The interaction of Selection and Linkage—Heterotic Models | 杂种优势模型

Nothing in Biology Makes Sense Except in the Light of Evolution. — Theodosius Dobzhansky

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Author: R.C. Lewontin, 1963

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Background | What it is?

In 1960s, we known that:

- ▶ Single loci, Selection, Population genetic change
- But two-loci or mulit-loci do not.

So the paper provide some two-loci model.

Background | What it is?

Here are results of Lewontin and Kojima:

- 1. If the fitnesses are additive between loci, linkage does not effect the final equilibrium state of the population.
- If linkage is tighter than the value demanded by the magnitude of the epistasis there may be permanent linkage disequilibrium.
- 3. The rate of genetic chagne with time is affected by the tightness of the linkage.
- 4. In some cases stable gene frequency equilibria are possible only if linkage is tight enough.

Background | What it is?

Three main modes of selection in natural and artificial populations:

- ► Heterotic Models(杂种优势)
- Series optimum selection
- Undirectional selection(Neutral Theory)

Mathematics of Selection and Linkage | What is the mean?

$$\Delta x_i = \frac{x_i \left(W_i - \overline{W}\right) - (-1)^i RDW_{12}}{\overline{W}}$$

Where,

 $W_{ij} = the \ fitness \ of \ genotype \ whose \ frequency \ is \ Z_{ij}$

$$W_i = \sum_{ij} W_{ij} x_j$$

$$\overline{W} = \sum_{i} W_{i} x_{i}$$

R is the recombination fraction between the loci.

$$D = x_0 x_3 - x_1 x_2$$

(the linkage disequilibrium determinat)

Mathematics of Selection and Linkage | What is the mean?

$$\Delta x_i = \frac{x_i \left(W_i - \overline{W}\right) - (-1)^i RDW_{12}}{\overline{W}}$$

At gene frequency equilibrium: - D=0, on linkage disequilibrium - D=/0, loss or gain of a gametic type by selection and by recombination

More locus can be expend by 2-locus equation.

Mathematics of Selection and Linkage | What is the mean?

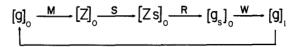


Figure 2.—The genetic transformation, T, broken up into its components during a single generation.

These operations are easy to perform in computer.

Heterotic Selection Model | How to representate?

Evidence:

Heterosis is important, then

 $degree\ of\ heterosis = f(number\ of\ heterozygosity)$

Hypothesis:

Epistatic(异位显性) ==> interaction of linkage and selection

Model to Test

- ► Two-locus model
- ► Five-locus model

Heterotic Selection Model | How to representate?

TABLE 3

Relative fitnesses of the nine genotypes for two-locus heterotic models

	AA	Aa	aa
BB	.40	.60	.30
Bb	.60	1.00	.50
bb	.50	.70	.40
o) Model 2: asymmetric p	eartially heterotic mode	el with epistasis	
BB	.5000	.5000	.3750
Bb	.5625	1.0000	.3125
bb	.3750	.4375	.3750
c) Model 3: mixed overdo	minance, underdomina	nce model	
BB	.90	$\overset{Aa}{.20}$.90
Bb	.20	1.00	.20
bb	.90	.20	.90

Figure 1: Relative fitness for two-locus heterotic models

Heterotic Selection Model | How to represent?

TABLE 4

Results of Model 1. Symbols are as explained in the text

R	g_{00}	g_{01}	g_{10}	g_{11}	p	r	D	D'	\overline{W}
.00	.50000	.00000	.00000	.50000	.50000	.50000	+.25000	+1.00000	.70000
	.00000	.58333	.41667	.00000	.58333	.41667	24306	-1.00000	.70836
.01	.46225	.05195	.01777	.46805	.51420	.48002	+.21543	+.92384	.69014
	.02359	.55936	.38914	.02791	.58295	.41273	21700	90191	.70378
.02	.42023	.10875	.03871	.43231	.52898	.45894	+.17746	+.82093	.68044
	.04984	.53246	.35855	.05915	.58230	.40839	18797	79042	.68902
.03	.37049	.17398	.06621	.38932	.54447	.43670	+.13272	+.66717	.67088
	.08051	.50089	.32332	.09528	.58140	.40383	15449	65799	.67950
.04									
	.11793	.46211	.28148	.13848	.58004	.39941	11374	49096	.67038
.06									
	.20082	.37418	.19621	.22879	.57500	.39703	02747	12033	.65954
.08									
	.21773	.35566	.18039	.24622	.57339	.39819	01054	04616	.65882
.10									
	.22172	.35125	.17676	.25032	.57297	.39848	00659	02886	.65878
.30									
	.22703	.34539	.17195	.25563	.57242	.39898	00135	00591	.65862
.50									
	.22766	.34473	.17141	.25620	.57239	.39907	00076	00327	.65862

Figure 2: Posults of Model1

Heterotic Selection Model | How to represent?

TABLE 10

Results of five-locus experiments in Drosophila melanogaster with genes se, ss, k, e and ro. Data of Dr. Grace B. Cannon

		Population and week									
		Population 20			Population 21			Population 22			
		0	28	50	0	28	50	0	28	50	
(a) Ger	ne freq	uencies									
se		.007	.102	.058	.007	.044	.073	.005	.026	.037	
SS		.012	.052	.216	.012	.078	.203	.009	.106	.186	
k		.012	.026	.200	.012	.100	.177	.009	.092	.175	
e		.012	.013	.174	.012	.133	.219	.009	.106	.181	
ro		.007	.064	.084	.007	.066	.094	.005	.026	.048	
(b) D a	and D'	values									
ss-k	D	+ .0247 +.1408			+.0610 +.1166			+.0693 +.1328			
	D'	-	-1.0000	+.8980		+.6616	+.8265		+.8426	+.932	
k-e	D	_	0003	+.1182		+.0781	+.1231		+.0823		
	D'	-	-1.0000	÷.8491	+.9008 +.8905			+1.0000 + .818			
ss-e	D	-	0123	+.1154		+.0588	+.0907		+.0810		
	D'	-	-1.0000	+.8459		+.8695	+.5721		+.8547		

Figure 3: Results of five-locus experiments

What about the following and question?

- ▶ Epistasis(异位显性) is required in order for linkage to be important in natural selection.
- ► Five-locus models show *cumulative* effect of the linkage along the chromosome.