumption when it was included as an independent variable in the regression model. In general, the joint contribution of the five independent variables accounted for 40 to 51 percent of the total sum of squares of feed consumption in any line. For example, including specific gravity as an independent variable accounted for an additional 1.88 and 1.61 percent of the total sum of squares of feed consumption in line B and cross AB, respectively. Including albumen height as an independent variable in cross AB, added only 0.93 percent in the total sum of squares of feed consumption of birds in that line.

Tables 6, 7, 8 and 9 give the analyses of variance of feed consumption for the different lines and crosses. The joint contribution of body weight and egg mass as independent variables and the additional contribution of age at first egg and egg quality traits to the sum of squares of feed consumption is also shown in the tables. The difference $Q_2 - Q_3$, represents the sum of squares of feed consumption jointly accounted for by including body weight and egg mass as independent variables in the regression equation; $Q_1 - Q_2$ represents the sum of squares of feed consumption accounted for by including age at first egg and the two egg quality traits in the regression equation.

Age at first egg and the egg quality traits together accounted for a significant component variance in feed

Table 5. Percent sum of squares of 8-week feed consumption due to regression on the different independent variables in the multiple regression equation

Variable	Lines and crosses			
	A	B	AB	BA
Body weight	20.65	19.18	20.46	15.85
Egg mass	11.93	11.41	13.75	25.68
Age at first egg	0.02	0.28	0.06	0.05
Albumen height	0.02	0.00	0.93	0.23
Specific gravity	0.16	1.88	1.61	0.00
All variables	39.77	50.68	43.49	46.46

consumption in line B and cross AB. In line A and cross BA, age at first egg and the two egg quality traits accounted for only 0.20 and 0.32 percent of the total sum of squares of feed consumption, respectively. Neither of these was statistically significant.

When body weight and egg mass were included as independent variables in the regression model, their combined contribution to the total sum of squares of feed consumption ranged from 38.70 to 46.71 percent for the various lines and crosses. Thus, residual effects accounted for about 53 to 61 percent of the total sum of squares in feed consumption.

Table 6. Analysis of variance of 8-week feed consumption test on line A as influenced by hatch (h), ration (r), and the regression on body weight (W), egg mass (M), age at first egg (A), and specific gravity (S) and albumen height (H) of eggs

Source of variation ^a	d.f.	S.S.	M.S.	Percent of total S.S.
Total	572	297,296,678		100.00
$Q_1 = R(r, h, b_W, b_M, b_A, b_H, b_S)$	8	121,011,082	15,126,385**	40.70
$Q_2 = R(r, h, b_W, b_M)$	5	120,410,707	24,082,141**	40.50
$Q_3 = R(r, h)$	3	5,341,712	1,780,570**	1.80
$Q_2 - Q_3$	2	115,068,995	57,534,497**	38.70
$Q_1 - Q_2$	3	600,375	200,125	0.20
Residual	564	176,285,595	312,563	59.30

^a Q_i = effect due to fitting the various factors in the model.

** $P < .01$.

Table 7. Analysis of variance of 8-week feed consumption test on line B as influenced by hatch (h), ration (r) and the regression of body weight (W), egg mass (M), age at first egg (A), specific gravity (S) and albumen height (H) of eggs

Source of variation ^a	d.f.	S.S.	M.S.	Percent of total S.S.
Total	214	85,554,238	-	100.00
$Q_1 = R(r, h, b_W, b_M, b_A, b_H, b_S)$	8	44,527,467	-	52.04
$Q_2 = R(r, h, b_W, b_M)$	5	42,326,887	-	49.07
$Q_3 = R(r, h)$	3	2,363,493	787,831*	2.76
$Q_2 - Q_3$	2	39,963,294	19,981,697**	46.71
$Q_1 - Q_2$	3	2,200,580	733,526*	2.57
Residual	206	41,026,770	199,159	47.96

^a Q_i = effect due to fitting the various factors in the model.

* $P < .05$.

** $P < .01$.

Table 8. Analysis of variance of 8-week feed consumption test on cross AB as influenced by body weight (W), egg mass (M), age at first egg (A), specific gravity (S) and albumen height (H) of eggs

Source of variation ^a	d.f.	S.S.	M.S.	Percent of total S.S.
Total	470	196,084,336		100.00
$Q_1 = R(b_W, b_M, b_A, b_H, b_S)$	5	85,227,615	17,055,522**	43.49
$Q_2 = R(b_W, b_M)$	2	80,742,427	40,371,213**	41.18
$Q_1 - Q_2$	3	4,535,185	1,511,728*	2.31
Residual	465	110,806,724	238,294	56.51

^a Q_i = effect due to fitting the various factors in the model.

** $P < .01$.

* $P < .05$.

Table 9. Analysis of variance of 8-week feed consumption test on cross BA as influenced by body weight (W), egg mass (M), age at first egg (A), specific gravity (S) and albumen height (H) of eggs

Source of variation ^a	d.f.	S.S.	M.S.	Percent of total S.S.
Total	648	296,810,447		100.00
$Q_1 = R(b_W, b_M, b_A, b_H, b_S)$	5	137,968,923	27,593,784**	46.48
$Q_2 = R(b_W, b_M)$	2	137,011,714	68,505,857**	46.16
$Q_1 - Q_2$	3	957,209	319,069	.32
Residual	643	158,841,523	264,648	53.52

^a Q_i = effect due to fitting the various factors in the model.

** $P < .01$.

* $P < .05$.

Because age at first egg and the two egg quality traits accounted for only a small portion of the variance of feed consumption, only body weight and egg mass were retained as the independent variables in further regression analyses of feed consumption.

Effect of genotype on the regression of feed consumption on body weight and egg mass

The regressions of feed consumption on body weight and on egg mass on each of the two pure lines and each of the two cross lines are given in Table 10. Line A and cross AB consumed somewhat more feed for body weight maintenance but consumed slightly less feed per gram of egg mass than line B and cross BA, respectively. The analyses of variance in Tables 11 and 12 however, indicated no significant difference in the regression coefficients for body weight and egg mass between the two pure lines or between the two cross lines.

It has already been shown (Table 2) that the difference in mean feed consumption between lines A and B and between cross lines AB and BA were significant. In Tables 11 and 12 however, the sum of squares due to fitting lines or crosses after adjusting for the regression on body weight and egg mass were not significant. This seems to demonstrate that the difference in feed consumption between the pure lines and between the crosses is a reflection of the differences in body weight and egg mass.

Table 10. Regressions of feed consumption on body weight and on egg mass in lines and crosses

Lines and crosses	Regression coefficients	
	b_W^a	b_M^b
A	1.9096 \pm 0.1288	0.4988 \pm 0.0418
B	1.6535 \pm 0.2227	0.5779 \pm 0.0814
Pure lines	1.8483 \pm 0.1114	0.5146 \pm 0.372
AB	1.7991 \pm 0.1416	0.7180 \pm 0.0666
BA	1.5878 \pm 0.1157	0.8072 \pm 0.0451
Crosses	1.6686 \pm 0.0895	0.7801 \pm 0.0379
Pure lines and crosses	1.7618 \pm 0.0702	0.6447 \pm 0.0247

^aGrams of feed per gram of body weight for 8 weeks.

^bGrams of feed per gram of egg mass.

The regressions of feed consumption on body weight and egg mass between the pure lines and the crosses, also given in Table 10, were significantly different at the $P < .01$ level. Since the pure lines were housed differently from the crosses, however, these differences could not be attributed to either genetic or environmental effects.

The regression of feed consumption on body weight and egg mass as influenced by ration

The effects of two rations differing in percent protein (14 and 19 percent) on the regression of feed consumption on

Table 11. Analysis of variance of feed consumption as influenced by line (ℓ), ration (r), hatch (h), and interactions and body weight (W)^a, and egg mass (M)^b

Source of variation	d.f.	S.S.	M.S.
Total	788	484,475,129	-
$Q_1 = R(\mu, \ell, r, h, (\ell r), (\ell h), b_{W_A}, b_{W_B}, b_{M_A}, b_{M_B})$	12	264,300,768	-
$Q_2 = R(\mu, \ell, r, h, (\ell r), (\ell h), b_W, b_M)$	10	263,876,435	-
Between lines	1	2,742	2,742
Between rations	1	673,638	673,638
Between hatches	2	1,358,945	679,472
Line x ration	1	769,943	769,943
Line x hatch	2	3,225,305	1,612,652**
$Q_1 - Q_2$	2	424,333	212,166
Residual	766	220,174,360	283,729

55

^a b_{W_A} or b_{W_B} is the regression on W in line A or line B, and b_W is the regression disregarding lines.

^b b_{M_A} or b_{M_B} is the regression on M in line A or line B, and b_M is the regression disregarding lines.

** $P < .01$.

Table 12. Analysis of variance of feed consumption as influenced by cross lines (ℓ) and by body weight (W)^a and egg mass (M)^b

Source of variation	d.f.	S.S.	M.S.
Total	1120	522,648,696	-
$Q_1 = R(\mu, \ell, b_{W_{AB}}, b_{W_{BA}}, b_{M_{AB}}, b_{M_{BA}})$	6	247,438,399	-
$Q_2 = R(\mu, \ell, b_W, b_M)$	4	246,871,119	-
Between crosses	1	698	698
$Q_1 - Q_2$	2	567,280	283,640
Residual	1114	275,210,296	247,046

^a $b_{W_{AB}}$ or $b_{W_{BA}}$ is the regression on W in cross AB or cross BA, and b_W is the regression disregarding cross line.

^b $b_{M_{AB}}$ or $b_{M_{BA}}$ is the regression on M in cross AB or cross BA, and b_M is the regression disregarding cross line.

body weight and egg mass in lines A and B are presented in Table 13. The analysis of variance of the regression of feed consumption for each line are presented in Tables 14 and 15.

In line A, the group fed the 19 percent protein diet consumed 0.72 grams more feed to maintain a gram of body weight in 8 weeks than the group fed the 14 percent protein diet. But the group fed the 19 percent diet consumed 0.14 grams less feed to produce a gram of egg than the group fed the 14 percent diet. The only significant difference between rations was the regression of feed consumption on body weight ($P < .01$).

In line B, ration differences had no effect on either regression coefficient. It appeared that the same amount of feed for body weight maintenance and for egg mass output was required on either ration.

Estimates of Phenotypic and Genetic Parameters of Body Weight, Egg Mass and Feed Consumption

Due to the very limited number of observations in line B, only the observations in line A and crosses AB and BA were used to estimate the phenotypic and genetic parameters of the various economic traits.

Coefficients of variation and phenotypic correlations

The coefficients of variation of body weight, egg mass and feed consumption for line A and crosses AB and BA are presented in Table 16. The phenotypic correlations between these traits

Table 13. Regressions of feed consumption on body weight (W)^a and egg mass (M)^b in two rations

Regression coefficient	Lines	
	A	B
$b_{W(14)}$	1.5293 \pm .1941	1.6751 \pm .2809
$b_{W(19)}$	2.2531 \pm .1841	1.6594 \pm .2610
b_W	1.9097 \pm .1350	1.6535 \pm .1903
$b_{M(14)}$	0.5770 \pm .0622	0.6475 \pm .0948
$b_{M(19)}$	0.4325 \pm .0593	0.5208 \pm .0874
b_M	0.4988 \pm .0438	0.5779 \pm .0696

^a $b_{W(14)}$ or $b_{W(19)}$ is the regression on W in 14% protein or 19% protein ration, and b_W is the regression disregarding ration.

^b $b_{M(14)}$ or $b_{M(19)}$ is the regression on M in 14% protein or 19% protein ration, and b_M is the regression disregarding ration.

are given in Table 17.

The coefficients of variation of body weight and feed consumption were consistently lower than those of egg mass. The coefficients of variation of all three traits, however, were noticeably higher in line A than in the crosses. This is to be expected because the performance of crosses usually tend to be more uniform than pure lines. The difference between the

Table 14. Analysis of variance of the effect of ration on the regressions of feed consumption on body weight (W) and egg mass (M) in line A

Source of variation	d.f.	S.S.	M.S.
Total	573	297,406,900	-
$Q_1 = R(\mu, r, h, b_{W(14)}, b_{W(19)}, b_{M(14)}, b_{M(19)})$	8	123,450,377	-
$Q_2 = R(\mu, r, h, b_W, b_{M(14)}, b_{M(19)})$	(7)	121,175,471	-
$Q_3 = R(\mu, r, h, b_W, b_M)$	(6)	120,540,841	-
Between rations	1	1,585,720	1,585,720**
Between hatches	2	2,132,461	1,066,230
$Q_1 - Q_3$	2	2,909,535	1,454,767**
$Q_1 - Q_2$	1	2,274,905	2,274,905**
$Q_2 - Q_3$	1	634,629	634,629
Residual	565	173,956,522	307,887

**P < .01.

Table 15. Analysis of variance of the effect of ration on the regressions of feed consumption on body weight (W) and egg mass (M) in line B

Source of variation	d.f.	S.S.	M.S.
Total	215	182,153,829	-
$Q_1 = R(\mu, r, h, b_{W(14)}, b_{W(19)}, b_{M(14)}, b_{M(19)})$	8	139,099,363	-
$Q_2 = R(\mu, r, h, b_W, b_{M(14)}, b_{M(19)})$	(7)	139,099,016	-
$Q_3 = R(\mu, r, h, b_W, b_M)$	(6)	138,845,527	-
Between rations	1	32,433	32,433
Between hatches	2	2,091,328	1,045,664**
$Q_1 - Q_3$	2	253,836	126,918
$Q_1 - Q_2$	1	346	346
$Q_2 - Q_3$	1	253,489	253,489
Residual	207	43,054,465	207,992

** $P < .01$.

Table 16. Coefficients of variation of traits

Traits	Line and crosses			Mean	
	A		AB		
	8-week test	24-week test			
Body weight	0.11	0.11	0.10	0.10	.10
Egg mass	0.28	0.31	0.13	0.18	.22
Feed consumption	0.12	0.14	0.11	0.11	.12

Table 17. Phenotypic correlations between traits

Traits	Line and crosses				Mean
	A		AB	BA	
	8-week test	24-week test			
Body wt. x egg mass	0.11**	0.04	0.15**	0.09**	0.10**
Body wt. x feed consumption	0.49**	0.60**	0.52**	0.44**	0.51**
Egg mass x feed consumption	0.43**	0.46**	0.46**	0.55**	0.48**

** P < .01.

coefficients of variation for all three traits observed in the 8-week and 24-week test periods in line A were small.

The phenotypic correlations between body weight and egg mass, ranging from 0.04 to 0.15, were consistently lower than those between feed consumption and body weight or between feed consumption and egg mass. The correlations between feed consumption and body weight and between feed consumption and egg mass were about the same.

Heritabilities and genetic correlations

The number of degrees of freedom in the analyses of variance used for estimating the different components of variance is given in Table 18. For all pullets in 8-week feeding test, the analyses of variance were hierarchical: between sires, dams/sire and progenies/dam. For the pullets in line A in the 24-week feeding test however, the analysis was between sires and between progenies/sire only. As a rule, the number of progenies within families and the number of dams mated per sire were unequal.

The estimates of heritability from the sire and dam components of variance are given in Tables 19 and 20. The estimates for body weight were consistently higher than those for either egg mass or feed consumption. On the other hand, the estimates for feed consumption were consistently higher than those for egg mass. The residual feed component had the lowest heritability estimate.

Table 18. Degrees of freedom for the various sources of variation in the analyses of variance

Source of variation	Degrees of freedom for line and crosses			
	A		AB	BA
	8-week test	24-week test ^a		
Sires	27	27	24	29
Dams/sires	142	-	180	236
Error	403	275	266	383
Total	572	302	470	648

^aAnalysis was based on sire classification only.

The heritability of body weight based on the sire component of variance was about equal to the estimate based on the dam component of variance. The heritability estimates of egg mass, feed consumption and of the residual based on the dam components of variance however, were consistently higher than the corresponding heritability estimates using the sire components of variance. This suggests that dominance may be important for these traits.

The genetic correlations between the traits, as estimated from the sire and dam components of variance and covariance are given in Tables 21 and 22. On the average, the estimated genetic correlation between feed consumption and body weight

Table 19. Heritabilities of traits estimated from sire components of variance

Traits	Line and crosses				Average ^a
	A		AB	BA	
	8-week test	24-week test			
Body weight	0.66 ± 0.25	0.70 ± 0.27	0.77 ± 0.28	0.58 ± 0.22	0.68 ± 0.18
Egg mass	0.04 ± 0.08	0.14 ± 0.12	0.03 ± 0.09	0.03 ± 0.06	0.06 ± 0.05
Feed consumption	0.20 ± 0.12	0.25 ± 0.16	0.19 ± 0.13	0.20 ± 0.11	0.20 ± 0.10
Residual	0.00 ± 0.06	-- ^b	0.00 ± 0.09	0.03 ± 0.06	0.01 ± 0.00

^aStandard errors were based on an approximation given by Robertson (1959) using 649 as the number of individuals in the sample.

^bNo estimate.

Table 20. Heritabilities of traits estimated from dam components of variance

Traits	Line and crosses				Average ^a
	A		AB	BA	
	8-week test	24-week test			
Body weight	0.54 ± 0.18	-- ^b	0.50 ± 0.21	0.94 ± 0.20	0.66 ± 0.18
Egg mass	0.29 ± 0.19	--	0.39 ± 0.21	0.17 ± 0.20	0.28 ± 0.12
Feed consumption	0.42 ± 0.20	--	0.61 ± 0.25	0.38 ± 0.20	0.47 ± 0.15
Residual	0.11 ± 0.18	--	0.67 ± 0.26	0.09 ± 0.19	0.29 ± 0.21

^aStandard errors were based on an approximation given by Robertson (1959) using 649 as the total number of individuals in the sample.

^bNo estimate.

Table 21. Genetic correlations between traits estimated from sire components of variance and covariance

Traits	Line and crosses				Average
	A		AB	BA	
	8-week test	24-week test			
Body wt. x egg mass	1.00	-0.04	0.92	0.50	0.60
Body wt. x feed consumption	0.96	0.82	0.99	1.00	0.94
Egg mass x feed consumption	1.00	0.44	0.94	0.02	0.60
Body wt. x residual	-- ^a	-- ^b	-0.46	1.00	0.27
Egg mass x residual	-- ^a	-- ^b	-0.41	-- ^a	-0.41

^aNot estimated due to negative component of variance.

^bNo estimate.

Table 22. Genetic correlations between traits estimates from dam components of variance and covariance

Traits	Line and crosses				Average
	A		AB	BA	
	8-week test	24-week test			
Body wt. x egg mass	-0.07	-- ^a	0.01	0.40	0.11
Body wt. x feed consumption	0.81	--	0.58	0.74	0.71
Egg mass x feed consumption	0.17	--	0.21	0.91	0.43
Body wt. x residual	0.68	--	0.21	-0.07	0.27
Egg mass x residual	-0.52	--	-0.11	0.85	0.22

^aNo estimate.

was higher than that between feed consumption and egg mass. The genetic effects of body weight and egg mass were also positively correlated. The estimates of genetic correlation between the residual and body weight and egg mass varied widely. However, due to the consistently low heritability estimate for the residual, ranging from 0.00 to 0.03, the true genetic correlations are probably very close to zero also. In view of the very limited number of degrees of freedom, however, the estimates of these parameters would have rather large sampling errors.

Typically, the estimates of the heritability of adult body weight of layers published in the literature are close to 0.6 (Kinney, 1969). The relatively low estimates of heritability of egg mass obtained in this study agrees with the estimates obtained by other workers (Waring et al., 1962; Casey, 1970).

As yet, there is no formally published literature (of which I am aware) on genetic studies of feed consumption of adult laying hens. However, Von Krosigk and Pirchner (1964), presented such a study to a poultry breeders meeting in England. From data on 545 cross line pullets from two White Leghorn lines, they estimated the heritability of feed consumption to be 0.15 and the respective genetic correlations with body and egg mass were estimated to be 0.62 and 0.24. These estimates were slightly lower than those obtained in the present study.

Economic Value of Body Weight, Egg Mass
and Feed Consumed

Evaluation of the expected gain in income over feed cost by selection requires information on the prices of eggs, poultry and feed. Table 23 presents the economic value for each unit of the traits used in this study.

Table 23. Annual average prices of cull hens, eggs and feed in 1969^a

Item	Unit	Value per unit (cents)
Cull hens	lb	9.70
	gm	.019
Eggs	doz	40.00
	egg	3.33
	gm	.058 ^b
Layer feed	lb	4.00
	gm	.008

^aBased on 1969 prices of eggs, feed and cull hens reported by the U.S. Department of Agriculture, Economic Research Service (1970).

^bAssumes one dozen eggs = 24 ounces.

In this study, each trait was measured in grams and the units of economic weight for each trait in the selection indexes were specified in cents per gram.

Expected Gain from the Different Selection Indexes

In the theory section, four different selection indexes were proposed. These can be characterized according to the variable they are designed to maximize and the kind of information required. In this frame of reference, the selection indexes are described as follows:

<u>Selection index</u>	<u>Variable maximized</u>	<u>Information required for the index</u>	<u>Descriptive notation of index</u>
Y_1	IF	W, M, F	$Y(IF:W, M, F)$
Y_2	IF	W, M, r_G	$Y(IF:W, M, r)$
Y_3	IF	W, M, b_p	$Y(IF:W, M, b)$
Y_4	I	W, M	$Y(I:W, M)$

where:

IF = income over feed cost

I = total income

W = body weight

M = egg mass

F = feed consumption

$r_G = r$ = genetic correlations between F and W, and between F and M

$b_p = b$ = phenotypic partial regressions of F on W and on M.

In an attempt to aid the reader in easily distinguishing the selection indexes, Y_1 through Y_4 , each is given a set of subscripts designating the objective which the index is designed to maximize (before the colon of the subscript) and the combination of records and information required to obtain the index (after the colon of the subscript). The corresponding change for each index is given in the above table. As an example from the table we read $Y_1 = Y(\text{IF}: W, M, F)$ as the index which maximizes income over feed cost (IF) when information on body weight (W), egg mass (M) and feed consumption (F) is used in constructing the index. Likewise, $Y_4 = Y(\text{I}: W, M)$ means the index which maximizes total income (I) from information only on W and M. This descriptive notation will be used consistently when referring to the different selection indexes in the text of the succeeding sections.

The expected gain in income over feed cost from the selection indexes were evaluated according to Equations 24, 25, 26 and 27. For all computations of the expected gain from selection, a selection intensity of $i = 1.4$, equivalent to selecting 20 percent of the population as parents of the next generation, was used. Although i was chosen arbitrarily, it

serves only as a constant in the equations, so that the generality of the results obtained in the relative gains of the selection indexes is not altered.

Expected gain from selection indexes using mass selection

The phenotypic standard deviations and partial regressions used in constructing the different selection indexes are given in Table 24. These standard deviations were obtained as an average of line A and crosses AB and BA. The standard deviations for egg mass and feed consumption were obtained after multiplying the values obtained for the 8-week test by 7 so that the expected gain from selection on the different indexes would be based on a standard 56-week production period. The estimates for the 24-week test were similarly adjusted by multiplying by 2.33. Likewise, the partial regression of feed consumption on body weight estimated from 8-week test was multiplied by 7. Thus, the partial regressions given above specify the grams of feed required to maintain a gram of body weight for the entire 56-week test.

The parameter estimates (phenotypic correlations, genetic correlation and heritability) were obtained by averaging line A and cross lines AB and BA and are given in Tables 17, 19 and 21. These were used in the computations of the selection indexes to estimate the expected gain in income over feed cost for each.

Table 24. Phenotypic standard deviations and partial regressions used in constructing the different selection indexes

Trait	Standard deviation	Partial regression of F
W (gm)	172	12.0094
M (gm)	3354	.6916
F (gm)	4917	-----

Table 25 gives the expected gain in income over feed cost from mass selection using the different selection indexes. The expected gains from the different selection indexes relative to $Y(I:W,M)$ is also given in Table 25.

Table 25. Expected gain from different selection indexes

Criteria	Selection indexes			
	$Y(IF:W,M,F)$	$Y(IF:W,M,r)$	$Y(IF:W,M,b)$	$Y(I:W,M)$
Expected gain (cents)	21.78	20.62	20.61	20.00
Expected gain relative to $Y(I:W,M)$ (%)	109	103	103	100

The highest expected gain in income over feed cost was by selection on index $Y(IF:W, M, F)$ which was 1.16 cents above index $Y(IF:W, M, r)$. This means that the inclusion of feed consumption information in an index is expected to give about 1.16 cents higher returns than by using instead estimates of the genetic correlations of feed consumption with body weight and with egg mass.

The expected gain from $Y(IF:W, M, r)$ was only .01 cents higher than the expected from $Y(IF:W, M, b)$. This very small difference suggests that using partial regressions to predict the breeding value of feed consumption from the breeding value of body weight and egg mass, was no more effective than using the estimates of the corresponding genetic correlations.

The expected gain from $Y(I:W, M)$ was 0.61 cents lower than $Y(I:W, M, b)$. The difference represents the extra gain from using feed consumption in the index estimated from partial regressions of feed consumption on body weight and egg mass.

Effect of family size on the expected gain from different selection indexes

Family selection or sib-testing is widely used in poultry breeding. Individuals are selected on their full-sib and half-sib family mean performance. Sib-selection is particularly applicable to sire selection for sex-limited characters as egg traits.

The heritability of a trait measured by sib-testing is,

$$h_s^2 = \frac{nr}{1 + (n-1)t} h^2$$

where:

n = number of individuals in the family

r = 1/2; genetic correlation between full-sibs

= 1/4; genetic correlation between half-sibs

h^2 = heritability of individual differences

t = phenotypic correlations between the members of full-sib or half-sib families; for full-sibs,

$t = (\sigma_s^2 + \sigma_d^2)/\sigma_p^2$ and for half-sibs, $t = \sigma_s^2/\sigma_p^2$

σ_s^2 = sire component of variance

σ_d^2 = dam component of variance

σ_p^2 = phenotypic variance among individuals.

The influence of family size on the expected gain from the different selection indexes was investigated for the arbitrary cases of 5, 10 and 15 mates per sire with 2, 6 and 10 progenies per dam. The average of the estimated phenotypic and genetic parameters given in Tables 17, 19, 20, 21, 22 and 24 were used to compute the different selection indexes. The computational methods used for constructing the indexes were the same as in mass selection except that for selection by sib-testing, family means were used instead of individual records.

Figures 4 and 5 show the expected gain in income over feed cost from the different selection indexes based on full-sib mean performance, half-sib mean performance, respectively.

The effect of family size on the expected gain in income over feed cost for the different selection indexes can be summarized as follows:

- (a) The expected gain, as averaged over all of the selection indexes increases as the number of progenies per dam and the number of dams per sire increases.
- (b) The value of including actual feed consumption as a variable in the index is enhanced with increasing family size. The relevant comparison here is the difference in expected gain between $Y(IF:W, M, F)$ and $Y(IF:W, M, r)$.
- (c) The difference between the genetic correlations and regression coefficients as used in the index to predict feed consumption from body weight and egg mass, i.e., $(Y(IF:W, M, r) \text{ minus } Y(IF:W, M, b))$, is not influenced by family size.
- (d) Using feed consumption information as estimated by regression, i.e., $Y(IF:W, M, b) \text{ minus } Y(IF:W, M)$, was enhanced by increasing family size.

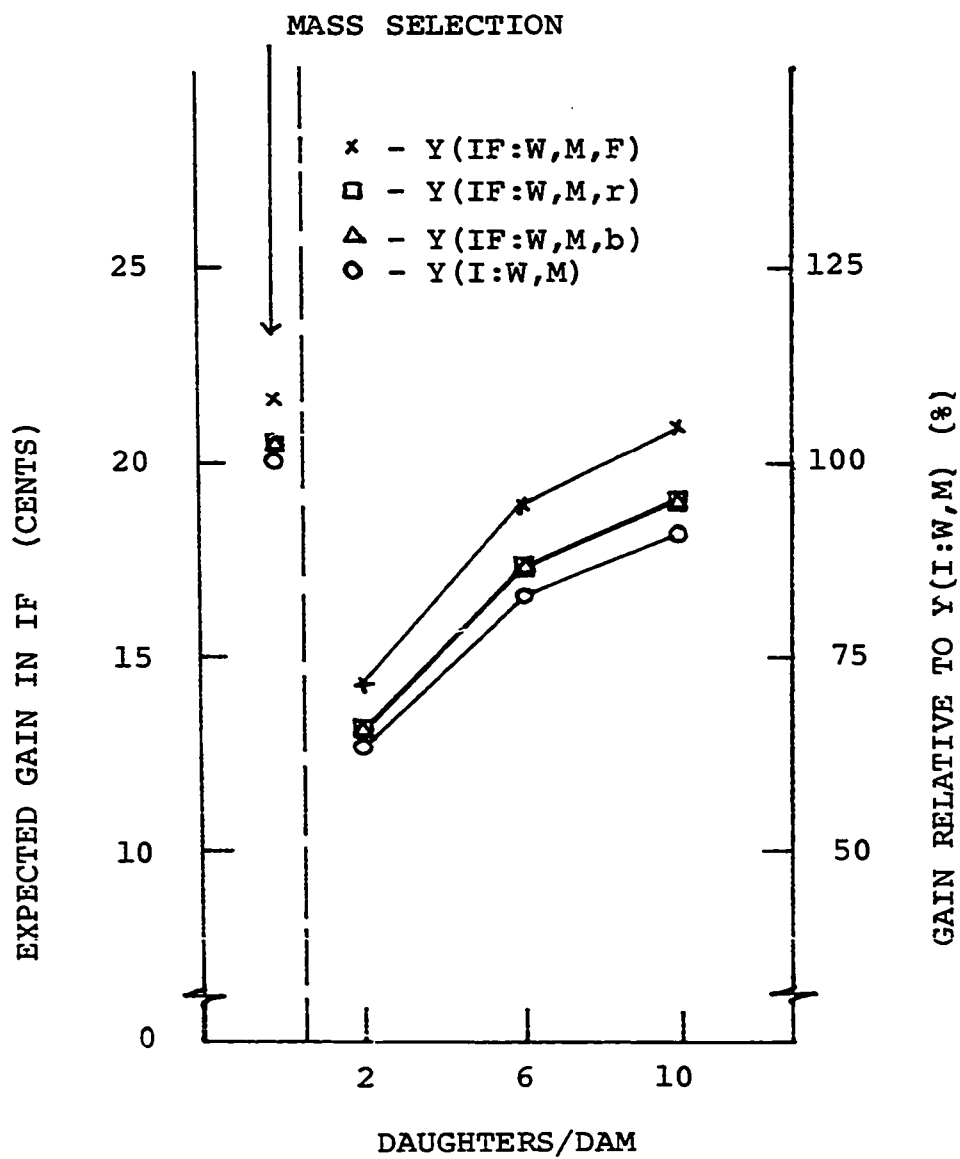


Figure 4. Expected gain from the selection indexes using full-sib selection

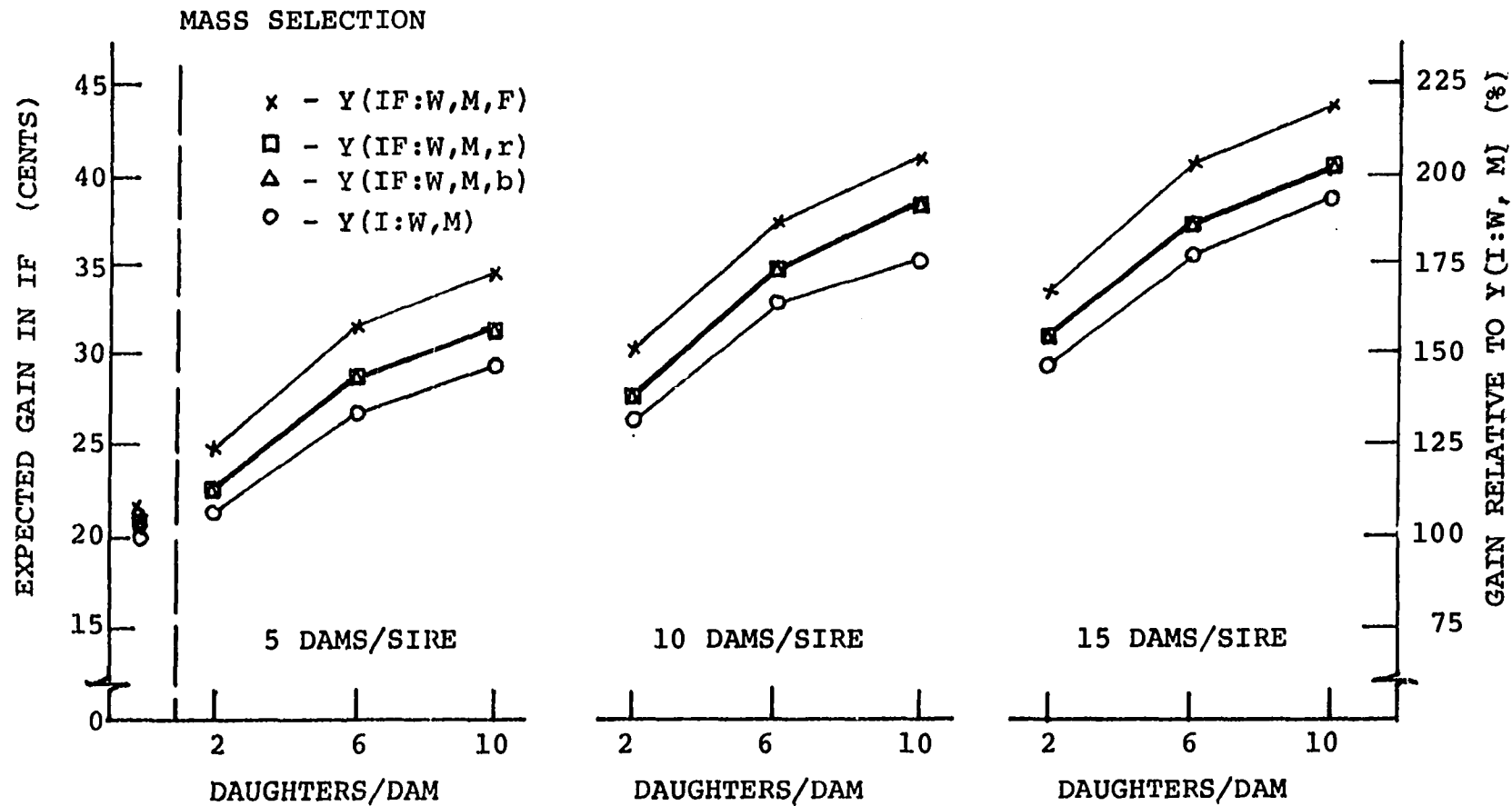


Figure 5. Expected gain from different selection indexes using half-sib selection

Effect of Residual Genetic Variation and Biased
Regression Estimates on the Expected
Gain from Selection Indexes

If feed consumption is a linear function of body weight and egg mass, then the expected genetic value of feed consumption is a linear function of the genetic values of body weight, egg mass and a residual. Based on this premise, formulas for obtaining the heritability of feed consumption and its genetic correlation with body weight and egg mass were derived in the theory section (Equations 8, 9 and 10). Within this linear regression framework, it is possible to evaluate the relative influence of a change in any feed consumption parameter on the efficiency of a given selection index. Also, it is possible to evaluate how much the effectiveness of index $Y(IF:W, M, b)$ is reduced because the partial regressions of feed consumption on body weight and egg mass are biased. In order to determine whether measuring feed consumption is useful in a testing program, the significance of the residual genetic variation as well as the partial regressions of feed consumption on body weight and egg mass are of particular importance.

From both theoretical consideration and the application of the estimated parameters obtained from feeding test, adding a direct measure of feed consumption to a selection program should enhance the expected gain in income over feed cost because it enables the breeder to more accurately evaluate

individual genetic differences in feed consumption including not only the part associated with regression on body weight and on egg mass, but also a part called a residual component attributed to differences in the efficiency of digestion and metabolism. Even if there is no residual genetic variation in feed consumption, its measurement may be justified on the basis that it will improve selection for the two components of efficiency; egg mass and body weight. Hence, if a breeder chooses not to include feed consumption as a variable in a selection index, the question is: how much gain in income over feed cost is he giving up by not taking full advantage of the possible residual genetic variation in feed consumption? On the other hand, if no residual genetic variation exists but the breeder uses an arbitrary regression equation to predict the breeding value of feed consumption from body weight and egg mass, the question is then: how much gain in income over feed cost is he giving up by not taking full advantage of feed consumption used as an auxiliary trait to improve selection for body weight and egg mass?

To evaluate the effect of the genetic variation of residuals and the bias of estimating feed consumption from a regression equation in terms of the expected gain from different selection indexes, several arbitrary values of the heritability of egg mass and its genetic correlation with body weight were chosen for study. This was done in order to examine the

possible effects of large sampling errors on the observed parameter estimates from the present experiment and from the estimates recorded by other workers. The range of values chosen for the genetic parameters of each independent trait plus the residual used in this part of this study are given in Table 26. These are thought to be realistic in the sense that the probability of the confidence interval represented by the range should be high (but really not known). Because we know that the heritability of body weight is high and because many estimates are reported in the literature, only a single value ($h^2 = .60$) was chosen. This simplifies the analysis because it reduces the number of combinations of parameter values. The average phenotypic correlations and standard deviations given in Tables 17 and 24 for body weight, egg mass and feed consumption were used. The partial regression coefficients of feed consumption on body weight and egg mass used to obtain Y (IF:W, M, b) were derived from the above standard deviations and phenotypic correlations. The partial regressions thus obtained are assumed to represent the true value for the population.

The derived heritability of feed consumption and its genetic correlations with body weight and egg mass were then computed for each combination set of the genetic parameters given in Table 26. The selection indexes were computed from the different combinations of these genetic parameters of body

Table 26. Values used for the genetic parameters of the independent traits

Parameter	Arbitrary values chosen
Heritability:	
Body weight	0.60
Egg mass	0.05, 0.15
Residual	0.00, 0.20
Genetic correlation:	
Body weight x egg mass	-0.20, 0.20, 0.60
Body weight x residual	0.00
Egg mass x residual	0.00

weight and egg mass and the genetic parameters of feed consumption were derived by substituting values of each set in Equations 8, 9 and 10 given in the theory section.

Effect of residual genetic variation

The expected gain in income over feed cost from the different values of the heritability of the residual, in combination with the heritability values of egg mass (h_M^2), and the genetic correlations between body weight and egg mass ($r_{G_{WM}}$) are given in Table 27.

Table 27. Expected gain in income over feed cost from different selection indexes for different values of genetic parameters

h_u^2	h_M^2	$r_{G_{WM}}$	Selection indexes			
			$Y(IF:W,M,F)$	$Y(IF:W,M,r)$	$Y(IF:W,M,b)$	$Y(I:W,M)$
0	0.05	-0.2	26.25	26.25	26.25	22.97
		0.2	12.82	12.82	12.82	5.92
		0.6	15.91	15.91	15.91	15.39
	0.15	-0.2	49.84	49.84	49.84	47.97
		0.2	36.03	36.03	36.03	33.34
		0.6	44.19	44.19	44.19	43.74
0.2	0.05	-0.2	26.64	26.25	26.25	22.97
		0.2	13.60	12.82	12.82	5.92
		0.6	16.54	15.91	15.91	15.39
	0.15	-0.2	50.04	49.84	49.84	47.97
		0.2	36.32	36.03	36.03	33.34
		0.6	44.42	44.19	44.19	43.74

The expected gain from index $Y(IF:W, M, F)$ increases as the heritability of the residual increases from 0.0 to 0.2. The expected gains from the other selection indexes, however, are not affected by increasing the heritability of the residual. This result is expected since the genetic variance of the residual is a component of the genetic variance of feed consumption. Also, because the genetic variation of the residual is not correlated with body weight or egg mass, it can be effectively utilized only by using $Y(IF:W, M, F)$ which includes direct information on feed consumption.

The additional expected gains in the index $Y(IF:W, M, F)$ by changing the residual heritability from 0.0 to 0.2 are of special interest. Overall, these are small ranging from 0.20 to 0.78 cents but could be an important source of variation in breeding for improved feed efficiency.

If the heritability of the residual has some real value as 0.2 rather than zero, this increases the expected gain from selection on the index $Y(IF:W, M, F)$ because the heritability of feed consumption would then be greater. Since the residual is not genetically correlated with body weight and egg mass, from Equation 20, increasing the residual heritability from $h_u^2 = 0$ to $h_u^2 = 0.2$ increases the heritability of feed consumption by $p_u^2 h_u^2$; where p_u is the proportion of the residual variance in the total phenotypic variance of feed consumption. In this experiment, the estimate of p_u was 0.5540. Hence the

heritability of feed consumption is increased only by 0.0613.

Influence of the regression bias on the expected gain when selection is on index $Y(IF:W, M, b)$

From the results just presented, the expected gain from index $Y(IF:W, M, b)$ was equal to the expected gain from index $Y(IF:W, M, F)$ with no genetic variation of the residual. The former index however, was formulated by using the true or unbiased regression coefficients of feed consumption on body weight and egg mass. From the comparisons of the partial regression coefficients presented earlier, such regressions could differ significantly from population to population. Thus, it seems that to obtain unbiased estimates of these partial regression coefficients would still require individual feeding records.

The selection index, $Y(IF:W, M, b)$ however, can be formulated without an individual feeding operation. Instead values of feed consumption are estimated by a regression equation of feed consumption on body weight and egg mass. Such equations for predicting feed consumption from adult body weight and egg mass are given in the literature. Even though these values may be biased and not agree exactly with the true population values appropriate to the population being subjected to selection, they may still be useful. To show the importance of such a bias, the expected gains from the index $Y(IF:W, M, b)$ using both biased and unbiased regression coefficients were

compared.

Two sets of partial regression coefficients were used. One set was obtained directly from the average phenotypic correlations along with the standard deviations given in Tables 17 and 24. This set was called the "unbiased" set. The other set was derived from an equation given by Card (1952) for predicting feed consumption from body weight and egg mass. This set was called the "biased" set. The values for the two sets of partial regression coefficients for body weight and for egg mass are given in Table 28.

Table 28. Unbiased and biased sets of partial regression coefficients used to predict feed consumption

Independent variable	Partial regression coefficients		
	Unbiased	Biased	Unbiased minus biased
Body weight (gm)	12.0994	8.6240	3.4754
Egg mass (gm)	.6916	1.1351	-.4435

The difference between the biased and unbiased coefficients were about 28 and 64 percent of the unbiased value for body weight and egg mass, respectively. Using the same genetic and phenotypic parameter estimates as in the previous study of the residuals, the selection index, $Y(IF:W, M, b)$ was formulated

with both an unbiased and a biased set. The expected gains from these two kinds of selection indexes are presented in Table 29a for $h_u^2 = 0$ and for different values of h_M^2 and $r_{G_{WM}}$.

For all combinations of h_M^2 and $r_{G_{WM}}$, the expected gain from the selection index using the unbiased set was consistently higher than from the other index with the biased set but the difference was rather small ranging from .07 to .96 cents.

Table 29a. Expected gain in income over feed cost from a selection index using unbiased and biased partial regression coefficients

h_u^2	h_M^2	$r_{G_{WM}}$	Selection index	
			$Y(IF:W,M,b)^a$	$Y(IF:W,M,b)^b$
0	0.05	-0.2	26.25	26.11
		0.2	12.82	11.86
		0.6	15.91	15.79
	0.15	-0.2	49.84	49.70
		0.2	36.03	35.71
		0.6	44.19	44.12

^aUsing unbiased regression coefficients.

^bUsing biased regression coefficients.

DISCUSSION

Value of Measuring Feed Consumption

From an investment point of view, the cost of measuring feed consumption in a poultry breeding operation can be justified only on the basis of the additional potential profit that it promises.

To simplify the evaluation of the economic feasibility of measuring feed consumption in a breeding operation, two assumptions are required: (1) the expected additional gain from measuring feed consumption is a genetically additive component; i.e., it produces a permanent genetic gain to the population; and (2) the breeding operation is integrated with a hatchery and a commercial egg production operation. The first assumption is required in order to apply the usual theory of selection indexes. The second assumption is required in order to directly credit the foundation poultry breeder with the genetic improvement realized by a commercial egg production operation using the improved stock. Clearly, in the case of a non-integrated operation, the uncertainties of marketing because of competition leading to irregularities between the three non-integrated operations, would make the problem very much more complex. On the other hand, an integrated model makes possible a more objective evaluation since the benefits as well as liabilities accruing from any change in procedure,

such as measurement of feed consumption, would directly affect the same organization.

Measuring feed consumption under mass selection

Because males do not produce eggs, we assume that the females are selected on individual records but that the males are selected on a half-sib test: i.e., the mean performance of their half-sisters, in say, a sire family of 5 dams and 6 daughters per dam.

For a 24-week testing period, the cost of taking individual feed consumption records was estimated to be \$1.92 per hen. Also, the additional gain accruing from using individual feed consumption record in a selection index in this study was estimated to be 1.8 cents and the expected gain from half-sib selection in males was estimated to be 4.0 cents. This gives an average additional expected gain of \$0.029.

If C is the cost of measuring feed consumption of a single pullet for some given period of time and if a fraction p of the individually fed pullets are selected as breeders, the feed record cost of a selected pullet is C/p . If the additional return resulting from the genetic improvement transmitted to the progeny because of selection on dams using an index with feed consumption records is D , then the number of pullet progeny descendants required to offset the cost of feed consumption measurement is C/pD .

If the reproductive rate, r , is defined as the number of female progeny a female breeder produces per generation, then the number of pullet progeny descendants in generation t is r^t .

If r^t is set equal to C/pD , then r^t defines the maximum reproductive rate required to pay in generation t for the cost of feed measurement in generation zero.

In a typical breeding program, the pullet chicks produced for commercial production would come no sooner than two generations removed from a foundation stock selection program. In this case,

$$r^2 = C/pD$$

and if $C = \$1.92$, $p = .20$, and $D = \$0.029$, then

$$r^2 = \$1.92/.2(\$0.029) = 331,$$

and $r = 18$ is an estimate of the minimum required reproductive rate to offset the additional cost of feed consumption measurement.

If the attainable reproductive rate is n , then $n-r$ is proportional to the additional profit resulting from selection on feed consumption records. At the end of two generations ($t = 2$), the total returns from measuring N birds in generation zero would be Npn^2D and the profit, P , would be

$$\begin{aligned} P &= (n^2 - r^2) NpD \\ &= (n^2 - C/pD) NpD \\ &= NpDn^2 - NC. \end{aligned}$$

The profit per bird measured in the original generation is then

$$P/N = pDn^2 - C.$$

If the maximum reproductive rate is 50,

$$\begin{aligned} P/N &= .2(.029)50^2 - 1.92 \\ &= 14.50 - 1.92 \\ &= \$12.58. \end{aligned}$$

Therefore, under the conditions specified, the expected profit at the end of two generations after an investment of \$1.92 per bird is \$12.58.

If it takes 4 years to complete two generations, for an investment of \$1.92 and with the expected total return of \$14.50, the yearly interest rate, q , can be computed from the relationship

$$1.92 = 14.50(1 + q)^{-4}.$$

Thus,

$$1 + q = \left[\frac{14.50}{1.92} \right]^{1/4} = 1.65.$$

Therefore, the annual interest rate expected from the capital investment in measuring feed consumption is 65 percent.

Measuring feed consumption under sib-selection

Under family or sib-selection only the record of the mean of a family is required in the index. This would reduce the cost of measuring feed consumption since a family group rather than individual would be measured. Although group feeding was

not done in this study, an approximation to the cost of measuring feed per hen, C' , would be inversely proportional to the number of full-sibs or half-sibs in the family. For full-sib selection using 5 full sisters in a family, $C' = \frac{C}{4}$. In this case, to offset the cost of measuring feed in the original generation, the total number of pullet progeny descendants required in two generations would be

$$r'^2 = \frac{C'}{pD} = \frac{C}{4pD} = 1/4 r^2 .$$

Hence, under sib-selection, the minimum required reproductive rate, r' , of the female breeders should only be about half as much as that of mass selection, i.e., $r' = 1/2 r = 9$.

Moreover, in measuring feed consumption by groups, the value of D should be slightly higher as family size is increased.

Economic risk from genetic uncertainties

In practice, the expected gain from selection indexes are predicted from genetic and phenotypic estimates of parameters. These parameters, especially the genetic parameters, are subject to rather high standard errors. Harris (1964) stated that a selection index with estimated parameters tended to over-estimate the "true" genetic gain. This however, would not be especially serious when the estimates are based on a large number of observations.

The parameter estimates used in a selection index are also subject to biases depending on the method of estimation. In the present study, for example, the genetic variances and covariances of the traits used in formulating the selection indexes were estimated from sire component of variance and covariance. If additive epistatic effects are important factors causing differences for these traits, then the additive genetic variance can be over-estimated. This will contribute to the inaccuracy of predicting the expected gain from selection.

Genetic advance from selection can also be attenuated by the effect of "genetic slippage" in the population (Dickerson, 1955). This may result from limited population size, heterozygote superiority of fitness and recurrent loss of favorable epistatic combination from one generation to the next.

The expected gain in a full-year performance record may not be fully realized if selection is based only on early or part-year performance records (Morris, 1963; Nordskog et al., 1967). In this study, for example, the length of a testing period was assumed to be only 24 weeks but prediction of progeny performance was based on a 56-week period.

In view of the genetic uncertainties that might affect a population, the assessment of the potential economic value of measuring feed consumption is, at best, speculative.

Possible Importance of a Residual Genetic Component of Feed Consumption

Since the genetic variance of feed consumption is a function of the genetic effects of body weight, egg mass and a residual, the intrinsic value of including feed consumption as a variable in a selection index is determined solely by the genetic variation in the residual component itself. Therefore, to realize the full value of this genetic component would require records of feed consumption.

In this study, the estimated heritability of the residual was very low and the standard error was relatively high. This suggests that most if not all of the residual variance is due to random environmental effects of measurement.

Results of studies on the regression of income over feed cost on economic traits of entries from random sample egg production tests also offer some evidence on the contribution of residual feed consumption. Nordskog (1960) reported that 93 percent of the variation in income over feed cost was accounted for by differences in body weight, egg production and egg size. McNally and Foster (1969) found that differences in body weight and egg mass accounted for 99 percent of the variation in income over feed cost of random sample test entries. Since other traits of economic importance (e.g., egg quality) may contribute to the variation in income over feed cost but were not included as independent variable in the

regression model, it seems likely that feed consumption could possibly account for only a small part of the remaining unexplained variation in income over feed cost.

The failure of this study to demonstrate positive evidence of the genetic differences in the residual, however, does not rule out the possibility that the real genetic differences in digestive and metabolic efficiency exist which are independent of body weight and egg mass. Nesheim (1966) reviewed the results of experiments indicating that breeds, strains, and individual birds may vary in the utilization of nutrients. He pointed out that the efficiency of the utilization of protein or energy in a diet depends on the metabolism of many individual compounds involving a large number of enzyme-controlled reactions which in turn, are probably under genetic control. Because of the highly complicated metabolic reactions, however, he concluded that the selection for better protein utilization is not likely to have success.

A study by Wilson (1969) on the genetic aspects of feed efficiency suggested that the genetic variation in feed efficiency not accounted for by body weight in broiler chicks may be important. He reported that selection for gain in body weight was only 75 percent as efficient in improving feed efficiency as direct selection for a low feed/gain conversion ratio. In beef cattle, Koch et al. (1963) reported the heritability for feed consumption adjusted for differences in

gain to be 0.28. They concluded that selecting for feed efficiency would increase feed efficiency and result in increased daily gain but feed consumption would not be affected.

Results from the present study show that even a relatively small amount of residual genetic variation may be sufficient to justify measuring feed consumption and including the record in an index. With family or sib selection the value of a feed consumption record is enhanced because the opportunity to identify superior genotypes is increased and at the same time the cost of measurement is lowered.

Use of Regression to Predict Breeding Value of Feed Consumption

The usual method for calculating the importance of a particular variable (e.g., feed consumption) in the index, is to construct a reduced index from which the particular variable has been excluded. In this study, the value of feed consumption in the index was determined by constructing two selection indexes Y_1 and Y_2 , i.e.,

$$Y_1 = b_{11}x_1 + b_{12}x_2 + b_{13}x_3$$

and

$$Y_2 = b_{21}x_1 + b_{22}x_2$$

where x_1 , x_2 and x_3 are the records for body weight, egg mass and feed consumption, respectively. The b_{ki} 's of the indexes

were obtained by maximizing the correlation of Y_k with the aggregate breeding value $H = a_1g_1 + a_2g_2 - a_3g_3$ where the a 's are the economic weights and the g 's are the breeding value of the respective traits. When there is no feed consumption residual genetic variation, the expected gain in H from selection is the same with both Y_1 and Y_2 . In this case, feed consumption does not enhance the effectiveness of the index.

As shown in the theory section, the construction of Y_2 requires an estimate of the genetic correlation between feed consumption and body weight and between feed consumption and egg mass in the population under selection. Even though the genetic correlations between these traits may be high and the residual genetic variation may be zero, the measurement of feed consumption can be justified as an "auxiliary" trait which helps to increase the correlation of the income-related traits in the index to the aggregate breeding value.

When the residual genetic variation is zero, however, an alternative approach to measuring feed consumption is to predict the breeding value of feed consumption from a pre-chosen regression equation. In this case, the aggregate breeding value of income over feed cost is a function only of the breeding values of body weight and egg mass. The breeding value of feed consumption can then be represented by the regression equation, $g_3 = \beta_1g_1 + \beta_2g_2$ where β_1 and β_2 are

partial regression coefficients for body weight and egg mass respectively. The aggregate breeding value can then be written as,

$$\begin{aligned} H^* &= a_1g_1 + a_2g_2 - a_3(\beta_1g_1 + \beta_2g_2) \\ &= (a_1 - a_3\beta_1)g_1 + (a_2 - a_3\beta_2)g_2 \end{aligned}$$

or

$$H^* = a_1^*g_1 + a_2^*g_2$$

where

$$a_1^* = (a_1 - a_3\beta_1) \text{ and } a_2^* = (a_2 - a_3\beta_2).$$

A selection index, $Y_3 = b_{31}x_1 + b_{32}x_2$ can be obtained by maximizing its correlation with H^* which does not require any genetic parameter estimates from a feeding experiment.

The development presented in the theory section, shows that the relative efficiency of Y_3 can only be equal to or less than Y_2 . This is understandable because for Y_3 , the linear genetic relationships between g_3 and g_1 and between g_3 and g_2 are only an approximation of the true biological relationships. In Y_2 , on the other hand, these genetic correlations would be obtained from actual data.

Results from this study indicate that when β_1 and β_2 are also estimated from the same population under consideration, the efficiency of Y_3 is very close to Y_2 . This suggests that a linear regression is a close approximation to the possible gains obtained from independent feed consumption measurement.

To obtain unbiased estimates of the regression coefficients in the population however, would still involve individual feeding experiment which entails the risk of an additional cost input.

Estimates of the regression of feed consumption on body weight and egg mass which have been published, might be used even though they would be biased estimates. Table 29b shows some of the published estimates on layers on the basis of a 56-week feeding test.

Table 29b. Some published estimates of partial regression of individual feed consumption on body weight and egg mass adjusted to 56-week period

Independent variable	Source of estimates		
	Card (1952)	Arboleda and Campos (1966)	Nordskog <u>et al.</u> (1969)
Body weight (gm)	8.6240	8.5456	13.5514
Egg mass (gm)	1.1351	1.4323	.8200

In this study, the differences of the regression between pure lines and cross lines were highly significant for body weight and egg mass. Because the experimental sources of variation may be different, the partial regression coefficients may be different. The coefficients from Card (1952) were 29

percent lower for body weight but 64 percent higher for egg mass than the average of pure lines and cross lines in the present experiment. The estimates given by Arboleda and Campos (1966) however, were 29 percent lower for body weight but 107 percent higher for egg mass than that obtained in the present experiment. The estimates given by Nordskog et al. (1969) on the other hand, were only 12 and 29 percent higher for each trait than the present experiment.

The conditions under which Card's and Arboleda and Campos' estimates were obtained, were probably highly different. In Arboleda and Campos' experiment, the ration used was much lower in quality than in the present experiment.

Since the regression coefficients of feed consumption on body weight and egg mass may vary from population to population, using an arbitrary set of published estimates might very well be different from the true values of the population under selection. If such a biased set of regression coefficients were then used to predict the breeding value of feed consumption in the formulation of a selection index, this will lower the effectiveness of the resulting selection index in improving the gain in income over feed cost. The decrease in effectiveness will be proportional to the degree of bias of the regression coefficients.

In this study however, the bias in the regression coefficients did not seem to markedly lower the expected gain in income over feed cost. Thus, commercial poultry breeders who wish to avoid the cost of measuring feed consumption, could improve their selection for gain in income over feed cost by choosing a set of regression equations to use in a selection index.

SUMMARY

Because of the high cost of measuring feed consumption and the high correlation between income over feed cost and the income-related traits (e.g., egg mass and body weight), up until now, the improvement of income over feed cost in breeding programs has been a result of correlated response from direct selection for these traits.

The primary objective of this study is to determine the conditions under which the expected gain in income over feed cost from selection can be improved by using feed consumption information in addition to body weight or egg mass.

Phenotypic and genetic parameters of adult body weight, egg mass and feed consumption were obtained from individual records of 788 pedigreed layers from two pure lines and 1120 pedigreed layers from corresponding reciprocal crosses. Records were obtained from an 8-week test period. Parameters of the same traits were also obtained from individual records of 303 pure line layers in a 24-week test.

A selection index using only records on egg mass output and body weight was compared with another containing the same information plus individual hen records on feed consumption. With truncation selection of the top 20 percent of the population, an index containing feed consumption records was 9 percent more efficient than from an index without feed records.

With sib-selection of males, the value of feed consumption records in an index was further enhanced by increasing family size.

Inclusion of feed consumption as a variable in a selection index theoretically increases the expected gain in income over feed cost because it contains a possible residual genetic component of variation apart from that contributed through its covariation with body weight and egg mass. The residual would be determined by genetic differences in the efficiency of digestion and metabolism. On the other hand, if there is no residual component of variation, there may be justification for measuring feed consumption. Its measurement would provide auxiliary information which could increase the effectiveness of selection for body weight and egg mass. Since these are highly correlated with feed consumption, the aggregate breeding value of income over feed cost would be more effectively improved.

The cost of individually measuring feed consumption was estimated to be \$1.92 per layer for a six-month testing period. For an integrated poultry operation, measuring feed consumption in a testing program can be made economically feasible if the female breeders selected by supplementary information of feed consumption are permitted to reproduce at the maximum rate possible.

The expected gain from a selection index using information on the breeding value of feed consumption as predicted from a regression on the breeding values of body weight and egg mass was also evaluated. Although this index is expected to be less effective than one using actual feed measurement, the breeder can still improve gain but avoid the cost of measurement by using a set of regression coefficients published in the literature.

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APPENDIX

Table 30. Coefficients^a for traits in the different selection indexes for mass selection

Selection index	b_1	b_2	b_3
Y(IF:W, M, F)	0.0841	0.0034	-0.0014
Y(IF:W, M, r)	0.0659	0.0025	--
Y(IF:W, M, b)	0.0666	0.0023	--
Y(I:W, M)	0.1444	0.0029	--

^a b_1 , b_2 and b_3 are the selection index coefficients for body weight, egg mass and feed consumption, respectively.

Table 31. Coefficients^a for traits in the different selection indexes for full-sib selection

Selection indexes	Progenies per dam								
	2			6			10		
	b_1	b_2	b_3	b_1	b_2	b_3	b_1	b_2	b_3
Y(IF:W, M, F)	0.0656	0.0031	-0.0013	0.1085	0.0070	-0.0029	0.1269	0.0094	-0.0039
Y(IF:W, M, r)	0.0482	0.0023	-	0.0675	0.0052	-	0.0717	0.0070	-
Y(IF:W, M, b)	0.0488	0.0021	-	0.0688	0.0048	-	0.0733	0.0065	-
Y(I:W, M)	0.1070	0.0026	-	0.1550	0.0058	-	0.1685	0.0078	-

^a b_1 , b_2 and b_3 are the selection index coefficients for body weight, egg mass and feed consumption, respectively.

Table 32. Coefficients^a for traits in the different selection indexes for half-sib selection with 5 dams per sire

Selection indexes	Progenies per dam								
	2			6			10		
	b_1	b_2	b_3	b_1	b_2	b_3	b_1	b_2	b_3
Y(IF:W, M, F)	0.1711	0.0131	-0.0052	0.2243	0.0264	-0.0098	0.2399	0.0332	-0.0119
Y(IF:W, M, r)	0.1033	0.0100	-	0.0943	0.0209	-	0.0814	0.0269	-
Y(IF:W, M, b)	0.1060	0.0093	-	0.0997	0.0194	-	0.0883	0.0249	-
Y(I:W, M)	0.2480	0.0109	-	0.2663	0.0223	-	0.2598	0.0285	-

^a b_1 , b_2 and b_3 are the selection index coefficients of body weight, egg mass and feed consumption, respectively.

Table 33. Coefficients^a for traits in the different selection indexes for half-sib selection with 10 dams per sire

Selection indexes	Progenies per dam								
	2			6			10		
	b_1	b_2	b_3	b_1	b_2	b_3	b_1	b_2	b_3
Y(IF:W, M, F)	0.2179	0.0230	-0.0087	0.2548	0.0419	-0.0142	0.2586	0.0504	-0.0162
Y(IF:W, M, r)	0.1056	0.0181	-	0.0670	0.0350	-	0.0436	0.0431	-
Y(IF:W, M, b)	0.1106	0.0168	-	0.0763	0.0324	-	0.0550	0.0399	-
Y(I:W, M)	0.2827	0.0192	-	0.2625	0.03666	-	0.2428	0.0449	-

^a b_1 , b_2 and b_3 are the selection index coefficients of body weight, egg mass, and feed consumption, respectively.

Table 34. Coefficients^a for traits in the different selection indexes for half-sib selection with 15 dams per sire

Selection indexes	Progenies per dam								
	2			6			10		
	W	M	F	W	M	F	W	M	F
Y(IF:W, M, F)	0.2400	0.0309	-0.0112	0.2593	0.0527	-0.0166	0.2536	0.0615	-0.0181
Y(IF:W, M, r)	0.0949	0.0250	-	0.0390	0.0453	-	0.0115	0.0541	-
Y(IF:W, M, b)	0.1017	0.0231	-	0.0512	0.0419	-	0.0260	0.0501	-
Y(I:W, M)	0.2861	0.0262	-	0.2437	0.0470	-	0.2187	0.0561	-

^ab₁, b₂ and b₃ are the selection index coefficients of body weight, egg mass and feed consumption, respectively.

Table 35. Coefficients^a for traits in the different selection indexes using different values of h_u^2 , h_M^2 and $r_{G_{WM}}$

h_u^2	h_M^2	$r_{G_{WM}}$	Y(IF: W,M,F)			Y(IF: W,M,r)		Y(IF: W,M,b)		Y(I: W,M)	
			b_1	b_2	b_3	b_1	b_2	b_1	b_2	b_1	b_2
0	0.05	-0.2	-0.0948	0.0033	0.0000	-0.0687	0.0029	-0.0687	0.0029	-0.0337	0.0030
		0.2	-0.0220	0.0026	0.0000	-0.0016	0.0024	-0.0016	0.0024	0.0453	0.0027
		0.6	0.0509	0.0019	0.0000	0.0655	0.0018	0.0655	0.0018	0.1243	0.0024
	0.15	-0.2	-0.1319	0.0089	0.0000	-0.1029	0.0080	-0.1029	0.0080	-0.0741	0.0090
		0.2	-0.0057	0.0077	0.0000	0.0134	0.0071	0.0134	0.0071	0.0628	0.0084
		0.6	0.1204	0.0065	0.0000	0.1296	0.0062	0.1296	0.0062	0.1997	0.0079
	0.2	-0.2	-0.0830	0.0039	-0.0009	-0.0687	0.0029	-0.0687	0.0029	-0.0337	0.0030
		0.2	-0.0101	0.0032	-0.0009	-0.0016	0.0024	-0.0016	0.0024	0.0453	0.0027
		0.6	0.0627	0.0025	-0.0009	0.0655	0.0018	0.0655	0.0018	0.1243	0.0024
0.2	0.15	-0.2	-0.1201	0.0094	-0.0009	-0.1029	0.0080	-0.1029	0.0080	-0.0741	0.0090
		0.2	0.0061	0.0083	-0.0009	0.0134	0.0071	-0.0016	0.0024	0.0628	0.0084
		0.6	0.1322	0.0071	-0.0009	0.1296	0.0062	0.0655	0.0018	0.1997	0.0079

^a b_1 , b_2 and b_3 are selection index coefficients for body weight, egg mass and feed consumption, respectively. These are the index coefficients used for computing the expected gain from the different selection indexes given in Table 27.