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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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.
2. 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**
- 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.

$$
\begin{tikzcd}
{[g]_0} \arrow[r, "M"] & {[Z]_0} \arrow[r, "S"] & {[Zs]_0} \arrow[r, "R"] & {[g_s]_0} \arrow[r, "W"] & {[g]_1} \arrow[llll, bend left]
\end{tikzcd}
$$

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 $==>$ 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

(a) Model 1: asymmetric heterotic model with epistasis

	AA	*Aa*	*aa*
BB	.40	.60	.30
Bb	.60	1.00	.50
bb	.50	.70	.40

(b) Model 2: asymmetric partially heterotic model with epistasis

	AA	*Aa*	*aa*
BB	.5000	.5000	.3750
Bb	.5625	1.0000	.3125
bb	.3750	.4375	.3750

(c) Model 3: mixed overdominance, underdominance model

	AA	*Aa*	*aa*
BB	.90	.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: Results 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) Gene frequencies										
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* and *D′* values										
ss–k	*D*		+ .0247	+.1408		+.0610	+.1166		+.0693	+.1328
	D′		+1.0000	+.8980		+.6616	+.8265		+.8426	+.9323
k–e	*D*		− .0003	+.1182		+.0781	+.1231		+.0823	+.1173
	D′		−1.0000	+.8491		+.9008	+.8905		+1.0000	+.8184
ss–e	*D*		+ .0123	+.1154		+.0588	+.0907		+.0810	+.1039
	D′		+1.0000	+.8459		+.8695	+.5721		+.8547	+.7052

Figure 3: Results of five-locus experiments

What about the following and question?

- Epistasis is required in order for linkage to be important in natural selection.
- Five-locus models show *cumulative* effect of the linkage along the chromosome.