AN EXPERIMENTAL EXAMINATION OF RESTRICTED SELECTION INDEX, USING *TRIBOLIUM CASTANEUM*.

I. THE RESULTS OF TWO-WAY SELECTION

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SOMETIMES it is desirable to change one character without altering another character. For this purpose the concept of a restricted selection index has been derived mathematically by KEMPTHORNE and NORDSKOG (1959), but only a few experiments have been devoted to its experimental verification.

ABPLANALP, OGASAWARA and ASMUNDSON (1963) selected Broad Breasted Bronze turkeys for seven generations using an index calculated to produce maximum gains in 9-week weight while holding 24-week body weight constant. The results were in fair agreement with predicted values. SCHEINBERG, BELL and ANDERSON (1967) compared relative efficiency of restricted index selection and uni-stage tandem selection on three traits in *Tribolium*. They reported that the results they obtained in general confirm the biological validity of the restricted selection index proposed by KEMPTHORNE and NORDSKOG.

The purpose of the present experiment was to test biologically the validity of the restricted selection index method and to measure its relative efficiency compared with mass selection for a single character under the same mating scheme. The results of the first seven generations of selection are presented.

MATERIALS AND METHODS

The experimental organism was the flour beetle, *Tribolium castaneum*. The population was originally formed at Purdue University in 1954 by combining eight noninbred stocks and a sample has been maintained by mass mating at the University of Alberta as a closed population since 1962. Fourteen-day larval weight and 30-day adult weight, recorded in units of 10^{-5} grams, were the variables studied. Progeny were reared on a culture medium of 95% sifted whole wheat flour and 5% dried brewers' yeast in a chick incubator modified to maintain 32°C and 70% relative humidity. The experiment consisted of two parts, the base experiment provided data for estimation of the parameters necessary for prediction purposes while the selection experiment allowed comparison of actual with predicted results.

Base experiment: Individuals for the base population were randomly chosen from the stock laboratory population. Forty sire groups (1 male, 3 females) comprised a replicate, and six replications were used. Females were mated and transferred to individual coffee creamers for 24-hour egg collection. Fourteen days later five progeny of each dam were weighed individually and placed into numbered creamers. As larvae pupated they were sexed and at 30 days an adult weight was obtained.

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Statistical analyses of the data were based on the analysis of variance according to the following model:

$$Y_{ijk} = u + R_i + S_{ij} + E_{ijk}$$

where Y_{ijk} was the measurement of the k th progeny of the j th sire within the i th replication. All factors of the model were considered random and analyses were carried out within each sex. Heritability was estimated according to the method presented by BOHREN, MCKEAN and FRIARS (1965). The estimates obtained were expected to include more nonadditive genetic variance than the half-sib model but less than the full-sib model. A restricted selection index, designed to increase 14-day larval weight without increasing 30-day adult weight, was constructed by the method of KEMPTHORNE and NORDSKOG (1959).

Selection experiment: The selection experiment consisted of three replications, two directions of selection, and four selection variables as outlined in Table 1. For each replication samples of adults were taken from the stock laboratory population. For each of the four samples per replicate, two consecutive 24-hour egg collections were made; progeny from the first collection were selected for high body weight and those from the second for low body weight. High selection in each replication was weighed on one day and low selection on the next. Replication 2 was initiated one week after Replication 1 and Replication 3, three weeks later.

Eggs were collected by allowing selected females to lay eggs for 24 hours in the rearing medium. At 14 days, larvae were weighed individually and placed in separate coffee creamers. Progeny were sexed as pupae and adult weights were taken at 30 days. Generation interval was six weeks. To assure the required number of progeny in all selections, 12 males and 30 females were selected and mass mated to reproduce the next generation. The mass mating of selected parents precluded estimates of heritable variation within generations from the selected parents.

RESULTS

Base population. Parameters estimated from the base population are given in Table 2. At 14 days of age there was no significant difference in weight between sexes, but at 30 days females were larger than males.

Estimates of heritability were calculated for each sex and the average of both sexes. For both 14-day larval and 30-day adult weights, the estimates for males were higher than for females. The opposite condition existed for genetic correlations in which the estimate for females was higher than the estimate for males. Using the parameters for both sexes, a restricted selection index was derived. The

TABLE 1
Outline of one replicate in selection experiment

Selection variable	Direction of selection	
	High	Low
14-day larval weight	H-14*	L-14
	150†	150
30-day adult weight	H-30	L-30
	150	150
Index	H-I	L-I
	150	150
Random	C ₁	C ₂
	100	100

* Population identification.

† Number of progeny measured each generation.

TABLE 2

Parameters estimated from base population

Parameter	Sex		
	Males	Females	Both sexes
14-day larval weight			
Mean (10^{-5} grams)	71.6	73.1	72.3*
Standard deviation	22.5	22.6	22.6*
Number	1,562	1,514	3,094*
30-day adult weight			
Mean (10^{-5} grams)	174.5	185.5	179.9
Standard deviation	21.5	23.8	23.3
Number	1,551	1,502	3,053
Heritability			
14-day larval weight	0.46 ± 0.06	0.35 ± 0.07	0.41 ± 0.05
30-day adult weight	0.40 ± 0.07	0.32 ± 0.06	0.36 ± 0.05
Correlation			
Phenotypic	0.15 ± 0.03	0.16 ± 0.03	0.16 ± 0.04
Genetic	0.12 ± 0.11	0.38 ± 0.12	0.24 ± 0.04

* Includes unsexed individuals.

FIGURE 1.—Mean 14-day larval weight (10^{-5} g) of selected lines averaged over sexes and replications. FIGURE 2.—Mean 30-day adult weight (10^{-5} g) of selected lines averaged over sexes and replications.

index obtained, after rounding, was $I = W_{14} - 0.3W_{30}$, where W_{14} and W_{30} are individual 14- and 30-day weights, respectively.

Selection experiments: Responses to selection, as deviations from control populations, are represented graphically in Figures 1 and 2 and the generation means for the control populations are presented in Table 3. Selection pressure in the low body weight lines was reduced after the 5th or 6th generation because some of the 150 larvae weighed at 14 days in these lines did not emerge in time to be weighed at 30 days.

The 14-day larval weight of the population selected for high index values (H-I) was greater than that of populations selected for high larval weight (H-14), but 30-day adult weight of H-I was less than that of H-14. Selection for high 14-day larval weight (H-14) was less effective than selection for low 14-day weight (L-14). Asymmetry of response was less for H-30 and L-30 selected for 30-day adult weight than for H-14 and L-14 selected for 14-day larval weight. Populations selected for low 14-day larval weight (L-14 and L-I) showed response through five generations, both direct and correlated, but populations selected for high 14-day larval weight (H-14 and H-I) reached a plateau in the first two or three generations of selection and produced essentially no change in 30-day weight. The 30-day adult weights of both high and low index lines (H-I and L-I) were quite similar although with successive generations they decreased slightly from the control.

For the selected trait, variations were smaller among the replications of H-30 and L-30 than among the replications of H-14 and L-14 (Table 4). Also 30-day adult weight fluctuated less from generation to generation than 14-day larval weight. These results suggest that 14-day larval weight was influenced more by environmental variations than was 30-day adult weight even though heritability

TABLE 3

Body weight of the control populations averaged over replications (10^{-5} grams)

Trait	Generation	Male	Female
14-day larval weight	0	72	73
	1	79	78
	2	85	83
	3	83	84
	4	91	91
	5	76	78
	6	63	67
	7	58	60
30-day adult weight	0	170	185
	1	175	187
	2	177	190
	3	174	190
	4	188	199
	5	185	198
	6	185	195
	7	187	199

TABLE 4

Mean squares of replications for the six selected populations and the two control populations

Population	Mean squares for replications	
	14-day larval weight	30-day adult weight
H-14	314	454
H-30	22	37
H-I	45	41
L-14	60	112
L-30	189	6
L-I	30	31
C ₁	38	36
C ₂	45	56

estimated in the base population was greater for 14-day larval weight than for 30-day weight.

Divergence between high and low selection gives the total response to selection (Figure 3). For 14-day larval weight all three methods resulted in divergence up to the sixth generation. However, most of this divergence was due to response to low selection rather than response to high selection. Although for 14-day larval weight there was little difference between populations selected for larval weight

FIGURE 3.—Divergence (10⁻⁵ g) between high and low lines averaged over sexes and replications. Code: X, H-14 minus L-14; O, H-30 minus L-30; and Δ, H-I minus L-I.

and for index score, there were considerable differences between the populations for 30-day adult weight.

As experimental design was the same for all populations, the number of larvae, determined by fecundity of parents and viability of larvae, is a measure of reproductive fitness (Figure 4). In all populations selected for smaller size the number of larvae decreased, whereas for larger size the number of larvae as a percentage of the control did not change for H-14 and H-I but did increase in H-30.

There were large differences between predicted response to selection and realized response (Table 5). Theoretically, response to selection depends upon heritability and selection differential, therefore, it was of interest to investigate whether deviation of predicted response versus realized response could be attributed to either.

Observed selection differentials averaged over sex and replications (Figure 5) indicated there were no real differences between generations except for a slight decrease for the sixth and seventh generations of L-14 and L-I. This decrease occurred because some of the small larvae were not emerging early enough to be selected to reproduce the next generation. Observed selection differentials were 20 to 30% less than predicted. Expected response for 30-day adult weight, using observed selection differentials, was comparatively close to the observed response, but for 14-day larval weight, the expected response was higher than the observed, markedly so in selection for larger larval weight.

FIGURE 4.—Number of larvae of selected populations as a percentage of a control line.

FIGURE 5.—Selection differentials (10^{-5} g) averaged over sexes and replications.

TABLE 5

Predicted and realized selection responses (10⁻⁵ g) replications and sexes combined

Character selected	Direction of selection	Selection differential		Response per generation			
				14-day larval weight		30-day adult weight	
		Predicted	Realized	Predicted*	Realized	Predicted*	Realized
14-day larval weight	High	27.7	22.6	11.2	—0.5	2.5	0.1
	Low		—18.6		—3.9		—3.1
30-day adult weight	High	28.0	21.5	2.5	0.2	10.0	4.7
	Low		—20.8		—2.6		—7.8
Index score	High	27.7	23.8	10.5	1.2	—0.5	—1.8
	Low		—18.3		—2.8		—1.2

* Based on predicted, not realized, selection differentials.

All estimates of realized heritability were smaller than estimates obtained from the base population (Table 6). There were large differences between estimates of realized and predicted heritability according to direction of selection, that is, realized heritabilities were asymmetrical. The difference between realized heritability for high and low selection was less for adult weight than for larval weight and realized heritabilities for low selection were higher than for high selection. LERNER (1958) indicated an estimate of heritability assessed in a base population may be expected to be close to the average of heritability for high and low selection rather than heritability in one direction of selection; therefore, predicted estimates could be compared with the mean value of both directions. Realized heritability for 14-day larval weight was about one eighth of the predicted value and, for 30-day adult weight, slightly less than the predicted value. The realized genetic correlations, contrary to results for heritability, were higher than predicted.

DISCUSSION

Generally, with selection for body weight at a specified time, there may be correlated response of body weight measured at some other age. This may or may not

TABLE 6

Realized heritabilities and genetic correlations

Direction of selection	Character selected	Realized*	
		Heritability	Genetic correlation
High	14-day larval weight	—0.07	0.29
	30-day adult weight	0.18	
Low	14-day larval weight	0.17	0.47
	30-day adult weight	0.35	
Mean	14-day larval weight	0.05	0.40
	30-day adult weight	0.27	

* Estimates obtained from the base population for heritability (14-day larval weight), heritability (30-day adult weight), and genetic correlations were 0.41, 0.36, and 0.24 respectively.

be desirable. The restricted selection index may be used for changing the mean of one trait while holding a second trait constant provided the two traits are heritable and the genetic correlation between the two traits is not 1.0.

As the number of traits selected increases, the selection differential for each of the different traits decreases, and consequently the expected change for each of the traits decreases. If restriction for one trait reduces rate of response in other economic traits of interest, the use of the restricted selection index may not be justified. Although in this experiment, restriction did not reduce selection response for 14-day larval weight, under other conditions this may not be true. Because there is some doubt that maximum selection intensity is necessarily the optimum selection intensity (LERNER 1962), and many populations which have been intensively selected have plateaued, a reduction in the selection pressure may be desirable. If such is the case, the possible value of utilizing the restricted selection index is enhanced.

In this experiment the populations selected on basis of the restricted selection index (H-I) compared favorably with the population selected for 14-day larval weight (H-14). However, H-14 did not respond to selection as predicted.

Realized heritability is not necessarily identical with estimates of heritability estimated by ANOVA or regression, but comparison of the two is informative. Two factors possibly contributing to the large difference between realized and predicted heritability were the presence of nonadditive genetic variance and/or common environmental variance. The possibility of nonadditive genetic variance was supported by response to selection ceasing in the first two or three generations of upward selection.

The predicted response to selection was made assuming symmetrical response, whereas the observed response was quite asymmetrical. CLARKE, SMITH and SONDHI (1961) and ABPLANALP (1961) indicated that it is a common experience to find the rates of response in two directions to be unequal. Direction of greater response depends upon the population under study and the trait selected. Greater response in the upward direction has been reported for bristle number in *Drosophila* (CLAYTON, MORRIS and ROBERTSON 1957) and for 12-week body weight in chickens (MALONEY, GILBREATH and MORRISON 1963). Greater response in the down direction has been reported for six-week body weight in mice (FALCONER 1955) for adult body weight in *Drosophila* (MARTIN and BELL 1960) and 13-day larval weight in *Tribolium* (HARDIN and BELL 1967).

FALCONER (1955) and CLARKE *et al.* (1961) suggested possible reasons for asymmetrical response to selection. Of the possible reasons, directional dominance and/or heterozygote superiority seem to be the most logical. ENGLERT and BELL (1960) found that 15-day larval weight of *Tribolium castaneum* was the most heterotic of three characters: 15-day larval weight, pupal weight and adult weight. This suggests that directional dominance of heterozygote superiority is more pronounced in larval weight than in adult weight, as asymmetry of response in this experiment was greater for larval weight than for adult weight. If alleles affecting body weight were mostly dominant for increasing body weight and their frequencies were intermediate, the response would be expected to be

greater for decreasing body weight. In the present experiment larval weight in the high population ceased to respond after the first two or three generations of selection. Although in other experiments the trait has responded, e.g. HARDIN and BELL (1967), lack of response in this experiment may be partly due to rapid decrease of additive genetic variance since such a decrease under the dominance model has recently been confirmed by YOUNG (1966) using computer simulation.

Asymmetry of response in 30-day adult weight was not large. Fluctuations between generations for adult weight were smaller than for larval weight, and variations among replicates was less. These results suggest that genetic variance of adult weight was mostly additive in agreement with the results reported by ENGLERT and BELL (1963).

The realized genetic correlation between larval and adult weight of upward selection was in close agreement with the estimate obtained from the base population, whereas in downward selection it was higher than expected. BOHREN, HILL and ROBERTSON (1966) have indicated that the normal situation is likely to be asymmetrical rather than symmetrical genetic correlation.

SUMMARY

This experiment was designed to test the validity of the theory that use of a restricted selection index (KEMPTHORNE and NORDSKOG 1959) allows change in one trait while holding another trait constant. Two traits, 14-day larval weight and 30-day adult weight, were the variables of interest.—The average relative efficiencies of the selection methods were in general agreement with expectations, though there was considerable variation among replications within selection methods. Although 30-day adult weight of the line selected for 14-day larval weight showed considerable correlated response, 30-day weight of the index line stayed near the control level. The line selected for 30-day adult weight responded as predicted with a large correlated response for 14-day larval weight. Thus, restricted selection index was effective for increasing larval weight while holding adult weight constant.—Responses to selection were considerably lower than predicted values obtained from the base population. Asymmetry of responses was observed, especially for 14-day larval weight; responses to upward selection were considerably lower than those for downward selection.

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