

"SURFACES" OF SELECTIVE VALUE*

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There have been many recent papers on evolutionary change in systems of interacting loci. Because of nonrandom combination, it has been necessary to use electronic computers in all but the simplest cases. If, however, the selective differences among genotypes are as small as seems usually to be the case in natural variability and the loci are in different chromosomes, as is usual in organisms with typical numbers, or even if they are loosely linked, useful approximations may be obtained by ignoring the small departures from random combination.

Formulae under Random Combination.—Under random combination, the genotypic frequency is by definition the product of the frequencies of the component genes, with doubling for each heterozygous locus. Under this assumption, the rate of change of a gene frequency p_x per generation is given¹ in terms of frequencies f_i and relative selective values w_i of genotypes by:

$$\Delta p_x = p_x(1 - p_x) \Sigma \left[w_i \frac{\partial f_i}{\partial p_x} \right] / 2\bar{w}. \quad (1)$$

In evaluating where there are multiple alleles²

$$\frac{\partial p_i}{\partial p_x} = -p_i / (1 - p_x). \quad (2)$$

We will deal here only with cases in which the selective values of genotypes are independent of their frequencies, under which³

$$\Delta p_x = p_x(1 - p_x) \frac{\partial \bar{w}}{\partial p_x} / 2\bar{w}. \quad (3)$$

Effect of Departure from Random Combination, a Simple Case.—The departure at metastable equilibrium of two-factor gametic frequencies from random combination was given many years ago^{4, 5} in a simple but important type of extreme interaction in which the optimum is at the midpoint of the scale.

Genotype	Grade	w
<i>AABB</i>	$M + 2\alpha$	$1 - 4s$
<i>AABb, AaBB</i>	$M + \alpha$	$1 - s$
<i>AAbb, AaBb, aaBB</i>	M	1
<i>Aabb, aaBb</i>	$M - \alpha$	$1 - s$
<i>aabb</i>	$M - 2\alpha$	$1 - 4s$

Homallelic *AAbb* and *aaBB* are both at the intermediate optimum and thus are at separate "selective peaks" (1,0) and (0,1) with respect to the gene frequencies p and q . The extremes, *aabb* and *AABB*, are in "selective pits" (0,0) and (1,1), respectively. There is metastable equilibrium at the "saddle" (0.5,0.5). Letting c be the amount of recombination in double heterozygotes, the equation expressing the lack of change in frequencies f_{Ab} and f_{aB} of the balanced gametes and in those

of the unbalanced gametes, f_{AB} and f_{ab} , is easily found at metastable equilibrium, at which $f_{aB} = f_{Ab}$ and $f_{ab} = f_{AB} = (1/2) - f_{Ab}$.

$$8sf_{Ab}^2 - 4(s - c)f_{Ab} - c = 0, \quad (4)$$

$$f_{Ab} = f_{aB} = [s - c + \sqrt{s^2 + c^2}]/4s \approx (1/4)(1 + s/2c) \quad \text{if } s \ll c, \quad (5)$$

$$f_{AB} = f_{ab} = [s + c - \sqrt{s^2 + c^2}]/4s \approx (1/4)(1 - s/2c) \quad \text{if } s \ll c, \quad (6)$$

$$\bar{w} = 1 - 4sf_{AB}.$$

Extension has been made to three equally spaced loci.⁶

A somewhat more general case, t for the selective disadvantage of $AABB$ and of $aabb$ and supplementation by additive heterosis h_1 and h_2 , at the loci, has been presented^{5, 6} and confirmed from a different viewpoint.⁷ The equation for gametic frequency f_{Ab} at equilibrium (metastable or stable) becomes

$$8(4s - t)f_{Ab}^3 - 8(3s - t)f_{Ab}^2 + 2(2s - t + 2c')f_{Ab} - c' = 0, \quad (7)$$

where $c' = c(1 + h_1 + h_2)$.

General Equations for Two Pairs of Alleles.—The general equations for rates of change of gametic frequencies in the case of two pairs of alleles were given by Kimura⁸ for continuously reproducing populations. The closely similar discrete rates per generation were given by Lewontin and Kojima.⁹

$$\left. \begin{aligned} \Delta f_{AB} &= [f_{AB}(w_{AB} - \bar{w}) - cDw_{AaBb}]/\bar{w} \\ \Delta f_{Ab} &= [f_{Ab}(w_{Ab} - \bar{w}) + cDw_{AaBb}]/\bar{w} \\ \Delta f_{aB} &= [f_{aB}(w_{aB} - \bar{w}) + cDw_{AaBb}]/\bar{w} \\ \Delta f_{ab} &= [f_{ab}(w_{ab} - \bar{w}) - cDw_{AaBb}]/\bar{w} \end{aligned} \right\} \quad (8)$$

where $D = f_{AB}f_{ab} - f_{Ab}f_{aB}$ measures departure from random combination.

$$w_{AB} = f_{AB}w_{AB/AB} + f_{Ab}w_{AB/Ab} + f_{aB}w_{AB/aB} + f_{ab}w_{AB/ab}, \text{ etc.}$$

$$\bar{w} = f_{AB}w_{AB} + f_{Ab}w_{Ab} + f_{aB}w_{aB} + f_{ab}w_{ab}.$$

Quasi-Equilibrium.—Kimura¹⁰ has shown that the ratio $R = f_{AB}f_{ab}/f_{Ab}f_{aB}$ approaches constancy, "quasi-equilibrium," during the evolution of systems under widely occurring conditions. It is convenient to use symbols that make R greater than 1 as far as practicable.

$$\Delta \log R \approx \frac{\Delta f_{AB}}{f_{AB}} - \frac{\Delta f_{Ab}}{f_{Ab}} - \frac{\Delta f_{aB}}{f_{aB}} + \frac{\Delta f_{ab}}{f_{ab}}, \quad (9)$$

$$w \Delta \log R \approx [w_{AB} - w_{Ab} - w_{aB} + w_{ab}] - cDw_{AaBb} \left(\frac{1}{f_{AB}} + \frac{1}{f_{Ab}} + \frac{1}{f_{aB}} + \frac{1}{f_{ab}} \right). \quad (10)$$

In a haploid population, $[w_{AB} - w_{Ab} - w_{aB} + w_{ab}]$ is a measure of the interactive

selection, s_I . In the diploid case, it requires four coefficients, each related to one of the four kinds of gametes.

$$s_{I(AB)} = w_{AB/AB} - w_{AB/Ab} - w_{AB/aB} + w_{AB/ab}, \text{ etc.}, \quad (11)$$

$$\bar{s}_I = f_{AB}\bar{s}_{I(AB)} + f_{Ab}\bar{s}_{I(Ab)} + f_{aB}\bar{s}_{I(aB)} + f_{ab}\bar{s}_{I(ab)}, \quad (12)$$

$$\bar{w} \Delta \log R \approx \bar{s}_I - cW_{AaBb} f_{Ab} f_{aB} (R - 1) \left(\frac{1}{f_{AB}} + \frac{1}{f_{Ab}} + \frac{1}{f_{aB}} + \frac{1}{f_{ab}} \right). \quad (13)$$

Kimura showed that with small selective differences and loose, if any, linkage, R changes so little in a single generation that $\bar{w} \Delta \log R$ may be treated as zero to obtain a useful approximate result. He gave a number of examples, calculated through hundreds of generations by electronic computer, in which R approached constancy. He also illustrated the failure of the principle where moderately great interactive selection is associated with very tight linkage and R increased without limit as fixation of one of the genotypes was approached.

It is convenient to let $x = R - 1$, and use $K = \bar{s}_I/cW_{AaBb}$ as an index that expresses the relation between interactive selection and recombination where the term $w \Delta \log R$ is negligible.

$$x^2 (f_{Ab} + f_{aB}) + x (1 - K) - K = 0.$$

If $\bar{w} \Delta \log R$ is not negligible in comparison with \bar{s}_I , it is possible to make provisional estimates and redefine K as $(\bar{s}_I - \bar{w} \Delta \log R)/cW_{AaBb}$ in the iteration process of solution:

$$x = [\sqrt{(1 - K)^2 + 4K(f_{Ab} + f_{aB})} - (1 - K)]/[2(f_{Ab} + f_{aB})]. \quad (14)$$

If K is always small, x is approximately $K/(1 - K)$, R is never much larger than 1 and sufficiently uniform that $\bar{w} \Delta \log R$ is unimportant, and there is consequently quasi-equilibrium in Kimura's sense. But even if K approaches 1, and R becomes indefinitely large as p approaches 0 or 1, there may be quasi-equilibrium in a broader sense.

The Quasi-Equilibrium Surface of Mean Selective Values.—The system of gametic frequencies in the case of pairs of alleles can be represented by points in an equilateral tetrahedron of unit height, to each of which a mean selective value can be assigned. Assuming that gametic frequencies change only slowly and K is not too large, there is a surface within this space, bounded by the edges $ab - Ab$, $Ab - AB$, $AB - aB$, and $aB - ab$, on which $\bar{w} \Delta \log R$ is less than for points on each side. Populations on this surface move along it in quasi-equilibrium, in a broad sense, even though R may change greatly with the changes in the set of gene frequencies.

If there is symmetry of the selective values about the line $q = p$, the gametic frequencies and the mean selective values along this line can readily be calculated. We will consider cases in which the selective peak or peaks are on this line. These values, in conjunction with those of homallelic $AAbb$ and $aaBB$, indicate fairly well the nature of the surface.

Along the line $q = p$, $f_{aB} = f_{Ab}$, $f_{AB} = p - f_{Ab}$, and $f_{ab} = 1 - p - f_{Ab}$,

$$R = 1 + x = (p - f_{Ab})(1 - p - f_{Ab})/f_{Ab}^2, \quad (15)$$

$$xf_{Ab}^2 + f_{Ab} - p(1 - p) = 0, \quad (16)$$

$$f_{Ab} = [\sqrt{1 + 4p(1 - p)x} - 1]/2x, \quad (17)$$

$$R - 1 = x = [\sqrt{(1 - K)^2 + 8Kf_{Ab}} - (1 - K)]/4f_{Ab} \text{ from (14)}. \quad (18)$$

The gametic frequencies and the values of K (if not constant), of R , and of w can be found by iteration of equations (17), (12) if necessary, and (18) for each desired value of $q = p$ for systems with given selective values w and given amounts of recombination for comparison with those given under the assumption of random combination ($R = 1$).

The following systems of constant genotypic values ($aabb$ at lower left, $AABB$ at upper right) will be considered.

I ($\bar{s}_I = 0.20$)			II ($\bar{s}_I = 0.20$)			III ($\bar{s}_I = 0.15$)			IV		
0.6	0.9	1	0.6	1.1	1	0.75	1	1.10	1	1	1
0.9	1	0.9	1.1	1.	41.1	0.95	1.05	1	1	1.25	1
1	0.9	0.6	1	1.	10.6	1	0.95	0.75	1	1	1
V			VI			VII ($\bar{s}_I = 0.25$)					
0.81	1	0.97	0.64	1	0.96	1	1.50	2			
1	1.03	1	1	1.05	1	1	1.25	1.50			
0.97	1	0.81	0.94	1	0.64	1	1	1			

Case I, symmetrical about both diagonals, is of the sort in which there is an optimum at the midpoint of the phenotypic scale, discussed above, but here with exchange of B and b . Case II is the same except for a bonus (0.2) for heterosis at each locus. Case III is somewhat like case I except that the selective peaks are unequal. In each of these three cases, the interactive selection is uniform. Case IV is a simple example of nonadditive heterosis. The interactive selection is variable (± 0.25 in the four corners) so that \bar{s}_I must be calculated for each p in the iteration process. It is a special case of a type discussed by Lewontin and Kojima.⁹ Cases V and VI were presented in a previous paper¹¹ to illustrate the possibility of two selective peaks that may be heterallelic at both loci. In both, \bar{s}_I varies. In VII, as in cases considered by Felsenstein,¹² mean selective value rises toward one extreme, but does so nonlinearly. Interactive selection is uniform.

Calculations for $c = 0.5$ and 0.2 were made, first treating $w \Delta \log R$ as negligible. Having estimated R for each value of p , at intervals of 0.1 , this term was estimated in each case from the formula $w \Delta p (d \log R / dp)$ in which

$$w \Delta p = [f_{AB}w_{AB} + f_{Ab}w_{Ab} - p\bar{w}].$$

The sums of the nine absolute estimates of $w \Delta \log R$ and of \bar{s}_I and the ratios are given in Table 1. The largest ratios are in case IV but involve only trivial deviation of w from its value under random combination. Of more interest is case I with relatively large deviations of w . Recalculations were made in these cases using $K = (\bar{s}_I - w \Delta \log R) / cW_{AaBb}$. The changes were trivial except for R in a few cases.

Tables 2 and 3 give the quantities indicated in the headings, using the recalculations where made.

Figure 1 shows the values of w for $c = 0.5, 0.2$, and 0 in cases I to VI in solid lines,

TABLE 1
RATIO OF THE TERM $\bar{w}\Delta \log R$ TO \bar{s}_I

Case	$c = 0.5$			$c = 0.2$		
	$\Sigma \bar{w} \Delta \log R $	$\Sigma \bar{s}_I $	Ratio	$\Sigma \bar{w}\Delta \log R $	$\Sigma \bar{s}_I $	Ratio
I	0.012	1.80	0.007	0.058	1.80	0.032
II	0.006	1.80	0.004	0.054	1.80	0.030
III	0.004	1.35	0.003	0.027	1.35	0.020
IV	0.043	0.62	0.068	0.129	0.66	0.193
V	0.002	0.51	0.031	0.004	0.49	0.009
VI	0.005	0.97	0.005	0.014	0.91	0.015
VII	0.060	2.25	0.027	—	—	—

for comparison with those under the assumption of random combination (broken lines). The latter are all outside the range of true values ($c = 0.5$ to $c = 0$) except at the extreme values of p , and at $p = 0.5$, in case IV.

In cases I to III, the curves represent \bar{w} along a ridge on the quasi-equilibrium surface ($aabb$ to $AABB$) between deep depressions at $AAbb$ and $aaBB$. The curves for $c = 0.5$ differ little from the approximation shown by the broken line. That for the curve on the surface at right angles to this, passing through the same value at $(0.5,0.5)$, can differ little from the approximation. Even with $c = 0.2$ there is rough approximation. The values for \bar{w} at $q = p = 0.5, c = 0.10, 0.05, 0.02,$ and 0.01 are shown by dots in cases I and II (formula 5).

In case IV, the true curves, even for $c = 0.2$, differ very little from the approximation, there being no difference at $(0.5,0.5)$.

Case V has the smallest selective differences and the least interactive selection on the average. The shallow saddle between heterallelic peaks is, however, close to the

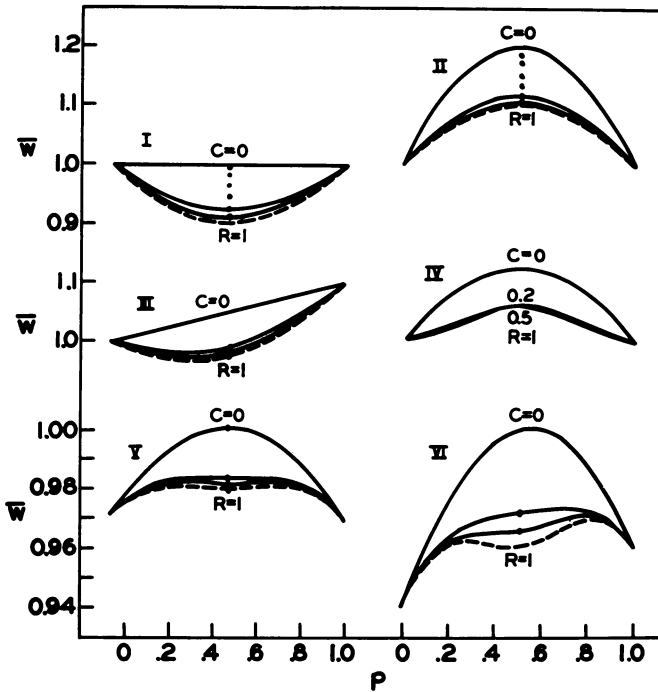


FIG. 1.—Mean selective values \bar{w} on the surface between $aabb$ and $AABB$ in six two-factor systems as described in the text.

TABLE
DATA ON THE QUASI-EQUILIBRIUM SURFACES OF MEAN SELECTIVE VALUE

Case	$R = 1$						
	p	f_{Ab}	$q = \frac{p}{\bar{w}}$	Δp	$q = \frac{1-p}{\bar{w}-p}$	$c = 0.5$	
						f_{Ab}	\bar{w}
I	0	0	1.000	0	0.600	0	1.000
	0.1	0.09	0.964	-0.0075	0.708	0.086	0.966
	0.2	0.16	0.936	-0.0103	0.792	0.148	0.941
	0.3	0.21	0.916	-0.0092	0.852	0.192	0.923
	0.4	0.24	0.904	-0.0053	0.888	0.217	0.913
	0.5	0.25	0.900	0	0.900	0.225	0.910
II	0	0	1.000	0	0.600	0	1.000
	0.1	0.09	1.036	+0.0069	0.780	0.087	1.037
	0.2	0.16	1.064	+0.0090	0.920	0.152	1.067
	0.3	0.21	1.084	+0.0077	1.020	0.197	1.089
	0.4	0.24	1.096	+0.0044	1.080	0.223	1.103
	0.5	0.25	1.100	0	1.100	0.232	1.107
III	0	0	1.000	0	0.750	0	1.000
	0.1	0.09	0.983	-0.0032	0.831	0.087	0.984
	0.2	0.16	0.972	-0.0033	0.894	0.152	0.974
	0.3	0.21	0.967	-0.0011	0.939	0.197	0.971
	0.4	0.24	0.968	+0.0025	0.966	0.223	0.973
	0.5	0.25	0.975	+0.0063	0.975	0.232	0.980
	0.6	0.24	0.988	+0.0097	0.966	0.223	0.993
	0.7	0.21	1.007	+0.0115	0.939	0.197	1.011
	0.8	0.16	1.032	+0.0109	0.894	0.152	1.034
	0.9	0.09	1.063	+0.0072	0.831	0.087	1.064
1.0	0	1.100	0	0.750	0	1.100	
IV	0	0	1.000	0	1.000	0	1.000
	0.1	0.09	1.008	+0.0032	1.008	0.087	1.009
	0.2	0.16	1.026	+0.0075	1.026	0.156	1.026
	0.3	0.21	1.044	+0.0084	1.044	0.206	1.044
	0.4	0.24	1.058	+0.0054	1.058	0.239	1.058
	0.5	0.25	1.063	0	1.063	0.250	1.063
V	0	0	0.970	0	0.810	0	0.970
	0.1	0.09	0.978	+0.0011	0.876	0.090	0.978
	0.2	0.16	0.981	+0.0004	0.923	0.157	0.981
	0.3	0.21	0.981	-0.0003	0.955	0.204	0.982
	0.4	0.24	0.980	-0.0004	0.974	0.232	0.982
	0.5	0.25	0.980	0	0.980	0.241	0.981
VI	0	0	0.940	0	0.640	0	0.940
	0.1	0.09	0.956	+0.0024	0.765	0.089	0.956
	0.2	0.16	0.962	+0.0009	0.855	0.155	0.963
	0.3	0.21	0.962	-0.0005	0.915	0.200	0.965
	0.4	0.24	0.961	-0.0005	0.950	0.225	0.966
	0.5	0.25	0.961	0	0.961	0.233	0.966
	0.6	0.24	0.963	+0.0019	0.950	0.224	0.968
	0.7	0.21	0.967	+0.0021	0.915	0.199	0.970
	0.8	0.16	0.970	+0.0008	0.853	0.155	0.971
	0.9	0.09	0.970	-0.0010	0.765	0.089	0.970
1.0	0	0.960	0	0.640	0	0.960	

threshold, and disappears by coalescence of the peaks if $c = 0.2$. Case VI with unequal peaks is even more sensitive, in spite of greater selective differences. There is loss of the saddle if $c = 0.50$, as brought out in a computer study by Jain and Allard.¹³ The saddle would persist, however, if selective differences from W_{AaBb} were less than one third as great.

In case VII, the deviation of \bar{w} , $c = 0.5$, from that under random combination would be barely perceptible in a figure of the scale of the others in spite of the large uniform value of K (0.40). The approximation under random combination falls outside the true range, however, by about 11 per cent at $p = 0.5$ (less elsewhere), which is somewhat similar to other cases.

In all of these cases, the calculation of \bar{w} under the assumption of random com-

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\bar{w} IN SIX CASES OF INTERACTING LOCI, $R = 1$, $c = 0.5, 0.2$, OR 0

$c = 0.5$		$c = 0.2$				$c = 0$
R	K	f_{Ab}	\bar{w}	R	K	$f_{Ab} = 0$ \bar{w}
1.67	0.400	0	1.000	∞	1.000	1.000
1.57	"	0.077	0.969	3.24	"	"
1.53	"	0.129	0.948	2.84	"	"
1.50	"	0.164	0.935	2.70	"	"
1.49	"	0.184	0.926	2.64	"	"
1.49	"	0.191	0.924	2.62	"	"
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1.40	0.286	0	1.000	2.50	0.714	1.000
1.37	"	0.081	1.040	2.40	"	1.072
1.35	"	0.138	1.073	2.17	"	1.128
1.34	"	0.177	1.097	2.07	"	1.168
1.33	"	0.199	1.112	2.03	"	1.192
1.33	"	0.207	1.117	2.01	"	1.200
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1.40	0.286	0	1.000	2.50	0.714	1.000
1.37	"	0.081	0.986	2.40	"	1.010
1.35	"	0.138	0.979	2.17	"	1.020
1.34	"	0.177	0.977	2.07	"	1.030
1.33	"	0.199	0.980	2.03	"	1.040
1.33	"	0.207	0.988	2.01	"	1.050
1.33	"	0.199	1.000	2.03	"	1.060
1.34	"	0.177	1.017	2.07	"	1.070
1.35	"	0.138	1.039	2.17	"	1.080
1.37	"	0.081	1.066	2.40	"	1.090
1.40	"	0	1.100	2.50	"	1.100
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1.67	0.400	0	1.000	∞	1.000	1.000
1.34	0.268	0.081	1.011	2.43	0.723	1.045
1.18	0.164	0.145	1.029	1.73	0.513	1.080
1.08	0.080	0.196	1.045	1.35	0.295	1.105
1.02	0.022	0.235	1.058	1.09	0.088	1.120
1.00	0	0.250	1.063	1.00	0	1.125
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1.00	0	0	0.970	1.00	0	0.970
1.06	0.056	0.089	0.978	1.16	0.138	0.981
1.11	0.098	0.153	0.982	1.28	0.238	0.989
1.14	0.127	0.196	0.983	1.36	0.305	0.995
1.16	0.144	0.220	0.983	1.41	0.342	0.999
1.16	0.149	0.228	0.983	1.42	0.354	1.000
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0.98	-0.019	0	0.940	0.95	-0.048	0.940
1.10	0.090	0.088	0.957	1.27	0.222	0.960
1.19	0.172	0.148	0.964	1.54	0.409	0.976
1.26	0.228	0.185	0.968	1.72	0.528	0.988
1.30	0.262	0.206	0.971	1.81	0.598	0.996
1.32	0.275	0.212	0.972	1.85	0.625	1.000
1.31	0.269	0.205	0.973	1.84	0.614	1.000
1.28	0.243	0.184	0.974	1.78	0.562	0.996
1.22	0.194	0.146	0.973	1.64	0.461	0.988
1.13	0.120	0.087	0.970	1.38	0.295	0.976
1.02	0.019	0	0.960	1.05	0.048	0.960

bination gives a good first-order approximation to the nature of the quasi-equilibrium surface for $c = 0.5$, except where a feature is close to the threshold. From the results for $c = 0.2$, it appears that rough approximations can be obtained up to values of K of at least 0.5, and that allowance for deviations from random combination is hardly necessary for this purpose where K is 0.05 or less. A number of cases in which there is frequency dependence of selective value have given similar results.

The concept of a multidimensional "surface" of mean selective values on which a population moves toward the immediately controlling peak (except as diverted by the other systematic pressures, recurrent mutation, and immigration, and by random processes) was developed¹⁴ for natural populations, assumed to have been

TABLE 3
DATA ON THE QUASI-EQUILIBRIUM SURFACE OF MEAN SELECTIVE VALUE
 \bar{w} IN CASE VII FOR $R = 1$, $c = 0.5$, AND $c = 0$

p	f_{Ab}	$R = 1$			$c = 0.5$				$c = 0$
		$q = \frac{p}{\bar{w}}$	Δp	$q = \frac{1-p}{\bar{w}}$	f_{Ab}	\bar{w}	R	K	$f_{Ab} = 0$ \bar{w}
0	0	1.000	0	1.000	0	1.000	1.67	0.400	1.000
0.1	0.09	1.010	+0.0045	1.090	0.086	1.012	1.57	"	1.055
0.2	0.16	1.040	+0.0160	1.160	0.148	1.046	1.53	"	1.120
0.3	0.21	1.090	+0.0318	1.210	0.192	1.099	1.50	"	1.195
0.4	0.24	1.160	+0.0493	1.240	0.217	1.172	1.49	"	1.280
0.5	0.25	1.250	+0.0666	1.250	0.225	1.262	1.49	"	1.375
0.6	0.24	1.360	+0.0828	1.240	0.217	1.372	1.49	"	1.480
0.7	0.21	1.490	+0.0967	1.210	0.192	1.499	1.50	"	1.595
0.8	0.16	1.640	+0.1085	1.160	0.148	1.646	1.53	"	1.720
0.9	0.09	1.810	+0.1178	1.090	0.086	1.812	1.57	"	1.855
1.0	0	2.000	0	1.000	0	2.000	1.67	"	2.000

breeding according to the same system long enough that there is divergence from random combination only as forced by interactive selection.

A cross between two inbred lines is likely to have a selective value higher than the nearest peak on the equilibrium surface. The randomly bred descendants will thus move *down* toward the latter. Because of this sort of situation, Moran¹⁵ has drawn the conclusion indicated by the title of his paper, "The nonexistence of adaptive topographies." This was based on a misunderstanding of the concept.

Summary.—Kimura's concept of "quasi-equilibrium" with respect to a ratio of gametic frequencies is used to clarify the concept of a "surface" of mean selective values, the gradient of which tends to control evolutionary change within a panmictic population. It is shown that the actual surface, where there is deviation from random combination because of interactive selection, differs little from that calculated under the assumption of random combination if selective differences, including the interactive coefficients, are as small as is probably usually the case in nature, and the loci are in different chromosomes, as is usual in organisms with typical numbers, or if in the same chromosome, are only loosely linked.

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