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Experimental comparison of selection methods to improve a non-linear trait in *Tribolium*

J. L. Campo and A. Sánchez de la Blanca

Departamento de Genética Cuantitativa y Mejora Animal, Instituto Nacional de Investigaciones Agrarias,
Apartado 8.111, E-28080 Madrid, Spain

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Summary. Five lines of *Tribolium castaneum* (flour beetle) were selected in each of three replicates for biomass, using quadratic (Q) and linear (L) selection indices, direct selection for biomass (B) and indirect selection for each component trait, i.e. pupal weight (P) and family size (F), respectively, for five generations. The highest response in biomass was obtained in the Q line using an exact quadratic index in which the genetic value for each trait was based on information from both traits. The expected results were that Q selection would not exceed L selection while the L method would be superior with respect to direct selection for biomass (B line); P selection would be better and F selection worse than B selection. Selection was effective for pupal weight in the Q, L, B and P lines, but was not effective for family size, although the Q line increased slightly. The lines had no linear response for family size. Selection for biomass was influenced more by family size than by pupal weight. It is advantageous to include terms such as "squares" and "products" in the selection index, even though the response to selection may have been non-linear because of the low heritability of family size and an intermediate optimum for this component trait.

Key words: Quadratic indices – Linear indices – Direct selection – Non-linear traits – *Tribolium*

Introduction

Traits in farm animals are sometimes defined as a product or ratio of two component traits. Litter weight, egg mass and feed conversion are examples of this type of trait. Selection index theory (Smith 1936; Hazel 1943) was originally developed to improve a quantity which is an additive combination of traits. Several methods of constructing selection indices to maximize non-linear functions have been proposed. Wilton et al. (1968) derived a quadratic and a linear index for quadratic models of total merit, in which total merit includes squares and cross-products as well as first-order powers of the traits involved. The quadratic index is equivalent to a maximum-likelihood estimate of total merit (Henderson 1963; Harris 1970). A conventional linear index can still be used in this situation, as the product or ratio function can be represented by the linear terms of its Taylor series expansion (Harris 1970) or, equivalently, the product or ratio trait and its components can be transformed to a logarithmic scale (Smith 1967). The linear index of Wilton et al. (1968) is identical to these conventional indices, but can not be used when the non-linear function is a ratio. Goddard (1983) examined the relationships between different methods of constructing selection indices to improve non-linear functions. Direct selection for the product or ratio character and indirect selection for a component trait are obvious alternatives.

The objective of this study was to compare the efficiency of quadratic and linear selection indices with the direct selection for biomass in *Tribolium* (a trait made up of two components: individual weights and family size) and with indirect selection on only one component, using a multigeneration experiment. Fairfull et al. (1977) compared the response in biomass obtained from quadratic and various linear selection indices with direct and indirect selection methods. However, they used a simplified quadratic index, in which the genetic value for each trait was estimated on information from only that trait rather than both traits, and the experiment was a single generation replicated test.

On the other hand, Berger (1977) described a long-term experiment designed to evaluate the efficiency of a linear selection index with respect to indirect selection for pupal weight or family size.

Materials and methods

The Consejo population of *Tribolium castaneum* was used in this experiment. All lines were kept at 33 °C and 70% relative humidity. The culture medium consisted of 95% wheat flour and 5% brewer's yeast. The variables analysed were family size and pupal weight was in tenths of milligrams; biomass was also recorded. Family size was recorded as the total number of pupae at 21 days from mating of the parents. Sexes were pooled without adjustment. Selection was carried out on full-sib families.

In each line and replicate 32 males and 32 females were sampled as pupae from the base population and paired randomly. Five lines were segregated according to the selection method applied, i.e. linear selection index (L), quadratic selection index (Q), direct selection for biomass (B), indirect selection for family size (F) and indirect selection for pupal weight (P). There were three replicates per line. Selection was carried out for five generations in each of the lines by retaining four sons and four daughters from the parents ranking highest on the designated criterion; the selected proportion of families was 25%.

The aggregate genotype is given by

$$H = (\mu_1 + G_1)(\mu_2 + G_2)$$

where G_1 and G_2 are the breeding values of family size and pupal weight, respectively, and μ_1 and μ_2 are the population means.

The linear index is given by Wilton et al. (1968)

$$L = b_1 x_1 + b_2 \bar{x}_2$$

where x_1 and $\bar{x}_2$ are the phenotypic value for family size and the mean of full-sib families for pupal weight. The coefficients b_1 and b_2 are given by

$$\begin{bmatrix} b_1 \\ b_2 \end{bmatrix} = 0.5 \begin{bmatrix} P_{11} & 0.5\,G_{12} \\ 0.5\,G_{12} & (P_{22} + 0.5\,(n-1)\,G_{22})/n \end{bmatrix}^{-1} \begin{bmatrix} G_{11} & G_{12} \\ G_{12} & G_{22} \end{bmatrix} \cdot$$

$$\cdot \begin{bmatrix} \mu_2 \\ \mu_1 \end{bmatrix} = 0.5\,P^{-1}\,G \begin{bmatrix} \mu_2 \\ \mu_1 \end{bmatrix}$$

where P_{ij} and G_{ij} are the phenotypic and genetic covariances between traits i and j, n is the family size for pupal weight and P is the phenotypic variance-covariance matrix. Since the estimate of the value of future offspring of parents is based on the phenotypic records of past offspring, the matrix of covariances between phenotypic and breeding values is 0.5 G, where G is the variance-covariance matrix of breeding values.

Population data used in constructing the selection indices are given in Table 1. In contrast to the linear case, non-linear total merit leads to the inclusion of means for each of the traits. The linear index was

$$L = 1.31\,x_1 + 6.66\,\bar{x}_2\,.$$

The quadratic index is given by Wilton et al. (1968)

$$Q = L + b_{11}\,x_1^2 + b_{12}\,x_1\,\bar{x}_2 + b_{22}\,\bar{x}_2^2\,.$$

The coefficients b_{11}, b_{12} and b_{22} are given by

$$\begin{bmatrix} b_{11} & 0.5\,b_{12} \\ 0.5\,b_{12} & b_{22} \end{bmatrix} = 0.25\,P^{-1}\,G \begin{bmatrix} 0 & 0.5 \\ 0.5 & 0 \end{bmatrix} G\,P^{-1}$$

where P and G are as defined earlier.
The quadratic index was

$$Q = 1.31\,x_1 + 6.66\,\bar{x}_2 + 0.0002\,x_1^2 + 0.0082\,x_1\,\bar{x}_2 + 0.0045\,\bar{x}_2^2\,.$$

Selection was based on the phenotypic value for family size (x_1) in the F line, on full-sib family means for pupal weight ($\bar{x}_2$) in the P line and on biomass ($x_1\,\bar{x}_2$) in the B line.

Estimates of heritabilities and genetic and phenotypic correlations for family size and pupal weight were obtained by analysis of regression of the progeny on parental mean. The mean responses per generation were calculated as the regression coefficient of the means on generations.

Expected response to selection for biomass in the linear index line is given by

$$i \sqrt{[b_1\,b_2]\,P \begin{bmatrix} b_1 \\ b_2 \end{bmatrix}}$$

where i is the standardized selection differential. For the intended value of the selected proportion (8/32), i = 1.235. Expected response for biomass in the quadratic index line (Wilton et al. 1968) is

$$i \sqrt{[b_1\,b_2]\,P \begin{bmatrix} b_1 \\ b_2 \end{bmatrix}} + i\,2\,\mathrm{tr}\left(\begin{bmatrix} b_{11} & 0.5\,b_{12} \\ 0.5\,b_{12} & b_{22} \end{bmatrix} P \right)^2$$

where tr denotes the trace of a matrix.

The expected direct response for biomass in the biomass line is

$$0.5\,i\,G_{33}/\sqrt{P_{33}}$$

where P_{33} and G_{33} are the phenotypic and genetic variances for biomass.

The expected indirect responses for biomass in the family size and pupal weight lines are

$$0.5\,i\,G_{13}/\sqrt{P_{11}}$$

$$0.5\,i\,G_{23}/\sqrt{[P_{22} + 0.5\,(n-1)\,G_{22}]/n}$$

respectively, where G_{13} (G_{23}) is the genetic covariance between family size (pupal weight) and biomass.

Results

The parameter estimates of the base population are shown in Table 1. Mean pupal weight agrees with that

Table 1. Parameter estimates of the base population

Parameter	Trait	
	Pupal weight (tenths of milligrams)	Family size
Mean	27.12 ± 0.12	28.55 ± 0.27
Phenotypic variance	5.70	29.94
Heritability	0.36 ± 0.07	0.09 ± 0.08
Correlation:		
Phenotypic	0.17 ± 0.05	
Genetic	0.13 ± 0.14	

Table 2. Biomass: observed responses per generation, regression coefficients of response on generation number and expected responses

Line	Generations					Mean response	Expected response
	G_1	G_2	G_3	G_4	G_5		
F	127.16	-23.70	17.00	-74.99	59.64	8.50 ± 12.70	8.79
P	188.88	7.00	63.37	-106.14	37.02	25.91 ± 19.45	19.73
B	148.37	-29.62	26.28	-40.20	-6.23	11.10 ± 13.36	15.33
L	172.40	-1.60	-16.60	-72.53	60.63	12.08 ± 17.05	21.64
Q	124.93	159.67	-56.07	-89.11	199.16	48.01 ± 22.24	21.85

Table 3. Line means and standard errors after five generations of selection

Line	Biomass	Pupal weight	Family size
F	850.00 ± 46.8	27.25 ± 0.25	32.41 ± 1.49
P	969.05 ± 46.8	30.69 ± 0.25	31.67 ± 1.49
B	910.49 ± 46.8	29.45 ± 0.25	31.01 ± 1.49
L	913.85 ± 46.8	30.11 ± 0.25	30.45 ± 1.49
Q	1092.31 ± 46.8	31.38 ± 0.25	34.91 ± 1.49

previously reported by Campo and Tagarro (1977) in the Consejo population. As shown in Table 1, family size is more variable than pupal weight with a coefficient of variation (19.2%) more than twice that for pupal weight (8.8%). Biomass had a coefficient of variation similar to that for family size. Fairfull et al. (1977) indicated larger values for the coefficients of variation of family size and biomass, approximately four times greater than that for pupal weight. Mean values were similar for both component traits. The heritability estimates of Campo and Tagarro (1977) agree very well with the values in Table 1. The small heritability for family size in Table 1 is similar to that reported by Berger (1977) and Fairfull et al. (1977). On the other hand, the positive phenotypic correlation in Table 1 is lower than that reported by Fairfull et al. (1977); Berger's (1977) estimate was small and negative. Regarding the genetic correlation, Berger (1977) reported a small negative value and Fairfull et al. (1977) a large positive value.

Average responses per generation for biomass are presented in Table 2 for all five lines (replicates pooled), with regression coefficients of response on generation number and expected responses. Line means after the five generations of selection are shown in Table 3. The response of the quadratic index line (Q) was better than that of the pupal weight (P), linear index (L), biomass (B) and family size (F) lines. The proportion of realized versus predicted response was 56% in the linear index line and 72.5% in the biomass line. The response obtained in the family size line was very similar to the expected response, while the observed response was greater than expected in the pupal weight line and was nearly two times greater than expected in the quadratic index line.

Average responses per generation for pupal weight are shown in Table 4 with regression coefficients of response on generation number and expected responses. Selection was effective in pupal weight except in the family size line (F). Response to selection was significant in all other lines ($P < 0.05$). The quadratic index, pupal weight, linear index and biomass selection methods were equally effective in changing pupal weight. The responses for pupal weight were greater than expected in all lines. In the biomass line, the observed response was two times greater than expected while in the family size line the change in pupal weight was not significant. The selection results for family size are given in Table 5. In general, selection was not effective in family size and the lines showed no linear response. Observed responses to selection were not significant in any line, even though the mean value in the quadratic index line (Q) after the five generations of selection (Table 3) was higher (at the 0.05 level) than that in the linear index line (L).

The procedure of estimating selection responses on a comparative basis by using the B line as a covariate (Muir 1986a, b) produced no improvement in the results. Mean responses for biomass calculated by adjusting both the independent (generation number) and dependent (observed response) variables for changes in the B line were positive in the Q and P lines (39.52 and 10.55, respectively); the lines responded in the same direction to common environmental effects, but with a different magnitude. Adjusted mean response for pupal weight was negative in the F line (-0.61) and fluctuation of the experimental lines was as before. Adjusted estimates of selection responses for family size were positive in the Q, P and F lines (0.89, 0.43, and 0.24, respectively); there was no genotype-environment interaction in the Q line, the fluctuations of this line matching those of the B line, while the environmental effects on all other lines were greater than on the B line, although in the same direction. The use of a line as a covariate violates the assumption that the independent

Table 4. Pupal weight: observed responses per generation, regression coefficients of response on generation number and expected responses

Line	Generations					Mean response	Expected response
	G_1	G_2	G_3	G_4	G_5		
F	− 1.87	0.59	0.55	1.31	− 0.03	0.30 ± 0.22	0.03
P	− 0.17	0.09	0.98	0.80	1.50	0.65* ± 0.15	0.53
B	− 0.32	0.33	0.98	0.44	0.94	0.52** ± 0.10	0.27
L	0.24	0.35	0.43	0.83	1.19	0.58** ± 0.09	0.50
Q	− 0.18	0.15	1.30	1.00	1.86	0.84** ± 0.18	0.50

* Significant at the 0.05 probability level
** Significant at the 0.01 probability level

Table 5. Family size: observed responses per generation, regression coefficients of response on generation number and expected responses

Line	Generations					Mean responses	Expected response
	G_1	G_2	G_3	G_4	G_5		
F	6.74	− 1.84	0.07	− 4.24	3.38	0.07 ± 0.70	0.30
P	7.08	0.15	0.97	− 4.51	− 0.35	0.21 ± 0.83	0.08
B	5.94	− 1.61	− 0.16	− 1.87	− 1.24	− 0.16 ± 0.59	0.29
L	6.24	− 0.94	− 0.76	− 3.45	0.94	− 0.17 ± 0.66	0.19
Q	5.22	4.85	− 3.37	− 3.96	4.56	0.73 ± 0.87	0.19

variable be measured without error, resulting in a biased estimate of the regression expressing the true relationship between the experimental lines; however, this bias is usually negligible (Muir 1986a, b).

The realized heritability for pupal weight, calculated in the pupal weight line (P) as the regression of means on cumulative realized selection differentials, was very close to the heritability estimate in the base population. At 0.39 ± 0.08 (replicates pooled), the realized value was significant ($P < 0.05$), reflecting the progress per unit of selection on this trait. Realized heritability for family size in the family size line (F) was small, negative and not significant (−0.27 ± 0.09); it did not differ appreciably from the estimate in the base population. Realized heritability for biomass in the biomass line (B) was very small and negative (−0.04 ± 0.03); the heritability estimate in the base population was small (0.15). Therefore, the realized heritability estimates were lower when selecting for increased reproduction (family size) than when selecting for increased growth (pupal weight), biomass influenced more by reproduction than by growth. Selection for increased reproduction or biomass tended to yield less response than expected.

Discussion

Although the expected selection efficiency of the linear index relative to the quadratic index was near unity, the quadratic index gave a much better response than the linear index for biomass, the mean response per generation being four times greater. When the non-additive genetic effects are substantial, it would be advantageous to include terms such as "squares" and "products" in the index; this could explain the very high response observed in the quadratic index line. On the other hand, the linear approximation correctly predicted the increase obtained from a small change in the mean value, but as selection changes this mean, the approximation becomes less accurate. Thus, the quadratic index could be used regardless of the mean value, but this is not true for the linear index. Obviously, the response to selection in the linear index line depends on the economic values of the component traits; the linear index of Wilton et al. (1968) used in this experiment assigns an economic value to each trait equal to the mean phenotypic value of the other trait. Fairfull et al. (1977) considered three linear indices in which the economic ratio of pupal weight to family size was 2:1, 1:1 and 1:2, respectively; they did not differ significantly and the quadratic index performed significantly better than the linear index. Linear selection indices appear to be inappropriate for the selection of a product trait like biomass, since the linear indices improve an aggregate genotype which does not necessarily reflect biomass.

Use of the exact quadratic index may have improved the relative efficiency of selection, because a more accurate identification of an individual's worth is utilized. It gave the highest response in biomass. The biomass and quadratic index lines were equal in response to selection for biomass in the experiment of Fairfull et al. (1977), which used a simplified quadratic index, adding product but not squares. On the other hand, if family size and pupal weight were high and positively correlated, the efficiency of the biomass line relative to that of the quadratic index line would be expected to increase; the genetic correlation used by Fairfull et al. (1977) was 0.72 and the phenotypic correlation was 0.32.

The expected superiority of the linear index over direct selection for biomass (Smith 1967) was not obtained; both lines were similar in the experiment. Expectation of response for the index line is calculated for a given set of parameter estimates, each with sampling errors; thus it may well overestimate the true response compared with the estimates from direct selection.

Although the pupal weight line was not better for biomass than the biomass line as expected, there was an indication of this superiority because the mean response per generation for biomass was two times greater for the pupal weight line. On the other hand, the expected inferiority of the line selected for the component trait with the least heritability (family size) was confirmed in practice. On the contrary, Fairfull et al. (1977) found that the line selected for offspring number was significantly better than the pupal weight line and was not significantly different from the line selected for biomass. The large response obtained by Fairfull et al. (1977) in the family size line could be explained by the high positive genetic correlation between pupal weight and family size; if these traits were lowly correlated, as in our experiment, the efficiency of selection on family size would be expected to decrease significantly. The Consejo population of *Tribolium* has a relatively high pupal weight and natural selection may have reduced the genetic correlation. The negative genetic correlation reported by Berger (1977) seems to be typical for reproduction and growth traits.

Generally, the response of all lines was poor for family size and very good for pupal weight except in the family size line. As a result, there was a lack of response in biomass in all lines, except in the quadratic index line in which the significant change in pupal weight and the insignificant change in family size may represent the optimal combination for biomass to be improved. In the experiment of Fairfull et al. (1977) response to selection for biomass seemed to be more dependent on family size than on pupal weight, especially in the linear index and the pupal weight lines in which response to selection was small for family size and high for pupal weight. Response to selection was greater for pupal weight than for family size in the experiment of Berger (1977); direct response of pupal weight in the pupal weight line was followed by intermediate response in the linear index line; the indirect response in the family size line was the worst. Response in family size increased in the family size and linear index lines and decreased in the pupal weight line.

The low heritability of family size seems to translate into a non-linear response after the first generation of selection as judged from the tendency of the mean to increase in later generations. However, natural fitness could be maximized at an intermediate value of family size. The change was very large in the first generation in all lines. Therefore, the replicated single generation experiment of Fairfull et al. (1977) is inadequate when comparing selection methods for improvement of non-linear traits and perhaps leads to the wrong choice of selection method. In this experiment, the line selected by the quadratic index was not significantly different from the biomass or family size lines. Four or more generations of selection would be advisable under these circumstances. The change in family size in the first generation of selection was accompanied by a small decrease in pupal weight, which suggests a small or negative correlation between these traits (Berger 1977).

Based on the results of this experiment, quadratic selection indices appear to be appropriate for the selection of a quadratic trait like biomass, in which the component traits are weakly and positively correlated and the heritability of one component trait, family size, is smaller than that of the other. The response to selection in traits of this type could be non-linear for both the product and one component trait. Indirect selection for the component trait with the higher heritability, pupal weight, could be the method of selection similar to that of the quadratic index but with the advantage of minimal requisite recording.

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