

AN EXPERIMENTAL COMPARISON OF INDIVIDUAL, FAMILY AND COMBINATION SELECTION¹

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ABSTRACT

Two selection experiments comparing the relative efficiencies of individual, family, and combination selection were conducted. The expected results for larval weight of *Tribolium* ($h^2 = 0.20$) and for pupal weight ($h^2 = 0.40$) were that combination selection would be a more efficient method than family selection, and that family selection would exceed individual selection. In experiment I, individual selection produced more response ($P < 0.05$) than did combination or family, which was not in agreement with expectation. There was confounding of inbreeding levels and random drift due to differential effective population sizes in the lines selected by different methods. Experiment II consisted of ten single-generation selection tests. An advantage of this approach is that it eliminates the inherent problems of differential inbreeding levels and differential rates of genetic drift due to unequal population sizes among the methods of selection. There were no statistically significant differences in efficiency among the three methods of selection for both traits. This was contrary to theoretical expectations but does suggest that with traits of 20% h^2 or higher, and where feasible, one may be justified in basing selection decisions on the phenotype of the individual only. Other advantages of single generation testing are that it allows more precise testing of selection theory and unbiased standard errors for estimates of realized heritability.

THEORETICAL developments describing the relative efficiencies of individual, family, and combination (family + individual) selection were published by LUSH (1947). He demonstrated that the comparative efficiencies of the three methods of selection can be determined if the correlations between genotypes (r) and between phenotypes (t) of members of a family are known. It is also necessary to know the number of individuals per family. OSBORNE (1957) converted LUSH's developments to depend on heritability (h^2) rather than r and t , but he assumed that $t = h^2r$, which in some cases may be substantially in error.

Results of the above-mentioned works have been utilized extensively, though very little experimental evidence concerning the relative efficiencies of these selection methods has been developed. McBRIDE and ROBERTSON (1963) did report that combination selection was slightly more effective than individual selection in increasing the number of abdominal chaeta in *Drosophila melanogaster*. Also,

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KINNEY *et al.* (1970) compared individual, sire family, dam family and index selection for egg production to 40 weeks of age in chickens. Family groups were predominantly half-sib but there were some full-sibs, and selection pressure was not equal in all lines. However, when selection pressure was standardized, individual selection was slightly more efficient than the other systems.

A problem inherent with experiments comparing selection systems is that differential effective population size is confounded with selection methods. Certainly, family and combination selection reduce effective population size (N_e) drastically relative to individual or random selection. Therefore, inbreeding levels and genetic drift are considerably different in the different lines. FRANKHAM, JONES and BARKER (1968) and JONES, FRANKHAM and BARKER (1968) clearly demonstrated with *Drosophila* that reducing effective population size does reduce both rate of response to selection and selection limits.

The first of the two experiments reported in this paper was a conventional selection approach comparing individual, family, and combination selection. In order to alleviate the problems encountered in experiment I with differential effective population size, experiment II utilized a scheme whereby comparisons were conducted in a series of 10 independent, one-generation selection experiments rather than in a conventional selection approach.

The objective of both experiments was to determine if the differences in efficiency among methods of selection, as projected by theory, can be experimentally demonstrated.

MATERIALS AND METHODS

Experiment I consisted of two separate, replicated selection studies. In one, selection was for the lowly heritable, heterotic trait 14-day larval weight. In the other, the selected trait was 19-day pupal weight, a trait of intermediate heritability and exhibiting little or no non-additive genetic variation. There were four lines in each replicate-trait subclass differentiated by the method by which potential parents were selected. The lines were: individual (I), selection based on individual phenotypes only; family (F), selection based on the mean of a family of full-sibs with the entire family selected or rejected; combination (X), selection based on individual phenotype and the weighted family mean; random (R), breeders randomly selected. In the combination selection system, the deviation of a given family mean from the overall mean was weighted by

$$\left[\frac{r-t}{1-t} \right] \left[\frac{n}{1+(n-1)t} \right] \left[Y - \bar{P} \right]$$

where n is the number of individuals in a family, Y is the family mean and $\bar{P}$ is the overall mean (LUSH 1947). Selection was continued for ten generations.

The genetic material utilized in this experiment was the Purdue Black population of *Tribolium castaneum* formed by crossing four stocks collected from widely separated geographical areas. The base population had been mass mated for many generations prior to the initiation of this experiment. Families were cultured in ¾-ounce glass creamers in control chambers at approximately 33° and 70% relative humidity. The culture medium consisted of whole wheat flour enriched with 5% dried brewer's yeast.

Each line was propagated by 22 single-pair matings per generation. Sib matings were avoided. Eggs were collected from each fertile mating over two consecutive 24-hour periods in separate containers. In most cases, six offspring from each of the two egg collection periods from each family were individually weighed, giving a total of 12 per family. However, on some occasions

fitness problems reduced the number of families available somewhat below the desired 20. When this occurred more offspring were weighed from the families that did produce for a total of 240 per line-generation-replication subclass. Since pupae can be sexed, the numbers of males and females weighed per family were equal in the lines selected for pupal weight. With larvae, sexes were undetermined when weighed so males were corrected to a female equivalent by multiplying male weights by 1.05 prior to the calculation of family means. With 22 males and 22 females selected each generation, the percentage selected was approximately 18 in all lines. Offspring were weighed in tens of micrograms and this unit of measurement was used throughout the experiment.

Inbreeding coefficients in each generation were calculated for all lines. In lines F and X, the replicates were crossed after generation seven in order to reduce the relatively high levels of inbreeding. One-half the selected males and one-half the selected females that produced generation eight in lines F and X came from each replicate.

In experiment II, the unselected generation 0 of each line, in each of the ten tests, was produced by mating males and females randomly selected from a large random-mating base population. The parents of the selected generation 1 were picked from generation 0 by the appropriate selection method and were mated in such a way that sib-matings were avoided. Each test was complete with the weighing of the individuals making up generation 1. The same base population was used to produce each of the ten tests.

Details of the population, traits, culture practices, designation of lines, number of matings and individuals per subclass, and other experimental procedures were described above under experiment I.

The phenotypic correlations among full-sibs (t) for larval and pupal weight, used in this study to compute expected relative efficiencies of selection methods and weighted family means for combination selection, were the same 0.16 and 0.20, respectively, calculated from generation 0 of experiment I. The reason for using these values was that they were much more precise, because of more data, than new estimates calculated from generation 0 of test 1 would be. However, at the completion of experiment II, t values were computed for both larval and pupal weight using generation 0 data from all ten tests. These estimates were very similar to those in experiment I. The correlation among genotypes of full-sibs (r) was 0.50 in all tests.

Statistical analyses of experiment I data consisted of standard analysis of variance procedures applied to regression coefficients of generation mean larval and pupal weights on generation number. In experiment II, the trait analyzed was the within-test response to selection (gen. 1—gen. 0) of each line. Duncan's new Multiple Range Test was used to make specific comparisons among selection methods. Heritabilities for each trait were calculated by regressing offspring phenotype on the average of the two parental phenotypes in the unselected zero generations. In experiment II, the h^2 values were averaged over the ten tests. Realized heritabilities (h_r^2) for experiment I were determined by regressing cumulative response, measured as deviations from the control, on cumulative selection differentials which were weighted by adjusting the parental phenotypes by the number of offspring measured. In experiment II, h_r^2 for each selected line in each test was calculated by dividing the selection response (ΔG), calculated as a deviation from the control, by the weighted selection differential (S). These ten within-test estimates of h_r^2 were then averaged for each selected line and standard errors were calculated.

RESULTS

Experiment I. Ten generations of selection utilizing individual, family and combination systems produced considerable increases in pupal and larval weight (Tables 1, 2, 3 and Figure 1, 2, 3, 4). The randomly selected control line remained rather constant over generations, indicating very little genetic drift or temporary environmental effects. Figures 1 and 2 indicate that individual selection produced a greater response than did family or combination selection when the selected trait was pupal weight. This became evident at generation 5 in repli-

TABLE 1

Pupal weight means by replication, line and generation

Line	Generations										
	0	1	2	3	4	5	6	7	8	9	10
Rep I											
I	234	248	260	286	307	326	344	354	370	384	393
F	239	251	259	279	298	302	326	326	342	343	352
X	233	252	266	264	286	299	303	311	328	348	354
R	238	237	236	236	231	234	232	230	229	231	231
Rep II											
I	234	247	277	282	307	322	338	351	371	383	397
F	231	239	250	265	275	294	296	309	342	343	343
X	232	247	260	269	286	300	316	334	345	350	374
R	236	230	230	230	232	236	235	236	233	227	229

TABLE 2

Larval weight means by replication, line and generation

Line	Generations										
	0	1	2	3	4	5	6	7	8	9	10
Rep I											
I	228	238	261	271	287	307	320	321	330	360	356
F	227	229	251	235	251	255	248	266	294	300	298
X	233	234	254	260	269	276	288	297	312	326	323
R	228	220	238	228	233	229	230	235	235	231	234
Rep II											
I	244	257	269	284	302	321	335	336	337	354	367
F	242	227	238	254	263	271	264	282	289	298	314
X	231	232	253	274	284	294	303	302	316	325	336
R	242	229	230	239	228	240	234	232	233	238	246

TABLE 3

Regressions of generation mean on generation number by replication, line and trait

Line	Pupal weight		Larval weight	
	Rep I	Rep II	Rep I	Rep II
I	16.72	16.41	12.43	12.23
F	11.84	12.41	7.54	7.51
X	11.66	13.98	9.92	10.52
R	-0.77	-0.19	0.70	0.53

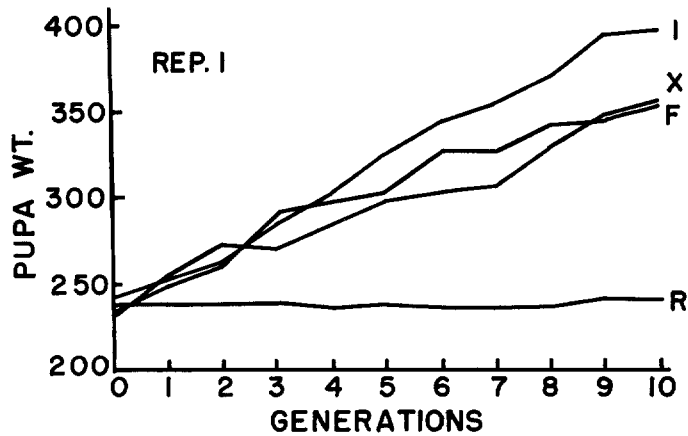


FIGURE 1.—Response to selection for pupal weight in replicate I.

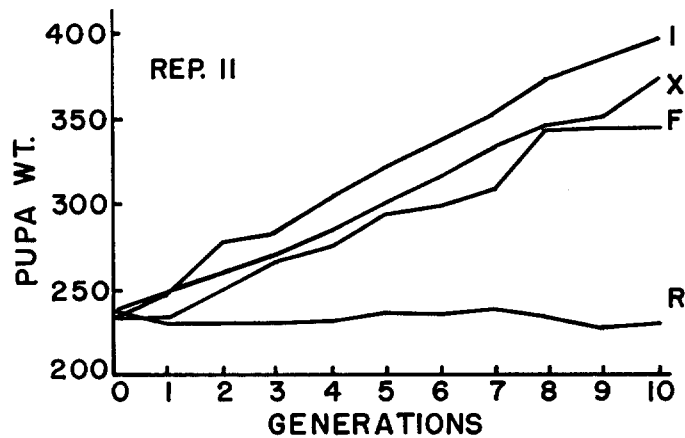


FIGURE 2.—Response to selection for pupal weight in replicate II.

TABLE 4

Analysis of variance and multiple range tests of regression coefficients in Table 3

Source	df	Pupal weight		Larval weight	
		MS	F	MS	F
Replications	1	1.25	2.84	0.01	0.14
Selection methods	3	110.24	250.55**	52.00	742.86**
R × Sm	3	0.44	...	0.07	...

Pupal weight				Larval weight			
I	X	F	R	I	X	F	R
16.6	12.8	12.1	— .5	12.3	10.2	7.5	0.6

Any two regressions not underscored by the same line differ significantly ($P < 0.05$).

** $P < 0.01$.

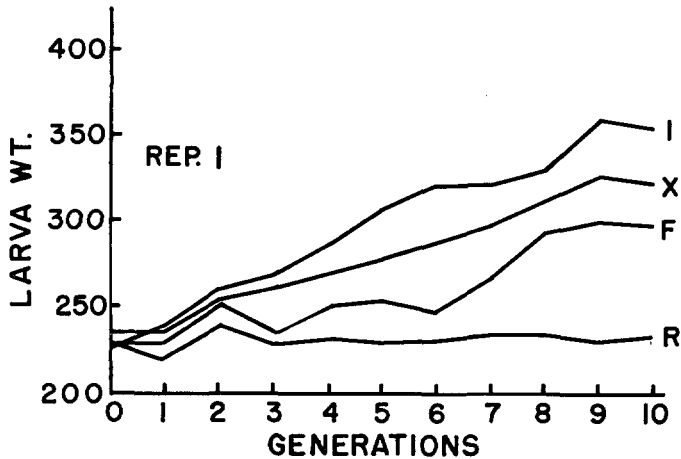


FIGURE 3.—Response to selection for larval weight in replicate I.

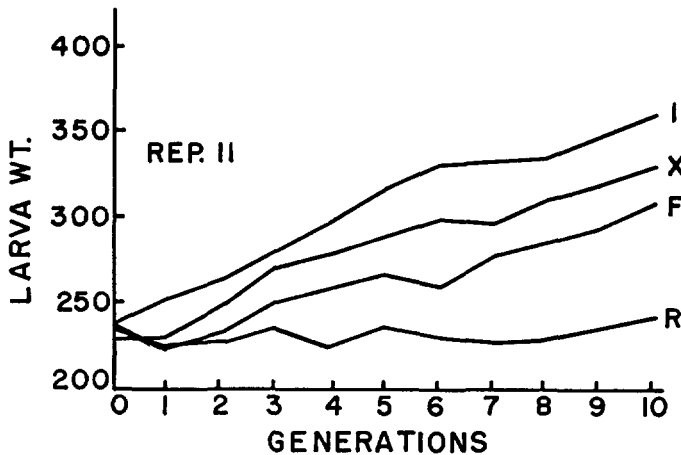


FIGURE 4.—Response to selection for larval weight in replicate II.

cate I and by generation 2 in replicate II. Statistical tests (Table 4) of the response, averaged over replicates, in the pupal weight lines indicate significant ($P < 0.05$) differences between the selected lines and the control and between I and X, and I and F. Average responses in X and F were very similar ($P > 0.05$). Figures 3 and 4, which illustrate response in the lines selected for larval weight, indicate a situation similar to that which occurred in the lines selected for pupal weight. Again, individual selection clearly surpassed combination and family selection; also, combination selection yielded more response than did full-sib family selection in both replicates. All paired comparisons of average response in larval weight lines were statistically significant ($P < 0.05$) (Table 4).

Estimates of heritability of pupal weight from the zero generation, by regression of offspring on mid-parent (b_{op}) were 0.39 ± 0.05 and 0.42 ± 0.04 in replicates I and II, respectively. For larval weight, these h^2 values were 0.15 ± 0.04

TABLE 5

Realized heritabilities by replication, line and trait

Line	Pupal weight			Larval weight		
	1-5	Generations 6-10	1-10	1-5	Generations 6-10	1-10
Rep I						
I	.42	.40	.41	.34	.18	.26
F	.66	.48	.57	.22	.37	.29
X	.42	.32	.37	.27	.32	.29
Rep II						
I	.40	.39	.39	.37	.20	.29
F	.55	.57	.56	.28	.29	.28
X	.30	.47	.42	.43	.29	.36

and 0.19 ± 0.03 . These estimates conform to previously reported heritabilities (WILSON, KYLE and BELL 1965; ENFIELD, COMSTOCK and BRASKERUD 1966; HARDIN and BELL 1967; WILSON *et al.* 1968). Realized heritabilities, calculated over five-generation increments and over the total ten generations, are given in Table 5 for each replicate-line-trait combination. Individual selection for pupal weight yielded h_r^2 values of 0.41 and 0.39 for the two replicates, very similar to h^2 values calculated from the zero generation. Those in the F lines were 0.57 and 0.56, reflecting increased accuracy from using family selection. However, the X lines, surprisingly, did not exhibit increased selection accuracy relative to individual selection. With the larval weight trait, individual selection was abnormally efficient for the first five generations with realized h^2 values of 0.34 and 0.37 in the two replicates. In generations 6-10, they were 0.18 and 0.20, very near expected values. Selection accuracy in lines F and X was improved slightly by the use of full-sib family and combination selection as h_r^2 values were higher than the ≈ 0.20 expected for individual selection. However, because of the unusually high h_r^2 values in generations 1-5 in the I lines, there was little or no advantage in using family information. Also, increasing inbreeding reduced realized h^2 in the first seven generations of lines F and X.

Since matings in all lines were single pair and, therefore, the family structure was full-sib, the correlation between the genotypes of family members was initially 0.50. When calculated over replications and traits, r increased with increased inbreeding to 0.56 and 0.54 in generation 10 in lines I and R. In lines F and X, r increased to 0.74 and 0.65 in generation 7, after which the two replications were crossed. The correlation between phenotypes of family members was estimated separately for each trait from the zero generation of both replications. They were 0.20 for pupal weight and 0.16 for larval weight. These values of t would probably increase over generations with increased r ; however, they were not recalculated during the experiment because the amount of data within generation-line subclasses was not sufficient to produce the necessary precision. Therefore, $r = 0.50$ in both lines, and $t = 0.16$ in the larval weight lines and 0.20 in the pupal weight lines were used to calculate weighting factors for the devia-

tions of family means from the overall mean in each generation of the X lines. The net effect of increasing r , which did happen in the F and X lines, would be to increase the efficiency of family and combination selection relative to individual selection.

Selection differentials averaged over five- and ten-generation increments for each replicate, line, and trait are given in Table 6. The absolute size of selection differentials changed very little during the experiment. There were, however, large differences among the lines with full-sib family selection reducing the average selection differential, as compared to individual selection, by approximately 50% in both traits. Combination selection reduced the selection differential by approximately 20% in pupal weight lines and 36% in larval weight lines.

Coefficients of inbreeding, averaged over replications, are given in Table 7 for each line and generation. Though sib matings were avoided, first-cousin and double-first-cousin matings were common in lines F and X. These consanguine-

TABLE 6
Average selection differentials by replication, line and trait

Line	Pupal weight Generations			Larval weight Generations		
	1-5	6-10	1-10	1-5	6-10	1-10
Rep I						
I	45.5	41.1	43.2	45.4	48.2	46.8
F	20.1	21.6	20.9	24.2	21.0	22.6
X	33.1	36.1	34.6	30.7	26.9	28.8
R	3.5	0.7	2.1	-4.0	-0.6	-2.3
Rep II						
I	43.8	42.1	43.0	43.2	39.1	41.1
F	22.8	19.7	21.3	21.4	26.3	23.9
X	35.5	34.4	35.0	29.8	23.9	26.9
R	0.8	-3.0	-1.1	1.6	0.1	0.8

TABLE 7
Inbreeding coefficients, averaged over replications, by generation, line and trait

Line	Generations										
	0	1	2	3	4	5	6	7	8	9	10
Pupal weight											
I	.00	.00	.01	.02	.02	.03	.04	.05	.05	.07	.08
F	.00	.00	.06	.15	.21	.26	.29	.35	.00	.05	.11
X	.00	.00	.02	.06	.09	.13	.16	.20	.00	.02	.05
R	.00	.00	.00	.00	.02	.02	.02	.03	.04	.04	.05
Larval weight											
I	.00	.00	.00	.02	.03	.03	.04	.05	.05	.06	.07
F	.00	.00	.05	.12	.18	.23	.27	.34	.00	.04	.09
X	.00	.00	.03	.05	.09	.12	.15	.19	.00	.03	.04
R	.00	.00	.00	.00	.01	.02	.03	.03	.03	.04	.05

ous matings led to generation 7 inbreeding levels of approximately 0.35 and 0.20 in lines F and X, respectively. The two replications of lines F and X were crossed to produce zero inbreeding in generation 8 and levels of approximately 0.05 and 0.10 in generations 9 and 10. Inbreeding in lines I and R at generation 10 did not exceed 0.08. Table 8 gives larval weight means adjusted for inbreeding depression by adding 11 micrograms for each 1% increase in inbreeding (WILSON *et al.* 1968). In lines F and X of both replicates, it seems that the adjustment was excessive. In no case, in these lines, did an eighth-generation mean with zero inbreeding exceed the adjusted seventh generation. The major point of interest in Table 8 with its adjusted means is that individual selection still produced more progress in both replicates than did full-sib family or combination selection. Pupal weight means were not adjusted since inbreeding has little or no effect on this trait.

Effective number (N_e) for each line was calculated by the formula

$$N_e = \frac{4N}{\bar{n} + \sigma_k^2}$$

as given by CROW (1954), where N , the number of breeders, was 36; $\bar{n}$, the average number of breeders per family, was 2.0; and σ_k^2 was the variance of the number of breeders per family. Information from both traits was used. The estimates of N_e were 30.0, 7.9, 11.2, and 33.4 for lines I, F, X, and R, respectively.

On the average, 18 of the 22 matings made each generation in each line were productive. Approximately 40 offspring were produced per productive mating. In line F of replicate II, selected for pupal weight, there were only 11, 10, and 9 productive matings in generations 6, 7, and 8. However, after the replicates were crossed, generations 9 and 10 had 18 and 16 productive matings, respectively.

Experiment II. Results from ten single-generation tests of the comparative efficiencies of individual, family and combination selection in increasing larval and pupal weight in *Tribolium* are shown in Tables 9 and 10. The consistency of the

TABLE 8

Larval weight means adjusted for the effects of inbreeding

Line	Generations										
	0	1	2	3	4	5	6	7	8	9	10
Rep I											
I	228	238	262	273	292	312	327	327	338	369	365
F	227	229	257	250	272	281	278	303	294	306	310
X	233	234	257	265	279	289	304	319	312	328	329
R	228	220	238	228	234	231	232	237	239	234	238
Rep II											
I	244	257	270	286	307	326	341	342	346	362	375
F	242	227	243	266	283	295	295	321	289	303	324
X	231	232	257	280	295	307	320	324	316	328	340
R	242	229	230	239	229	242	236	235	235	241	250

TABLE 9

Body weight means by trait, line, generation and test

Test	Gen.	Pupal weight				Larval weight			
		I	F	X	R	I	F	X	R
1	0	225.6	227.6	228.5	229.3	231.0	232.5	234.4	229.5
	1	240.5	244.5	239.0	231.1	247.2	248.6	250.7	234.3
2	0	224.4	228.4	225.1	228.3	226.5	225.7	226.1	226.1
	1	238.7	242.1	237.3	229.1	238.5	234.9	236.1	228.1
3	0	223.8	229.2	232.3	222.5	214.3	213.5	212.6	216.7
	1	243.2	241.8	250.2	231.4	219.3	220.0	218.3	210.8
4	0	226.0	229.4	223.2	222.1	229.9	229.2	239.3	233.1
	1	241.1	240.4	235.9	226.9	238.1	237.6	243.4	232.6
5	0	233.1	233.9	234.3	235.4	213.2	220.9	217.8	205.5
	1	243.3	240.4	241.4	234.7	237.9	245.6	240.9	217.3
6	0	222.4	226.1	224.5	226.1	213.7	208.9	199.9	207.8
	1	231.4	233.3	237.4	226.5	241.1	234.1	226.5	220.6
7	0	228.9	231.1	230.2	231.0	222.4	236.5	234.7	228.7
	1	233.9	237.6	236.8	227.2	225.1	239.1	234.7	223.4
8	0	228.3	224.7	225.7	227.6	233.1	226.6	230.7	227.8
	1	238.3	229.8	235.5	222.8	241.7	235.6	240.7	224.8
9	0	226.9	237.1	236.1	235.2	214.0	230.8	208.2	220.3
	1	242.8	247.0	243.6	232.8	236.6	249.6	236.8	227.6
10	0	231.5	232.2	230.0	231.8	231.8	237.1	229.1	233.6
	1	237.2	240.8	244.9	231.2	249.3	250.9	244.8	239.9

TABLE 10

Response to selection in single generation tests, calculated as deviations from the control

Line	Tests										Total ΔG
	1	2	3	4	5	6	7	8	9	10	
Pupal weight											
I	13.1	13.5	10.5	11.1	10.9	8.6	8.8	14.8	18.3	6.3	115.9
F	15.1	12.9	3.7	6.2	7.2	6.8	10.3	9.9	12.3	9.2	93.6
X	8.7	11.4	9.0	7.9	7.8	12.5	10.4	14.6	9.9	15.5	107.7
Larval weight											
I	11.4	10.0	10.9	8.7	12.9	14.6	8.0	11.6	15.3	11.2	114.6
F	11.3	7.2	12.4	8.9	12.9	12.4	7.9	12.0	11.5	7.5	104.0
X	11.5	8.0	11.6	4.6	11.3	13.8	5.3	13.0	21.3	9.4	109.8

randomly selected generation 0 means (Table 9) indicates that the base population from which each of the ten tests originated was genetically stable for the duration of this experiment. There were some within-test deviations in the control lines which were assumed to be environmentally caused; therefore, the responses in the selected lines were measured as deviations from the appropriate controls (Table 10). In no test did the selection methods fail to produce positive response for either trait. Total progress from each selection method indicates

TABLE 11

Analysis of variance and multiple range tests of response to selection

Source	df	Pupal weight		Larval weight	
		MS	F	MS	F
Tests	9	45.3	6.4**	257.4	52.5**
Selection methods	3	288.0	40.6**	301.5	61.5**
R × Sm	27	7.1	..	4.9	..

** P < 0.01.

I	Pupal weight X	F	R	I	Larval weight X	F	R
12.0	11.2	9.8	0.4	14.5	14.0	13.4	3.0

Any two means not underscored by the same line differ significantly ($P < 0.05$).

rather similar results for both traits. In each case, I exceeded F and X, and X exceeded F (Table 10).

An analysis of the selection progress realized, not adjusted for control deviations, is shown in Table 11. Tests and selection methods were highly significant sources of variation ($P < 0.01$) when tested by the interaction variance. However, when all possible comparisons among the selection method means were made, the only significant differences were between the controls and the selected lines.

Within-test selection differentials for larval weight consistently exceeded those for pupal weight (Table 12). As expected, selection differentials in line I were highest, followed by lines X and F for both traits. The reductions in *S* from the use of F and X were 47.8 and 19.7% for pupal weight and 51.7 and 24.7% for larval weight, respectively.

Since there was no evidence of maternal effects for either trait, regression of offspring phenotype on the average of parental phenotypes was used to estimate

TABLE 12

Selection differentials and total S for all lines, and percent reduction in S in lines F and X

Line	Tests										Total S	Percent Red.
	1	2	3	4	5	6	7	8	9	10		
Pupal weight												
I	31.8	26.6	32.8	25.7	37.3	33.6	29.6	29.5	31.5	30.3	308.7	...
F	16.0	18.6	13.7	18.3	13.9	14.4	13.9	17.8	17.6	16.9	161.1	47.8
X	23.4	26.2	25.0	21.1	34.4	21.1	23.2	25.6	22.4	25.6	248.0	19.7
R	-2.3	2.1	4.8	-0.1	4.0	-1.3	2.6	0.1	-1.6	-0.7	7.6	...
Larval weight												
I	35.0	39.4	47.8	40.1	54.6	65.1	46.2	36.9	48.4	42.7	456.2	...
F	17.6	15.7	22.4	16.7	30.3	29.4	18.6	26.8	22.4	20.6	220.5	51.7
X	31.0	32.7	29.7	28.0	41.4	47.8	30.6	28.8	35.8	37.6	343.4	24.7
R	-9.5	4.9	-7.5	-3.7	1.3	1.7	2.4	7.7	6.1	1.9	5.3	...

heritability. These h^2 values for pupal and larval weights were approximately 0.40 and 0.20. Realized heritabilities and standard errors in lines I, F and X were 0.38 ± 0.04 , 0.58 ± 0.06 , and 0.44 ± 0.04 for pupal weight. For larval weight, they were 0.26 ± 0.02 , 0.48 ± 0.03 , and 0.32 ± 0.04 , respectively.

DISCUSSION

Experiment I. The expected progress from family selection was given by LUSH (1947) as

$$\frac{1 + (n-1)r}{\sqrt{n[1 + (n-1)t]}}$$

times the progress from individual selection. Family selection should be superior to individual when $t < r^2 - \frac{(1-r)^2}{n}$. Therefore, family selection is expected to produce less progress than individual selection anytime t is as large as r^2 . In this experiment, when selection was for pupal weight with $r = 0.50$, $t = 0.20$ and $n = 12$, the expected efficiency of full-sib family selection was (1.05) (h^2S) where h^2 is the heritability of individual deviations and S is the selection differential. With family selection for larval weight ($r = 0.50$, $t = 0.16$, $n = 12$), the expected efficiency was (1.13) (h^2S).

The expected progress from combination selection was given as

$$\sqrt{1 + \frac{(r-t)^2}{1-t} \frac{n-1}{1 + (n-1)t}}$$

times the progress from individual selection. Theoretically, combination selection equals or exceeds individual and family selection for all combinations of r and t . In this study, the expected progress from combination selection for pupal weight was (1.19) (h^2S) and for larval weight (1.24) (h^2S).

It is difficult to reconcile the results of this study to the expected results. In all cases, family and combination selection should have produced more progress than individual selection. However, in no case did this occur. Even when larval weight means were adjusted for the effects of differential inbreeding, progress from individual selection was still superior. Adjusted selection differentials were reduced by family selection approximately 50% when compared to those produced by individual selection. Therefore, for family selection to be as efficient as expected, selection accuracy, as measured by h_r^2 , would have had to have been more than doubled; this did not occur. The reduction in realized selection differentials with combination selection was much less than with family selection in both traits, but the increase in selection accuracy was again not enough to offset this reduction.

A possible explanation for the unexpected results of this study is that differential rates of random fixation of loci, due to differential effective population sizes, were responsible. Certainly, if the effective size of the population is small many unfavorable alleles may be fixed by chance, thus reducing both rate of response and selection limits. ROBERTSON (1960), FRANKHAM, JONES and BARKER (1968), and JONES, FRANKHAM and BARKER (1968) have demonstrated very clearly that differential effective population sizes produce unequal rates of and limits to re-

sponse. Information in the RESULTS section of this paper indicates that effective population sizes in the lines selected by different methods were quite different, with family and combination selection each producing a much smaller N_e than individual or random selection. In spite of the fact that there were not consistent reductions in realized heritabilities in the last five generations of lines F and X relative to h_r^2 values in the first five generations of those lines, it seems that differential effective population size is the most likely explanation for the differences between observed results and theoretical expectations.

Experiment II. The use of repeated one-generation selection experiments completely alleviates the problem of differential inbreeding levels being confounded with selection methods. This is true since the mating of related individuals can be avoided for generations 0 and 1, but not thereafter. However, due to non-random distribution of family size, where family size indicates the number of progeny of an individual mating that survived to produce offspring, the effective population size does continue to differ among selection methods. Utilizing the development given by Crow (1954), the estimates of N_e , including data from both traits, were 32.4, 8.4, 12.8, and 35.1 for lines I, F, X and R, respectively. With the conventional selection approach, any loci fixed by chance in a negative state are, barring mutation, lost to selection. And, those fixed in positive state do not enhance selection response greatly, for selection would fix most of those in positive state anyway. Therefore, the net result of small population size is to reduce selection response. In this study, there was differential genetic drift in the lines due to differential effective population sizes. But, genetic drift is random in direction, and repeated one-generation selection tests are independent; therefore, selection response in one is not affected by negative state fixation in a previous test. The result of this is that, over all ten tests, plus and minus effects of drift should cancel or nearly so; the net effect of differential population sizes among the different selection methods should be of no consequence.

As in the first experiment, the expected increases in efficiency of family over individual selection for pupal and larval weights were 5 and 13%. The expected increases in efficiency of combination over individual selection for those two traits were 19 and 24%. Though there were no statistically significant differences among the total responses produced by the three methods of selection, the results, as in experiment I, do not follow theoretical expectations. For each trait, combination and family selection should have produced more progress than individual selection. In neither case did this occur. In fact, for both traits individual selection was slightly superior. This occurred even though the problems of differential inbreeding and genetic drift among selection methods were alleviated.

The reductions in selection differentials due to the use of family selection were approximately 48% and 52% for pupal and larval weight. These reductions are relative to the selection differentials in the I lines and they are almost exactly the expected values. The reductions for combination selection were 20% and 25% for pupal and larval weight. Realized heritability, which is a measure of the accuracy of the selection system, was not increased enough by the use of family

or combination selection to offset the reductions that occurred in the adjusted selection differentials.

There is no obvious explanation for the discrepancies that exist between these experimental results and the theoretical expectations. However, these data are extensive and they do suggest that with traits of 20% heritability or higher, and where feasible, one may be justified in basing all selection decisions on the phenotype of the individual only.

It should be mentioned that there are other advantages to using single-generation testing. Firstly, since theoretical developments do not account for the effects of changes in gene frequencies that occur during conventional selection experiments, the single-generation test approach alleviates this problem and allows a more precise test of selection theory. Secondly, this approach allows for unbiased estimates of standard errors for realized heritabilities, in contrast to conventional selection where the standard errors have been shown to be biased downward (HILL 1972).

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