Efficiency of Selection in Layer-type Chickens by Using Supplementary Information on Feed Consumption

I. Selection Index Theory*

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Summary. Selection indexes to maximize net income for egg laying chickens were constructed with information on egg mass output, body weight and individual feed records. Relative selection efficiencies were then compared with different kinds of information in the index. If the genetic variation in feed consumption is completely determined by egg mass output (M) and body weight (W), using reliable estimates of genetic correlations or pehnotypic regressions of these traits with feed consumption in the index is equally efficient to an index with individual feed records. If real genetic differences in feed efficiency exist which are independent of egg mass and body weight, (h_0^2) , then there is greater justification in using individual feed consumption records. For example, if $h_u^2 = 0.2$, $h_w^2 = 0.6$, $h_{M}^{2} = 0.15$ and $r_{G_{M}}$ (genetic correlation) = 0.2, the use of individual feed records is expected to improve efficiency of the selection for net income by 9p. On the other hand, if the genetic correlations of feed consumption on bo-

dy weight and on egg mass are substituted in the index for records on individual feed consumption, only slightly less selection efficiency would result.

Introduction

Even though feed represents about two-thirds of the cost of egg production, genetic studies on individual variation in feed consumption have been very few indeed. Rather, research has been devoted mostly to the genetic evaluation of traits related to income such as egg production, viability and body weight. This is understandable because the measurement of individual feed consumption records in large numbers would be expensive.

To improve net performance, or net income the breeder has three basic options in his choice of selection criteria: (I) records on both income-related traits and feed consumption, (2) records on incomerelated traits supplemented with indirect information on feed consumption, and (3) records only on income related traits. The basic question is what is the efficiency of a selection program directed towards increasing net income when feed consumption is known relative to that when it isn't. The problem can be conveniently handled in terms of selection index theory. In particular, we shall specify the conditions under which a selection index for net income can be im-

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proved and by how much with supplementary information on feed consumption.

Table I lists 4 selection indexes developed in accordance with the options listed above. Y_1 is designed to maximize income over feed costs (IF), using information on body weight, W, egg mass, M and feed consumption, F (Option 1). Y_2 supplements information on W and M with estimates of genetic correlations of W and M with F. $Y₃$ supplements information on W and M with phenotypic partial regressions of F on W and M. Y₂ and Y₃ are variations of Option 2. Y₄ is designed to maximize total income, I, using information only on W and M. To aid the reader, a shorthand description of each index is given in the last column of Table 1. Thus, the shorthand description of Y_1 is $Y(IF: W, M, F)$ where the trait maximized is to the left of the colon and the input information is indicated on the right.

Selection Index Theory

The maximization of genetic gains in net income over feed cost is readily derived in terms of a standard selection index as developed by Smith (1939) and Hazel (1943).

Valid application of selection index theory requires that :

(a) the phenotypic value of trait x_i is expressible as $x_i = g_i + e_i$, where g_i is the additive genetic com-

Selection	Variable	Information required	Descriptive	
index	maximized	for the index	notation of index	
$\begin{smallmatrix} \texttt{Y}_1 \ \texttt{Y}_2 \ \texttt{Y}_3 \ \texttt{Y}_4 \end{smallmatrix}$	ΙF ΙF ΙF	W.M.F W, M, r_G W, M, b_n W.M	Y(IF:W, M, F) Y(IF:W, M, r) $Y(IF:W, M, b)$ $Y(IF:W, M)$	

Table I. Selection index options using supplementary information on feed consumption

IF = income over feed cost

 $I = total income$

 $W = body weight$

 $M = egg$ mass

 $F = feed consumption$

 $G = r =$ genetic correlations between F and W and between F and M

 $p = p$ = phenotypic partial regressions of F on W and F on M

ponent and e_i is the environmental and non-additive genetic component; $¹$ </sup>

(b) for trait $i = 1, \ldots, t$, the additive genetic component, or breeding value, H, of an individual is det fined as $H = \sum_{i=1}^{\infty} a_i g_i$, where a_i is the economic value of a unit of the ith trait;

(c) the regression of H on any linear function of the x_i 's is linear. When selection is based on a linear is the contract of the contra function of x_i, say, $Y = \sum_{i=1}^{n} b_i x_i$, the expected imi:1 provement in H is $\Delta H = B_{HY} \Delta Y$, where ΔY is the selection differential and B_{HY} is the regression of H on Y. This may also be written,

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

If Y is normally distributed, if the b's are known without error and if the top p proportion is selected by truncation, then $\Delta Y/\sigma Y = z/p = i$ is defined as the selection intensity where z is the ordinate of the standardized normal distribution. The expected gain in H, when selection is on Y, is then $\Delta H(Y)$ = $=$ i Cov(H, Y)/ $\sigma_{\mathbf{v}}$.

A linear statistical model is the simplest choice of a model to represent feed consumption. Let,

$$
x_3 = \beta_1 x_1 + \beta_2 x_2 + u \tag{1}
$$

where x_3 , x_1 and x_2 are the records of feed consumption, body weight and egg mass, respectively, of a hen measured as deviations from the respective population means; β_1 is a feed constant for maintenance of body weight and β_2 is a feed constant to produce egg mass. The quantity u is a residual representing the amount of feed either wasted or used for digestion and metabolism.

It is obvious from the model given in (1) that with no additive genetic component in the residual, the genetic parameters of feed consumption are functions only of body weight and egg mass and are estimable when β_1 and β_2 are known.

Application to Improve Income Over Feed Cost

The net breeding value of income over feed cost, H, is defined as a linear combination of the breeding values of body weight (g_1) , egg mass (g_2) and feed consumption (g_3) ,

$$
H = a_1 g_1 + a_2 g_2 - a_3 g_3 \tag{2}
$$

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

If the breeding value of feed consumption is a linear function only of body weight and egg mass, i.e., $[$ g₃ = β_1 g₁ + β_2 g₂] then the net breeding value of income over feed cost equation can be written,

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

= $(a_1 - a_3 \beta_1) g_1 + (a_2 - a_3 \beta_2) g_2$

 $\mathbf 1$ Henceforth e_i will be called the environmental component but it will be understood that it contains also any non-additive genetic variance.

Finally, the net breeding value can be defined in terms of total income,

$$
H^{***} = a_1 g_1 + a_2 g_2.
$$

From these breeding values we define four selection indexes :

For each index the b's are chosen such that the correlation between the respective Y and H is maximized. The normal equations for each of the indexes are,

Index

$$
Y_{1}: \begin{bmatrix} p_{11} & p_{12} & p_{13} \\ p_{21} & p_{22} & p_{23} \\ p_{31} & p_{32} & p_{33} \end{bmatrix} \begin{bmatrix} b_{11} \\ b_{12} \\ b_{13} \end{bmatrix} = \begin{bmatrix} g_{11} & g_{12} & g_{13} \\ g_{21} & g_{22} & g_{23} \\ g_{31} & g_{32} & g_{33} \end{bmatrix} \begin{bmatrix} a_{1} \\ a_{2} \\ -a_{3} \end{bmatrix}
$$

$$
Y_{2}: \begin{bmatrix} p_{11} & p_{12} \\ p_{21} & p_{22} \end{bmatrix} = \begin{bmatrix} b_{21} \\ b_{22} \end{bmatrix} = \begin{bmatrix} g_{11} & g_{12} & g_{13} \\ g_{21} & g_{22} & g_{23} \end{bmatrix} \begin{bmatrix} a_{1} \\ a_{2} \\ a_{3} \end{bmatrix}
$$

$$
Y_{3}: \begin{bmatrix} P_{11} & P_{12} \\ P_{21} & P_{22} \end{bmatrix} \begin{bmatrix} b_{31} \\ b_{32} \end{bmatrix} =
$$

\n
$$
= \begin{bmatrix} g_{11} & g_{12} & (g_{1}g_{11} + g_{2}g_{12}) \\ g_{21} & g_{22} & (g_{1}g_{12} + g_{2}g_{22}) \\ g_{21} & g_{22} & (g_{1}g_{12} + g_{2}g_{22}) \end{bmatrix} \begin{bmatrix} a_{1} \\ a_{2} \\ -a_{3} \end{bmatrix}
$$

\n
$$
Y_{4}: \begin{bmatrix} P_{11} & P_{12} \\ P_{21} & P_{22} \end{bmatrix} \begin{bmatrix} b_{41} \\ b_{42} \end{bmatrix} = \begin{bmatrix} g_{11} & g_{12} \\ g_{21} & g_{22} \end{bmatrix} \begin{bmatrix} a_{1} \\ a_{2} \end{bmatrix}
$$

In Y_1 we require full information on W, M and F. In Y_2 we collect no information on F but we utilize information on the genetic correlations of feed consumption on the other traits, i.e., g_{12} and g_{13}' , in deriving the index. In Y_3 we assume that g_3 is completely determined by body weight and egg mass, i.e., $g_3 = \beta_1 g_1 + \beta_2 g_2$. This ignores any residual genetic variation for feed consumption.

Relative Efficiencies

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

$$
\Delta H(Y_k) = \frac{\text{Cov}(H, Y_k)}{\sigma_{Y_k}^2} \left(\overline{Y}_{k_S} - \mu_{Y_k}\right) = \frac{\text{i Cov}(H, Y_k)}{\sigma_{Y_k}}
$$
(3)

where

 \overline{Y}_k = mean of the individuals selected on index Y_k S

$$
\Psi_{Y_k} = \text{population mean for index } Y_k
$$
\n
$$
i = (\overline{Y}_{k_S} - \mu_{Y_k}) / \sigma_{Y_k}
$$
\nis the standardized selection differential.

In matrix notation, let

$$
H = \mathbf{a}^T \mathbf{g}
$$

$$
y_K = \mathbf{b}_k^T \mathbf{x}_k
$$

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

$$
\mathbf{P}_{k}\mathbf{b}_{k} = \mathbf{G}_{k}\mathbf{a}
$$
 (4)

so that

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

where P_k^{-1} is the inverse of the variance-covariance matrix P_k , of the traits in Y_k ; G_k is the genetic varianee-eovariance matrix generated by the elements in g and x_k . From equation 4,

$$
Cov(YK, H) = \mathbf{bKt \mathbf{GK} \mathbf{a} = \mathbf{bKt \mathbf{P}K \mathbf{bK}
$$
\n
$$
= \sigma_{YK2
$$
\n(5)

From equations 3 and 5, the expected gains in H But if using Y_1 and Y_2 are

$$
\Delta H(Y_1) = i \frac{\text{Cov}(Y_k, H_1)}{\sigma_{Y_1}} = i \sigma_{Y_1}
$$
 (6)

$$
\Delta H(Y_2) = i \frac{\text{Cov}(Y_2, H_1)}{\sigma_{Y_2}} = i \sigma_{Y_2}
$$
 (7)

Because the coefficients of indexes Y_3 and Y_4 are obtained for alternative definitions of $H(H^*$ and H^{**}), the identity given by (5) does not hold and the expected gain in H from these indexes can be expressed only as

$$
\Delta H(Y_3) = \frac{i \operatorname{Cov}(Y_3, H)}{\sigma_{Y_3}}
$$
 (8)

$$
\Delta H(Y_4) = \frac{i \operatorname{Cov}(Y_4, H)}{\sigma_{Y_4}}
$$
 (9)

In general, the efficiency of index Y_K relative to an index Y_1 is,

$$
\mathbf{E}_{\mathbf{k},\mathbf{l}} = \frac{\Delta \mathbf{H}(\mathbf{Y}_{\mathbf{k}})}{\Delta \mathbf{H}(\mathbf{Y}_{\mathbf{l}})}
$$

Hence, the efficiency of Y_2 relative to Y_1 is

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

Cunningham (1969) showed that $\sigma_{Y_2} = \sigma_{Y_1} - b_{1i}/W_{1i}$ where W_{11} is the igratagonal of the inverse of the P_4 matrix corresponding to the i trait with the index b_{1i} that is deleted from the selection index Y₁. Since b_{1i}^2/W_{ii} cannot be negative, the range of values for σ_{Y_2} is $0 \leqslant \sigma_{Y_2}^{\sim} \leqslant \sigma_{Y_1}^{\sim}$. Consequently, $E_{2,1} \leqslant 1$. The efficiency of \overline{Y}_3 relative to Y_2 is,

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

which in matrix notation is,

$$
E_{3,2} = \frac{b_3^1 G_3 a}{\left[(b_3^1 P_3 b_3)(b_2^1 P_2 b_2) \right]^{1/2}}.
$$

$$
\mathbf{G}_3 = \mathbf{G}_2 = \begin{bmatrix} \varepsilon_{11} & \varepsilon_{12} & \varepsilon_{13} \\ \varepsilon_{21} & \varepsilon_{22} & \varepsilon_{23} \end{bmatrix}
$$

i. e., there is no residual genetic component for feed consumption, and since

$$
P_3 = P_2 = \begin{bmatrix} P_{11} & P_{12} \\ P_{21} & P_{22} \end{bmatrix} = P
$$
,

where g_{ii} is the genetic covariance between x_i and x_j , and \overrightarrow{P}_{ij} is the phenotypic covariance between x_i and x_i , then from equation 4,

$$
E_{3,2} = \frac{\mathbf{b}_3^{\prime} \mathbf{P} \mathbf{b}_2}{\left[(\mathbf{b}_3^{\prime} \mathbf{P} \mathbf{b}_3) (\mathbf{b}_2^{\prime} \mathbf{P} \mathbf{b}_2) \right]^{1/2}}
$$

which reduces to a correlation between the index values, Y_2 and Y_3 . Hence, in terms of a correlation, $E_{3,2} \le 1$ and therefore $\Delta H(Y_2) \ge \Delta H(Y_3)$. A similar reasoning can be applied to $E_{4, 2}$. Hence, $E_{4, 2} \le 1$ and $\Delta H(Y_2) \ge \Delta H(Y_4)$.

The efficiency of Y_4 relative to Y_3 is,

$$
E_{4,3} = \frac{i \operatorname{Cov}(H, Y_4) \sigma_{Y_3}}{i \operatorname{Cov}(H, Y_3) \sigma_{Y_4}} = \frac{\operatorname{Cov}(H, Y_4) \sigma_{Y_3} \sigma_H}{\operatorname{Cov}(H, Y_3) \sigma_{Y_4} \sigma_H} =
$$

=
$$
\frac{r_{HY_4}}{r_{HY_3}}
$$

and is not as determinate as Y_4 relative to Y_2 . However, in choosing between Y_3 and Y_4 , the one whose correlation with H is highest is judged the more efficient index.

To summarize, the relative expected gain from the four different selection indexes we have defined are in the following order,

$$
\Delta H(Y_1) \ge \Delta H(Y_2) \ge \text{L}\Delta H(Y_3) \le \Delta H(Y_4)
$$

If the heritability of the residual is greater than zero then $\Delta H(Y_1) > \Delta H(Y_2) > \Delta H(Y_3) > \Delta H(Y_4)$. If the residual is not genetically correlated with body weight and egg mass, the heritability of feed consumption is increased by $\beta_{11}^2{}_{n_{11}}^2$; where $\beta_{11}^2{}_{n_{21}}^2$ is the proportion of the residual variance in the total phenotypic variance of feed consumption.

Example

The expected gains from the selection indexes were evaluated according to Equations 6, 7, 8 and 9. For all computations, a selection intensity of $i = 1.4$, equivalent to selecting 20 percent of the population as parents of the next generation, was assumed. Because the arbitrarily chosen i serves only as a constant in the equations, the generality of the results is not altered.

The economic values are taken from Table 10 of the companion paper (Arboleda et al., 1976) and the assumed genetic parameters in the equations are given in Table 2. Because different populations have different parameters, and few, if any, estimates are recorded in the literature, we have chosen a range of arbitrary values for h_M^2 , h_R^2 and r_G _{WM}. These are thought to be realistic although they are not really known. On the other hand, because body weight is known to be highly heritable, and many estimates have been recorded in the literature, only a single value $(h^2 = 0.60)$ was used. The estimates of phenotypic correiations and standard deviations as well as the partial regression coefficients of feed consumption on body weight and egg mass were taken from the companion paper (Arboleda et al. 1976). These are

assumed to represent the true values for the population. Finally, the residual component, u, was assumed to be uncorrelated with W and M.

From each combination set of the genetic parameters given in Table 2, the derived heritability of feed consumption and its genetic correlations with body weight and egg mass were computed in addition to the selection indexes. Finally, the expected gain in income over feed cost from the different combinations of parameter estimates were computed as given in Table 3. The b coefficients for the four types of index for each combination of parameters are presented in Table 4 and aid in interpreting Table 3.

The gain from index Y_1 increases as the heritability of the residual increases, but the gains from the other selection indexes are not affected. This is an expected result since the genetic variance of the residual

Table 3. Expected gain in income over feed cost from different selection indexes for different values of genetic parameters

 $^4\,$ See Table 1 for the complete description of the selection indexes

	h_u^2 h_M^2	$\mathrm{^{r}G}_{\mathrm{WM}}$	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}	$\mathbf{b}_{\mathbf{1}}$	b_{2}	b_{1}	b_{2}
Ω	0.05	-0.2 0.2 0.6	-0.0948 0.0033 -0.0220 0.0026 0.0509 0.0019		0.0000 0.0000	$0.0000 - 0.0687 0.0029$ -0.0016 0.0024	0.0655 0.0018	-0.0687 0.0029 -0.0016 0.0024	0.0655 0.0018	-0.0337 0.0030 0.0453 0.0027	0.1243 0.0024
	0.15	-0.2 0.2 0.6	$-0.13190.0089$ -0.0057 0.0077	0.1204 0.0065	0.0000 0.0000 0.0000	$-0.10290.0080$	0.0134 0.0071 0.1296 0.0062	$-0.10290.0080$	0.0134 0.0071 0.1296 0.0062	-0.0741 0.0090	0.0628 0.0084 0.1997 0.0079
	0.05	-0.2 0.2 0.6			-0.0830 0.0039 -0.0009 -0.0101 0.0032 -0.0009 0.0627 0.0025 -0.0009	-0.0687 0.0029 -0.0016 0.0024	0.0655 0.0018	-0.0687 0.0029 -0.0016 0.0024	0.0655 0.0018	-0.0337 0.0030 -0.0453 0.0027 0.1243 0.0024	
0.2	0.15	-0.2 0.2 0.6			-0.1201 0.0094 -0.0009 0.0061 0.0083 -0.0009 0.1322 0.0071 -0.0009	$-0.10290.0080$	0.0134 0.0071 0.1296 0.0062	-0.1029 0.0080	0.0134 0.0071 0.1296 0.0062	-0.0741 0.0090	0.0628 0.0084 0.1997 0.0079

Table 4. Coefficients^a for traits in the different selection indexes using different values of h_u^2 , h_w^2 and $r_{G_{\text{max}}}$

 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 3.

is a component of the total genetic variance of feed consumption. Furthermore, if the genetic variation of the residual is not correlated with body weight or egg mass, it can be effectively utilized only by directly recording feed consumption.

When $h_{ij}^2 = 0.2$, the gains are small, from 0.5% to 6.0% within the range of parameter values chosen. Nevertheless, this might be a useful source of genetic variation in breeding for improved feed efficiency.

When $h_{\mathrm{u}}^{\mathrm{u}}$ = 0 there is no advantage to recording F in preference to using auxiliary information on r_G or β in the index (as Y₂ or Y₃). On the other hand, Y₂ and Y₃ still show a substantial advantage over Y₄ although this depends on the magnitude of the parameters h_{M}^2 and $r_{G_{\text{WM}}}$. When $r_{G_{\text{WM}}}$ is near zero and h_M is small Y_2 and Y_3 are much better than Y_A , but when r_G is substantially negative or positive, the advantage is much less. This seems to be related to the change in direction of selection for body size for $r_{G_{WM}}$ near zero. Note that in some indexes, body size is selected against because of its relationship to higher feed consumption, whereas in other indexes, it is selected for as a genetic indicator for egg mass (Table 4).

Although $\Delta H(Y_2) \leq \Delta H(Y_3)$ on theoretical grounds, no difference between them could be demonstrated within the limits of the decimal places used in Table 3.

Discussion

From theoretical considerations a direct measure of feed consumption should increase the expected gain in income over feed cost because it would enable the breeder to more accurately evaluate individual genetic differences in feed efficiency. This would include, not only the components of feed correlated with body weight and egg mass, but also a residual component correlated with differences in efficiency of digestion and metabolism. Even if there is no residual genetic variation in feed consumption, its measurement could be justified on the basis that it will improve production efficiency as an indicator trait (Purser 1960) for greater egg mass output and lower body weight.

The usual method for calculating the importance of a particular variable (e.g., feed consumption)in an index is to construct a reduced index from which the particular variable has been excluded. Thus, the value of feed consumption can be determined from the two indexes,

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

and

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

When there is no real residual genetic component, the expected gain would be the same for both Y_1 and Y_2 .

In this case, the actual measurement of feed consumption would be useful only to estimate genetic correlations between F and W and between F and M. By using feed consumption as an auxiliary trait, the correlation of the income-related traits in the index with the net breeding value would be increased.

An alternative approach to measuring feed consumption is to predict the breeding value of feed consumption from a pre-chosen regression equation, such as in $Y_3 \sim Y(IF:W, M, b) = b_{31}x_1 + b_{32}x_2$. In this case, the breeding value of F is $g_3 = \beta_1 g_1 + \beta_2 g_2$ and the net breeding value is,

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

where

$$
\mathtt{a}_{1}^{*}=\left(\mathtt{a}_{1}-\mathtt{a}_{3}\mathtt{\beta}_{1}\right) \text{ and } \mathtt{a}_{2}^{*}=\left(\mathtt{a}_{2}-\mathtt{a}_{3}\mathtt{\beta}_{2}\right).
$$

Theoretically the relative efficiency of Y_3 is equal to or less than Y_2 . This is because the linear genetic relationships of g_3 to g_1 and to g_2 is approximated by the linear phenotypic relationship for Y_3 but for Y₂ the genetic correlations are assumed to be known. Practically, however, the advantage of Y_2 relative to $\frac{y}{3}$ is negligibly small as demonstrated in Table 3.

Thus, if the residual genetic component of feed consumption is small, a linear regression equation would nearly equal the efficiency in gains made with independent feed consumption records.

Gjedrem (1972) considered the same general problem presented here but viewed in terms of the aggregate genetic value, $\Sigma a_i g_i$, in a selection index. He compared two indexes, one with two observed traits, X_1 and X_2 , and the other with an unobserved

Received October 20, 1975 Communicated by H. Abplanalp trait, G_3 , included in $\Sigma a_i g_i$. In our notation, they compared Y_2 with Y_4 and their conclusions are in general accord with our results. However, they also showed that the advantage of Y_2 over Y_4 is higher when $r_{G_1G_3}$ and $r_{G_2G_3}$ are large and opposite in sign. In our study these were assumed to be zero, i.e., that the correlations of W and M with the residual were zero. Also they showed that when X_1 and X_2 (or W and M in our study) are of equal importance, i.e., $a_1 \sigma_{G_1} = a_2 \sigma_{G_2}$, the value of including G_3 in an index is proportional to the magnitude of $a_3 \sigma_{G_2}$.

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