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Multiple-trait selection experiments: Current status, problem areas and experimental approaches

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INTRODUCTION

In species of economic importance, the value of a potential replacement individual usually is a function of several quantitative traits. Those traits that determine aggregate breeding value may differ in their degree of genetic determination and may be either positively or negatively correlated, genetically and phenotypically.

Selection among individuals usually involves many traits. The process of selection, both voluntary and involuntary, must ultimately reduce to the classification of individuals into one of two categories, the selected or the culled. To determine the relative role of each trait and the role of an entire set of traits in selection, it is necessary to consider the interrelationships among those traits considered in the selection process.

Selection experiments have been used to study the effectiveness of selection and to estimate "realized" genetic parameters. Such estimates are used to estimate the genetic parameters in a large random-mating population. The theory of 'correlated responses' is well known and has been reviewed by Falconer (1960a). In this theory, the genetic correlation between the two traits plays an important part and determines the predicted pattern of direct and indirect responses found in different experiments. Hill (1971, 1972) discussed several methods of estimating genetic parameters and the variances of such estimates from single-trait and double-selection experiments. Berger and Harvey (1975) gave procedures for the estimation of realized heritabilities and genetic correlations from populations selected simultaneously for two traits.

Estimates of realized genetic correlations from selection experiments have been characteristically unstable. Falconer (1960b) selected mice for growth on high and low planes of nutrition and observed the correlated responses on the alternate nutritional level. The realized genetic correlations were equal for the first four generations of selection (0.67, 0.65) but were markedly different for generations 5 to 13 (1.25, -0.02). This discordance of the pattern of correlated responses from expectation was attributed to changes in the basic parameters, due to the selection applied, and to large changes in the phenotypic standard deviations.

Asymmetry of the realized genetic correlations also was observed by Bell and McNary (1963), who selected Tribolium castaneum for increased pupa weight in both a wet and a dry environment, and by Yamada and Bell (1963) where selection was for increased and decreased 13-day larval weight under good and poor nutritional levels. Siegel (1962) found a realized genetic correlation of 0.55 when selection was for body weight and 0.45 when selection was for breast angle in poultry. In another selection experiment with poultry, Nordskog and Festing (1962) observed asymmetry of the realized genetic correlation between body and egg weight when either the direction of selection or the trait being selected was considered. In both poultry studies, the asymmetry was attributed to differing genetic variances or heritabilities for the two traits.

The purpose of this paper will be to present selection index procedures that may be used to estimate realized genetic parameters under a multiple trait objective and to describe their application to an experiment designed to evaluate the efficiency of index selection.

EXPERIMENTAL PROCEDURE

Tribolium castaneum were selected for pupa weight, as a measure of growth, and family size, as a measure of reproduction. The basic design of the experiment is described in Table I. Mass selection in each line was based on the designated criterion. Selection for family size in the family size line and the index line was accomplished by mating all females from the previous generation and retaining families from the highest ranking parents on the designated criterion. Males were chosen strictly at random in these two lines. The index was constructed to allow an equal contribution by both traits to the response in aggregate genotype.

TABLE I

Design of Experiment

Line	Selection Criterion	Matings/Gen. Males	Matings/Gen. Females	Individ.
$PW^{+}FS^{\circ}$	Pupa Weight	18	54	324
$PW^{\circ}FS^{+}$	Family Size	54	162	324
Index	$I = 0.0024PW + 0.094FS$	54	162	324
Control	Random	54	54	324

All populations were cultured on standard medium (whole wheat flour enriched with 5% dried brewer's yeast) in an environmental chamber at 38 ± 1° C and 70 ± 5% relative humidity. The base population originated from 24-hour egg lays taken from females obtained from a stock with a pearl eye mutant gene maintained in the laboratory. The stock is maintained by transferring 200 unsexed pupa every 30 days to new media. Individuals obtained from 24 hour egg lays of this random mating population were divided equally into the four lines. Families were cultured for 19 days in a 3/4 oz. creamer containing 2 g. medium. Three males and three females were randomly chosen from each family at 19 days, weighed individually, and placed in separate bottles. Matings in each generation were randomly divided into three sets, with matings and egg lays started across a 3-day period to distribute the work.

SELECTION INDEX PRINCIPLES

The criterion upon which the selection decision is made arises from a condensation of many factors. A linear function of total productivity might be represented as

$$I = \sum_{i=1}^{n} \alpha_i X_i + Z \tag{1}$$

where I is the ultimate measure upon which selection is practiced, the α_i describe the attention given to the ith trait, X_i is the phenotypic measure of the ith trait and Z is the collection of remaining factors involved in selection.

In the absence of knowing I, it is possible to construct an index

$$I^* = \sum_{i=1}^{n} a_i X_i \tag{2}$$

such that the r_{II^*} is maximized. The relative attention given in the intended index (α_i) would be identical to the relative attention in the actual index (a_i) if Z were independent of the X_i's. Allaire and Henderson (1966) and others have shown that to maximize this correlation the weights of the index I^* are obtained by solution of the following equations, where s_i is the observed selection differential for the ith trait in standard deviation units and $r_{P_1P_2}$ is the phenotypic correlation:

$$\begin{bmatrix} 1.0 & r_{P_1P_2} & \cdot\cdot & r_{P_1P_n} \\ \vdots & \vdots & & \vdots \\ r_{P_nP_1} & r_{P_nP_2} & & 1.0 \end{bmatrix} \begin{bmatrix} a_1 \\ \vdots \\ a_n \end{bmatrix} = \begin{bmatrix} s_1 \\ \vdots \\ s_n \end{bmatrix} \qquad (3)$$

This technique was first used by Dickerson et al. (1954) to examine selection in retrospect for traits in swine.

With selection based on (2), it can be shown that

$$E(\Delta G_i) = \mathrm{Cov}(G_i I)\,\frac{(I-u)}{\sigma_I^2} \quad .$$

Dividing both sides of the equation by the phenotypic standard deviation for the i^{th} trait and evaluating the covariance term

$$E(\Delta G_i/\sigma_{P_i}) = a_i g_i^2 + a_j r_{G_iG_j} g_i g_j \ ,$$

where

$$g_i = \frac{\sigma_{G_i}}{\sigma_{P_i}} \quad .$$

Thus from each experimental line selected simultaneously for two traits, there are two equations for expected genetic progress and three unknown genetic parameters. Equations from two experimental lines may be combined as follows:

$$\begin{bmatrix} a_{11} & a_{21} & 0 \\ 0 & a_{11} & a_{21} \\ a_{12} & a_{22} & 0 \\ 0 & a_{12} & a_{22} \end{bmatrix} \begin{bmatrix} g_1^2 \\ g_1 r_{G_1G_2} g_2 \\ g_2^2 \end{bmatrix} = \begin{bmatrix} \Delta G_{11}\,\frac{\sigma_I^2}{s_I} \\ \Delta G_{21}\,\frac{\sigma_I^2}{s_I} \\ \Delta G_{12}\,\frac{\sigma_I^2}{s_I} \\ \Delta G_{22}\,\frac{\sigma_I^2}{s_I} \end{bmatrix} \qquad (4)$$

where a_{ij} is the attention given to the i^{th} trait in the j^{th} line, and the ΔG_{ij}'s are the estimates of genetic response in standard deviation units. By considering these equations as

$$X\beta = Y ,$$

then estimates of the realized genetic parameters may be obtained from the solution of the least squares equations

$$\hat{\beta} = (X'X)^{-1}X'Y .$$

It has been shown (Berger and Harvey, 1975) that the ratio, σ_I^2/s_I, equals one for each experimental line and therefore does not affect the solution for the realized genetic parameters. However, the a_i's from the index in retrospect are proportional to the α_i's of the intended index. Because the intended index may be different from one experimental line to another, this proportionality constant will be different for each experimental line. This suggests that the magnitude of the a_i's from one experimental line to another will influence the accuracy of the estimates combining lines.

RESULTS

The weight given each trait through selection is shown in Table II. To facilitate comparison, the actual attention achieved in selection for pupa weight has been expressed relative to the attention to family size. A positive sign indicates positive attention in selection, and a negative sign indicates negative attention in selection. The sign designating attention in selection does not necessarily follow the direction of the selection differential for individual traits. This is due to the correlation among traits, although for the two traits considered here, the attention in selection did follow the direction of the selection differentials.

TABLE II

Relative Attention in Selection for Pupa Weight (a_1') and Family Size (a_2')^a

	Line					
	PW$^+$	FS$^\circ$	PW$^\circ$	FS$^+$	$I = b_1$ PW + b_2 FS	
Gen	a_1'	a_2'	a_1'	a_2'	a_1'	a_2'
1	0.9	1.0	0.2	1.0	0.6	1.0
2	58.6	1.0	0.2	1.0	0.7	1.0
3	193.4	1.0	0.2	1.0	0.5	1.0
4	3.7	-1.0	0.3	1.0	0.5	1.0
5	2.8	1.0	0.2	1.0	0.5	1.0
6	86.5	1.0	0.2	1.0	1.2	1.0
7	6.6	1.0	0.1	1.0	0.9	1.0
8	4.9	-1.0	0.1	1.0	0.3	1.0
9	2.6	-1.0	2.2	1.0	18.2	1.0
10	65.6	1.0	18.2	1.0	0.5	1.0
11	94.9	-1.0	0.0	1.0	0.6	1.0
12	10.6	-1.0	0.1	1.0	0.6	1.0
13	2.1	-1.0	-0.0	1.0	0.4	1.0
14	2.8	1.0	0.2	1.0	0.7	1.0
15	3.9	-1.0	0.0	1.0	0.6	1.0
16	4.4	-1.0	-0.0	1.0	0.4	1.0
Ave.	12.1	-1.0	0.1	1.0	0.6	1.0

^{a}a_1 and a_2 were obtained by expressing a_1 and a_2 proportional to the absolute value of a_2.

As expected for single trait selection, pupa weight received considerably more attention than family size in the pupa-weight line. There was considerable variation in the attention given to pupa weight from generation to generation. In later generations of the experiment, the attention to family size became negative. In the family-size line, there was less variability in the attention given to family size, and pupa weight received positive attention throughout the experiment. Selection on the index, in the index line, was effective in giving positive attention to both traits and more attention to pupa weight than was achieved in the family-size line.

TABLE III

Relative Attention in Selection of Males and Females for Pupa Weight (a_1) and for Family Size (a_2)

	PW$^+$	FS$^\circ$	PW$^\circ$	FS$^+$	I = b_1 PW + b_2 FS	
Sex	a_1	a_2	a_1	a_2	a_1	a_2
Males	18.2	1.0	-18.4	-1.0	19.6	1.0
Females	6.4	-1.0	0.3	1.0	1.1	1.0

The attention to pupa weight and to family size was different in the selection of males than females (Table III). Despite the random selection of males in the family-size and index lines, pupa weight received about the same relative attention to family size in all three lines. However, negative attention was given to pupa weight in selection of males in the family-size line. Pupa weight of females received positive attention, and for both sexes combined, the overall attention for the experiment was positive.

The responses of pupa weight in Figure 1 are expressed as deviations from the control population. Direct response of pupa weight in the pupa-weight line was 136 ± 3 ug per generation. This was followed by the intermediate response of 35 ± 2 ug in the index line. The indirect response in pupa weight in the family-size line was 9 ± 2 ug per generation.

Figure 2 shows the responses in family size expressed as deviations from the control population. The correlated response in family size, in the pupa-weight line, resulted in the loss of 1.11 ± 0.09 individuals per generation. This continued loss resulted in the eventual extinction of this line by generation 16 because of this loss in fertility. Response in family size increased 0.34 ± 0.12 and 0.27 ± 0.11 individuals per generation in the family-size and index lines, respectively.

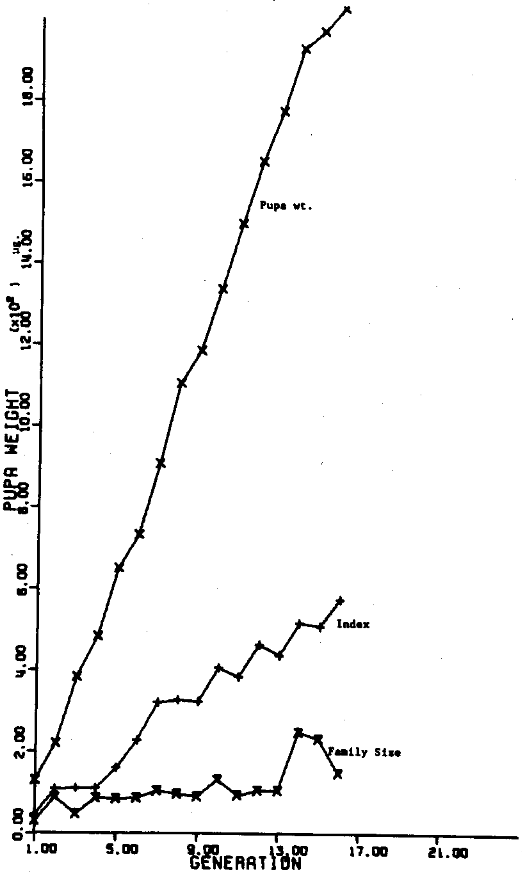

FIGURE 1. Response in Pupa Weight

Estimates of the realized genetic parameters in Table IV were obtained by the procedure described earlier. Estimates describing selection for increased growth were obtained by combining the pupa weight and index line. The family size and index line describe selection for improved reproduction. In general, the realized heritability estimates for both traits were lower selecting for increased reproduction than those selecting for increased growth. The differences between the

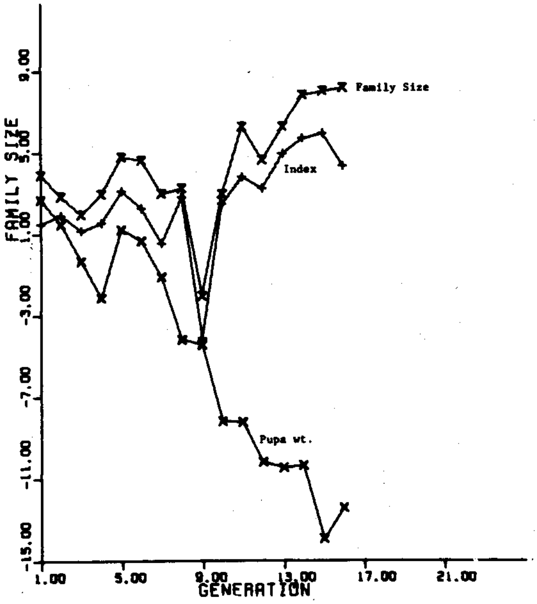

FIGURE 2. Response in Family Size

realized heritabilities and base population estimates (Table V) could be due to sampling error, although there was an indication that selection for increased growth yielded a higher direct response, while selection for increased reproduction yielded less direct response than expected.

Realized genetic correlations agreed least with expectations. The realized genetic correlation was larger selecting for increased growth and positive selecting for increased reproduction. This could be due to sampling error or further evidence supporting conclusions from other multiple trait experiments (Berger and

TABLE IV

Realized Heritability and Genetic Correlation Estimates[a]

Selection for High Pupa Weight		Selection for High Family Size	
Pupa Weight	Family Size	Pupa Weight	Family Size
0.36	-.43	0.33	0.03
	0.11		0.06

[a] Heritabilities are on the diagonal and the genetic correlation above the diagonal.

Harvey, 1975; Rutledge et al., 1973). Under the antagonistic selection practiced in these experiments, the realized genetic correlation was overestimated, suggesting that the pleiotropic effects of genes may be more powerful in retarding response in aggregate genotype than current theory would allow. On the other hand, some experiments have shown no change in the genetic correlation between two selected traits. For example, Bell and Burris (1973) concluded that either initial upward bias, a gradual decline in the genetic variances, or both accounted for predicted changes consistently greater than those observed.

TABLE V

Base Population Parameter Estimates[a]

Trait	Pupa Wt.	Family Size
Pupa Wt.	0.33 ± 0.04	-.17
Family Size	-.05	0.10 ± 0.05

[a] Heritabilities are on the diagonal, genetic correlation above the diagonal and phenotypic correlation below the diagonal.

There are several difficulties with the procedure used. It was not possible to obtain standard errors for the realized genetic parameters. On the other hand, it is impossible to determine the effect of antagonistic selection on indirect responses with single trait selection. In a recent Monte Carlo simulation study, Bruns and Harvey (1976) found the accuracy of realized heritability estimates depended on the attention in selection. More accurate estimates were obtained for the trait receiving the most attention in selection. In this experiment this would correspond to the estimates for pupa weight under high pupa weight selection and family size under high family size selection. In addition, Bruns and Harvey (1976) further concluded that the reduction in genetic and phenotypic variances and covariances, due to the selection of parents, biased realized heritabilities downward and the genetic correlation upward.

The generality of these results is uncertain. They do raise some question concerning the conclusions of some theoretical studies comparing the efficiency of selection for production and reproduction. In comparisons between the efficiency of selecting males and females on different indices with the efficiency of selecting both sexes on the same index, Moav and Hill (1966) and Smith (1964) concluded that the most efficient method of selection was one of splitting the original line into separate sire and dam lines, each selected on a specialized index. The correlated response of reduced fertility in the pupa weight line would suggest that it might be difficult to maintain a specialized sire line selected entirely on productivity. The index line demonstrates that index selection for both productivity and reproductivity is possible and may be used in developing specialized dam lines.

CONCLUSION

The seeming conflict between selection index principles and the results from selection experiments can be explained by two types of errors made in the development and utilization of multiple trait selection schemes. The first is that the true parameter estimates are often unknown, and the second is the failure to account for important correlated traits. The major benefit to come from multiple trait selection experiments is to identify the errors in parameter specification and the way these may change with selection. Once these errors are identified, the additional pertinent information must be considered.

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