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Experimental study of the influence of errors of genetic correlation estimates on unrestricted, optimum, and desired gains selection indices

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Summary. Effects of errors in estimates of the genetic correlation on the accuracy of unrestricted, optimum, and desired gains selection indices were examined experimentally in *Tribolium castaneum.* Three lines were selected for three generations for pupal weight at 21 days and adult weight at 31 days, using unrestricted (I9), optimum (O9), and desired gains (G9) index selection methods. The genetic correlation between pupal and adult weights in the base population was 0.95. The optimum index was designed to set the response of pupal weight by a fixed amount, while in the desired gains index the responses of pupal and adult weights were specified as being equal to 3:1. Three other indices were constructed using a deliberately incorrect genetic correlation (0.25), i.e., unrestricted (I2), optimum (O2), and desired gains (G2). Responses observed in unrestricted index lines (I9 versus I2) and optimum index lines (O9 versus O2) did not differ significantly, even though lines I9 and I2 differed in a practical sense. Responses in desired gains index lines (G9 versus G2) differed significantly. Responses obtained for aggregate genotype (pupal weight + adult weight) and for the component traits were greater in line I9 than those obtained in line I2. Responses obtained in the O9 and O2 lines for pupal and adult weights were similar, while those obtained in the G9 and G2 lines were similar for pupal weight but not ($P<0.05$) for adult weight. Therefore, underestimation of the genetic correlation seems to affect the efficiency of a desired gains index more than that of unrestricted or optimum indices.

Key words: Estimation errors – Genetic correlation – Unrestricted index – Restricted index – *Tribolium*

Introduction

Several potential problems are frequently associated with the use of a selection index. One of the most serious limitations is that the true population parameters are usually unknown and have to be estimated from samples. There has been an extensive discussion of the effects of errors in the parameter estimates on the efficiency of unrestricted indices (Smith 1936; Hazel 1943), but the sampling formulae are so complex that it is difficult to identify situations where poor indices are likely to arise in practice.

Harris (1963, 1964) reported that use of the Smith-Hazel index is justified if the parameter estimates deviate only slightly from the parameters. Heidhues (1961) and Sales and Hill (1976b) investigated the effect of errors on the accuracy of a selection index that is based on the trait under selection and on a genetically correlated trait. When estimates of the phenotypic or genetic covariance matrix exceed theoretical limits, Heidhues (1961) suggested that they should be modified to increase the accuracy. Hill and Thompson (1978) discussed the effect on selection indices of estimates of heritability and genetic correlation that are outside their valid limits (0 to 1 and -1 to $+1$, respectively). Hayes and Hill (1981) described a general procedure (bending) for modifying estimates of parameters in the construction of selection indices. The main difficulty lies in choosing an appropriate value for the bending factor; complete bending implies the use of the base index (Williams 1962). Meyer and Hill (1983) showed that losses of accuracy of index selection may be substantial for small samples but losses can be reduced by bending. On the other hand, there has been little discussion of the effects of errors on the accuracy of restricted indices. Hill and Meyer (1984) have studied the effect of variation in genetic parameters for a Kempthorne and Nordskog (1959) completely restricted index. They found that a restricted index can be an effective procedure if based on reliable estimates of parameters. Simm et al. (1986) studied the sensitivity of completely restricted and unrestricted indices to changes in parameters in cattle.

Lin et al. (1979) experimentally evaluated in *Tribolium* the effect of errors of heritability estimates on the efficiency of a selection index involving larval weight and pupal weight. As far as we know, no experimental investigations of the effect of errors of genetic correlation estimates have been reported. Estimation error of the genetic correlation seems to have a larger effect than estimation error of heritability (Pease et al. 1967), especially if the sign of the genetic correlation does not equal the sign of the ratio of the economic weights of traits.

Here we describe the effects due to a grossly incorrect genetic correlation estimate on the efficiency of three selection indices involving pupal weight and adult weight of *Tribolium castaneum*. Experiment 1 considered an unrestricted index designed to improve both weights (Smith-Hazel index), and experiment 2 involved two restricted selection indices, i.e., the optimum (Tallis 1962) and desired gains (Pesek and Baker 1969) indices.

Materials and methods

The Consejo population was used in both experiments. The traits selected were pupal weight at 21 days and adult weight at 31 days measured to the closest 0.01 mg. The culture medium consisted of 95% wheat flour and 5% dried brewer's yeast. All lines were kept at 70% relative humidity and 33 °C.

To start each line and replicate, 20 males and 20 females were sampled as pupae from the population cage. In experiment 1, with two replicates per line, two unrestricted selection indices were used based on values of the genetic correlation between pupal and adult weight of either 0.95 (line I9) or 0.25 (line I2). The correlation values of 0.95 and 0.25 represent an estimate of the "true" genetic correlation in the base population and a deliberate underestimate, respectively. In experiment 2, four restricted selection indices were used representing the four combinations of optimum index (lines O9 and O2) or desired gains index (lines G9 and G2) with the two contrasting values of the genetic correlation (0.95 or 0.25). Two replicates were used in the O2 and G2 lines. Three replicates, set 4 months before the others in experiment 2 (Campo and Velasco 1989), were used in lines O9 and G9.

In each generation and line, 20 pair matings contributed 5 male and 5 female offspring, all individually weighed. The appropriate index was calculated for each individual, and the best 20 males and 20 females from a given line were selected and mated in pairs, avoiding sib-matings. The selected proportion was therefore 20%. Three generations of selection were carried out in all lines.

Variances and covariances used in constructing the selection indices for lines I9, O9, and G9 in Table 1 are based on the "true" genetic correlation of 0.95. The incorrect genetic correlation of 0.25 was used in calculating indices for lines I2, O2, and G2; variances and covariances were those in Table 1 except that the genetic covariance was 58.03 ($=0.25 \cdot \sqrt{355.86} \cdot \sqrt{151.42}$).

Table 1. Variances and covariances used in construction of the selection indices for lines I9, O9, and G9

	Pupal weight	Adult weight
Pupal weight	1,012.39[a] 355.86[b]	651.02[a]
Aduld weight	221.30[b]	503.38[a] 151.42[b]

[a] Phenotypic values
[b] Genetic values

Table 2. Index coefficients used in each line for pupal weight (b_1) and adult weight (b_2)

Type of line	Index coefficients	
	b_1	b_2
Unrestricted (I9)	0.5581	0.0186
Unrestricted with genetic correlation = 0.25 (I2)	0.8467	−0.6807
Optimum (O9)	−0.0260	0.1551
Optimum with genetic correlation = 0.25 (O2)	0.0143	0.3438
Desired gains (G9)	4.7100	−6.2600
Desired gains with genetic correlation = 0.25 (G2)	0.7839	0.3612

The aggregate genotype for the unrestricted and optimum indices was: $H = G_1 + G_2$, where G_1 and G_2 are the breeding values for pupal and adult weights, respectively. In the optimum index, the genetic gain for pupal weight was specified as being equal to 0.13 mg, which was approximately equal to 80% of the expected gain from the unrestricted index. The relative expected genetic responses in the desired gains index for pupal and adult weights were specified as being equal to 3:1. Values of index coefficients are given in Table 2.

Mean response obtained per generation was calculated as the regression coefficient of observed means on generation number. Standard errors of observed responses were calculated from the square root of the variance among replicate slopes divided by the number of replicates. Three types of predicted response were calculated (Harris 1963, 1964; Sales and Hill 1976a). In the I9, O9, and G9 lines, we calculated the response possible (Δ) given the parameter values in Table 1. For the I2, O2, and G2 lines, two types of predicted response were calculated: that predicted ($\hat{\Delta}$) from the index using the "wrong" genetic covariance (58.03) and that predicted (Δ') when the index computed with this "wrong" genetic covariance is applied in the population.

Analyses of variance of the cumulative genetic gains obtained by line, generation, and replicate were calculated. In experiment 1, replicates from the I9 and I2 lines were contemporaneous and thus unrestricted selection indices were compared in a mixed model with replicates as a factorial effect. In experiment 2, the three replicates of the O9 (G9) line were not contemporaneous with the two replicates of the O2 (G2) line. Thus, optimum (desired gains) indices were compared in a mixed model with replicates nested within lines. In both experiments, lines and generations were treated as fixed effects and replicates as random variables.

Table 3. Mean values by generation and replicate for aggregate genotype in the unrestricted index lines (I9 and I2)

Line	Replicate	Generations				Mean response
		0	1	2	3	
I9	1	492.42	502.23	526.72	573.84	26.88
	2	468.31	490.83	514.19	537.00	22.94
	Pool	480.37	496.53	520.46	555.42	24.91 ± 1.97
I2	1	466.76	517.84	519.08	545.20	23.66
	2	493.60	499.86	516.72	526.52	11.56
	Pool	480.19	508.86	517.91	535.86	17.61 ± 6.05

Table 4. Mean values by generation and replicate for pupal and adult weights in the unrestricted index lines (I9 and I2)

Trait	Line	Replicate	Generations				Mean response
			0	1	2	3	
Pupal weight	I9	1	267.41	273.24	287.78	317.98	16.62
		2	257.32	269.57	287.09	301.10	14.89
		Pool	262.37	271.41	287.44	309.54	15.75 ± 0.86
	I2	1	256.04	285.72	290.53	307.45	15.90
		2	272.05	276.63	287.68	294.42	7.82
		Pool	264.05	281.18	289.11	300.94	11.86 ± 4.04
Adult weight	I9	1	225.01	228.99	238.94	255.86	10.25
		2	210.99	221.26	227.10	235.90	8.06
		Pool	218.00	225.13	233.02	245.88	9.15 ± 1.09
	I2	1	210.72	232.12	228.55	237.75	7.75
		2	221.55	223.23	229.04	232.10	3.75
		Pool	216.14	227.68	228.80	234.92	5.75 ± 2.00

Results

Generation means for aggregate genotype (pupal weight + adult weight) and for pupal and adult weights separately are presented in Tables 3 and 4, respectively, for the unrestricted index lines (I9 and I2), with mean responses and variation between replicates. Since the selection index is designed to maximize genetic gain in the aggregate genotype, the combined pupal + adult weight response is of main interest and the responses in pupal and adult weights separately are secondary; they are included for analyses of the effect of error in the genetic correlation estimate on the individual traits of an index. Selection led to a significant response over the three generations in both lines for pupal, adult, and combined weights. Consistent differences between lines were observed over three generations. Responses in the I9 line exceeded those in the I2 line in both replicates. Pupal weight responded more to unrestricted index selection than adult weight in lines I9 and I2, i.e., the response obtained in the aggregate genotype was mainly due to the increase in pupal weight. The index coefficients were greater in both lines for pupal than for adult weight.

Table 5. Analyses of variance of cumulative genetic gains. Unrestricted selection indices

Sources of variation	Degrees of freedom	Mean squares		
		Pupal weight	Adult weight	Aggregate genotype
Indes (I)	1	1.62	16.50	28.45
Replicate	1	341.01	161.41	971.63
Generation (G)	2	846.25*	204.36	1,877.87
I × G	2	84.81	45.60	254.47
Error	5	132.27	52.42	344.80

* $P < 0.05$

The analyses of variance of cumulative genetic gains did not detect significant differences between I9 and I2 in pupal, adult, or combined weights (Table 5). Since the responses of line I2 were as much as 24.7% and 37.2% lower for mean response per generation (21.8% and 32.6% lower for total response), the analyses apparently was not stringent enough to detect important differences.

Generation means for pupal and adult weights and mean responses are presented in Table 6 for the optimum

Table 6. Mean values by generation and replicate for pupal and adult weights in the optimum index lines (O9 and O2)

Trait	Line	Replicate	Generations				Mean response
			0	1	2	3	
Pupal weight	O9	1	276.46	285.13	304.04	302.12	9.59
		2	269.58	291.13	288.90	295.08	7.43
		3	280.01	298.23	299.07	335.41	16.70
		Pool	275.35	291.50	297.34	310.87	11.24±2.80
	O2	1	269.03	271.24	293.02	297.47	10.71
		2	259.99	286.41	292.72	290.05	9.65
		Pool	264.51	278.83	292.87	293.76	10.18±0.53
Adult weight	O9	1	229.12	231.94	249.69	245.33	6.64
		2	224.70	239.10	242.20	241.43	5.33
		3	230.64	244.41	249.38	269.04	12.02
		Pool	228.15	238.48	247.09	251.93	7.99±2.05
	O2	1	220.93	222.41	234.49	241.76	7.46
		2	216.26	230.92	239.84	239.95	8.00
		Pool	218-60	226.67	237.17	240.86	7.73±0.27

Table 7. Mean values by generation and replicate for pupal and adult weights in the desired gains index lines (G9 and G2)

Trait	Line	Replicate	Generations				Mean response
			0	1	2	3	
Pupal weight	G9	1	276.78	281.43	287.42	283.72	2.68
		2	266.41	283.94	290.42	291.38	8.14
		3	267.91	275.05	289.61	286.62	7.07
		Pool	270.37	280.14	289.15	287.24	5.96±1.67
	G2	1	278.90	273.74	296.75	306.06	10.45
		2	261.72	266.43	271.15	276.69	4.96
		Pool	270.31	270.09	283.95	291.38	7.71±2.74
Adult weight	G9	1	227.07	222.10	225.86	226.84	0.31
		2	222.06	228.70	229.74	226.68	1.49
		3	225.79	219.62	229.79	226.72	1.30
		Pool	224.98	223.47	228.46	226.75	1.03±0.37
	G2	1	228.79	223.38	239.89	250.37	8.13
		2	212.07	219.89	222.93	224.56	4.05
		Pool	220.43	221.64	231.41	237.47	6.09±2.04

index lines (O9 and O2) and in Table 7 for the desired gains index lines (G9 and G2). Observed responses to selection in the optimum index lines were significant for pupal and adult weights over the three generations of selection. Differences between lines O9 and O2 (3.3% and 9.4% for mean response) were smaller than corresponding differences in the other types of index. The response was slightly larger in pupal weight than in adult weight, even though the index coefficients for pupal weight were smaller. The desired gains index lines responded significantly in pupal weight; observed response for adult weight was significant in the G2 line but not in the G9 line. There was a very large difference for mean response in adult weight between G9 and G2 lines and responses were larger for G2 than for G9, the reverse of trends in the other types of index. Pupal weight was more

Table 8. Analyses of variance of cumulative genetic gains. Optimum (O) and desired gains index (G) lines

Sources of variation	Degrees of freedom	Mean squares			
		O lines		G lines	
		Pupal weight	Adult weight	Pupal weight	Adult weight
Index (I)	1	1.20	6.88	47.96	259.22*
Replicate (within indices)	3	127.83	95.44	116.09	40.72
Generation (G)	2	387.29	246.54*	238.75*	98.69
I×G	2	49.38	1.09	62.42	48.19
Error	6	113.04	44.19	28.88	26.59

* $P<0.05$

Table 9. Expected response and obtained response (in brackets; replicates pooled) per generation for each line

Type of line			Trait	
			Pupal weight	Adult weight
Unrestricted	(I9)	Δ	15.6 (15.75)	9.7 (9.15)
Unrestricted	(I2):	$\hat{\Delta}$	25.4 (11.86)	−5.1 (5.75)
		Δ'	14.7 (11.86)	8.2 (5.75)
Optimum	(O9)	Δ	13.0 (11.24)	9.1 (7.99)
Optimum	(O2):	$\hat{\Delta}$	4.3 (10.18)	9.1 (7.73)
		Δ'	14.0 (10.18)	9.5 (7.73)
Desired gains	(G9)	Δ	6.7 (5.96)	2.2 (1.03)
Desired gains	(G2):	$\hat{\Delta}$	12.9 (7.71)	4.3 (6.09)
		Δ'	15.5 (7.71)	9.8 (6.09)

Δ is the response possible given the "true" genetic correlation of 0.95, $\hat{\Delta}$ is the response predicted from the index using the deliberately "wrong" genetic correlation estimate (0.25), and Δ' is the response predicted when the index computed from this "wrong" genetic correlation estimate is used in the population

Table 10. Average selection differentials for unrestricted index lines (I9 and I2)

	I9 line		I2 line	
	Rep. 1	Rep. 2	Rep. 1	Rep. 2
Selection differentials	25.83	22.07	17.91	19.00
Standardized selection differentials	1.42	1.22	1.24	1.32
Standardized selection differentials (intended)	1.39	1.37	1.34	1.35

responsive to desired gains index selection than adult weight in the G9 line, while observed responses for pupal and adult weights were similar in the G2 line. The index coefficient for pupal weight was smaller than for adult weight in the O9 line, although the standardized index coefficient for pupal weight was greater, i.e., more attention was paid to pupal than adult weight. Nonstandardized and standardized index coefficients were greater for pupal than for adult weight in the G2 line.

The analyses of variance of cumulative genetic gains did not detect significant differences for responses in pupal and adult weights between lines O9 and O2 (Table 8). On the other hand, significant differences ($P<0.05$) for adult weight due to the desired gains index (lines G9 and G2) were found. Gains in pupal weight did not differ significantly between lines G9 and G2.

Expected responses to selection per generation are shown in Table 9 for the three types of line. Underestimation of the genetic correlation coefficient in the unrestricted index (I2 line) had no apparent effect for the response predicted when the index computed from this estimate was used in the population (Δ versus Δ'), either for the aggregate genotype or for the individual traits. By contrast, responses predicted in the I2 line from the index using the underestimated genetic correlation ($\hat{\Delta}$) were very different for pupal and adult weights from those expected in the I9 line, even though the values for the aggregate genotype were very close. The proportion of realized versus predicted response in the I9 line was very high for the aggregate genotype (98%). Responses observed for pupal weight and adult weight agreed very well with those predicted (101% and 94%, respectively). Responses obtained in the I2 line also agreed with the theo-

Table 11. Average selection differentials for optimum index lines (O9 and O2)

	O9 line			O2 line	
	Rep. 1	Rep. 2	Rep. 3	Rep. 1	Rep. 2
Selection differentials	3.34	3.40	3.45	9.95	9.35
Standardized selection differentials	1.23	1.26	1.28	1.23	1.15
Standardized selection differentials (intended)	1.26	1.33	1.21	1.39	1.39

Table 12. Average selection differentials for desired gains index lines (G9 and G2)

	G9 line			G2 line	
	Rep. 1	Rep. 2	Rep. 3	Rep. 1	Rep. 2
Selection differentials	86.81	72.20	68.77	38.98	39.06
Standardized selection differentials	1.41	1.18	1.12	1.20	1.20
Standardized selection differentials (intended)	1.32	1.34	1.26	1.38	1.48

retical expectations (Δ'), although the proportions of realized versus predicted values were not as high as those in the I9 line (70% and 81%). In the optimum index lines, $\hat{\Delta}$ for the unrestricted trait (adult weight) accurately predicted the expected response in the O9 line. In the desired gains index lines, both Δ' and $\hat{\Delta}$ overestimate the response possible using the parameter value of the genetic correlation, although $\hat{\Delta}$ for pupal and adult weights kept the ratio of 3:1 intended in the desired gains index. The proportion of realized versus predicted response was high in the O9 and O2 lines for pupal weight (86.5% and 73%, respectively) and for adult weight (88% and 81%).

Average selection differentials for each line and replicate are summarized in Tables 10, 11, and 12. Average standardized selection differentials were slightly smaller in the lines whose indices were constructed with the incorrect genetic correlation (I2, O2, and G2) than in the lines whose indices used the "true" genetic correlation (I9, O9, and G9). Average standardized values were similar to the intended values based on the normality assumption.

Genetic correlation estimates within each line did not deviate markedly from 0.95, and all exceeded 0.90. The correlation did not change significantly during the three generations of selection. Only in replicate two of lines O9 and G9 did it decrease slightly but significantly, as shown by the regression coefficients of correlation estimates on generation number of -0.05 ± 0.01 and -0.08 ± 0.01, respectively.

Discussion

The genetic correlation between pupal weight and adult weight was estimated as 0.95 in the base population. Indices for lines O9, G9, and I9 were based on this "true" value, while indices for lines O2, G2, and I2 were based on a deliberate underestimate of this coefficient of 0.25. Unrestricted index lines (I9 versus I2) and optimum index lines (O9 versus O2) were found not to differ significantly, suggesting that the incorrect genetic correlation had no significant effect on the efficiency of either type of index. Despite this lack of a statistical difference, lines I9 and I2 differed by 29.3% for mean response in aggregate genotype, an apparent difference in a practical sense. Desired gains index lines (G9 versus G2) differed significantly and, therefore, underestimation of the genetic correlation had an important effect on the efficiency of the desired gains index.

The results obtained in the unrestricted index lines are in agreement with the theoretical findings by Harris (1963, 1964), Meyer and Hill (1983), and Simm et al. (1986) with respect to the effects of errors of genetic correlation estimates. Harris (1963, 1964) indicated that the influence of sampling errors is largest when the genetic correlation is -0.5; the magnitude of the decrease in the expected progress decreases as the genetic correlation increases. Meyer and Hill (1983) found that sampling errors tend to be greater when traits have a low genetic correlation and high heritability than vice versa. The loss in efficiency appears to be roughly proportional to the inverse of the squared covariance of any trait with the aggregate genotype, increasing faster with decreasing genetic correlations than with decreasing heritabilities. Simm et al. (1986) indicated that when individual genetic correlations were increased or decreased by 0.2, the change in single correlations never reduced the efficiency of unrestricted indices below 0.99; single changes of 0.4 in these correlations only reduced the efficiency to 0.97.

The results of the unrestricted index lines also agree with the experimental results of Lin et al. (1979), who found that overestimation of heritability appears to affect the efficiency of index selection more than underestimation. Increasing the heritability value resulted in larger genetic covariance between traits and vice versa, even though the genetic correlation was fixed. In our experiment, the genetic covariance decreased from 221.30 when the genetic correlation was 0.95 (line I9) to 58.03 when the genetic correlation was 0.25 (line I2), and this underestimation did not significantly affect the efficiency of the unrestricted index. It should be noted that in the experiment of Lin et al. (1979), the effects of errors of heritability estimates were confounded with simultaneous errors of the genetic correlation and, hence, the significant differences among lines were a result of joint effects of incorrect heritabilities and genetic covariances. In our experiment, the effect of errors of parameter estimates was due exclusively to incorrect genetic covariances.

The results obtained in the optimum and desired gains index lines show that caution should be exercised in generalizing about the theoretical findings of Hill and Meyer (1984) upon the effects of errors in parameter estimates on efficiency of the Kempthorne-Nordskog (1959) restricted index. On the one hand, results from the desired gains index line do agree with their finding that with poor estimation of the parameters, the actual response in the restricted variable may differ quite markedly from that expected. On the other hand, results from the optimum index line do not agree with their result, since the response in the restricted variable did not differ from that expected. Finally, results of Simm et al. (1986) for the Kempthorne-Nordskog (1959) restricted indices agree with ours in the optimum index line, since the change in the genetic correlation did not significantly reduce the efficiency of selection.

Despite the magnitude of the deliberate error in the genetic correlation coefficient (-0.7), the efficiency of the optimum index and essentially also that of the unrestricted index was not affected, suggesting that even larger deviations from the true genetic correlation are needed to overcome the effects of random errors under conditions such as those used here: two traits of equal importance, medium heritabilities, and high positive genetic correlation between them. The susceptibility of the efficiency of desired gains index selection to discrepancies in the genetic correlation, as shown by a relatively large error contribution from this parameter, suggests that this type of restricted index should be applied with caution. Implications from this study cannot be completely generalized because the conditions considered here for two trait indices are not completely representative of all possible combinations of parameters which might be relevant for two trait and more complex indices, especially with simultaneous changes in all genetic correlations between several traits. Furthermore, no negative genetic correlations were involved in this study. Subsequent experiments should be done to generalize the implications of this study.

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