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An Empirical Comparison of Selection Methods for the Improvement of Biomass

R.W. Fairfull, G.W. Friars and J.W. Wilton
Department of Animal and Poultry Science, University of Guelph, Guelph, Ontario (Canada)

Summary. A single generation of upward truncation selection on families with 20 % selected was carried out in each of five replicates using *Tribolium castaneum* as the test organism. The experiment involved eight lines: N - selected for offspring number; W - selected for pupal weight; B - selected for biomass; Q - quadratic index selected; L_{21} - linear index selected with relative economic weights of 2:1 offspring number to pupal weight; L_{11} - linear index selected with relative economic weights of 1:1 offspring number to pupal weight; L_{12} - linear index selected with relative economic weights of 1:2 offspring number to pupal weight; C - an unselected control.

Biomass (weight of offspring per family), offspring number, and pupal weight were measured. No differences in response to selection were found among the linear index lines and the pupal weight line with regard to any trait analysed. Generally, response to selection in the linear index lines and pupal weight line was small for offspring number and high for pupal weight. Selection pressure on offspring number in these lines seemed to be dependent on the correlation between offspring number and pupal weight. As a result, response to selection for biomass was poor in the linear index and pupal weight selected lines. In the case of the linear indices, poor response to selection for biomass appeared to be due to the violation of the assumption of additivity of the traits included in the definition of aggregate genotype.

The responses in the quadratic index, biomass, and offspring number selected lines were equal with respect to selection for biomass. The response of the quadratic index selected line was less than the responses of the biomass and offspring number selected lines for offspring number, but the response in the quadratic index line was as large as that of any other line included in the experiment and greater than the biomass and offspring number selected lines where pupal weight was the criterion.

Highly significant amounts of variation were found for all traits indicating that more replicates are needed for precise evaluation of selection systems.

Key words: Selection - Pupal Weight - Biomass - *Tribolium*

Introduction

Smith (1936) and Hazel (1943) developed linear selection indices for the simultaneous improvement of several characters. Index selection, independent culling levels, and tandem selection were compared theoretically by Hazel and Lush (1942) and Young (1961, 1964). Their findings were confirmed experimentally by Sen and Robertson (1964) and Doolittle, Wilson, and Hubert (1972). The development of linear indices is based on the assumption that the total merit of an individual for a number of characters can be found as an additive combination of the characters each weighted by its economic value. Cases exist in which the assumption of additivity is not valid. Wilton, Evans, and Van Vleck (1968) suggested three such cases and developed indices for them. In particular, the economic value of one character may depend on the level of another character, the economic value of a character may not be linear, or a character may be a non-linear function of two or more other characters.

This study was conducted using *Tribolium castaneum* as a pilot organism in order to:

1. Examine the response in biomass to selection and the correlated responses for offspring number and pupal weight obtained by index selection using various indices, and selection on biomass.
2. Examine the response in offspring number to selection and the correlated responses for biomass and pupal weight.
3. Examine the response in pupal weight to selection and the correlated responses for biomass and offspring number.

4. Determine the number of replicates needed for the critical comparison of the selection systems included in the experiment.

Biomass is the weight of the offspring in a full sib family. It is made up of two components: individual weights and numbers of individuals. The linear indices and quadratic index were functions of the component traits of biomass: offspring number and pupal weight.

Material and Methods

In each of five replicates, 160 males and 160 females were chosen at random from the base population and paired randomly as pupae. Twenty pairs were assigned randomly to each of eight lines (Table 1) and a single generation of upward truncation selection on families with 20% selected was carried out in all lines with the exception of the control.

The quadratic index (Wilton et al. 1968) was of the form:

$$Q = (\mu_N + I^*_N)(\mu_W + I^*_W),$$

where, $I^*_N = \frac{1}{2} h^2_N p_N$,

$$I^*_W = \left| \left(\frac{1}{2} n\, h^2_W \right) / \left(1 + \frac{1}{2} \{n - 1\} h^2_W \right) \right| p_W,$$

μ_N is the population mean for offspring number, μ_W is the population mean for pupal weight, h^2_N is the heritability of offspring number, h^2_W is the heritability of pupal weight, p_N is the phenotypic expression of the number of offspring in a family measured as a deviation from the population mean, p_W is the phenotypic expression of family mean pupal weight measured as a deviation from the population mean, and n is the number of offspring per family. The parameters used in the indices (Table 2) were based on literature values reported by Jui (1972), Friars, Nayak, Jui and Raktoe (1971), Capparossa and Van Vleck (1969), Scheinberg, Bell, and Anderson (1967), and Hardin (1962). Each I^*_i was based on information from trait i (i = N or W) alone. This is a "simplified" quadratic index (Wilton et al. 1968) since it uses information from only one trait rather than both traits in each I^*.

The linear indices were of the form,

$$L = b_N p_N + b_W p_W,$$

where

$$\begin{pmatrix} b_N \\ b_W \end{pmatrix} = \begin{pmatrix} 113.80 & 87.95 \\ 87.95 & r \end{pmatrix}^{-1} \begin{pmatrix} 5.70 & 87.95 \\ 87.95 & 2618.50 \end{pmatrix} \begin{pmatrix} a_N \\ a_W \end{pmatrix},$$

$$r = [\{1 + 0.26(n-1)\}\ 10072.0]/n,$$

$\begin{pmatrix} a_N \\ a_W \end{pmatrix} = \begin{pmatrix} 2 \\ 1 \end{pmatrix}, \begin{pmatrix} 1 \\ 1 \end{pmatrix}$, and $\begin{pmatrix} 1 \\ 2 \end{pmatrix}$ for L_{21}, L_{11}, and L_{12}, respectively.

Table 1. Description of Lines

Line	Description
N	Selected for offspring number
W	Selected for pupal weight
B	Selected for biomass
Q	Selected for a quadratic index
L_{21}	Selected for a linear index with a 2:1 economic ratio offspring number to pupal weight
L_{11}	Selected for a linear index with a 1:1 economic ratio offspring number to pupal weight
L_{12}	Selected for a linear index with a 1:2 economic ratio offspring number to pupal weight
C	An unselected control

Table 2. The Variance-Covariance Values Used in Index Calculations

	Offspring Number	Pupal Weight
Offspring Number	113.8 11.4	342.6
Pupal Weight	175.9	10072 5237

Phenotypic values are above the main diagonal and genotypic values are below

For the purposes of this study, offspring number and pupal weight were arbitrarily designated as the only traits of economic importance. Total merit was the sum of the two traits weighted by their economic values. The economic values were on a per unit basis, not on a per standard deviation basis.

The data were analysed as a randomized complete block design using analysis of variance techniques and Tukeys ω-procedure (Steel and Torrie 1960). Three variables were analysed: Biomass, offspring number, and pupal weight. The number of replicates required to detect a true difference of a required magnitude was calculated using the procedure of Cochran and Cox (1957).

Results

For each variable analysed (biomass, offspring number, and pupal weight) the interaction of replicates and method of selection proved to be non-signficant. As the ratio of the residual and interaction variances closely approximated unity in each case, the interaction term was dropped from the model and pooled with the residual (Bozivich et al. 1956).

Table 3. Influences of Selection Method on Response in Biomass, Offspring Number, and Pupal Weight Expressed as Absolute Mean Differences

	Mean Difference		
Comparison	Biomass (μgx10^2)	Offspring Number	Pupal Weight (μg)
Analysis of Variance			
C vs all Others	144**	3*	144**
N, W, B vs Q, L_{21}, L_{11}, L_{12}	98**	5**	105**
B vs N, W	108	5*	32
N vs W	188**	10**	187**
Q vs L_{21}, L_{11}, L_{12}	143**	7*	16
L_{11} vs L_{21}, L_{12}	62	3	11
L_{21} vs L_{12}	106	4	0
Residual Mean Squares (Degrees of Freedom = 148)	42,995 (μgx10^4)	69 (individuals × 10^2)	22436 (μgx10^2)
Tukey's ω-procedure			
Q vs B	93	6	114**
W vs L_{12}, L_{11}, L_{21}	67	1	6

* Significant at $\alpha = 0.05$
** Significant at $\alpha = 0.01$
α is the probability of type one error
N is a line selected for offspring number
W is a line selected for pupal weight
B is a line selected for biomass
Q is a quadratic index selected line
L_{21}, L_{11} and L_{12} are lines selected with a linear index having economic weights for offspring number to pupa weight as denoted by the subscript
C is an unselected control line

Biomass

The selected lines were significantly better than the unselected control line for biomass (Tables 3 and 4). In general, selection on biomass was effective. At $\alpha = 0.05^1$, the line selected for the quadratic index (Q) was not significantly different from the biomass selected line (B) and the pupal weight selected line (W) was not significantly different from the linear index selected lines (L_{21}, L_{11}, L_{12}; Table 2). The quadratic index selected line (Q) was significantly better than the linear index selected lines (L_{21}, L_{11}, L_{12}) which were not significantly different from each other (Tables 3 and 4). The line selected for offspring number (N) was not significantly different from the line selected for biomass (B), but was significantly better than the pupal weight selected line (W; Tables 3 and 4).

The quadratic index selected line (Q), the biomass selected line (B), and the offspring number selected line (N) were equally effective in changing biomass.

Table 4. Line Means and Standard Errors after One Generation of Selection

Line	Biomass (μgx10^2)	Offspring Number	Pupal Weight (μg)
N	915 ± 46	38.6 ± 1.9	2370 ± 34
W	729 ± 46	28.6 ± 1.9	2560 ± 34
B	931 ± 46	38.3 ± 1.9	2430 ± 34
Q	838 ± 46	32.8 ± 1.9	2550 ± 34
L_{21}	663 ± 46	26.1 ± 1.9	2560 ± 34
L_{11}	654 ± 46	25.4 ± 1.9	2570 ± 34
L_{12}	770 ± 46	30.1 ± 1.9	2560 ± 34
C	642 ± 46	28.0 ± 1.9	2370 ± 34

N is a line selected for offspring number
W is a line selected for pupal weight
B is a line selected for biomass
Q is a quadratic index selected line
L_{21}, L_{11} and L_{12} are lines selected with a linear index having economic weights for offspring number to pupa weight as denoted by the subscript
C is an unselected control line

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[1] α is the probability of type one error.

The response of these lines for biomass was better than that of the pupal weight selected line (W) and the three linear index selected lines (L_{21}, L_{11}, and L_{12}).

There was a highly significant amount of variation among replicates for biomass (F, $P < 0.01$). Since the relative efficiencies of the selected lines do not change among the replicates, this heterogeneity indicates that a great deal of variability for biomass exists in the base population.

Offspring Number

After one generation the selected lines were significantly higher than the unselected control line for offspring number (Tables 3 and 4). The biomass selected line (B) was significantly better than the quadratic index selected line (Q) with regard to response for offspring number. The biomass selected line (B) and the offspring number selected line (N) were very similar for offspring number (Table 4). The quadratic index selected line (Q) was significantly better than the three linear index selected lines (L_{21}, L_{11}, L_{12}) and the pupal weight selected line (W) which were not significantly different from each other (Tables 3 and 4). Furthermore, there were highly significant differences among replicates (F,$P < 0.01$).

Pupal Weight

The selected lines were highly significantly better than the unselected control (Tables 3 and 4). The quadratic index selected line (Q) was significantly better than the biomass selected line (B), but was not significantly different from the pupal weight (W), or linear index (L_{21}, L_{11}, L_{12}) selected lines which were not significantly different from one another (Table 2). The biomass selected line (B) was very similar to the offspring number selected line (N) for pupal weight (Table 4). Both line B and line N were significantly less than the pupal weight selected (W) line for pupal weight (Tables 3 and 4). There was a significant amount of variation among replicates for pupal weight (F, $P < 0.05$).

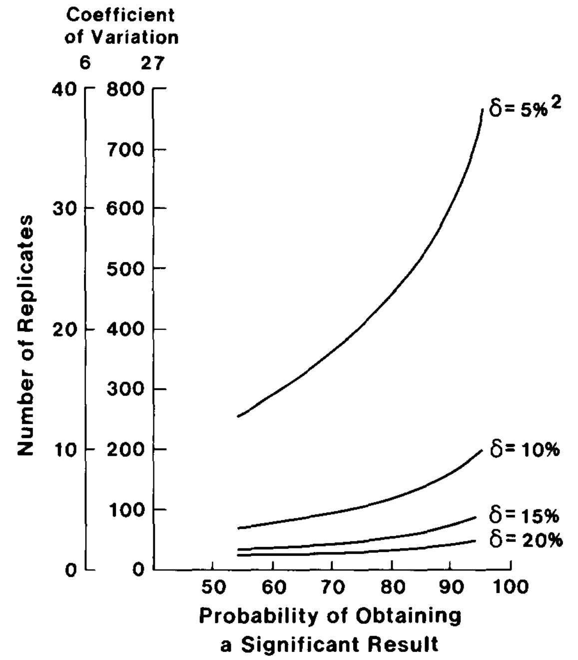

Fig.1. A plot of the number of replicates required to detect a true difference versus the probability of obtaining a significant result testing at $\alpha = 0.05^1$. $^1\alpha$ = Probability of type one error. $^2\delta$ = Difference to be detected as a percentage of the mean

Replication

A plot of an estimate of the number of replicates required to detect a true difference in mean values is shown in Fig.1. Estimates are presented at probability levels of obtaining a significant result ranging from 55% to 95%, testing at $\alpha = 0.05$ (Cochran and Cox 1957, pp. 17-23). The "replicate" referred to here consists of one experimental unit (family) per line. Changes in the proportion selected or the type of selection would influence the coefficient of variation (C.V.). The new C.V. would then determine the number of experimental units required.

In this experiment biomass had a coefficient of variation (C.V.) of 27.0% while offspring number and pupal weight had C.V.'s of 26.9% and 6.0%, respectively. The detection of a true difference of 5% in mean values for biomass would require 250 replicates 55% of the time (Fig.1). The detection of true differences in mean values of 10% or higher for biomass and offspring number are probably more realistic. A maximum of 194 replicates would be required. In traits with C.V.'s of 6.0 as opposed to 27 only 1/20th of the number of replicates are required to detect any difference at all probability levels (Fig.1).

Discussion

Selection

In this experiment three of the indices considered were linear. They were functions of the component traits of biomass: offspring number and pupal weight. There were no significant differences found between the linear indices. Generally, the response of these lines was poor for offspring number and very good for pupal weight. In fact it seemed that selection pressure on offspring number was dependent solely on the correlation between offspring number and pupal weight. As a result response for biomass was very poor in the linear index lines. On a standard deviation basis the relative economic weights were approximately 1:5, 1:10 and 1:20 for the three linear indexes which would explain the different response in the two traits.

Wilton et al. (1968) suggested that cases exist in which the assumption of additivity implicit in linear additive indices is not valid. The selection of biomass using a linear index appears to be such a case. In instances of this kind in which the assumption of linearity is violated, response to selection depends on heritability, amount of information available and the arbitrarily chosen economic values of the component traits.

Based on the results of this experiment, linear selection indices appear to be inappropriate for the selection of a quadratic trait, even where the component traits are positively correlated phenotypically. The linear index lines behaved as the pupal weight selected line, being neither greater nor smaller with regard to offspring number, pupal weight, or biomass. The linear indices improve an aggregate genotype, but this genotype does not necessarily reflect biomass.

The quadratic index selected line was as good with regard to response for biomass as the biomass selected line and the offspring number selected line. Although the response of the quadratic index selected line was not as great as the response of the biomass selected line and the offspring number selected line for offspring number, its response was as good for pupal weight as any other line included in the experiment and better than the biomass and offspring number selected lines.

The efficiency of the offspring number line with respect to response for biomass is is partially dependent on the positive genotypic and phenotypic correlations of offspring number and pupal weight. Were offspring number and pupal weight low or negatively correlated, the efficiency of that line compared to the biomass or quadratic index would probably decline. Likewise, the efficiency of the biomass line relative to that of the quadratic index line would be expected to decrease.

The biomass line and the quadratic index line were equal in response to selection for biomass. As the quadratic index can include information from relatives, other correlated traits or both, the relative efficiency of the index should improve as more information and thus more accurate identification of an individual's worth is utilized. The use of the exact quadratic index (Wilton et al. 1968) should result in higher responses than the simplified index used here. Furthermore, the quadratic index can form a portion(s) of a linear index where applicable, i.e. $I = a_{12}(\mu_1 + I_1^*)(\mu_2 + I_2^*) + a_3(\mu_3 + I_3^*) + a_4(\mu_4 + I_4^*) + \ldots + a_n(\mu_n + I_n^*)$, where a_{12} is the economic weight of trait 1 by trait 2. Biomass itself can be included in a linear index, but is not likely to be so effective as an index that takes into account component traits separately. In indices with two or more quadratic traits included, the efficiency of the quadratic index relative to any other form of selection will probably become greater.

This experiment was initiated as a comparison of selection methods and the influence of different selection goals. The results are partially dependent on the parameters used, that is literature values or more variable estimates of population parameters. Literature values were used here and the expectations differ from those resulting from the use of population values.

Variation and Replication

Hill (1973, 1974) considered the variation of response to selection. He showed that in selection experiments designed to compare selection methods the efficiency of the experiment is not improved a great deal with selection beyond a few generations because of cummulative drift variance and the correlation between generation means.

The amount of variation found in this single generation selection experiment exceeds (χ^2, $P > .95$) that expected by Hill (1973, 1974), but variance due to sampling the base population is not considered per se by Hill (1973, 1974). This variation is contributed by random, finite sampling of a practically infinite population and is likely as substantial as the drift variance. In selection experiments of few generations, variance due to sampling from the base population will probably form an important part of the total variation. Increased replication will allow more accurate prediction of this variance and will also insure an adequate, unbiased representation of the base population in the experiment.

In any generation a realized heritability estimate will reflect response from 1/2 of any additive by additive genetic effects, 1/4 of any additive by additive by additive genetics effects, and fractions of the genetic effects due to maternal effects and sex linkage if present. Each of these variances in the base population will be reduced by the appropriate fraction in each succeeding generation of selection from the first onward. If the non-additive genetic effects were substantial or unequal between selection methods (traits), the results of a single generation selection experiment could be misleading and perhaps support the choice of the wrong selection system as "best".

Given limited resources of time and space, there is an optimum balance between the number of generations of selection and replication. Although the number of generations of selection are less crucial than replication, two or three generations of selection may be prudent under most circumstances. Replication is the more important and for traits with high coefficients of variation becomes critical in terms of facilities.

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R.W. Fairfull
G.W. Friars
J.W. Wilton
Department of Animal and Poultry Science
University of Guelph
Guelph, Ontario (Canada)

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