

## Comparison of three selection methods for pupal weight of *Tribolium castaneum*

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### Summary

Two experiments comparing the relative efficiencies of individual, family and combined selection for pupal weight at 21 days, were conducted in *Tribolium castaneum*. In experiment 1 the family size was ten (five males and five females) and in experiment 2 it was four (2 males and 2 females). There were no statistically significant differences in efficiency among the responses obtained by the three methods of selection. This was contrary to theoretical predictions. The expected results for pupal weight ( $h^2 = 0.40$ ) were that combined selection would be a more efficient method than family or individual selection, and that family selection could exceed slightly individual selection depending on the family size. Experiment 1 presented larger responses than those obtained in experiment 2.

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### Introduction

The relative efficiencies of individual, family and combined selection were first calculated by LUSH (1947) as a function of the family size ( $n$ ), and the genetic ( $r^G$ ) and phenotypic ( $r^P$ ) correlations between the members of the families. OSBORNE (1957) transformed the initial formulae of LUSH as a function of the heritability ( $h^2$ ), with the restriction  $r^P = r^G h^2$  which is only true in additive models. The value of the genetic correlation depends on the family structure (0.50 for full sibs families, 0.25 for half sibs, etc.). LERNER (1958) and FALCONER (1960) analyzed the value to the expected responses for the different methods of selection.

These theoretical comparisons showed that family selection is more efficient than individual selection only for characters of low heritability. The value of the heritability under which this superiority is true depends on the magnitude of the genetic correlation and on the family size, as shown in Table 1. Combined selection has been proven to be always more efficient than any one of the other two

TABLE I

*Relative superiority of family to individual selection*  
*Supériorité relative de la sélection familiale sur l'individuelle*

Family size	Heritability								
	Full sibs families						Half sibs families		
	0,00	0,10	0,20	0,30	0,40	0,50	0,00	0,10	0,20
2	1,06	1,04	1,01						
4	1,25	1,17	1,10	1,04					
6	1,43	1,28	1,17	1,08	1,01				
8	1,59	1,37	1,22	1,11	1,03				
10	1,74	1,44	1,26	1,13	1,04		1,03		
20	2,35	1,68	1,38	1,20	1,07		1,29	1,06	
50	3,61	1,94	1,48	1,25	1,10		1,87	1,26	1,01
100	5,05	2,07	1,53	1,27	1,11	1,00	2,58	1,38	1,06

TABLE 2

*Relative superiority of combined to individual selection*  
*Supériorité relative de la sélection combinée sur l'individuelle*

Family size	Heritability									
	Full sibs families					Half sibs families				
	0,00	0,20	0,40	0,60	0,80	0,00	0,20	0,40	0,60	0,80
2	1,12	1,08	1,05	1,02	1,01	1,03	1,02	1,01	1,01	1,00
4	1,32	1,19	1,10	1,04	1,01	1,09	1,05	1,03	1,01	1,00
6	1,50	1,26	1,13	1,06	1,01	1,15	1,08	1,04	1,02	1,00
8	1,66	1,32	1,15	1,06	1,02	1,20	1,10	1,05	1,02	1,00
10	1,80	1,36	1,17	1,07	1,02	1,25	1,12	1,06	1,02	1,01
20	2,40	1,47	1,20	1,08	1,02	1,48	1,19	1,08	1,03	1,01
50	3,64	1,57	1,23	1,09	1,02	2,02	1,26	1,10	1,03	1,01
100	5,07	1,62	1,24	1,09	1,02	2,68	1,30	1,11	1,04	1,01

methods, and only if the heritability is high individual selection is as efficient as combined selection. The superiority over individual selection increasing with lower heritabilities and larger family size (Table 2).

Therefore, the magnitude of the heritability enables to choose the type of selection more suitable to the improvement of a given character. There is very

little experimental evidence with respect to the relative efficiency of the three methods of selection. MC BRIDE and ROBERTSON (1963) and CLAYTON *et al.* (1957) found a good agreement with theory when practising selection for abdominal chaetae number in *Drosophila melanogaster*. On the other hand, KINNEY *et al.* (1970) selecting for egg production in chickens and WILSON (1974) selecting for larval and pupal weight in *Tribolium castaneum*, obtained results contrary to the theoretical expectations.

Our work is a selection study in *Tribolium castaneum*, in which the relative efficiency of the three selection methods is compared for the character pupal weight. The influence of family size on the responses to family and combined selection has been also investigated.

### Material and methods

The genetic material used in the experiment was the *Consejo* population of *Tribolium castaneum*; this population was founded in 1964 from a great number of adults captured in different grain stores in the neighbourhood of Madrid. The population is kept without any type of selection and with a minimum inbreeding coefficient (OROZCO and BELL, 1974).

Cultures was made in chambers at 33 °C and 70 per cent of relative humidity. The culture medium was wheat flour (95 %) with 5 per cent of brewer's yeast. The medium was dry-sterilized at 65 °C for 12 hours previously to its use.

Selection was applied to the character pupal weight at 21 days from mating of the parents. This character has a high heritability and a small non-additive genetic variance (YAMADA, 1974). Pupae were weighed in a METTLER precision balance, the unit of measure being the  $\mu\text{gr.}$ , although the results are presented in hundredths of mg.

From a sample of pupae taken from the population cage, three different lines were segregated, each one distinguished by the selection type, i.e. individual (I), family (F) or combined (C). Selection was based on the individual phenotypes in line *I*, it was made on the full sibs family means in line *F*, and both types of information were combined in an index in line *C*.

Two different experiments were made, each one qualified by the different family size studied. This size was ten (experiment 1) and four (experiment 2). Six generations of selection were carried out in each of the three lines of the two experiments.

Each line was reproduced by 25 pair matings, each mating individualized in a different vial. All families were full sibs families. Brother-sister mating were always avoided in order to reduce as much as possible the inbreeding effect (restricted random). The number of males taken in the progeny of each mating was equal to the number of females (five in experiment 1 and 2 in experiment 2). From 250 or 100 individuals scored in experiments 1 and 2 respectively, 25 males and 25 females were selected in each generation. The selected proportion was therefore 20 per cent in experiment 1 and 50 per cent in experiment 2.

In line *C* each individual was given a value by the expression:

$$b_1X + b_2\bar{X} = h^2 \frac{1 - r^G}{1 - r^P} X + h^2 \frac{r^G - r^P}{1 - r^P} \frac{n}{1 + (n - 1)r^P} \bar{X}$$

where  $X$  is the phenotypic value of the individual and  $\bar{x}$  the mean phenotype of the family to which that individual belongs. The value of the phenotypic correlation between sibs used in the expression above was 0.20, taking the genetic correlation equal to 0.50, as our estimate of the heritability in the *Consejo* population was 0.40.

Estimates of the heritability in consecutive generations of selection were obtained by analysis of variance of full sibs families. Standard errors of the estimates of heritability were calculated by the formula of OSBORNE and PATERSON (1952).

The mean responses per generation were calculated as the regression coefficient of the means on generations. Realized heritabilities were calculated as the coefficients of regression of means on cumulative realized selection differentials (FALCONER, 1960), and their standard errors were estimated according to the formula reported by HILL (1972).

The predicted responses to selection for the lines  $I$ ,  $F$  and  $C$  are respectively:

$$\begin{aligned} & \bar{i} \sigma_P h^2 \\ & \bar{i} \sigma_P h^2 \frac{I + (n - I)r^G}{\sqrt{n\{I + (n - I)r^P\}}} \\ & \bar{i} \sigma_P h^2 \frac{b_1 + b_2 \frac{I + (n - I)r^G}{n}}{\sqrt{b_1^2 + (2b_1b_2 + b_2^2) \frac{I + (n - I)r^P}{n}}} \end{aligned}$$

The corresponding standard errors are:

$$\begin{aligned} & \sqrt{h^2 \sigma_P^2 \{I + (a\bar{i} - \bar{i}^2)h^2\} / N} \\ & \sqrt{h^2 \sigma_P^2 \{I + (a\bar{i} - \bar{i}^2)h^2 \frac{\{I + (n - I)r^G\}^2}{\{I + (n - I)r^P\}n} \} / N} \\ & \sqrt{h^2 \sigma_P^2 \{I + (a\bar{i} - \bar{i}^2)h^2 \frac{\{b_1 + b_2 \frac{I + (n - I)r^G}{n}\}^2}{b_1^2 + (2b_1b_2 + b_2^2) \frac{I + (n - I)r^P}{n}} \} / N} \end{aligned}$$

where  $N$  is the number of selected individuals,  $\bar{i}$  the standardized selection differential,  $a$  the corresponding abscissa at the truncation point, and  $\sigma_P$  the phenotypic standard deviation.

## Results

The estimated genetic parameters in the *Consejo* population are summarized in Table 3. The heritabilities were calculated by three different methods: regression of the progeny on parental mean ( $h^2_{OP}$ ), analysis of variance of half sibs families ( $h^2_{HS}$ ), and analysis of variance of full sibs families ( $h^2_{FS}$ ). As  $h^2_{FS}$  can be vitiated by the presence of non-additive genetic effects, the estimate used in the prediction was the weighted mean of the first two ( $h^2_{OP+HS}$ ). On the other hand, twice the difference between  $h^2_{FS}$  and  $h^2_{OP+HS}$  estimates the deviations due to non-additive effects, which in this case turns out to be zero.

TABLE 3

*The parameters of the Consejo Base Population*  
*Paramètres de la population-base Consejo*

Mean . . . . .	281,95 ± 0,55	
Phenotypic variance . . . . .	823,69	
Coefficient of variation . . . . .	11 %	
Heritability* {	$h^2_{OP}$ . . . . .	0,45 ± 0,05
	$h^2_{HS}$ . . . . .	0,23 ± 0,09
	$h^2_{OP+HS}$ . . . . .	0,40 ± 0,04
	$h^2_{FS}$ . . . . .	0,40 ± 0,07

(\*) For symbols see explanation in the text.

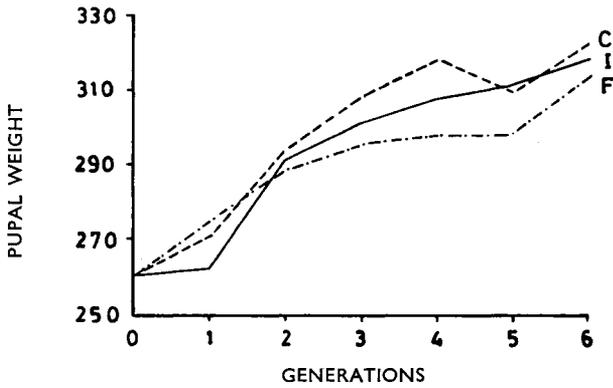


FIG. 1. — *Response to selection for pupal weight in experiment 1.*  
*Réponse à la sélection pour le poids de la pupe dans l'expérience 1.*

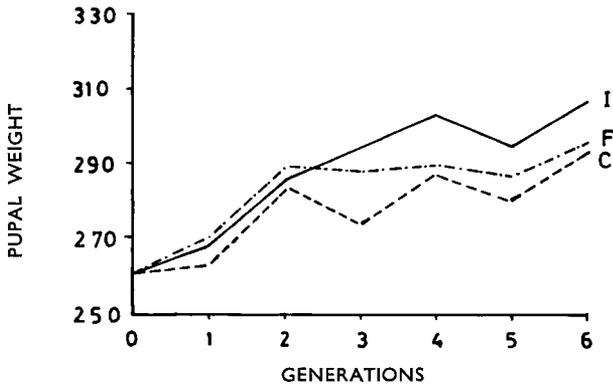


FIG. 2. — *Response to selection for pupal weight in experiment 2.*  
*Réponse à la sélection pour le poids de la pupe dans l'expérience 2.*

The estimates of the heritability shown in Table 3 agree quite well with those reported by other authors. ENFIELD *et al.* (1966) find  $h^2_{HS} = 0.27$  in females and 0.36 for males,  $h^2_{OP} = 0.36$  in females and 0.34 for males. WILSON *et al.* (1965) estimate  $h^2_{OP} = 0.46$ . BELL and BURRIS (1973) in two different repetitions give the value  $h^2_{FS} = 0.67$  and 0.69 respectively. Finally, WILSON (1974) in two repetitions finds  $h^2_{OP} = 0.39$  and 0.42 respectively.

The means of the character are shown for each line and generation in Figures 1 and 2 and Table 4. In experiment 1 the response is considerable, and combined selection produces greater response than individual selection, this last being superior to family selection. The superiority of line C over line I is observed until generation 4; from this point the mean of both lines are practically equal. In experiment 2, the greatest response is shown by line I while lines F and C almost do not respond to selection from the second generation onwards.

The mean responses per generation with its corresponding standard errors are included in Table 4. The comparison between the responses obtained in each experiment were made by the method indicated by SNEDECOR (1956). Significant differences between the responses obtained by the three methods of selection could not be detected in any of the two experiments.

TABLE 4

*Pupal weight means and mean responses to selection per generation*  
*Valeurs moyennes du poids de la puppe et réponse moyenne à la sélection par génération*

Line	Generations							Mean responses
	0	1	2	3	4	5	6	
Experiment 1								
I	260	263	292	303	309	312	319	9,89 ± 2,13
F	260	274	289	296	299	298	315	6,71 ± 1,28
C	260	272	295	309	318	310	322	8,69 ± 2,28
Experiment 2								
I	260	268	286	295	304	295	308	6,74 ± 1,82
F	260	269	289	288	290	287	296	3,74 ± 1,57
C	260	264	285	274	288	281	295	4,49 ± 1,88

The responses to selection were predicted from the expected selection differentials and the initial heritabilities. The values founded were 16.000 ± 4.52, 16.15 ± 4.36 and 18.75 ± 3.89 in lines I, F and C of experiment 1, respectively, and 9.09 ± 4.90, 8.85 ± 4.94 and 10.07 ± 4.61 in the lines of experiment 2. In every case the predicted responses are greater than the mean responses obtained per generation.

Realized and predicted (BECKER, 1964) selection differentials through generations are shown in Table 5. In all cases the realized values were smaller than the predicted. The mean realized selected proportions did not differ very much from the calculated when the experiment was designed: 0.21, 0.22 and 0.21 in lines I, F and C of experiment 1, respectively, and 0.52, 0.53 and 0.52 in the lines of experiment 2.

TABLE 5

*Average predicted ( $i_1$ ) and realized ( $i_2$ ) selection differentials and their corresponding standardized values ( $\bar{i}_1$  and  $\bar{i}_2$ )*

*Différentielles de sélection des procédés prédits ( $i_1$ ) et réalisés ( $i_2$ ) et leurs valeurs correspondantes typifiées ( $\bar{i}_1$  et  $\bar{i}_2$ )*

Line	Experiment 1				Experiment 2			
	$\bar{i}_1$	$i_1$	$\bar{i}_2$	$i_2$	$\bar{i}_1$	$i_1$	$\bar{i}_2$	$i_2$
I	1,394	40,01	1,260	37,83	0,792	22,73	0,638	19,00
F	1,345	38,60	0,842	24,17	0,774	22,21	0,552	15,83
C	1,394	40,01	1,053	32,00	0,792	22,73	0,516	14,67

The pool of the estimated heritabilities in each generation is presented in Table 6. The values agree quite well with the estimate in the base population, specially in experiment 1. In this table the regression coefficients of the estimated heritabilities on generation number is also included. This coefficient is practically zero in all cases although a decreasing trend is also apparent.

TABLE 6

*Heritabilities pooled over generations ( $h^2$ ) and regression of heritability on generation number (b)*  
*Héritabilité poolée sur des générations ( $h^2$ ) et régression de celle-ci sur le nombre de générations (b)*

Line	Experiment 1		Experiment 2	
	$h^2$	$b$	$h^2$	$b$
I	0,42 ± 0,06	0,05 ± 0,06	0,49 ± 0,09	— 0,10 ± 0,05
F	0,42 ± 0,04	0,01 ± 0,03	0,34 ± 0,06	— 0,04 ± 0,03
C	0,34 ± 0,05	— 0,01 ± 0,03	0,21 ± 0,08	— 0,04 ± 0,02

The realized heritabilities are shown in Table 7. In every case the values obtained are smaller than the values calculated in the base population and also smaller than the estimated values through generations. The line with larger

realized heritability in experiment 1 was line *F* which produced the smaller response in general terms. The differences between realised heritabilities were not significant in any case.

TABLE 7  
*Realized heritabilities by line and experiment*  
*Héritabilités réalisées par lignée et expérience*

Line	Experiment 1	Experiment 2
I	0,19 ± 0,02	0,21 ± 0,10
F	0,26 ± 0,07	0,09 ± 0,05
C	0,17 ± 0,07	0,20 ± 0,20

### Discussion

The theoretical efficiency of family selection compared with individual selection is given by the expression:

$$\frac{1 + (n - 1)r^G}{\sqrt{n\{1 + (n - 1)r^P\}}}$$

For  $n = 10$  (experiment 1) the efficiency results to be 1.04 given the special conditions of the experiment ( $h^2 = 0.40$  and  $r = 0.50$ ). For  $n = 4$  (experiment 2) the result equals 0.99. It would then be expected a greater response in line *F* of the first experiment compared with line *I*, and the reverse in the second experiment.

The efficiency of combined selection with respect to individual selection is:

$$\frac{b_1 + b_2 \frac{1 + (n - 1)r^G}{n}}{\sqrt{b_1^2 + (2b_1b_2 + b_2^2) \frac{1 + (n - 1)r^P}{n}}}$$

In the particular conditions already pointed out the efficiencies are 1.17 in experiment 1 and 1.10 in experiment 2; therefore it would be expected a greater response in line *C* of both experiments than in the other two lines.

The results of this study do not agree with the theoretical expectations because the differences between lines are not significant. In experiment 1 lines *I* and *C* exceeded line *F* throughout the experiment, while the superiority of line *C* over *I* disappears from the fourth generation of selection. The absence of agreement with theory in experiment 2, is perhaps largely due to the lack of response in lines *F* and *C* from the second generation and this fact rules out any possible comparisons between lines.

The mean responses obtained per generation do not confirm the predicted superiority of lines *C* and *F*. The proportions of predicted responses that were realized were 0.62, 0.42 and 0.46 in lines *I*, *F* and *C* of the first experiment, respectively, and 0.74, 0.42 and 0.45 for the same lines of the second experiment.

The realized selection differentials were generally greater in line *I* than in the other two lines, compensating the increase in precision which should be obtained by practising family or combined selection. On the other hand, the realized heritability values do not agree with the theoretically expected results.

The principal consequence which could be extracted from this experiment is that with characters of heritability equal or greater than 0.40, the information based in the individual phenotypes would be sufficient in the design of a selection experiment.

It is convenient to remark that in the experimental checks of selection systems, the effective population size ( $N_e$ ) cannot be equalled for all lines. Clearly, the family selection and, in lesser proportion, the combined selection reduce the effective population size and, consequently, the rate of response to selection should decrease.

In experiment 1, the mean effective sizes were 34.6, 18.2 and 9.9 in the individually, combined and familiar selected lines, respectively. The reduction in size was not so drastic in experiment 2, where the corresponding values were 53.2, 46.1 and 32.4. All effective sizes were calculated by the following 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 (not very different of two), and  $\sigma_k^2$  the variance of family size.

This strong reduction in the effective size can also be a reason for the lack of concordance found between expected and obtained results in this experiment, as lines *F* and *C* are in disadvantage with respect to line *I*. This disadvantage could have made up for the greater response expected in the first two lines.

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### Résumé

#### *Comparaison entre trois méthodes de sélection pour le poids de la puppe de Tribolium castaneum*

Deux expériences ont été réalisées pour confirmer l'efficacité relative des méthodes de sélection individuelle, familiale et combinée, sur le caractère poids de la puppe de 21 jours de *Tribolium castaneum*. Dans une de ces expériences le nombre d'individus était dix (5 mâles et 5 femelles), dans l'autre quatre (2 mâles et 2 femelles). Aucune différence significative n'a été relevée entre les trois lignées de sélection, caractérisées chacune, par les types indiqués précédemment. L'expérience

avec dix individus dans chaque famille avait une plus grande réponse, en général, que celle réalisée avec quatre. Les résultats théoriquement attendus, pour ce caractère ( $h^2 = 0,40$ ) nous montrent que la sélection combinée serait la plus efficace de ces trois expériences, avec un léger avantage de la sélection familiale sur l'individuelle dans la première et de celle-ci sur la familiale dans la deuxième. Une analyse est faite sur les raisons par lesquelles ces résultats théoriques ne s'accordent pas avec ceux qui ont été obtenus dans l'expérience.

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