AN EXPERIMENTAL EXAMINATION OF RESTRICTED SELECTION INDEX, USING *TRIBOLIUM CASTANEUM*. II. THE RESULTS OF LONG-TERM ONE-WAY SELECTION

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THE first seven generations of a selection experiment designed to allow experimental evaluation of a restricted selection index were reported by OKADA and HARDIN (1967). The index was computed to produce maximum response in 14-day larval weight of *Tribolium castaneum* while preventing a correlated increase in 30-day adult weight. Not only was the index effective for restricting the change of 30-day adult weight but also the results obtained from the index selection compared favorably with results obtained from direct selection for 14-day larval weight.

NORDSKOG (1966) stated ". . . the elementary prediction equation of genetic gains in terms of heritability and selection intensity follows according to theory reasonably well in the earlier stages of a selection program but that for selection carried out over many generations, the prediction equation has almost no value." To obtain additional information concerning what happens when the restricted selection index is used, the selection experiment reported by OKADA and HARDIN (1967) was continued to generation thirteen. The results are presented in this paper.

MATERIALS AND METHODS

A complete outline of materials and methods was reported by OKADA and HARDIN (1967). A closed population of flour beetles, *Tribolium castaneum*, was reared in 95% sifted whole-wheat flour and 5% dried brewers' yeast in a chick incubator modified to maintain 32°C and 70% relative humidity. 14-day larval weight and 30-day adult weight were the variables studied.

TABLE 1

Outline of one replication in the selection experiment

Selection variable	Population identification	Number of progeny measured each generation
14-day larval weight	H-14	150
30-day adult weight	H-30	150
Index	H-I	150
Random	Control	100

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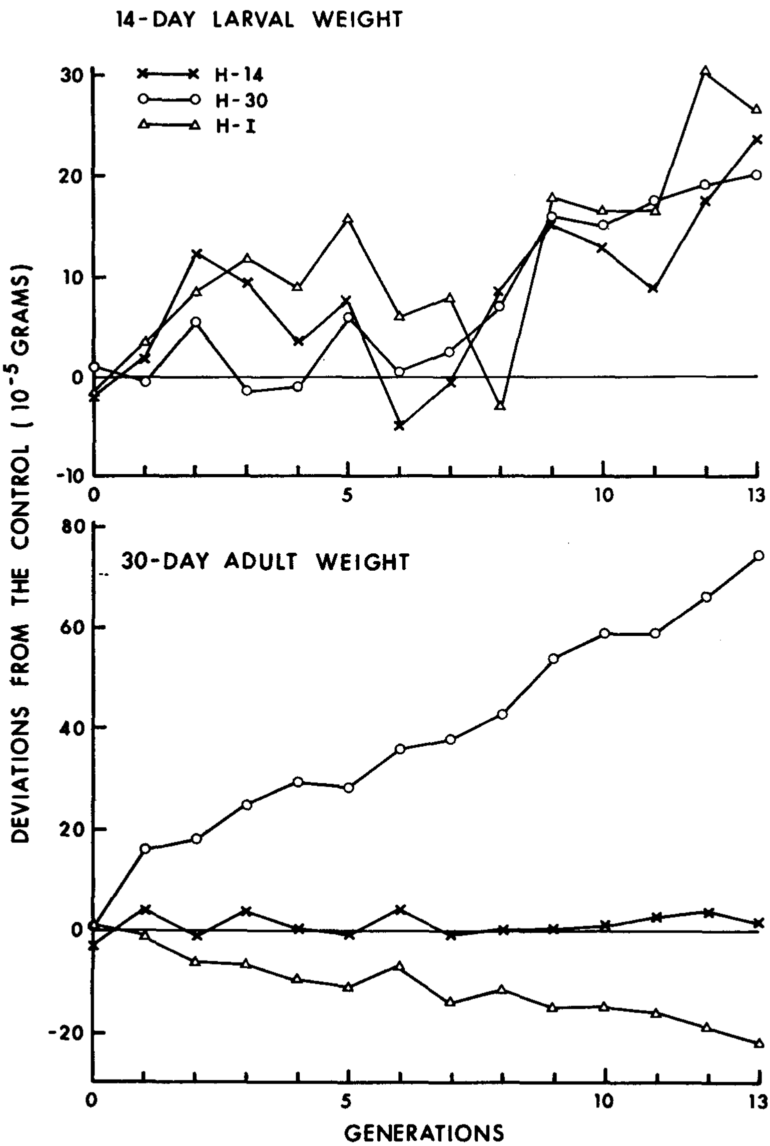

FIGURE 1.—Generation means (10^{-5} grams) of the three selected lines plotted as deviations from the Control.

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). The index derived was $I = W_{14} - .3W_{30}$ where W_{14} and W_{30} are 14- and 30-day body weights, respectively. The experiment consisted of three replications and four selection variables (Table 1). The populations selected for 14-day larval weight (H-14), 30-day adult weight (H-30) and index (H-I) were selected for large (high) body weight while selection in the Control was at random. In each population 12 males and 30 females were selected and mass mated to reproduce the next generation. During the first seven generations, two-way selection was made; however, only selection for large (high) body weight was continued beyond generation seven.

RESULTS

The population means for 13 generations of selection are shown in Figure 1 as deviations from the Control (Table 2). For 14-day larval weight there were no outstanding differences among H-14, H-30, and H-I although in most generations H-I weighed the most.

Although the means indicate response to selection for 14-day larval weight resumed in the seventh generation, the behavior of each replicate was different (Figure 2). There was considerable variation between replications for 14-day larval weight not only in H-14 but also in H-30 and H-I. In H-14, Replication 1 showed practically no response through 13 generations while in Replications 2 and 3, response resumed after six or seven generations of selection. In H-I the response observed in Replication 3 was much greater than that observed in Replications 1 and 2.

For 30-day adult weight, selection (H-30) resulted in a marked and consistent increase over the Control while in H-I, there was a small but consistent decline from the Control (Figure 1). For 30-day adult weight the differences between replications were very small, not only for H-30 but also H-14 and H-I (Figure 2).

Examination of the data indicated that variation for larval weight increased from the 6th or 7th generation, reached a peak around the 10th generation and by the 13th generation had declined to the original level. As ENGLERT and BELL (1963) have shown that the growth pattern of larval weight in Tribolium is multiplicative, the increase in larval weight may have been a scale effect, that is, as the mean increased, the variation increased. The increase of the coefficients of variation for 14-day larval weight (Figure 3) indicated that scale was not the cause and the exact cause of this increase is not known.

TABLE 2

Body weight (10^{-5} grams) of the Control population averaged over replications for Generations 8 through 13

Trait	Sex	Generation 8	9	10	11	12	13
14-day larval weight	♂	62	63	70	81	64	82
	♀	62	65	74	86	64	81
30-day adult weight	♂	187	184	185	180	190	197
	♀	206	200	200	198	203	211

TABLE 3

Realized parameters

Generations	Populations	Character selected	Average selection differential (10^{-5} grams)	Realized heritability ($h^2 \pm$ SE)	Realized genetic correlation
1 to 7	H-14	14-day larval weight	23	—0.07 ± 0.04	0.29
	H-30	30-day adult weight	21	0.18 ± 0.02	
8 to 13	H-14	14-day larval weight	29	0.07 ± 0.03	0.22
	H-30	30-day adult weight	23	0.23 ± 0.03	

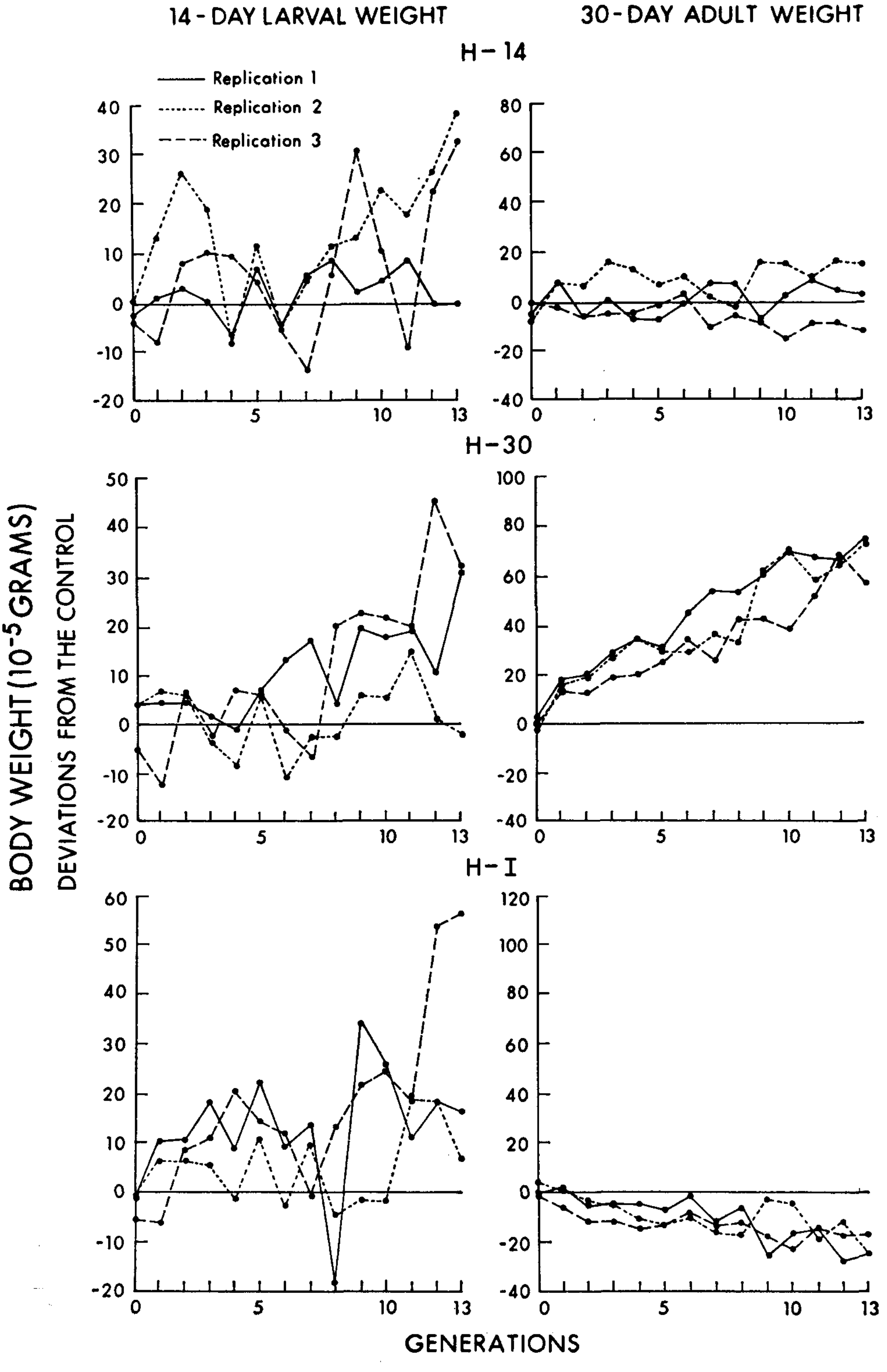

FIGURE 2.—Generation means (10^{-5} grams) of each replication of the three selected lines.

Although the increase in phenotypic variation resulted in increased selection differentials in later generations (Table 3), this was not the only cause of increased response. The realized heritabilities (Table 3), which were calculated as the regression of responses to selection differentials (FALCONER 1960), were higher in later generations than in early generations.

Because the genetic correlation between 14-day larval weight and 30-day adult weight was utilized in computation of the index, there was interest in whether the phenotypic correlation between 14-day larval and 30-day adult weight may have changed during the selection experiment (Figure 4). The correlation in H-14 was generally lower than in the Control and the correlation in H-30 higher than in the Control. On the other hand, the correlation in H-I fluctuated greatly.

DISCUSSION

The results of the first seven generations of selection (OKADA and HARDIN

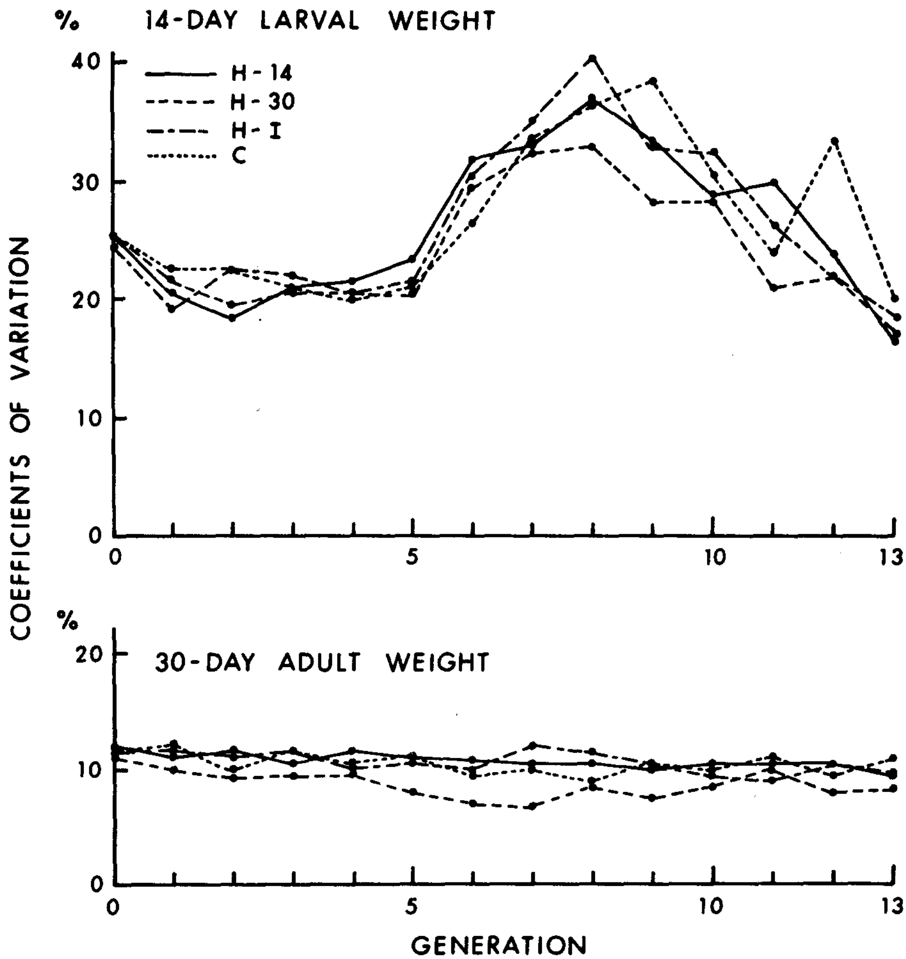

FIGURE 3.—Coefficients of variation for 14-day larval and 30-day adult weight.

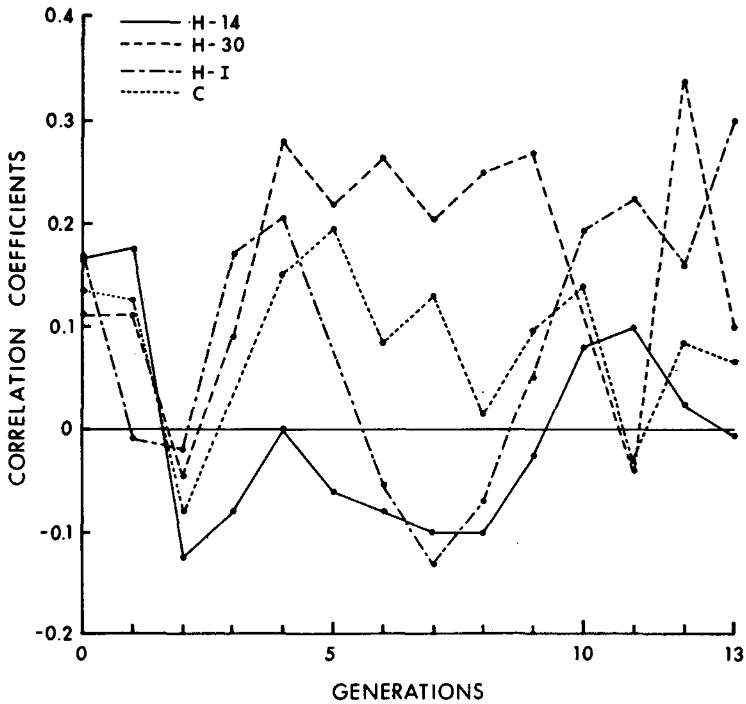

FIGURE 4.—Phenotypic correlation coefficients between 14-day larval and 30-day adult weights.

1967) showed that the restricted selection index was effective for changing 14-day larval weight without a correlated response in 30-day adult weight. Although considerable variation existed between replications, the results reported here indicated that the trend continued for generations 8 through 13. Among the selected populations, 14-day larval weight was largest in H-I while 30-day adult weight of H-I was reduced below that of H-14. The results suggest that the restricted selection index is biologically valid.

Another point of interest concerned the pattern of response to selection for 14-day larval weight. Analysis of the first seven generations of selection (OKADA and HARDIN 1967) showed no consistent change after the first two or three generations. However, after Generation 6 the populations resumed response to selection. Although this resumed response could be partly due to the increase of the selection differentials, the realized heritability also increased in the later generations. The resumption of response occurred in the early generations and, therefore, differs from the results in Drosophila of MATHER and HARRISON (1949) and of CLAYTON and ROBERTSON (1957) in which response to selection resumed in later generations after loss of reproductive fitness necessitated relaxation of selection. However, in neither of the two cited cases was the maximum level attained after relaxation much greater than that obtained prior to relaxation.

One possible explanation of this result could be that artificial selection led to the breakdown of buffering capacity, after which recombination between balanced polygenic blocks released new variability which was useable for response. If this were true, there should have been a reduction in the fitness of the population (LERNER 1954, 1968). Although in the present study, no experiment on fitness was carried out to verify this, the increase in phenotypic variation indicates that this could have occurred. However, the increase in variation occurred not only in the selected populations but also in the Control, which suggests that some unknown environmental causes may have been involved.

SUMMARY

A selection experiment designed to allow experimental evaluation of a restricted selection index was performed. The index was computed to produce maximum response in 14-day larval weight of *Tribolium castaneum* while preventing a correlated increase in 30-day adult weight. The response of 14-day larval weight for 13 generations of selection was as large in the index population (H-I) as in the population selected directly for 14-day larval weight (H-14), while 30-day adult weight of H-I was considerably less than 30-day adult weight of H-14. Selection for 30-day adult weight (H-30) was effective. For 14-day larval weight, considerable variation existed between replicates while for 30-day adult weight the replicates were quite consistent. The response to selection for 14-day larval weight was very small in the early generations but resumed after generation 6. This increase was accompanied by an increase in phenotype variation. No increase in phenotypic variance was observed for 30-day adult weight.

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