

小数派有利型淘汰と連鎖遺伝子

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ORGANIZATION OF LINKED GENES UNDER FREQUENCY-DEPENDENT SELECTION OF MINORITY ADVANTAGE

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Frequency-dependent selection is often considered to be responsible for the maintenance of a large amount of polymorphisms in natural populations (e.g. Kojima and Yarbrough 1967; Ehrman 1966).

In the present note I intend to report on the results of Monte Carlo experiments which I carried out to investigate the effects of linkage on the formation of adapted gene complex (cf. Franklin and Lewontin 1970) under the assumption of frequency-dependent selection of minority advantage at each locus. The experiments were carried out using Tosbac 3400 at the National Institute of Genetics, under the following assumption: (1) The population consists of 100 diploid individuals. (2) The number of linked loci on a chromosome is 88. (3) Recombination fraction between adjacent loci is 0.002, and there is no interference. The number of crossing-over to be produced among chromosomes in the population was calculated following Poisson distribution of mean λ . If the chromosome length is x morgan and the number of gamete in the population is y , the number of crossing-over in the population is $\lambda=xy/2$. (4) Individual fitness is determined by the multiplication of fitness values among loci, and the fitnesses of genotypes at each locus are

$$F11_i = 1 + m(0.5 - p1_i)$$

$$F12_i = 1$$

$$F22_i = 1 + m(0.5 - p2_i)$$

where $p1_i$ and $p2_i$ are respectively the frequencies of allele 1 and 2 at the i th locus, and m is the constant which specifies the intensity of selection ($0.25 \leq m \leq 1$). In this system of selection, all three genotypes have the same fitness at equilibrium. Though several experiments were performed using different values of m , the results were essentially the same. Therefore the results for the case of $m=0.5$ are reported in this paper. As the gene frequency deviates from 0.5, the difference in fitness among genotypes increases. In the simulation experiments, the gene frequencies used to determine fitnesses were obtained by surveying the gene pool of the previous generation. Therefore, the effect of gene frequency on the fitnesses lags one generation behind.

Each experiments was continued until generation 500. Starting from random combination of alleles between loci, the amount of linkage disequilibrium between adjacent loci increased substantially as the generation number increased: the squared correlation between gene frequencies of two adjacent loci was approximately 0.6 and did not appear

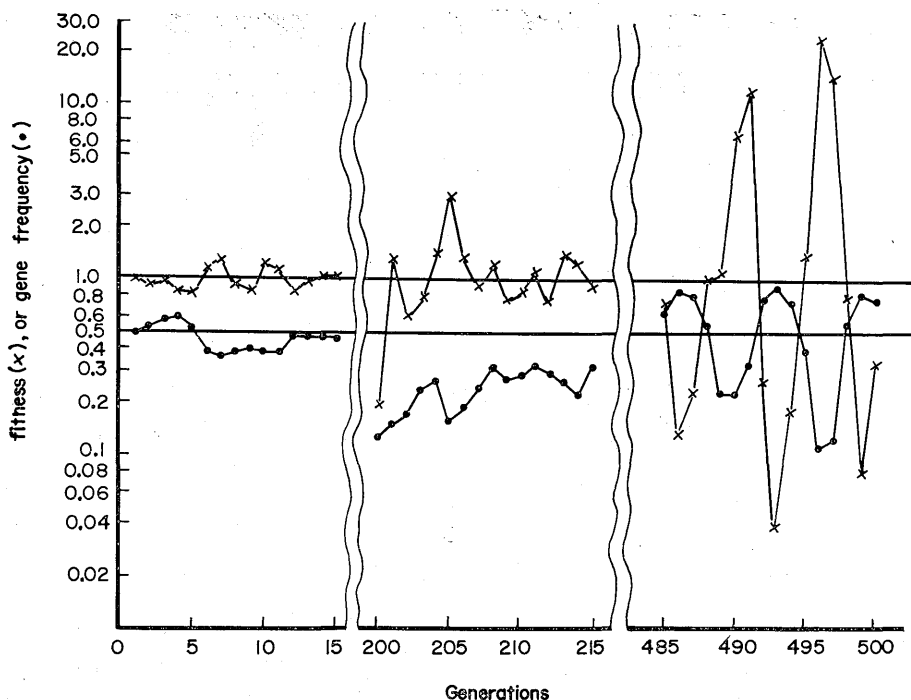


Fig. 1. Individual fitness and gene frequency at the particular locus under the assumption of frequency-dependent selection ($m=0.5$).

- indicates the frequency of allele 1 at the 45th locus from one end.
- ×— indicates the individual fitness of 1/1 genotype at the same locus.

to be at equilibrium yet at generation 500. Figure 1 and Table 1 show clearly what is happening on the organization of chromosomes as selection proceeds. Figure 1 illustrates the course of change in the frequency of allele 1 at a particular locus (45th locus from one end of a chromosome) and in the fitness of individuals whose genotype at this locus is homozygous for allele 1. We would not see strong correlation between gene frequency at the locus and fitness of an individual if allelic combinations between loci were at linkage equilibrium. In early generations neither gene frequency nor fitness fluctuated much. However, the variance among generations in fitness as well as the variance of gene frequency increased as generation increased, and a regular fluctuation with a cycle of 5-7 generations was observed. Also, a strong negative correlation between the gene frequency and the individual fitness appeared in later generations. The negative correlation means that the decrease of an allele frequency at a locus accompanies the increase of fitness of an individual. Namely, if one allele becomes a minority at a locus, genes linked to this particular allele are also minorities, and therefore a number of minority alleles gather on the same chromosome. The same situation occurs among majority alleles. This phenomenon can be generalized to other loci, though 45th locus was examined in this particular case. Allelic combinations and their frequencies (a section of chromosome) after 500 generations of selection are shown in Table 1. Although every chromosome was different from each other at the beginning

Table 1. Gametic arrays after the selection of 500 generations under the assumption of frequency-dependent selection ($m=0.5$). Only 25 out of 88 loci are shown in the table. Fixed loci are indicated by asterisks. The first three chromosomes are identical as far as the loci shown are concerned. The differences appear in the rest of chromosomes which are not shown in the table.

Frequency dependent selection ($m=0.5$)																									
locus																									
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
gene frequencies at each locus																									
67.5	67.5	67.5	67.5	32.5	67.5	55.0	45.0	87.5	45.0	32.5	45.0	0	12.5	0	17.5	17.5	17.5	82.5	17.5	45.0	45.0	45.0	45.0	55.0	chromosome frequencies
1	1	1	1	2	1	1	2	1	2	2	2	2	*	2	*	2	2	2	1	2	2	2	2	1	28.8 %
1	1	1	1	2	1	1	2	1	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	1	10.0 %
1	1	1	1	2	1	1	2	1	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	1	8.8 %
1	1	1	1	2	1	1	2	1	1	1	2	2	2	2	2	2	2	1	2	2	2	2	2	1	5.0 %
2	2	2	2	1	2	2	1	1	1	1	1	2	2	2	2	2	2	1	2	1	1	1	1	2	13.8 %
Others																									33.6 %

of experiments, the number of different chromosome types in the population decreased substantially as selection proceeded and only a few types of chromosomes dominated the population after 500 generations. The degree of complementarity of chromosomes is not so strong as in the case of overdominance (cf. Franklin and Lewontin 1970; Wills, Crenshaw, and Vitale 1970). Complementarity does not extend through the whole chromosome, but it is restricted to a segment of about ten genes which form a block. However, two main groups—majority and minority—are established as a whole. The relative frequencies of them alternated in every 5-7 generations.

The present study suggests that the formation of organized blocks of linked genes might be more common than previously considered. It will be of interest to know whether the organization effect of genes as mentioned above is prevalent in natural populations or not. Accumulation of more data concerning linkage disequilibrium in natural populations will be needed before we can make judgement on this problem.

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