CONCURRENT INBREEDING AND SELECTION IN *DROSOPHILA PSEUDOOBSCURA*¹

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IN artificial selection programs inbreeding is generally minimized in order to eliminate possible deleterious effects. Surprisingly little work, however, has been done on animal populations simultaneously subjected to both inbreeding and selection. KING (1918a, 1918b, 1918c, 1919) was able to select for heavy body weight in rats in spite of using full-sib matings. TANTAWY (1956a, 1956b), CLAYTON, MORRIS and ROBERTSON (1957) and REEVE and ROBERTSON (1952) have studied selection and regular systems of inbreeding for various quantitative traits in *Drosophila*; SHULTZ (1953) conducted a similar experiment with chickens. In general these workers found that selection was effective despite inbreeding, although TEBB (1957) found inbreeding to have a depressing effect on selection response in a long-term experiment with egg production in chickens.

The theoretical consequences of simultaneous selection and inbreeding have been worked out by HAYMAN and MATHER (1953) and REEVE (1955). KOJIMA (1961) considered a more general case and found that gain from selection was dependent upon three factors: (1) additive effects of genes, (2) dominance deviations, and (3) the joint contribution of dominance and the variance of change in gene frequency.

Selection for a quantitative trait should be effective if additive genetic variance is present. That is, the response to selection equals the heritability times the selection differential. Inbreeding depression on the other hand, depends, in part, on dominance deviations (FALCONER 1960).

The present study was undertaken to determine the degree of interaction between directional selection and inbreeding depression.

MATERIALS AND METHODS

Experimental technique: Sixteen inbred lines derived from a random-mating population of *Drosophila pseudoobscura* formed the basic material for the study. The base population was monomorphic for the Arrowhead arrangement. Inbreeding was accomplished by brother-sister mating for eleven to fourteen generations. Each line was then maintained by transferring adults to new culture bottles each generation. At the initiation of the present study the lines had been maintained in the laboratory in this way for at least two years. Neither the base population nor the inbred lines had any prior history of artificial selection.

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The study was conducted in a temperature controlled laboratory at 19–20°C with constant humidity and no illumination. The flies were cultured in 25 mm × 95 mm vials containing 15 mm of cream-of-wheat medium (DEMEREK and KAUFMANN 1957).

The trait selected for study was body weight of adult flies. The flies were weighed on a Mettler microbalance to the nearest 0.01 milligram (mg).

Body weight is a trait affected by many environmental factors. Accordingly, precautions were taken to minimize the effect of age and sex of flies, and age and larval density of the culture. Since the effects of desiccation become apparent approximately one and one-half days after emergence, equal numbers of male and female flies were measured within twenty-four hours after emergence. Only freshly prepared vials were used for rearing the flies to minimize the effects of the age of the culture. An equal number of eggs (30) was put into each vial to standardize larval density. Even though these environmental effects were minimized, considerable variation in body weight was still found.

All pair matings were made within 6 days after the flies had emerged from the pupae. Twenty-four hours after mating, the flies were transferred to half-pint milk bottles. The bottles were stoppered with ordinary milk bottle caps, on which a black agar-molasses-charcoal medium had been placed for oviposition. Fresh caps were placed in the bottles every twenty-four hours. The bottles were inverted and samples of thirty eggs were collected on the first and third day after the flies were placed in the bottles, so that two samples of eggs were collected from each mating.

The first sample of eggs was always used in the continuation of the group described below. In the event that the first sample of eggs did not provide sufficient numbers of flies, the additional ones were obtained from the second sample.

In order to eliminate possible selection for faster development, the first two flies of each sex to emerge were discarded in each culture. The next five flies of each sex were then weighed, and the sexes stored in separate vials. A female mean and a male mean were obtained for the two samples of each culture (there was no significant difference between the means of the first and second samples) and averaged to give a family mean. Thus, a family mean consisted of twenty total observations. Selection was based on family means.

Mating scheme: Suppose that ten families had been chosen to be parents for the next generation with these families randomly designated as A, B, . . . , J. The matings would be as follows, where the first letter is a female and the second letter a male:

A × B	B × C	C × D	D × E	E × F	F × G	G × H	H × I	I × J
C × A	D × B	E × C	F × D	G × E	H × F	I × G	J × H	
A × D	B × E	C × F	D × G	E × H	F × I	G × J		
E × A	F × B	G × C	H × D	I × E	J × F			
A × F	B × G	C × H	D × I	E × J				
G × A	H × B	I × C	J × D					
A × H	B × I	C × J						
I × A	J × B							
A × J								

All the above matings are pair matings with each member of the pair being chosen at random from the respective family. This scheme can be modified for any number of selected families. Ignoring reciprocal differences and omitting the diagonal of a diallel, the above scheme condenses into the upper half of a diallel. The system is very convenient to use and consumes very little time in preparing matings for the next generation.

It can be noticed in the scheme that there are no reciprocal matings and no full-sib matings. Each line is used as a female five times and four times as a male, when ten families are selected as above.

Experimental design: The sixteen inbred lines were randomly divided into two groups of eight each, one group used as male and the other as female parents in a factorial design. From the 64 F_1 families so formed, a balanced sample of 16 families (Figure 1) was chosen for parents of the F_2 generation. These 16 families were randomly mated in a diallel fashion, omitting reciprocals and the diagonal, giving a total of $(16)(15)/2 = 120 F_2$ families.

		Inbred lines used as female parents							
		1	2	3	4	5	6	7	8
Inbred lines used as male parents	9	X				X			
	10		X				X		
	11			X				X	
	12				X				X
	13	X				X			
	14		X				X		
	15			X				X	
	16				X				X

FIGURE 1.—The 16 families (X) used as a control in the experiment.

The F_1 was analyzed statistically to estimate the variance components which were used to derive estimates of genetic variance (COCKERHAM 1963). In the F_1 analysis it was assumed that the inbred lines were homozygous. If this assumption is not correct, the estimated values of additive and dominance variance would be biased upwards, with the bias being greater in the dominance than in the additive variance.

Two groups were initiated from the F_2 populations: a directionally selected group (selected for heavy body only) with two replicates (S and S', where S' was derived from a separate F_2 generated identically the same way as the F_2 described above) and a randomly selected group (R) where the families were chosen for parents on a random basis. If a family in the F_2 happened to be included in both the S and R groups, the additional pairs of flies were taken from the 2nd sample of eggs. A control group consisted of a balanced sample of 16 families from the F_1 , i.e., each inbred line was represented twice in the control (see Figure 1). The control was reconstituted each generation from the original inbred lines.

Table 1 gives the number of families selected in each generation for each of the groups (S, S', and R). In the selected groups both inbreeding and selection were present, while the random group was inbred without selection. For all groups a complete pedigree of each family was kept so that expected inbreeding coefficients could be computed.

TABLE 1

Number of observed families and number of families selected in each generation for each of the S, S' and R groups

Generation	Number of families observed	Number of families selected
0	120	12
1	66	10
2	45	10
3	45	10
4	45	10
5	45	9
6	36	8
7	28	7
8	21	7
9	21	

After five generations of family selection, the twenty-five families with the highest means (including the nine families chosen to continue selection in the S group) in the S group were each full-sib mated for three generations without further selection. This gave two sets of lines in the S group after the fifth generation; one selected and one inbred without further selection. Similarly, 25 families in the R group were chosen at random from the fifth generation and full-sib mated for three generations.

An additional inbreeding test was conducted to estimate the effects of inbreeding on body weight. F_1 progeny from crosses between the 16 inbred lines could be mated in such a fashion as to form F_2 families with expected inbreeding coefficients of 0, 1/8, and 1/4.

RESULTS

The factorial design used to generate the F_1 population permitted the estimation of genetic variance of body weight. The analysis of variance for the F_1 data, presented in Table 2, shows that the mean squares for male parents, female parents, and male-by-female interaction were all significant at the 1% level. The higher female mean square (compared to the male mean square) could possibly be accounted for by a maternal effect, but unfortunately no estimate of maternal effects was possible in this study. However, DEFRIES and TOUCHBERRY (1961) have suggested that a negative maternal effect is present in body weight in *Drosophila affinis*, although larval density was not controlled. They found a significantly positive relationship between body weight of the female parent and number of offspring, but a negative relationship between number of offspring and body weight of the offspring. The significant male-by-female interaction in Table 2 indicates the presence of nonadditive genetic variance.

Heritability of body weight can be estimated from the F_1 by $(\sigma_F^2 + \sigma_M^2)/\sigma_T^2$ where $\sigma_T^2 = \sigma_e^2 + \sigma_F^2 + \sigma_M^2 + \sigma_{FM}^2$ and the inbred lines are assumed to be completely homozygous (COCKERHAM 1956). This gives a value of .38 for heritability on a family basis.

The results of the F_1 analysis, then, indicate that selection should be effective in increasing body weight (due to additive genetic variance) and that inbreeding depression should be present, assuming the male $\times$ female interaction to be attributable, at least in part, to dominance effects of genes.

TABLE 2
Analysis of F_1 variability

Source	df	SS	MS	E(MS)
Replications	2	.62809		
Males (M)	7	.85245	.12178**	$\sigma_e^2 + 3 \sigma_{FM}^2 + 24 \sigma_M^2$
Females (F)	7	1.22294	.17471**	$\sigma_e^2 + 3 \sigma_{FM}^2 + 24 \sigma_F^2$
M $\times$ F interaction	47	1.09809	.02336**	$\sigma_e^2 + 3 \sigma_{FM}^2$
Error	110	1.45946	.01327	σ_e^2
$\sigma_e^2 = .01327$		$\sigma_F^2 = .00631$		$\bar{x}_{F1} = 1.191$
$\sigma_{FM}^2 = .00336$		$\sigma_M^2 = .00410$		$\bar{x}_P = 1.106$

** Significant at the 1% level.

Since the control group was reconstituted each generation, the genetic composition remains the same. Hence, any variation observed between "generations" of the control should be entirely environmental. The data for mean body weight of the control for each "generation" are shown in Table 3 and indicate considerable environmental effects between "generations." To remove the variation due to environmental differences among generations, the response of the S, S', and R groups was expressed as deviations from the control group.

The random group data (Table 4) reflect the influence of forces other than artificial selection operating within the population. Deviations of the R group from control were essentially random. The apparent increase in the last two generations might have been due to random drift, since only seven cultures were

TABLE 3
Mean body weight of the control for each generation of the study

Generation	Mean body weight (mg)	Standard error
0	1.135	.021
1	1.168	.023
2	.990	.028
3	1.225	.025
4	1.136	.038
5	1.114	.040
6	1.075	.039
7	.940	.031
8	1.071	.031
9	.799	.018

TABLE 4
A summary of mean raw body weight with its standard error, deviation from control, average expected inbreeding coefficient, range of expected inbreeding coefficients within a generation, and regression coefficient of body weight on inbreeding within generations for each generation of the random group

Generation	Mean body weight (mg)	Standard error	Deviations from control	$\bar{F}$	Range of $\bar{F}$	Within generation regression*
0	1.173	.010	+.038	0	0	
1	1.094	.014	— .074	.060	0—.19	— .3213
2			(not measured)	.089	0—.22	
3	1.321	.017	+.096	.129	.03—.28	+.1806
4	1.105	.021	— .031	.163	.04—.31	— .0257
5	1.022	.016	— .092	.220	.11—.31	+.4944
6	1.069	.020	— .006	.246	.18—.37	+.3660
7	1.007	.019	+.067	.272	.20—.36	+.1739
8	1.250	.030	+.179	.318	.27—.40	— .6931
9	.940	.028	+.141	.363	.28—.42	— .2650

* Pooled within generation regression = $\pm .0785 \pm .4102$.

randomly chosen for parents to produce generations 8 and 9 (see Table 1). Figure 2 shows the response, measured as deviations from control, of the R group each generation.

Since the inbreeding coefficient of each family in the R group was known and within each generation there was a range of inbreeding coefficients (column 6, Table 4), a regression coefficient of mean body weight on inbreeding could be obtained (column 7, Table 4). The regression coefficients of each generation were pooled to estimate the effects of inbreeding on body weight. The pooled value was $0.0785 \pm .4102$ mg per generation at 100% inbreeding. If one assumes that body weight is very slightly increased by inbreeding (although the pooled value is not significantly different from zero) then by adjusting the deviations of the R group for inbreeding (e.g., if $F = .129$ and the deviation from control is $+.096$, then the adjusted deviation would be $+.096 - (.129 \times .0785) = +.086$), the effects of natural selection can be estimated by computing the regression of the adjusted deviations on generation number. This linear regression coefficient was found to be $+.0082 \pm .011$ mg per generation. Thus, the effects of natural selection appear to be nil.

The response to selection for heavy body weight was very similar for the S and S' groups. Summaries of the data for the S and S' groups are presented in Tables 5 and 6, respectively. Response to selection was measured as deviations from control. Although mean body weight of the selected groups does not exhibit an absolute response to selection (column 2 in Tables 5 and 6), deviation from control shows good response (column 4, Tables 5 and 6). Figure 2 shows that after the initial generations of no response, for which no explanation seems

FIGURE 2.—Response to directional and random selection in the select and random groups, respectively, plotted as deviations from control (SFS = select full sibs, RFS = random full sibs).

TABLE 5

A summary of mean raw body weight with its standard error, deviation from control, cumulative selection differential, average expected inbreeding coefficient, range of expected inbreeding coefficients within a generation, and regression coefficients of body weight on inbreeding for each generation of the S group

Generation	Mean body weight (mg)	Standard error	Deviations from control	Cumulative selection differential	$\bar{F}$	Range of F	Within generation regression
0	1.173	.010	+.038	0	0	0	
1	1.157	.013	-.011	.179	.065	0-.25	+.3447
2	.948	.013	-.042	.323	.138	0-.38	+.0458
3	1.377	.015	+.152	.373	.177	.06-.29	+.2570
4	1.341	.021	+.205	.468	.215	.10-.37	-.4392
5	1.360	.023	+.246	.617	.239	.14-.33	+1.3057
6	1.330	.023	+.255	.770	.276	.18-.38	+.4776
7	1.212	.026	+.272	.898	.309	.21-.40	+.0108
8	1.453	.022	+.382	1.041	.344	.26-.43	-.0569
9	1.178	.030	+.379	1.110	.369	.28-.47	-.7693

plausible, selection was very effective. The realized heritability, calculated by finding the regression of deviations from control on cumulated selection differential, of the S group was $.371 \pm .058$, while that of the S' group was $.276 \pm .056$. Assuming that the effects of inbreeding and natural selection were to increase body weight (albeit very slightly), then these effects are included in the observed response to selection. Therefore, by adjusting the observed response to selection for inbreeding and natural selection, the "true" response should be estimated. After adjustment of deviations for inbreeding and natural selection, as done previously, realized heritabilities of the S and S' group were $.279 \pm .056$ and $.205 \pm .068$, respectively.

TABLE 6

A summary of mean raw body weight with its standard error, deviation from control, cumulative selection differential, average expected inbreeding coefficient, range of expected inbreeding coefficients within a generation, and regression coefficients of body weight on inbreeding with generations for each generation of the S' group

Generation	Mean body weight (mg)	Standard error	Deviations from control	Cumulative selection differential	$\bar{F}$	Range of F	Within generation regression
0	.982	.014	-.008	0	0	0	
1	1.284	.022	+.059	.172	.095	0-.19	-.0004
2	1.200	.021	+.064	.404	.134	.03-.23	-.0046
3	1.108	.017	-.006	.564	.174	.10-.28	+.1445
4	1.207	.020	+.132	.692	.207	.14-.30	-.3010
5	1.224	.019	+.284	.838	.237	.17-.33	-.1284
6	1.359	.024	+.288	.993	.269	.20-.37	+.1978
7	1.049	.024	+.250	1.097	.286	.21-.42	-.4846

TABLE 7
Heterosis tests

Group	Mean body weight (mg)	Variance	Number of cultures
S	1.114	.011	5
S'	1.219	.023	8
R	1.065	.016	8
S × R	1.073	.010	12
S × S'	1.105	.008	11
SFS			
Within	1.108	.024	9
Between	1.113	.012	7
RFS			
Within	.969	.021	10
Between	1.051	.021	9
SFS × RFS	1.103	.014	20

As an additional check on the effects of inbreeding on body weight, two types of inbreeding tests were conducted. The first test consisted of a series of full-sib, half-sib, and non-sib matings formed from the F_1 population. No appreciable difference in mean body weight among the three levels of inbreeding was found. The mean body weights (in mg) for the levels of inbreeding 0, $\frac{1}{8}$, and $\frac{1}{4}$ were $1.243 \pm .033$, $1.255 \pm .033$ and $1.244 \pm .032$, respectively.

The second test on inbreeding effects was provided by the full-sib lines derived from the S and R groups. After three generations of full-sib mating in which the expected inbreeding coefficient was raised from .23 to approximately .64, no significant change in deviation from control was observed in either group (Figure 2).

The F_1 did not show any significant heterosis. Nevertheless, additional crosses were made to test for this effect. The crosses included S × R, S × S', selected full sibs (SFS) by random full sibs (RFS), between SFS, and between RFS. The results of these crosses are shown in Table 7.

In the SFS × RFS crosses families of the SFS were crossed to families of the RFS. The within SFS mean listed in row 6 of Table 7 is simply the mean of the SFS lines used for the between SFS crosses. This provides a check for heterosis. The inbreeding coefficient of the within SFS mean is .64 and that of the between SFS is the same as generation 5 of the S group, or .24. No significant heterosis was detected in any of the crosses, although some was expected due to the significant nonadditive variance component found in the F_1 analysis.

Unfortunately, these experiments did not provide separate estimates of epistatic variances. The possibility exists that the epistatic variances could have had some influence on the results of the study. It is clear that they could cause an overestimate of the additive and dominance variances.

DISCUSSION

From the relative magnitude of additive genetic variance found in the F_1 analysis, one would have predicted the observed response to selection. On the

other hand, from the F_1 variability analysis one would have expected inbreeding depression to be evident; however, essentially no depression was observed. The apparent lack of inbreeding depression in body weight of *Drosophila* supports what has been found by other workers (MARTIN and BELL 1960; KIDWELL and KIDWELL 1966).

Inbreeding tends to cause a decrease in frequency of heterozygotes and an increase in frequency of homozygotes. If epistatic effects are considered negligible, inbreeding can produce an increase or decrease in the mean, depending on the direction of dominance. On the other hand, if the dominance of the loci involved are equally divided between plus and minus directions and gene frequencies are equal, then one would expect no change in the mean.

In order to compute the expected change of the mean due to inbreeding, so as to have a basis of comparison, certain assumptions must be made. These assumptions include 1) there are n loci controlling body weight, each with two alleles; 2) the deviation of the heterozygote from mid-parental value, d , is the same for all loci; 3) gene frequency, q , is the same for all loci, and 4) there is no linkage disequilibrium. FALCONER (1960) gives the dominance variance as $V_D = (2pqd)^2$. With several loci $V_D = \Sigma(2pqd)^2$ summed over all loci, which equals $n(2pqd)^2$ under the above assumptions. The change of the mean upon inbreeding can be shown to equal $2F\Sigma pqd$, or with n loci, $2Fn pqd$. Using the estimate of dominance variance from the F_1 analysis, $2pqd = \sqrt{.00336}/\sqrt{n}$. Also, the change of the mean with complete inbreeding was $1.191 - 1.106 = .085 = 2npqd$, or $.085/n = 2pqd$. Equating and solving for n yields approximately 1.2. This means that if the dominance of all genes were in the same direction, then essentially only one gene would account for the observed inbreeding depression. However, body weight would seem to be a quantitative character controlled by many genes. This suggests that the dominance of the genes was not all in the same direction or that the dominance variance is incorrect. On the assumption that the estimate of nonadditive variance contains little or no epistatic variance, a balanced dominance system is proposed to account for the results. That is, if we designate alleles for heavy body weight as + and alleles for light body weight as -, then some of the + alleles are dominant over the - alleles and some of the - alleles are dominant over the + alleles. An analysis of variance would show a significant dominance variance, but there would be no change in the mean upon inbreeding. This supports KIDWELL and KIDWELL's (1966) postulate of a balanced dominance system for body weight in *D. melanogaster*.

Along the same line of reasoning, if the inbreeding coefficient, F , were, say, 25%, and the number of loci involved was 9, then the change of the mean expected would be $2 \times \frac{1}{4} \times 9 \times pqd = .044$ or .021, depending on whether the estimate of pqd comes from the F_1 estimate of dominance variance or from the change of the mean with complete inbreeding. This clearly does not agree with the full-sib, half-sib, and non-sib inbreeding test. The change of the mean in full sibs was only .001 mg. This is only 1/44 to 1/21 of what might be expected with equal frequency and the same direction of dominance for all genes.

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SUMMARY

Selection for heavy body weight in *Drosophila pseudoobscura* was effective in spite of inbreeding. No significant inbreeding depression was seen in any of the tests, whether inbreeding was increased by full-sib or half-sib matings, or increased by effective population size as in the selected and random groups. A statistically significant nonadditive variance was found in the F_1 analysis. To account for the discrepancy between the expected results of inbreeding and the observed results, a balanced dominance system was proposed. This system allows for a significant dominance variance but no inbreeding depression. Additional tests for heterosis were likewise negative, thus lending further support for a balanced dominance system.

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