

# The interaction of Selection and Linkage—Heterotic Models |

*Presentor: Yuejian Mo*

*Author : R.C. Lewontin, 1963*

*2018.06.11 @ SUSTech*

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

## 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.  
*(need picture)*

## 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
- ▶ Unidirectional selection(Neutral Theory)  
*(need picture)*

# Mathematics of Selection and Linkage | What is the mean?

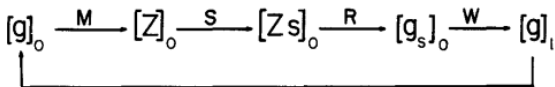


FIGURE 2.—The genetic transformation,  $T$ , broken up into its components during a single generation.

Figure 1: The genetic transformation  $T$

# Heterotic Selection Model | How to represent?

## Evidence:

Heterosis is important, then

$$\text{degree of heterosis} = f(\text{number of heterozygosity})$$

## Hypothesis:

Epistatic( )  $\implies$  interaction of linkage and selection

## Test

- ▶ Two-locus model
- ▶ Five-locus model

# Heterotic Selection Model | How to represent?

TABLE 3

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

|                                                                  |           |           |           |
|------------------------------------------------------------------|-----------|-----------|-----------|
| (a) Model 1: asymmetric heterotic model with epistasis           |           |           |           |
|                                                                  | <i>AA</i> | <i>Aa</i> | <i>aa</i> |
| <i>BB</i>                                                        | .40       | .60       | .30       |
| <i>Bb</i>                                                        | .60       | 1.00      | .50       |
| <i>bb</i>                                                        | .50       | .70       | .40       |
| (b) Model 2: asymmetric partially heterotic model with epistasis |           |           |           |
|                                                                  | <i>AA</i> | <i>Aa</i> | <i>aa</i> |
| <i>BB</i>                                                        | .5000     | .5000     | .3750     |
| <i>Bb</i>                                                        | .5625     | 1.0000    | .3125     |
| <i>bb</i>                                                        | .3750     | .4375     | .3750     |
| (c) Model 3: mixed overdominance, underdominance model           |           |           |           |
|                                                                  | <i>AA</i> | <i>Aa</i> | <i>aa</i> |
| <i>BB</i>                                                        | .90       | .20       | .90       |
| <i>Bb</i>                                                        | .20       | 1.00      | .20       |
| <i>bb</i>                                                        | .90       | .20       | .90       |

Figure 2: 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*

| $R$ | $g_{00}$ | $g_{01}$ | $g_{10}$ | $g_{11}$ | $p$    | $r$    | $D$     | $D'$     | $\bar{W}$ |
|-----|----------|----------|----------|----------|--------|--------|---------|----------|-----------|
| .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 3: 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              |                     |      |       |               |       |       |               |       |       |       |       |   |       |        |       |       |
| <i>se</i>                         | .007                | .102 | .058  | .007          | .044  | .073  | .005          | .026  | .037  |       |       |   |       |        |       |       |
| <i>ss</i>                         | .012                | .052 | .216  | .012          | .078  | .203  | .009          | .106  | .186  |       |       |   |       |        |       |       |
| <i>k</i>                          | .012                | .026 | .200  | .012          | .100  | .177  | .009          | .092  | .175  |       |       |   |       |        |       |       |
| <i>e</i>                          | .012                | .013 | .174  | .012          | .133  | .219  | .009          | .106  | .181  |       |       |   |       |        |       |       |
| <i>ro</i>                         | .007                | .064 | .084  | .007          | .066  | .094  | .005          | .026  | .048  |       |       |   |       |        |       |       |
| (b) <i>D</i> and <i>D'</i> values |                     |      |       |               |       |       |               |       |       |       |       |   |       |        |       |       |
| <i>ss-k</i>                       | <i>D</i>            | +    | .0247 | +             | .1408 |       | +             | .0610 | +     | .1166 |       | + | .0693 | +      | .1328 |       |
|                                   | <i>D'</i>           |      | +     | 1.0000        | +     | .8980 |               | +     | .6616 | +     | .8265 |   | +     | .8426  | +     | .9323 |
| <i>k-e</i>                        | <i>D</i>            | -    | .0003 | +             | .1182 |       | +             | .0781 | +     | .1231 |       | + | .0823 | +      | .1173 |       |
|                                   | <i>D'</i>           |      | -     | 1.0000        | +     | .8491 |               | +     | .9008 | +     | .8905 |   | +     | 1.0000 | +     | .8184 |
| <i>ss-e</i>                       | <i>D</i>            | +    | .0123 | +             | .1154 |       | +             | .0588 | +     | .0907 |       | + | .0810 | +      | .1039 |       |
|                                   | <i>D'</i>           |      | +     | 1.0000        | +     | .8459 |               | +     | .8695 | +     | .5721 |   | +     | .8547  | +     | .7052 |

Figure 4: 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.