NATURAL SELECTION IN EXPERIMENTS WITH POPULATION INVERSIONS

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(With Three Text-figures)

Dubinin & Tiniakov (1945–6) discovered that the karyotypes of urban and rural populations of *Drosophila funebris* are different.

Dobzhansky (1943), Dubinin, Sokolov & Tiniakov (1937), and Dubinin & Tiniakov (1945) described cyclic changes in inversion frequencies during the course of the year. All these researches give evident, though indirect, proof that natural selection acts on the karyotype of populations. The work here described is the first attempt at a direct proof of this very important principle.

Dubinin & Tiniakov (1945) found that the frequency of inversions in *D. funebris* is lowest in the spring after hibernation. In summer, during the period of reproduction, this frequency rises, and it reaches its maximum when the populations are in their prime. The inversion frequency falls in the winter. It is of great interest to discover which environmental factors cause the difference between the karyotypes of urban and rural populations, and the changes in inversion frequencies with the seasonal cycle.

We have investigated the changes occurring during hibernation. The flies hibernated in veneer boxes ($30 \times 20 \times 20$ cm.) with one glass side, and a hole for ventilation in one of the other sides. Each box contained 1000–5000 flies. During the winter of 1944–5 the boxes, containing a total of 22,512 flies, were kept in a cellar at temperatures from -2 to 3° C. The populations were examined cytologically before and after hibernation, in order to observe changes in the frequency of inversions due to natural selection.

The initial populations had three inversions, II-1, II-2 and IV-1. They remained in the cold for 1, 1½ and 2½ months. Table 1 and Fig. 1 show that the mortality is very heavy, and increases with the length of hibernation, till after 2½ months only 0·56% of flies survived. Males and females survived in roughly equal numbers. Table 2 shows that in each population the frequency of individuals heterozygous for inversions II-1 diminished, while that of individuals heterozygous for IV-1 increased. The behaviour of heterozygotes for inversion II-2 is so far not clear. But it is clear that fitness, as shown by differential survival during hibernation, is increased by IV-1, and diminished by II-1.

Table 1

Population	Duration of hibernation months	Initial no.	No. of survivors ♂	♀	Total	% survivors
Samoteka, Moscow, boxes 10, 11	1	5,100	171	176	347	6·80
Samoteka, Moscow, boxes 3, 6; Ivanovo, box 2	1½	5,960	83	70	153	2·57
Ivanovo, boxes 3, 4, 5	2½	11,452	35	29	64	0·56
Total		22,512	289	275	564	2·50

It is very important that the results obtained in an experiment on hibernation agree with those on the changes of inversion frequency during the summer months. The frequency of inversion II-1 rises in summer, but falls in winter. Inversion IV-2 shows the opposite behaviour.

In this experiment the number of flies which survived hibernation and were studied cytologically is comparatively low (130). We therefore carried out a second experiment

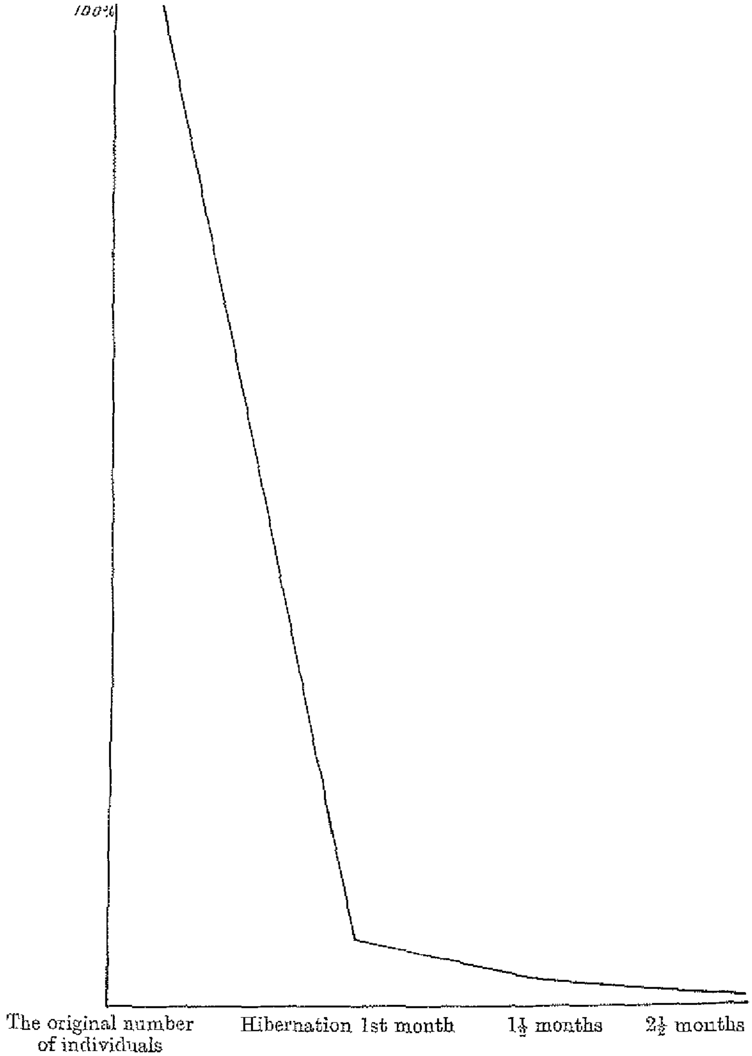

Fig. 1. Comparative viability during winter months.

Table 2

Population	Category	Non-hibernating controls No.	Non-hibernating controls %	Survivors of hibernation No.	Survivors of hibernation %
Ivanovo	Total	367	—	72	—
	Heterozygotes for inversion II-1	116	31·60	10	13·88
	,, ,, ,, II-2	6	1·63	2	2·77
	,, ,, ,, IV-1	20	5·44	6	8·31
Samoteka	Total	261	—	58	—
	Heterozygotes for inversion II-1	134	51·34	18	31·03
	,, ,, ,, II-2	70	26·93	10	17·24
	,, ,, ,, IV-1	7	2·69	13	22·41

with stocks specially bred for the purpose. One stock was homozygous for inversion II-4, another for the standard gene order, while the third was made by crossing these two, and was therefore heterozygous for the inversion. These karyotypically different categories of flies were placed in boxes under conditions of hibernation, and samples were taken after 15, 30 and 45 days. Fig. 2 and Table 3 show the results of the experiment.

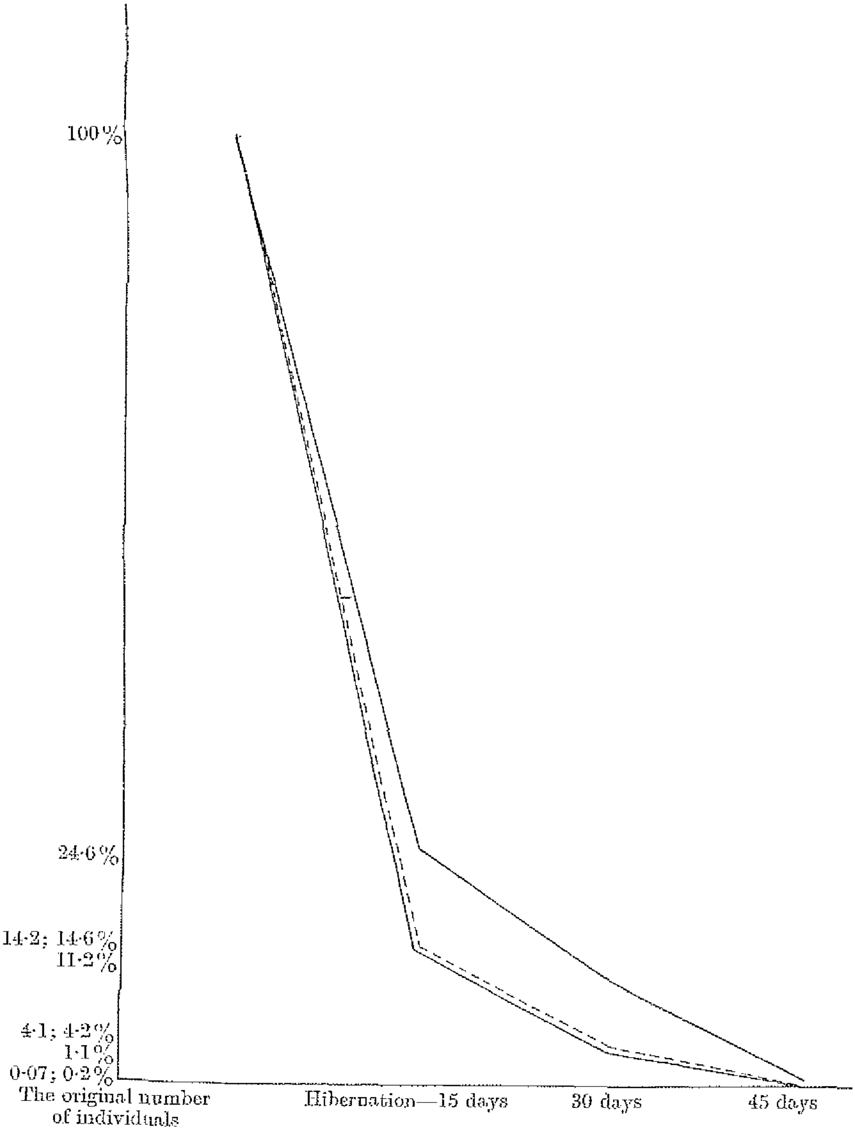

Fig. 2. Comparative viability of different genotypes during hibernation. The upper curve—the standard gene arrangement. The broken curve—homozygotes for the inversion No. 1. The lower curve—heterozygotes for the inversion No. 1.

Table 3. *Comparative survival of different karyotypes during hibernation*

Duration of hibernation days	Normal order			Heterozygotes for inversion II-1			Homozygotes for inversion II-1		
	Initial no.	No. of survivors	% survival	Initial no.	No. of survivors	% survival	Initial no.	No. of survivors	% survival
15	2000	593	24·6	2000	285	14·2	1847	270	14·1
30	3092	367	11·2	2318	94	4·1	3483	147	4·2
45	1092	12	1·1	1483	1	0·07	1471	3	0·2

The table and diagram show the enormous mortality of the flies during hibernation. Once more, and this time more clearly, we see the differential survival of different karyotypic categories. Flies with a normal karyotype survived better than either homozygotes or heterozygotes for the inversion. The degree of survival of the homozygotes and heterozygotes was equal. This speaks for the complete dominance of those genes which, being

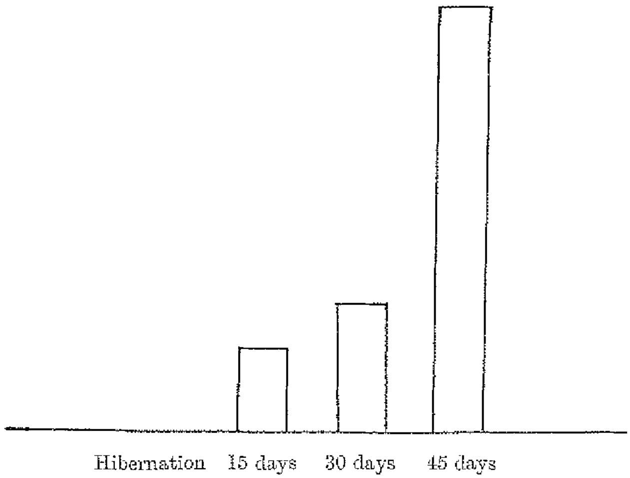

Fig. 3. The degree of viability of the normal karyotype as compared with inversions.

located in the inversion, determine their selective value. It will be very interesting to investigate the manifestation of those factors in homozygotes and heterozygotes, which determine the preferential increase of inversions in summer, and to ascertain whether they are due to a single group of genes which acquire a different selective value under different environmental conditions, or whether two different groups of factors are responsible, one for the selection in summer, the other for that in winter. Fig. 3, also derived from Table 3, shows the predominant survival of flies with a normal karyotype as compared with those with one or two chromosomes with an inverted order, as a function of length of hibernation. After 15 days the normal flies were 1·7 times as viable, after 30 days they were 2·6 times more viable, and after 45 days 8·5 times.

Conclusions

1. Our data show that the karyotypic differentiation of *Drosophila funebris* populations into urban and rural races, the diminution of inversion frequency in the towns destroyed by the war, and the changes in inversion frequencies with the months of the seasonal cycle, must all be regarded as vivid manifestations of the action of natural selection on the evolution of the karyotype.

2. Our material for the first time gives direct experimental evidence of the effect of natural selection on the karyotypic structure of populations. The experiments on hibernation show the differential survival of different karyotypic structures which are widespread in populations in nature. Different inversions react differently to the same experimental conditions.

3. This work has therefore discovered a new trend in the genetics of populations. It will become possible to apply natural selection as a method of direct experimental analysis for the solution of the several principal problems of the evolution of populations.

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