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Experimental comparison of methods for simultaneous selection of two correlated traits in *Tribolium*

1. Empirical and theoretical selection indexes

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Summary. Two lines of *Tribolium castaneum* were selected in each of three replicates for egg laying between 7 and 11 days after adult emergency and for adult weight at 12 days, using theoretical (IT) and empirical (IP) index selection methods. Index coefficients were given empirically in the IP line and they were adjusted in the successive generations of selection according to the results obtained in the previous ones. Highly repeatable selection responses in all replicates occurred in both lines for the aggregate genotype (egg laying plus adult weight) and for each individual trait. The IP line tended to increase slightly more than the IT line for aggregate genotype and egg laying, while the highest response in adult weight was obtained with the IT method. The two methods gave consistently different responses in each replicate. The expected results were that IT selection should not exceed IP selection for the aggregate genotype and egg laying while theoretically the IT method should have been superior for increase adult weight. Theoretical expectations for adult weight have been fulfilled in practice. The IP method would be preferred in a practical sense because of its simplicity and freedom from need of parameter estimation.

Key words: Selection indexes – Sampling errors – Correlated traits – *Tribolium*

Introduction

The theory of selection indexes (Smith 1936; Hazel 1943) is based on the assumption that the parameters that need to be known (economic weights, heritabilities and genetic correlations) are estimated without error. However, only estimates of these parameters are available in practice and such a selection index will be likely less efficient than one calculated from the parameters themselves.

Harris (1964) investigated the influence of errors in the estimation of heritabilities and genetic correlations. He concluded that there may be a serious loss of efficiency unless sample sizes are rather large, which is most marked when heritability is low and when there is negative genetic correlation. If there were not sufficient data available, it could be better to use the economic weights as coefficients of the index directly. Williams (1962) called that a "base index".

Sales and Hill (1976a, b) analyzed the effects of sampling errors on the efficiency of selection indexes used to improve a single trait. When information from relatives is used, the loss of efficiency is small; when information on associated traits is used, the expected selection response will be overpredicted. Lin et al. (1979) determined experimentally the effects on selection efficiency due to deviations of heritability from the true value. They showed that an overestimation of the parameter would affect the selection efficiency more than an underestimation.

Instead of using either the index computed from the parameter estimates or the base index, it may be possible to modify index weights in the course of selection to avoid the effects of the errors mentioned above. Hayes and Hill (1981) have described a general procedure for modifying estimates of parameters; the complexity of this method is greatly reduced with the use of the reparameterization suggested by Hayes and Hill (1980).

Another method is the use of an empirical selection index for which coefficients are assigned empirically to each trait according to the importance being applied to the selection of each one. This empirical index is adjusted in successive generations of selection according to selection results obtained in the previous generations and it is free from errors of parameter estimation although necessarily biased.

The object of this work is to compare such an empirical index with a selection index based on least squares coefficients using two correlated traits, egg laying and adult weight, in *Tribolium castaneum.*

Materials and methods

The genetic material used in the experiment was the Consejo population of *Tribolium castaneum*. This population has been kept in our department since 1964. Cultures were made in chambers at 33 °C and 70% relative humidity. The culture medium was wheat flour (95%) supplemented with brewer's yeast (5%); it was dry-sterilized at 65 °C for 12 h prior to its use.

The traits selected were number of eggs laid by virgin females scored from the 7th to the 11th day after adult emergency and adult body weight at the 12th day after emergency, in tenths of milligrams.

In each line and replicate, 25 males and 25 females were sampled as pupae from the population cage; two different lines were segregated, distinguished by the selection index applied, i.e. theoretical (IT) or empirical (IP); there were three replicates per line. Selection was carried out for high egg laying and high adult weight. In each generation and line 25 pair matings contributed five male and five female offspring each of which were individually weighed; the females were additionally scored for egg laying. The appropiate index was calculated for each individual and the best 25 males and 25 females from a given line were selected and mated in pairs avoiding sib-matings. The selected proportion was therefore 20%. Six generations of selection were carried out in each of the lines.

The aggregate genotype H is given by:

$$H = k_1G_1 + k_2G_2$$

where G_1 and G_2 stand for the breeding values of the egg laying and adult weight, respectively. The weights k_1 and k_2 were taken as being equal to 1.00.

The selection indexes were based on family information for egg laying and on individual performance for adult weight. In the IT line each individual was given a value by the expression:

$$I = b_1\bar{x}_1 + b_2x_2$$

where $\bar{x}_1$ and x_2 stand for the mean of full-sib families for egg laying and the individual phenotypic value for adult weight, respectively. The coefficients b_1 and b_2 are given in females by (Campo 1978):

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

and, in males:

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

where P_{ij} and G_{ij} are the phenotypic and genetic covariances between traits i and j; n is the family size for egg laying.

Variances and covariances used in constructing the theoretical selection index are given in Table 1. The theoretical index was, in females:

$$I = 0.69\,\bar{x}_1 + 1.34\,x_2$$

and, in males:

$$I = 0.57\,\bar{x}_1 + 1.53\,x_2$$

In the IP line the initial index coefficients $b_1 = b_2 = 1$ ($I = \bar{x}_1 + x_2$) were given a priori. Those coefficients were modified throughout the experiment according to the obtained results in the previous generations, as shown in Table 2; if a trait had not adequate response to selection, and the other had, its coefficient was increased in the index of the next generation.

Table 1. Variances and covariances used in construction of the theoretical selection index

	Egg laying	Adult weight
Egg laying	165.56^a 75.54^b	7.06^a
Adult weight	5.44^b	4.77^a 3.42^b

^{a} Phenotypic values (P_{ij})
^{b} Genetic values (G_{ij})

Table 2. Values of the coefficients of the empirical index in the successive generations of IP line

Coefficient	Generations					
	0	1	2	3	4	5
b_1	1	1	1	1	1	1
b_2	1	3	3	6.5/3.5	6.5/3.5	1.5

Estimates of heritabilities and genetic and phenotypic correlations for both traits were obtained by analysis of variance-covariance of full-sib families. The mean responses per generation were calculated as the regression coefficient of the means on generations. Expected responses to selection for each trait in females are given by:

$$\begin{aligned}&\Delta G_1=i\,\{b_1G_{11}\,(1+\,(n-1)\,0.5)/n+b_2G_{12}\}/\sigma_I\\&\Delta G_2=i\,\{b_1G_{12}\,(1+(n-1)\,0.5)/n+b_2G_{22}\}/\sigma_I\end{aligned}$$

where i is the standardised selection differential, σ_I is the standard deviation of the index and,

$$\begin{aligned}\sigma_I^2=&\,b_1^2\,\{P_{11}+(n-1)\,0.5\,G_{11}\}/n+b_2^2\,P_{22}+\\&+2\,b_1b_2\,\{P_{12}+(n-1)\,0.5\,G_{12}\}/n\end{aligned}$$

Expected responses to selection in males are:

$$\begin{aligned}&\Delta G_1=i\,\{b_1\,0.5\,G_{11}+b_2\,G_{12}\}/\sigma_I\\&\Delta G_2=i\,\{b_1\,0.5\,G_{12}+b_2\,G_{22}\}/\sigma_I\end{aligned}$$

where now

$$\begin{aligned}\sigma_I^2=&\,b_1^2\,\{P_{11}+(n-1)\,0.5\,G_{11}\}/n+b_2^2\,P_{22}+\\&+2\,b_1b_2\,0.5\,G_{12}\end{aligned}$$

Genetic improvement in aggregate genotype is then

$$\Delta H=\Delta G_1+\Delta G_2$$

and ΔH is equal to $i\sigma_I$ in the theoretical selection index.

Results

The parameters estimated in the base population are summarized in Table 3; they correspond to generation 0 of this experiment. Mean egg production is larger than previously observed in the Consejo population by Fuentes (1974); Ruano et al. (1975) and Orozco et al.

Table 3. Parameters of the base population estimated at generation 0 of selection

Parameter	Trait	
	Egg laying	Adult weight[a]
Mean	32.58±0.43	21.73±0.04
Coefficient of variation (%)	43.65	10.78
No. offspring	1091	2260
No. parents	272	266
Heritability	0.34±0.05	0.45±0.05
Correlation:		
Phenotypic	0.28±0.09	
Genetic	0.69±0.04	

[a] Sexes pooled

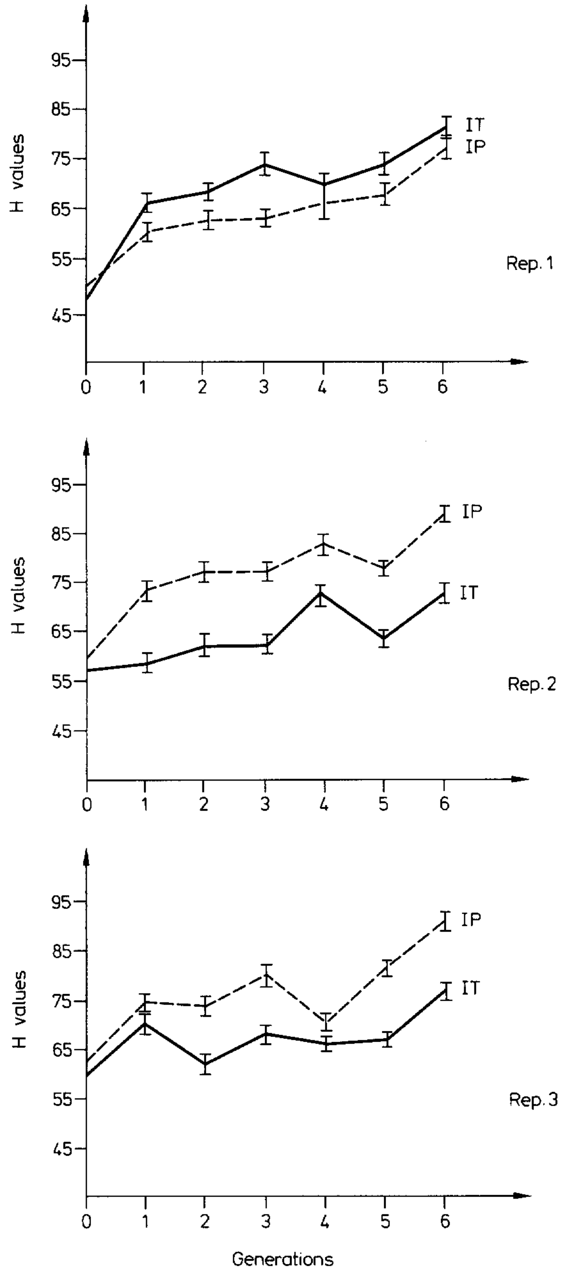

Fig. 1. Observed responses for H values for the theoretical (IT) and empirical (IP) index lines

(1980); the mean for adult weight agrees very well with those reported by Fuentes (1974) and Orozco et al. (1980). As is shown from Table 3, egg laying is a trait with great variability (CV=43.6) while adult weight has a small variation (CV=10.8).

The heritability estimated in the Consejo population by other authors ranges approximately from 0.20–0.40 for egg laying (Fuentes 1974; Orozco and Bell 1974; Ruano et al. 1975; Orozco 1976; López-Fanjul and Jodar 1977; Toro 1978; Bolet et al. 1979; Orozco et al. 1980) and from 0.30–0.50 for adult weight (Fuentes 1974; Toro 1978; Orozco et al. 1980). The small and positive phenotypic correlation showed in Table 3 agrees very well with those reported by Fuentes (1974) and Orozco et al. (1980). With regards to the genetic correlation, although Fuentes (1974) and Orozco et al. (1980) reported very small values, Orozco et al. (1980) indicated other estimates with moderate and positive value. A positive value for the genetic correlation is consistent with the behaviour of both selected lines.

Although there was a significant difference between male and female adult weight, there were no significant differences between heritabilities of this trait in both sexes, thus they were pooled in the experiment. The females were heavier (22.14±0.07) than the males (21.36±0.06); similar differences have been reported by Okada and Hardin (1967); Fuentes (1974) and Toro (1978).

Generation means for H values for both lines and three replicates are shown in Fig. 1. Selection led to a significant response during the six generations studied. Regression coefficients of mean on generation number are given in Table 4, both for the aggregate genotype and for each individual trait. Observed total responses are summarised in Table 5. Rather consistent selection differences between methods and highly repeatable selection responses were obtained over six generations. The response for the aggregate genotype in the empirical index line exceeded that in the theoretical index line in two replicates; differences between both lines were significant in a practical sense in each of the three replicates. The empirical index line showed very little variation between replicates.

Generation means for egg laying are presented in Fig. 2. A significant response was detected during the

Table 4. Regression coefficients of response on generation number for the theoretical (IT) and empirical (IP) index lines

Trait	Line	Replicates			Pool
		1	2	3	
H-values	IT	4.10±1.09	2.45±0.73	1.78±0.84	2.78±0.54
	IP	3.71±0.61	3.65±0.85	3.36±1.05	3.57±0.47
Egg laying	IT	3.28±1.11	1.65±0.68	0.98±0.88	1.97±0.55
	IP	3.17±0.61	3.34±0.83	2.80±1.11	3.10±0.48
Adult weight	IT	0.82±0.09	0.80±0.08	0.80±0.13	0.81±0.06
	IP	0.54±0.10	0.31±0.18	0.55±0.12	0.47±0.08

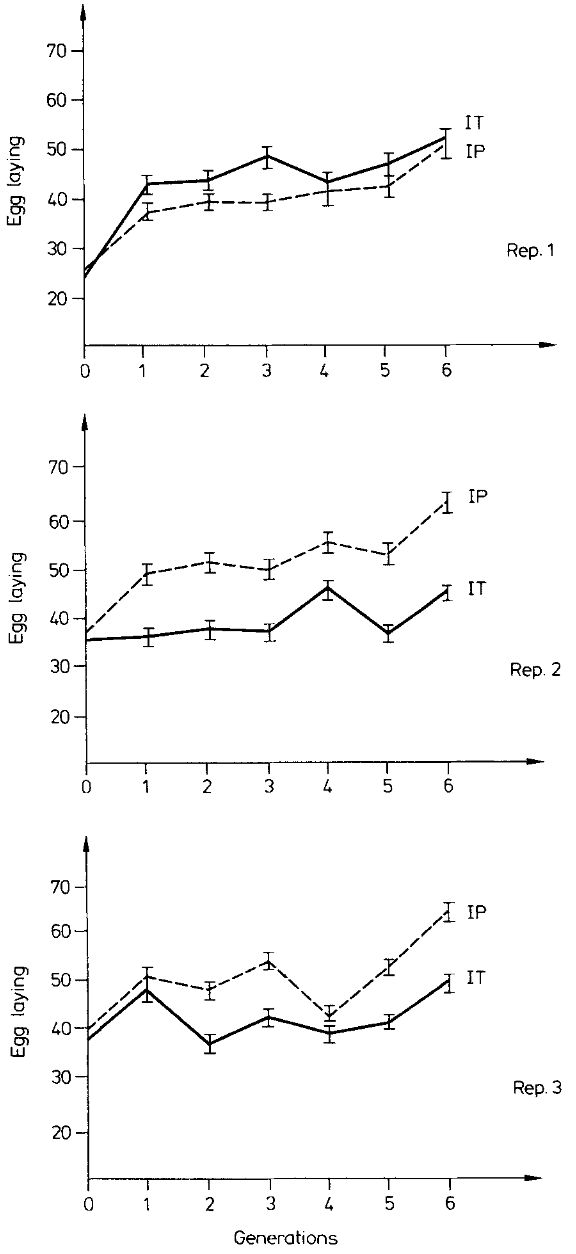

Fig. 2. Observed responses for egg laying for the two selection lines

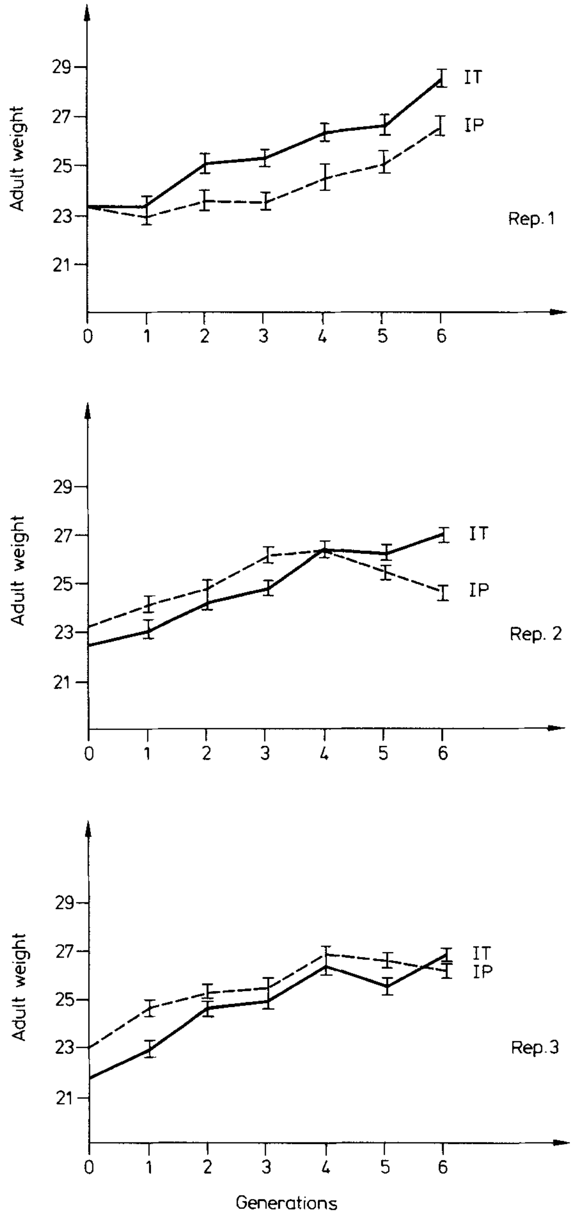

Fig. 3. Observed responses for adult weight for the two selection lines

selection; mean responses of the empirical index were again larger in two replicates. Finally, generation means for adult weight are shown in Fig. 3. Response is apparent in both lines, even though replicate two of the IP line had no linear response. A higher rate of response for this trait was observed in the three replicates for the theoretical index line.

Since there was not heterogeneity between mean responses for the three replicates in both lines, replicates were pooled to give a comparison between lines in the experiment as a whole (Tables 4 and 5). Empirical index selection was better than the theoretical index, both for the aggregate genotype and for egg laying. On the other hand, the theoretical index line had a higher response than the empirical index line for increasing adult weight.

Population and selection data are summarised in Table 6 for each line and replicate. Average standardised selection differentials were slightly greater in the empirical index line than in the theoretical index line. There was a close aggreement between these values and that based on the normality assumption, this value being 1.394 for the intended value (20%) of selected proportion. Effective population size was calculated by the formula given by Crow (1954):

$$4N/(\bar{k}+\sigma_k^2)$$

where N is the number of breeders (50 in this experiment), $\bar{k}$ the mean number of breeders per family and σ_k^2 the variance of family size.

All lines showed a clear reduction in effective population size, consequently with the use of family information in the selection. The reduction in effective size was not so drastic in the theoretical index line, its value being almost two times greater than those calculated in the empirical index line.

The pool of heritabilities, estimated in each generation for both individual traits, is presented in Table 7; the regression coefficients of estimated heritabilities on generation number are also included in this table. The values of heritabilities agree quite well with the estimates on the base population, specially in IT line for egg laying and in IP line for adult weight; both traits again presented intermediate heritability and adult weight showed a trend toward high values. The magnitude of the heritabilities did not significantly change during the six generations of selection considered.

Pooled genetic and phenotypic correlation estimates in each generation and the regression coefficients of these parameters on generation number are shown in Table 8. Average values calculated for the correlations were similar to those estimated in the base population. Neither genetic nor phenotypic correlation significantly changed during selection; this stability does not agree with the expected change toward negative values postulated by Lerner (1958) for the genetic correlation between two traits.

Table 5. Observed total responses for each line and replicate

Trait	Line	Replicates			Pool
		1	2	3	
H-values	IT	33.12	15.79	17.10	22.00
	IP	28.25	28.93	27.96	28.38
Egg laying	IT	27.91	11.25	12.02	17.06
	IP	24.84	27.53	24.73	25.70
Body weight	IT	5.21	4.54	5.08	4.94
	IP	3.41	1.40	3.23	2.68

Table 6. Average selection differentials, number of individuals measured and selected, selected proportions and effective population size, for each line and replicate

	Replicate					
	1		2		3	
	Line		Line		Line	
	IT	IP	IT	IP	IT	IP
Selection differentials	14.45	4.09	14.36	5.62	12.52	4.74
Standardised selection differentials	1.253	1.382	1.302	1.366	1.235	1.243
No. measured	213	189	229	234	202	209
No. selected individuals	47	41	50	50	48	50
Selected proportion (%)	22	22	22	21	24	24
Effective population size	27.71	11.76	24.14	11.85	28.18	14.96

Table 7. Heritabilities pooled over generations and regression coefficients (in brackets) of heritability on generation number

Replicate	Egg laying		Adult weight	
	Line		Line	
	IT	IP	IT	IP
1	0.31±0.07 (0.06±0.03)	0.14±0.16 (−0.03±0.03)	0.36±0.05 (−0.01±0.04)	0.51 ±0.08 (0.04 ±0.04)
2	0.35±0.07 (−0.02±0.08)	0.12±0.05 (−0.08±0.05)	0.35±0.05 (−0.01±0.02)	0.38 ±0.07 (0.001±0.06)
3	0.19±0.06 (−0.03±0.05)	0.33±0.07 (−0.03±0.04)	0.34±0.05 (−0.02±0.04)	0.50 ±0.08 (0.04 ±0.04)

Table 8. Correlations pooled over generations and regression coefficients (in brackets) of correlations on generation number

Replicate	Genetic correlation		Phenotypic correlation	
	Line		Line	
	IT	IP	IT	IP
1	0.88±0.06 (−0.06±0.11)	0.69±0.10 (0.08±0.17)	0.28±0.03 (−0.02±0.04)	0.16±0.03 (0.02±0.01)
2	0.47±0.06 (−0.02±0.17)	0.69±0.10 (0.03±0.08)	0.29±0.04 (−0.10±0.02)	0.23±0.03 (−0.01±0.02)
3	0.74±0.09 (−0.08±0.06)	0.24±0.12 (−0.10±0.16)	0.27±0.03 (−0.03±0.02)	0.17±0.04 (−0.02±0.02)

Table 9. Expected response per generation for each line

Trait	Line	
	IT	IP
H-values	8.95	8.86
Egg laying	7.47	7.47
Body weight	1.50	1.39

Discussion

Although the theoretical selection index gave a better response than the empirical selection index for adult weight, the empirical index tended to give the greater response for egg laying and the aggregate genotype. There were highly repeatable selection responses and the two methods give consistently different responses in each replicate that is significant in a practical sense. It appears that theoretical selection index was not appreciably better than empirical selection index. Possible differences between the two procedures are biased in favor of IP because it was continuously adjusted to current genetic response.

Expected responses to selection per generation are given in Table 9. The variances and covariances used for the calculation of the theoretical index (Table 1) were utilised in the equations of the predicted responses. Since the coefficients of the selection index in the empirical line were adjusted in the successive generations of selection the responses given for this line are the means of the expected response in each generation.

The results of this study do not agree with the theoretical expectations for the aggregate genotype as the small better response that should be expected in the IT line (Table 9) was only found in one replicate, the IP line being superior in the other two replicates. Theoretical prediction of the superiority of the IT line over the IP line for adult weight has been fulfilled in practice, while the theoretical equality of both lines for egg laying has not, empirical index being better in two replicates.

The efficiency of the theoretical selection index could have been reduced by the use of overestimated heritabilities in the calculation of index coefficients, especially for adult weight. Heritabilities estimated from the phenotypic and genetic variances indicated in Table 1 (0.45 and 0.72 for egg laying and adult weight, respectively) were larger than the values reported by other authors and those found throughout the experiment, showing that smaller values would have been more adequate for that calculation.

The sampling errors of the estimates used for the calculation of the theoretical index do not seem to explain the small proportion of observed versus predicted response. Expectations of gains for the theoretical index line calculated using the generation 0 parameters (as the index equation calculated from these values was similar to the previously calculated index) resulted in 9.05, very close to those calculated before. On the other hand, the response that should have been expected with the index calculated with generation 0 estimates is also very similar (9.13). These results agree with those of Harris (1964), since both traits have intermediate heritability and there is positive genetic correlation between them, and also with the results reported by Sales and Hill (1976 a). However, they do not agree with those indicated by Lin et al. (1979) where the adult weight heritability used for the calculation of the index was much greater than the value estimated in generation 0.

The small proportion of predicted response that was observed in the experiment is probably a consequence of the action of genetic drift interfering on the selection effects since it does not seem to be produced by sampling errors of parameter estimates nor by parameters changes during the generations of selection considered. The stability of the parameters throughout the process of selection justifies that the theoretical index were not recalculated in each generation. Effective population size was small enough to produce important effects from random changes.

The empirical index used in this experiment is similar to the base index (Williams 1962) and they both are identical in the first generation of selection. In theory, the theoretical index is better than the base index since the regression of aggregate genotype on the index value is equal to 1.00 in the theoretical index and less than 1.00 in the base index. Nevertheless, Elgin et al. (1970) reported that the base index proved equally effective and Eagles and Frey (1974) showed that the two indexes were about equally efficient.

The very good behaviour of the empirical selection index shows that in practice it could be the best solution for simultaneous improvement of two traits. This is so because of its simplicity and because it can be easily recalculated in each generation of selection, according to the obtained results in the previous ones, and also because it is free from sampling errors in parameters estimation. In addition, in some cases parameters are not available for calculating a theoretical selection index.

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