

Saura, A. and S. Lakovaara, University of Helsinki, Finland. A study of alcohol dehydrogenase isoenzymes in *D. subobscura* and *D. obscura*.

isopropanol as substrate. We have analyzed a total of 17 strains of *D. subobscura* collected from different natural populations in SW Finland and 23 strains of *D. obscura* collected from

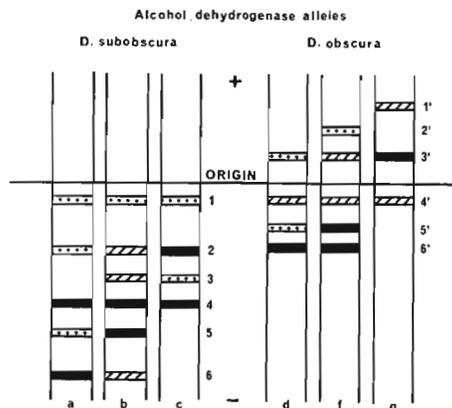
natural populations in Finland and N Norway along with strains of *D. alpina*, *D. ambigua*, *D. bifasciata*, *D. pseudoobscura* and *D. silvestris*.

The most common ADH pattern of *D. subobscura* is marked 'c' in the figure. It has two strongly staining bands at positions 2 and 4, and two very weakly staining bands at 3 and 1. The pattern 'c' has been found in all populations of *D. subobscura* studied this far, and it is identical with a pattern found in *D. alpina* and *D. pseudoobscura*. Like 'c', pattern 'a' also breeds true and it is found in two Finnish populations with pattern 'c'. The hybrid progeny of 'a' and 'c' shows the pattern 'b' (shaded bands 2, 3 and 6 are minor ones but stronger than the stippled ones.)

Patterns 'd' and 'g' appear to be identical with *D. melanogaster* Adh<sup>Slow</sup> and Adh<sup>Fast</sup>, respectively.

ADH of *D. obscura* shows two true-breeding forms 'd' and 'g', and a hybrid between these, 'f'. Pattern 'd'

is found also in *D. bifasciata* and *D. silvestris*, whereas 'g' is found in *D. ambigua*. Most Finnish populations of *D. obscura* contain all three types, only four being homozygous for 'g'. Type 'd' has not been found homozygous in any population of *D. obscura*.



Moree, R. Washington State University, Pullman, Washington. Heterozygosis and segregation ratio in *D. melanogaster*.

competitors, and in the backgrounds of both. The eight resulting combinations (three factors, two levels each) were made by using the following four strains of flies: a Canton-S strain into which Dr was introduced by 35 generations of back crossing; a wild type strain collected at Wawawai, Washington on 27 September 1964; two derived strains, one having Canton-S 2nd and Wawawai 3rd chromosomes, and the other the contrary, constructed by the use of a double balancer, SMI/Pm;TM6/D1<sup>7</sup>. The X chromosomes consist of material from the balancer, Canton-S, and Wawawai lines in about a 4:1:1 ratio. The crosses, the eight heterozygosity combinations, the total number of flies for each combination, and the percentage of Dr carriers are summarized as follows:

1) S/S;S/S x S/S;S/S <sup>0</sup>	→ S/S;S/S <sup>0</sup> and S/S;S/S	3162	47.94*
2) S/S;S/S <sup>0</sup> x W/W;S/S	→ W/S;S/S <sup>0</sup> and W/S;S/S	3082	48.51
3) S/S;S/S x S/S;W/S <sup>0</sup>	→ S/S;S/S <sup>0</sup> and S/S;W/S	2022	35.16***
4) W/W;S/S x S/S;W/S <sup>0</sup>	→ W/S;S/S <sup>0</sup> and W/S;W/S	3012	47.01**
5) S/S;W/W x S/S;W/S <sup>0</sup>	→ S/S;W/S <sup>0</sup> and S/S;W/W	2652	49.32
6) W/W;W/W x S/S;W/S <sup>0</sup>	→ W/S;W/S <sup>0</sup> and W/S;W/W	3050	48.33
7) S/S;S/S <sup>0</sup> x S/S;W/W	→ S/S;W/S <sup>0</sup> and S/S;W/S	2703	48.58
8) W/W;W/W x S/S;S/S <sup>0</sup>	→ W/S;W/S <sup>0</sup> and W/S;W/S	3186	49.27

S indicates a Canton-S chromosome, S<sup>0</sup> a Canton-S chromosome carrying Dr, and W a Wawawai chromosome. \*, \*\*, and \*\*\* indicate statistically significant deviation from 50% at the 5%, 1%, and 0.1% levels, respectively. Further X<sup>2</sup> tests show that combination 3 differs signifi-

We have recently studied the isoenzyme patterns of the *D. (Sophophora) obscura* group by means of starch and agar gel electrophoresis at pH 8.6. The flies are reared on the malt medium devised by Lakovaara (1969 DIS 44). ADH isoenzyme patterns are observed using ethanol or

cantly from all other combinations and that, aside from this, no other combination differs significantly from any other with respect to Dr carrier frequency. Sex and Drop phenotype frequencies were found to be independently distributed.

It is clear that changes in heterozygosity can change the relative viability of the Drop carriers, and hence the segregation ratio, but only under certain conditions; these conditions are summarized in the following table:

Combination	1	2	3	4	5	6	7	8
Drop type	(L:L)	(H:L)	(L:L)	(H:L)	(L:H)	(H:H)	(L:H)	(H:H)
Wild type	(L:L)	(H:L)	(L:H)	(H:H)	(L:L)	(H:L)	(L:H)	(H:H)
% Drop type	47.94*	48.51	35.16***	47.01**	49.32	48.33	48.58	49.27

For a given type and combination, in parentheses, relative heterozygosity is given as background:3rd chromosomes and may be either low (L) or high (H) for a given category, i.e., (H:L) for Drop type of combination 4.

In combination 1, Drop frequency falls significantly below 50% while in combination 2 it is intermediate between that of combination 1 and 50% without being significantly different from either; the intermediacy ostensibly relates to the increased background heterozygosity in both types. In combination 3 Drop frequency is drastically reduced; interestingly, the difference between the total heterozygosities of the two types is proportionally greater in this combination than in any other. In combination 4 Drop frequency very significantly increases relative to combination 3; the difference between the total heterozygosities of the two types is proportionally less than in combination 3 owing to the increase in background heterozygosity. Combinations 5 and 6 might reasonably be expected to give results just the opposite of those of combinations 3 and 4, but obviously do not. The wild type flies of combinations 5 and 6 have 3rd chromosomes W/W, rather than S/S, as occurs in all other combinations in which the two members of a pair are from the same strain. Third chromosomes W/W and W/S appear to be about equal as far as viability effects are concerned. Why do the S and W chromosomes differ in this respect? Canton-S is an old laboratory stock, necessarily somewhat inbred, and has probably accumulated mildly detrimental mutations that would ordinarily be eliminated by the rigors of selection in nature. Wawawai, by contrast, is a new laboratory strain taken from a natural population about five years ago. It seems possible that such a difference may characterize a fair proportion of chromosomes taken from laboratory and natural populations. It is reasonable to suppose that if Dr were transferred to a Wawawai chromosome (now under way) the viability relations  $W^0/W^0 < W^0/S > S/S$  would obtain since the carriers of  $W^0/S$  would be highly heterotic. In combinations 7 and 8 Drop frequencies are intermediate, as in combination 2; and, as in combination 2, the total heterozygosities of the two types are essentially equal in both combinations.

Excluding the apparent effect of the Drop gene (or region) and the exceptional behavior of the W/W 3rd chromosomes, the simplest consistent explanation of the results, applicable to wide deviations from the theoretical 1:1 ratio (combinations 3 and 4) and to failure to depart significantly from it (combinations 2, 5, 6, 7 and 8) may be summarized as follows:

(a) If total heterozygosities of two coexisting types tend toward equality, their frequencies tend toward equality also, whether background heterozygosity is high or low; if background heterozygosity is higher, the tendency toward equality is slightly greater (combinations 1, 2, 7, and 8, exclusive of the Dr effect).

(b) If total heterozygosities of two coexisting types are unequal, the less heterozygous type has the lower frequency; the difference is more pronounced when background heterozygosity is low, less when it is high (combinations 3 and 4).

(c) Aside from the heterozygous effect of the Dr gene (or region), differences in segregant viability are correlated with differences between the total heterozygosities of the two segregants. Genetic background is effective to the extent, and only to the extent, that it contributes to the magnitude of this difference.

(d) The results depend as much on the distribution as on the mere quantity of heterozygosity, in a given combination.

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