

Further evidence for coadaptation in crosses between geographic populations of *Drosophila pseudoobscura*

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1. INTRODUCTION

Genes are considered as separate entities in the simple models which population geneticists customarily set up to follow the fate of genes in populations. The situation in actual populations, however, is far more complex. Linkage and interactions between genes are two important factors which force us to consider the genotype as a whole. Only in the last few years have mathematical geneticists begun to incorporate these refinements into the theory of populations. The mathematical treatments suggest key roles for linkage and interactions in evolution (see, for instance, Lewontin, 1967).

Organisms will vary quantitatively in many characters as we consider populations in different environments. The geographic variations result from selection to adapt the organisms to the specific local conditions. Within each population the genes may also be selected to operate together for maximal fitness. Specific, favourable linkage relations will be established, and genes which interact epistatically for increased adaptation and reproduction will be selected. The gene pool, that is, the collection of all genes in the population, adjusts itself; Dobzhansky (1949) has called this internal adjustment *coadaptation*.

Vetukhiv (1953, 1954, 1956, 1957, 1959) performed a series of experiments to determine the extent of coadaptation in natural populations of *Drosophila pseudoobscura*. Crossing flies from different populations, he obtained F_1 and F_2 generations and compared the performance of both hybrid generations and the parental strains for longevity, viability, and fecundity. The F_1 hybrids often outperformed their parents as judged by the several criteria; the F_2 hybrids fell below the F_1 's and below the parental strains. The F_1 heterosis, or hybrid vigour, reflects perhaps the increased heterozygosity of the F_1 's; crosses between geographically disparate populations should give the maximal heterozygosity. Each F_1 inherited a complete, integrated set of genes and chromosomes from each parent. These balanced complexes of genes were disrupted and shuffled by recombination in the F_1 parents of the F_2 's (Wallace & Vetukhiv, 1955; Wallace, 1959). The more important the mutual adjustment of the genes within each population, the greater will be the decline of the performance in the F_2 's. Wallace (1955) studied viability in crosses between geographically separated populations of *D. melanogaster* and found the F_2 breakdown expected for coadapted genetic

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systems. Brncic (1954) extended Vetukhiv's work with *D. pseudoobscura* by studying viability under intense competition; he found the F_2 breakdown and was able to show its basis in recombination. King (1955*a, b*) found that coadapted gene pools had evolved in experimental populations of *D. melanogaster* selected for resistance to DDT. Kitagawa (1967) studied viability in crosses among six experimental populations of *D. pseudoobscura* and found the F_2 breakdown characteristic of crosses between coadapted gene pools. Genetically alike at their inceptions, these populations diverged appreciably during 8 years of maintenance at three different temperatures. Anderson (1966) had previously studied body size in crosses among these same populations; he found a pronounced F_1 heterosis and a far less dramatic F_2 breakdown. The study with body size is thus consistent with that utilizing viability; body size might be expected to be the more conservative index of coadaptation, since it was studied under nearly optimal conditions, while the viability was measured under more intense competition.

The recent work of McFarquhar & Robertson (1963) on *D. subobscura*, a wide-ranging European species, has raised some interesting questions concerning coadaptation in *Drosophila*. These authors found no evidence of F_1 heterosis or F_2 breakdown in crosses of widely separated populations. Their chief criterion was body size, which is a polygenic character that should reflect coadaptation about as well as any other. Since their criterion of body size was not employed in any of the experiments cited above, however, they might have been so unlucky as to pick an insensitive trait. On the other hand, the difference between their results with *D. subobscura* and the previous work on *D. pseudoobscura* and *D. melanogaster* might be due to different genetic systems in the species. Differences in genetic structures between species would constitute a valuable addition to our knowledge of the various paths populations may take in response to selection. Experiments were therefore set up to determine whether body size in different geographic populations of *D. pseudoobscura* is coadapted.

2. MATERIALS AND METHODS

D. pseudoobscura is an American species confined to the West. Populations exist from Canada through Guatemala, and from the Pacific coast to the western margin of the great plains. Eleven widely separated localities were selected to represent, as far as possible, the whole range of the species; they are shown in Fig. 1. The flies were collected from April to August 1964. Buckets of fermenting bananas were set out in likely spots, usually under trees and near a stream. The flies attracted to the bait were recovered with a sweep net, tentatively classified in the field, and shipped to New York.

Experimental populations as representative of the natural ones as possible were established in the laboratory. Each female inseminated in nature was placed in a separate culture bottle. Twenty female and 20 male offspring of each female were placed in plastic population cages, one cage per natural population. The number of founder genotypes (twice the number of inseminated females) represented

in each population ranged between 48 and 232, depending on the success in collecting. The numbers of founder genotypes in each population are given in another study of these populations (Anderson, Dobzhansky & Kastritsis, 1967). The populations were maintained at 16 °C until December 1964; genetic changes are known to be slight at this temperature (Wright & Dobzhansky, 1946). Hence

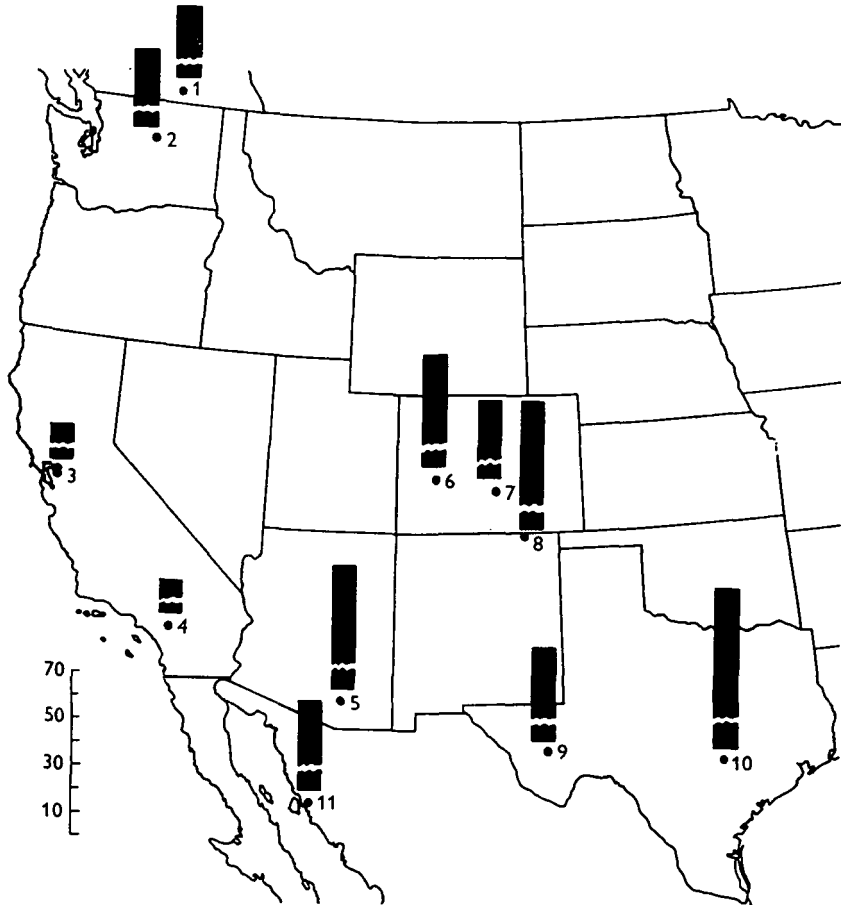


Fig. 1. Body size in natural populations of *Drosophila pseudoobscura*. The bars are proportional to the mean wing length of females in the populations. The scale is explain in the text. The localities are the same as in Table 2.

each population reached a large size with a minimum of selection. The population cages are plastic boxes, 31 cm by 26 cm by 11 cm, with 15 food cups inserted into the bottom. Large and fairly stable populations (1000–4000 flies) are maintained in these cages. Late in December 1964, after they were sampled to study differences in body size, the populations were transferred to a constant temperature room at 25 °C; they remained there until the end of the experiments. The temperature in this room has accidentally fluctuated on several occasions as much as two or three degrees below and one degree above, 25 °C. The relative humidity was not controlled and fluctuated with the seasons from a low of 25% in the winter to a high of

65% in the summer. Spassky's (1943) cream-of-wheat medium was used in the food cups until September 1965. Thereafter, a food enriched with brewer's yeast, Ohba's (1961) 10% medium, was used for its convenience in the sampling of the populations. All the populations were exposed to the same conditions of food, temperature and humidity. The generation time of *D. pseudoobscura* in the population cages at 25 °C is about 30 days.

The body weight of individual flies is difficult to measure and is sensitive to environmental conditions, to humidity in particular. Following other workers, I chose wing length as the index of size. Wing length does not vary with the conditions at the time of measurement, and accurate measurement of each individual is possible. Studies of wing length are highly repeatable (see Anderson, 1966, for an example). Sokoloff (1966) studied body size in *D. pseudoobscura* and measured both wet weight and wing length to see how they were correlated. For flies from six localities he found the correlation to be 0.81. The sizes of males and females (measured as weight or wing length) were even more highly correlated. My own data show similar correlations. We may, then, confidently use the wing length of one sex as an index of the body size in a given population. The length of the wing along the third longitudinal vein, from the outer margin of the anterior cross-vein to the tip of the wing, was used as the measure of size. Flies were stored in 70% ethyl alcohol; left wings were later removed and mounted in Canada balsam. The measurements were made under a compound microscope at magnification $\times 63$, with an ocular micrometer of 100 divisions; all measurements were recorded to the nearest unit of the micrometer scale.

Samples of approximately 1000 eggs were taken from each cage and subdivided among six bottles. The adults coming from the initial egg sample were then placed in vials with spoons containing Kalmus's (1943) medium, blackened with charcoal, for the collection of eggs. Several hundred parents were used per population, distributed over five to ten vials. Counted samples of 50 eggs were then placed in yeasted half-pint bottles with Spassky's (1943) cream-of-wheat medium. For each experiment these bottles were kept at the same temperature in which the initial egg sample was incubated. All of the flies actually measured were one generation removed from the cages and were raised under uncrowded, nearly optimal conditions. Wings were removed from a random sample of all the flies hatching in a given culture. All experimental cultures were kept in circulating air incubators in which the temperatures only rarely varied as much as 0.5 °C on either side of those desired. Bottles were randomized, and wherever possible all the bottles for a single experiment were kept on the same shelf within the incubator.

The F_1 and F_2 generations of all combinations of the seven populations listed in Table 4 were studied, a sample of the parental populations being raised simultaneously with each hybrid generation. All reciprocal crosses were made. Ten female wings from each of seven replicate bottles per reciprocal cross were measured. Occasionally a bottle was lost due to mould or breakage. There was no evidence of a dependence of within-bottle variance on the mean body size. The statistical analyses were therefore carried out on the untransformed data.

3. RESULTS

In all the experiments, counted numbers of 50 eggs were placed in the bottles. The viability varied from cross to cross, however. An experiment was conducted at 25 °C to see whether variation in the number of adults emerging in each bottle affected wing length over the range of densities encountered in the main experiments. The number of adults emerging is an accurate index of eggs which hatched, since very few larvae fail to reach adulthood under these uncrowded conditions. The results are summarized in Table 1. The dependence of wing length on density is small and insignificant.

In Table 2 the body sizes in eleven widely separated geographic populations are given, along with the names of the physiographic provinces. Ten female wings

Table 1. *The relationship of wing length and larval density in Drosophila pseudoobscura raised under standard laboratory conditions*

No. adults emerging in bottle	Mean wing length, ♀♀*	Mean wing length, ♂♂*	No. adults emerging in bottle	Mean wing length, ♀♀*	Mean wing length, ♂♂*
7	81.67	74.50	35	80.80	73.70
8	79.67	72.00	36	81.20	72.00
8	80.00	72.25	37	81.30	74.20
9	81.17	74.68	37	80.00	73.50
9	80.00	71.00	40	80.30	73.60
14	79.50	75.20	40	79.70	72.80
16	80.71	72.56	41	79.90	73.30
19	81.00	73.30	42	80.40	73.70
22	79.90	73.13	50	80.60	73.10
25	79.60	71.78	51	81.00	74.90
26	81.40	75.00	51	80.30	73.30
28	79.30	72.50	53	80.70	73.80

Regression of ♀♀ wing length on density: $b = 0.003 \pm 0.009$

Regression of ♂♂ wing length on density: $b = 0.013 \pm 0.018$

* One unit = 20.8 μ

Table 2. *Body size in geographic populations of Drosophila pseudoobscura; females only*

Population	Map no.	Province	Wing length at 19 °C*
Austin, Texas	10	Texas	91.79
Raton, New Mexico	8	Rocky Mountains	90.48
Tucson, Arizona	5	Basin and Range	90.25
Black Canyon, N.M., Colorado	6	Rocky Mountains	89.80
Davis, Texas	9	Texas	89.02
Sonora, Mexico	11	Basin and Range	88.76
Hayden Creek, Colorado	7	Rocky Mountains	88.33
Methow, Washington	2	Pacific Coast	88.24
Okanagan, British Columbia	1	Pacific Coast	88.11
Berkeley, California	3	Pacific Coast	86.53
Riverside, California	4	Pacific Coast	86.37
Average standard error	—	—	0.618

* Mean of 100 measurements: One unit = 20.8 μ

were measured from each of ten replicate bottles per population. The differences in size among the populations are highly significant, as shown in Table 3. Figure 1 presents the geographic variation in size visually; to accentuate the differences between the populations, the scale and the heights of the bars are in units of (wing length - 85) × 10. The localities from the Pacific coast are generally smaller than those from the interior. Lumping the populations to form 'interior' and 'coastal' groups, Scheffe's (1953, 1959) test was applied to test the significance of the difference between the two groups. The average size in the four Pacific coast localities was highly significantly different ($P < 0.005$) from the average size in the interior populations. The collection from Sonora, Mexico, was included among the interior populations since it came from a desert area typical of the interior.

Table 3. *Analysis of variance of body size in geographic populations of Drosophila pseudoobscura; females only, at 19 °C*

	D.F.	M.S.	F
Populations	10	269.02	7.04***
Error	99	38.23	

*** $P < 0.005$

Table 4. *Body size in geographic populations of Drosophila pseudoobscura after 1.5 years in the laboratory at 25 °C; females only*

Population	Abbreviation	Wing length* at 25 °C
Okanagan, British Columbia	C	82.057
Austin, Texas	A	81.483
Tucson, Arizona	T	81.096
Black Canyon N.M., Colorado	B	80.882
Hayden Creek, Colorado	H	80.296
Berkeley, California	S	80.157
Riverside, California	R	79.133
Average standard error	—	0.175

* Mean of 280 measurements. One unit = 20.8 μ .

The populations established from the collections in nature were kept at 25 °C for 1.5 years. Sampling them in the usual way, body sizes were again determined in seven of the populations, but this time at 25 °C; the data are given in Table 4. Ten female wings were measured from each of 28 replicate bottles per population. The ranking by size is the same as in the determination 1.5 years previous at 19 °C, excepting only the Canadian population. The population from Okanagan, British Columbia, had a larger mean size in the later sample. On the whole, the sizes changed very little; the crosses between the populations will very likely reflect the genetic systems for body size in the natural populations.

Variations in body size in *Drosophila* is known to be polygenic. If the various genes for size act *additively*, then each hybrid generation should be the average of the sizes of its parents. This average is usually called the *mid-parent*. *Heterosis* occurs when the hybrids are larger than the midparent; *breakdown* occurs when

they are smaller than the mid-parent. *Overdominant* loci often contribute to heterosis; the heterozygotes for such a locus have a phenotype higher on the scale by which we judge performance than either homozygote. With body size as our criterion, over-dominant loci would yield larger flies when the loci were heterozygous than when homozygous (see Robertson (1954) for an example).

Vetukhiv & Beardmore (1959) found that F_1 heterosis and F_2 breakdown, as indices of coadaptation, depend on the environment of the experiment. Under stringent conditions, the effects are pronounced; under optimal conditions they may not be detected. My experiments were therefore conducted at 25 °C, to accentuate the effects of coadaptation and to make their measurement more accurate. The data are presented in Tables 5 and 6; maternal effects appeared, so the data have been divided into crosses in which the reciprocals were the same and into crosses in which the reciprocals were different. Splitting the data this way allows us to see if the maternal effects bias the interpretation of the comparisons F_1 -midparent, F_2 -midparent, and F_1 - F_2 . In Table 6 the reciprocal crosses are grouped where they did not differ significantly. The results of these comparisons are summarized below:

Numbers of statistically significant comparisons of parents and hybrids

	F_1 -midparent		F_1 - F_2	
	Positive	Negative	Positive	Negative
Crosses with maternal effects	4	4	8	2
Crosses without maternal effects	2	2	5	0
Total	6	6	13	2

There is no pattern to the comparisons F_1 -midparent; in half the cases the differences are positive and in the other half, negative. The comparisons F_2 -midparent and F_1 - F_2 , by contrast, are more frequently significant and are mostly positive. There was no strong F_1 heterosis, but there was a pronounced F_2 breakdown. The findings are the same in the crosses which showed no maternal effects on size and in those which did. Body size in *D. pseudoobscura* is evidently part of an integrated, internally adjusted genetic system. Recombination between different coadapted systems results in a loss of this integration and a consequent breakdown in the F_2 hybrids.

The reciprocal crosses are compared in Table 7. Only in one case did a maternal effect persist for both hybrid generations. The maternal effects probably arose from interactions of the genotypes with the maternal cytoplasm. Each reciprocal line had an originally different maternal cytoplasm; the genotypes changed, however, by recombination in the F_1 's. Similar maternal effects on body size in this (Prout, 1959) and other (McFarquhar & Robertson, 1963) species of *Drosophila* have been reported.

The within-bottle variance was used as the index of variability; this variance contains both genetic and environmental components. The differences in variability among the parental populations and the hybrid generations, however, should

be largely genetic. The variabilities of the F_1 and F_2 generations are compared with those of the sets of parental populations raised as standards with each in Table 8. The variabilities of the F_1 and F_2 hybrids are also compared, after adjustment of the F_2 means for the size difference between the parents raised with the

Table 5. Comparisons of wing length in hybrids between geographic populations and their parents. A. Crosses not involving maternal effects; females only, at 25 °C

Cross †	F_1 -MP	F_2 -MP	F_1 - F_2
SB and BS	0.45	0.04	0.37
SH and HS	-1.33***	-2.15***	0.94**
SR and RS	0.87**	-0.69*	1.53***
AB and BA	0.05	-0.28	-0.21
AR and RA	0.72*	-0.69*	0.90**
AC and CA	-0.24	1.45**	1.05**
BH and HB	0.25	0.11	0.00
BR and RB	0.22	0.55	-0.63
RC and CR	-0.72*	-1.57***	0.91**

All comparisons are in micrometer scale units; one unit = 20.8 μ .

*, **, and *** denote significance at 0.05, 0.01, and 0.001 levels, respectively.

† Female parent given first; abbreviations are as in Table 4.

Table 6. Comparisons of wing length in hybrids between geographic populations and their parents. B. Crosses involving maternal effects; females only, at 25 °C

Cross †	F_1 -MP	F_2 -MP	F_1 - F_2
ST	1.38***	-0.06	{ 1.59***
TS	-0.23		{ -0.02
SA	2.00***	1.68***	0.07
AS	-2.23***	-2.04***	-0.44
SC	0.18	{ -1.35***	1.85***
CS		{ 0.10	0.40
TA	1.45***	-0.75**	{ 1.85***
AT	-0.58		{ -0.18
TB	-1.36***	1.34***	{ -2.83***
BT	0.74		{ -0.73
TH	0.35	0.35	{ 0.05
HT	-0.86*		{ -1.16*
TR	0.34	{ 0.85*	0.36
RT		{ -0.86*	1.08*
TC	-0.43	{ -0.27	0.07
CT		{ -1.27***	1.07*
AH	1.18***	{ -0.14	0.97*
HA		{ -1.67***	2.50***
BC	0.24	{ -1.68***	1.95***
CB		{ 0.31	-0.04
HR	-1.21*	-0.81**	{ -0.53
RH	-0.21		{ 0.90
HC	0.01	{ -0.23	0.46
CH		{ 0.81*	-0.58

All comparisons are in micrometer scale units; one unit = 20.8 μ .

*, **, and *** denote significance at 0.05, 0.01 and 0.001 levels, respectively.

† Female parent given first; abbreviations are as in Table 4.

F_1 's and the parents raised with F_2 's. The adjustment removes the average effect on size which different batches of food usually produce. The F_1 's were highly significantly less variable than the parents, and the F_2 's were highly significantly more variable than either the parents raised with them or than the F_1 's. These findings corroborate the evidence for coadaptation from the comparisons of size among parents and hybrids. The means of the crosses, the numbers of flies measured and the standard errors are given for reference in an appendix to Anderson (1967).

Table 7. *Maternal effects on body size in crosses between geographic populations of Drosophila pseudoobscura; females only, at 25 °C*

Cross †	Difference of F_1 reciprocals	Difference of F_2 reciprocals	Cross †	Difference of F_1 reciprocals	Difference of F_2 reciprocals
ST-TS	1.61**	0.27	AB-BA	-0.57	0.41
SA-AS	4.23***	3.71***	AH-HA	0.97	1.53***
SB-BS	-0.16	-0.10	AR-RA	-0.47	-0.85
SH-HS	0.56	0.69	AC-CA	0.79	0.06
SR-RS	0.37	-0.74	BH-HB	0.23	0.47
SC-CS	0.24	-1.46***	BR-RB	0.58	-0.13
TA-AT	2.03***	-0.07	BC-CB	0.32	-1.99***
TB-BT	-2.10***	-0.01	HR-RH	-1.42**	0.07
TH-HT	1.21*	0.44	HC-CH	0.59	-1.04*
TR-RT	-0.45	1.72***	RC-CR	0.24	0.35
TC-CT	0.20	1.00*			

All comparisons are in micrometer scale units; one unit = 20.8 μ .

*, **, and *** denote significance at 0.05, 0.01 and 0.001 levels, respectively.

† Female parent given first; abbreviations are as in Table 4.

Table 8. *Comparison of pooled within-bottle variances of wing length in parents and hybrids from the geographic populations; females only, at 25 °C*

	D.F.	M.S.	F
(a) Parents	837	3.23	1.22**
F_1	2354	2.66	
(b) F_2	2296	3.50	1.24**
Parents	882	2.83	
(c) F_2 †	882	4.00	1.24**
F_1	837	3.23	

† Adjusted for the difference in average sizes of F_1 's and F_2 's.

** Significant at the 0.01 level.

4. DISCUSSION

Body size in *D. pseudoobscura* is known to be a polygenic character with a rather high heritability. The heritability of body size in *D. pseudoobscura* lies somewhere between 25 and 35% (Frahm & Kojima, 1966); that is, of all the variation in size under the carefully controlled conditions in the laboratory, from one-fourth to one-third is genetic. Thus, size is a character rather accessible to selection in this

species. Body size in *D. pseudoobscura* is correlated with fitness in the sense of evolutionary success; Tantawy & Vetukhiv (1960) and Tantawy (1961) found that larger flies lay more eggs and live longer than do smaller ones. Geographical gradients in body size have been described in several species of *Drosophila*, and temperature seems to be an important factor in the variation (see Anderson (1966) for references). Sokoloff (1965) found no evidence of a general cline in size correlated with latitude or any other factor in *D. pseudoobscura*. As Sokoloff noted, however, the complex topography of the territory which this species inhabits may obscure such relationships. My studies confirm Sokoloff's (1965) demonstration that size is different in geographic populations of *D. pseudoobscura*. Not only are the sizes different in the eleven populations which I studied, but there is some *pattern* of sizes among the populations. Those from the Pacific coast were smaller than those from the interior, although the effect was small in some localities. We expect such a pattern of physiographic variation in an organism which adapts to so varied a territory as does *D. pseudoobscura*.

The geographic variation we have considered indicates selection on a grand scale, differentiating populations over a range of 2000 miles. The crosses among the experimental populations derived from the parents collected in nature, on the other hand, illustrate selection at a narrower level, within each population. The crosses between the experimental populations begun from the collections in nature clearly indicate the coadaptation within them. There was a significant 'breakdown' of size, and a significant increase in variability among the F_2 's. The breakdown indicates the breaking apart, by recombination, of gene complexes which had been selected for favourable interactions. The increased variability reflects the many new combinations, made possible by recombination, among the different collections of genes for body size in the various populations.

The irregular behaviour of the F_1 's suggests either a minor role for overdominant loci in determining body size in *D. pseudoobscura*, or that the populations are already heterozygous for a large fraction of the possible overdominant loci for size. The former possibility seems more likely in view of the increased heterozygosity expected in crosses between such geographically separated populations. The maternal effects on size complicate but in no way obscure our conclusions. Prout (1959) has found similar maternal effects in *D. pseudoobscura*, and workers with other species have reported them for a variety of characters (Wallace, 1955; Poulson, 1934; Moriwaki & Tobar, 1963).

Heterosis in the F_1 generation is often found in crosses between geographically separated populations but is not a necessarily expected phenomenon in crosses between coadapted populations. F_1 heterosis and F_2 breakdown are probably the results of different genetic mechanisms. F_2 breakdown occurs through the reassortment of genes by recombination and the consequent disruption of synergistic combinations of genes. F_1 heterosis, on the other hand, is most likely the result of increased heterozygosity for genes with overdominant effects. Many genes with overdominant effects may be fixed in a parental population, by chance or by selection. The fixation occurs at different loci in different populations, since

the selections are different. Crossing two populations restores heterozygosity at the overdominant loci, with a corresponding heterosis. Whether the populations have highly integrated, interacting genetic systems is another matter. The experiments of Kojima and his collaborators bear on this last idea. Kojima & Kelleher (1963) compared the effectiveness of purebred and crossbred selection on fecundity in *D. pseudoobscura*. In purebred selection, parents are chosen for their performance, mated and the process repeated again and again; it is the usual directional selection. In crossbred selection, parents are chosen for the performance of their hybrids with other, unrelated populations. Those parents whose hybrids with other lines are most successful by the particular criterion of selection being employed are remated, each within its own line. Thus there is no exchange of genes between lines; separate lines are developed which perform well when crossed. Kojima & Kelleher found crossbred selection more successful in increasing fecundity than was purebred selection. After 19 generations the crossbred lines were combined into one mixed population (Richardson & Kojima, 1965). The fecundity scarcely changed; there was no breakdown through recombination in six generations of the mixed population. The crossbred selection produced lines which yielded F_1 heterosis but which were not individually coadapted. And conversely, as my experiments indicate, populations with coadapted genetic systems may not display F_1 heterosis when crossed. We do not expect F_1 heterosis for a trait that is determined by genes with largely additive, and less often overdominant, effects.

The experiments I report plainly corroborate Vetukhiv's earlier work, showing that the 'breakdown' expected of coadapted systems occurs in crosses between natural populations of *D. pseudoobscura*. The populations in the present experiments were composed of a large number of strains, mixed in the same proportions in which they occurred in the samples from nature. In this respect my experiments are similar to those of McFarquhar & Robertson (1963) with *D. subobscura*. Yet the results with the two species were different. Why?

The likeliest explanation is that the genetic structures of the two species are different. Interactions among genes are more important in the genetic adjustment of *D. pseudoobscura* for maximal fitness than they are in *D. subobscura*. There are several experiments, other than those on coadaptation cited above, which lend support to this hypothesis. The extensive series of experiments on the release of variability through recombination (see Dobzhansky & Spassky (1960) for a list of the relevant papers) revealed that *synthetic lethals*, which are lethals arising through interactions among genes rather than through lethality at specific loci, were more frequent in *D. pseudoobscura* than in most of the other species investigated. Several workers, in particular Sperlich, Dobzhansky, and Krimbas (see Anderson *et al.* (1967) for references), have noticed that the chromosomal polymorphism in *D. subobscura* is *rigid* as compared to the *flexible* polymorphism in *D. pseudoobscura*. The polymorphism in *D. pseudoobscura* is delicately adjusted and varies widely with many environmental factors, in both nature and the laboratory. *D. subobscura*, in contrast, shows less change to either natural or experimental variation in its environment. This species seems to possess a genetic

system more generalized in the sense of allowing adjustment over a fairly wide range of environments; there is variation, but nothing so extensive as in *D. pseudoobscura*. The genetic system of *D. pseudoobscura*, on the other hand, seems to adjust to environmental changes with rapid and often extensive alteration of gene or chromosome frequencies. Both species are wide-ranging, with flourishing populations. They seem to have achieved success by different modes of adjustment within their gene pools.

SUMMARY

Body size in *Drosophila pseudoobscura* is a continuously varying character with a high heritability; it is almost certainly related to fitness. Natural populations of *D. pseudoobscura* from Canada to Mexico have been sampled and found to vary geographically in body size. The geographic variation for the genes determining size is to some extent correlated with the physiographic division of the West. The populations from the Pacific coast have genetically smaller flies than do those from the interior provinces. Experimental populations derived from the samples of seven widely separated natural populations were crossed to yield F_1 and F_2 hybrid generations. Body size in the F_1 's varied irregularly, while the F_2 's showed a consistent 'breakdown', the F_2 's being significantly smaller than their F_1 parents. The F_1 's were significantly less variable than their parents, while the F_2 's were significantly more variable than their parents of the F_1 generation. The natural populations possess coadapted genetic systems, with genes mutually adjusted by selection for favorable interactions. Recombination disrupted the balanced genic complexes to give the F_2 breakdown and the increased F_2 variability. *D. pseudoobscura* differs from *D. subobscura* in showing the effects expected in crosses between coadapted systems. This species difference lends additional support to the hypothesis that the gene pools of these two successful species respond in different ways to environmental variation. The gene pool of *D. pseudoobscura* is flexible and changes readily, while that of *D. subobscura* is relatively rigid.

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