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SELECTIVE FORCES IN WILD POPULATIONS OF *PARATETTIX TEXANUS*

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1. The biological interest of collections of polymorphic species

THE data used in the following paper were supplied by Dr Nabours of Manhattan, Kansas, and obtained during the Nabours-Sabrosky Tetrigid expedition in Mexico and Texas in 1933. The data on only one of the species collected, *Paratettix texanus*, will be discussed at present.

One of the objects of the expedition was to obtain random samples from different local populations sufficiently large to check and verify the theoretical consequences of the theory of selective equilibrium which in 1930 I had applied to these insects.

When, in 1928, I first put forward the suggestion that Mendelian dominance was a secondary phenomenon induced by the selection of modifying factors, I was influenced principally by the facts as ascertained in *Drosophila* (Fisher, 1928). First, that about twelve out of thirteen of the non-lethal mutants observed in culture were completely recessive, while the remainder were incompletely dominant, and secondly, that in multiple allelomorphic series the situation commonly found was that the wild allelomorph was dominant to all others, while the mutant allelomorphs showed no dominance *inter se*. These facts clearly suggested that the wild-type genes had become dominant in the course of time by the same selective process which assured their predominant frequency in the wild population.

The theory of dominance modifiers was quickly found to explain a number of facts, respecting the incidence of dominance, which I had not at first considered. Among these the situation found in several polymorphic species was strikingly different from that found in *Drosophila*, and in the other species most widely studied in genetics. In a prolonged series of investigations Nabours had shown that in a number of species of American grouse locusts polymorphism was due to several factors completely dominant to the prevalent type. This suggested that there also dominance was associated with selective advantage, but that some counter-selection, presumably acting on the homozygotes, prevented these from supplanting the universal recessive, as it seemed also to do (Fisher, 1927) with some polymorphic butterflies.

In 1930 I published an examination of Nabours's extensive breeding experiments with *Apotettix eurycephalus* (Nabours, 1925), from which it appeared that in culture the homozygotes of nearly all the dominants concerned were less viable than double heterozygotes from the same matings. In some cases the apparent difference in viability was considerable, and on the average it amounted to about 7 %. An examination of the frequency of recessives showed no significant difference. The data on these were not very extensive, and their

discussion requires one correction, since Dr Nabours informs me that one group of matings, which I had noted as aberrant, should have been omitted, as the females were probably not virgin.

The correction occurs in Table IV, p. 395, where mating 287 yielding $77 + / +$ against $114 + /Q$, or Q/Q, should be omitted. The totals are thus 144 against 481, showing a deficiency in place of an excess of recessives, so confirming Tables V and VI. In the summary (Table VII) the numbers expected and observed from this group of matings should now be 160 and 144, and, in the total, 2209 and 2086. The recessives may thus in culture show a deficiency of 5 or 6 %, nearly as great as that of the homozygous dominants.

The observed viabilities in culture thus unquestionably confirm the advantage of the heterozygotes postulated as a basis for genetic equilibrium. Although the breeding experiments were not designed to measure viability, they may be taken as showing that other selective agencies must exist in nature beyond those affecting viability in culture, for in nature the universal recessive is much the most frequent type. It will be seen that the data from the collected samples reveal some very high selective intensities not suspected from the broods raised in culture.

2. SAMPLES OF *PARATETTIX TEXANUS*

Six samples in all were obtained of this species, amounting in all to 3644 individuals. Eighteen different dominants could be distinguished, all rare, and some only represented by one or two specimens. In addition, four insects showed a recessive character **sf**, which has not been included in my tables. On Dr Nabours's advice I have also disregarded a few modifications of which the genetics is not clear.

Since in all samples the same dominant **D** is constantly the most frequent, I have arranged Table I so as to show the frequencies of all genotypes with **D** and not-**D** (+) in parallel columns. The compounds (double dominants) which do not involve **D** are then sufficiently infrequent to be listed separately.

3. MUTUAL AVOIDANCE OF DIFFERENT DOMINANTS

These samples afford an excellent demonstration of the mutual aversion of the different dominants, suggestive of a selective disadvantage of the dominant compounds, so powerful as to have suppressed combinations in coupling almost completely.

The largest collection of 1219 individuals was taken at Tynan, Texas, on 15 and 16 July. By far the most frequent dominant was that designated **D**, which was represented in 158 individuals out of the 1219. If we divide the sample into four classes with and without **D**, and with and without any of the other dominants taken together, we have the 2 by 2 table shown in Table II.

In the absence of other dominants, therefore, those with **D** are more than a sixth of those without **D**, while in the presence of other dominants they are less than a nineteenth. The

disproportion is clearly significant, having $\chi_c^2 = 11\cdot3658$, using Yates's correction, for one degree of freedom. The success of this test is rendered possible by the relatively high frequency of the dominant **D**, and by the circumstance that the other dominants largely concur in their behaviour, and therefore reinforce the effect when they are treated together in a single aggregate. Individually, they do not occur with sufficient frequency for the aversion

Table I. *Six samples of* Paratettix texanus

Source	Tynan		Irish Creek		Canvassback Lake		Kerrville		Tamos		Topila	
	+	D	+	D	+	D	+	D	+	D	+	D
+	888	149	747	150	495	153	166	56	114	15	107	7
J	18	3	7	4	23	7	15	—	3	—	2	—
H	17	1	19	1	22	4	6	2	1	—	1	—
θ	22	1	23	1	8	—	10	1	4	1	—	—
E	29	1	11	1	6	1	3	—	1	—	—	—
B	19	—	7	—	14	—	3	—	1	—	—	—
P	13	2	18	2	7	—	—	—	2	—	2	—
C	8	—	19	—	8	—	12	—	—	—	—	—
N_1	9	—	25	1	4	—	2	—	1	—	1	—
N	7	—	10	—	10	—	2	—	—	—	—	—
Cof	7	—	6	—	9	—	2	—	1	—	2	—
S	7	—	6	—	5	1	2	1	—	—	1	—
I	3	—	6	—	—	1	5	—	—	—	—	—
F	1	—	7	—	—	—	2	—	—	—	—	—
L	4	1	1	—	1	—	2	—	—	—	1	—
K	4	—	2	—	—	—	1	1	—	—	—	—
Hm	—	—	—	—	—	—	—	—	1	1	—	—
Hn	—	—	—	—	—	—	—	—	—	—	1	—
	1056	158	914	160	612	167	233	61	129	17	118	7
	θN	1	JS	1	HP	1	Jθ	1			SI	1
	EB	2	Hθ	1	BI	1						
	EN	1			BF	1						
	PN	1										
	1219		1076		782		295		146		126	

Table II

	+	D	Total
+	888	149	1037
Others	173	9	182
Total	1061	158	1219

to be asserted separately for each, and, in some cases, such as **J** with three **D** out of twenty-one individuals, **P** with two **D** out of fifteen, and **L** with one **D** out of five, there may really be no such aversion. There is, however, no evidence of attraction in any case, and the behaviour of the aggregate indicates that a great many at least of the other dominants must appear with **D** in a substantially lower proportion than in the general population.

The question arises whether these other dominants also show a mutual aversion amongst

themselves. Clearly no pair of these can be tested independently, for even the two most frequent, **E** with thirty-three observations, and **θ** with twenty-four, give an expectation of less than one combination **Eθ**, in a sample of 1219. The absence of this combination in our sample does not therefore provide evidence adequate for asserting that there is mutual aversion between the dominants **E** and **θ**. On the other hand, there are, in the sample, five compounds, not including **D** (2 **BE**, 1 **EN**, 1 **NP**, 1 **Nθ**), and it may be asked whether these are fewer than the totality of compounds among dominants other than **D**, which would be expected from the actual frequencies of these dominants, supposing that the compounds occurred with proportionate frequency. In principle, we could evaluate the frequency of each possible compound of two dominants, such as **Eθ**, by multiplying the total number of observations, 1219, by a series of fractions, of which two represent the probability of the presence of **E**, 33/1219, and the presence of **θ**, 24/1219, while thirteen others are the probabilities of the absence of the other thirteen dominants. There are, however, 105 such products to be added to obtain the total frequency to be expected of compounds involving only two dominants, and it will therefore be worth while to set out a quicker method of calculation, by which the total numbers of individuals containing 0, 1, 2, 3, ... dominants to be expected, may be calculated from the frequencies with which each of the dominants has been found to occur.

If q stand for the proportion of individuals in the observed sample in which a particular dominant does not occur, and p stand for the proportion in which it occurs, then the expression

$$n(q_1 + p_1 x)(q_2 + p_2 x) \ldots (q_k + p_k x),$$

supposing we are concerned with k dominants, when expanded in powers of x, will have as its coefficients of x^0, x^1, x^2, x^3, ... the numbers of individuals containing 0, 1, 2, 3, ... dominants. The expansion may equally be written

$$n q_1 \ldots q_k \left\{ 1 + t\Sigma\frac{p}{q} + t^2 \Sigma\Sigma\frac{pp'}{qq'} + t^3 \Sigma\Sigma\Sigma\frac{pp'p''}{qq'q''} + \ldots \right\},$$

where $\Sigma p/q$ stands for the sum of the fractions p/q for each dominant, and $\Sigma\Sigma pp'/qq'$ stands for the sum of the products of these fractions taken two at a time.

In the case, which is that before us, in which all the fractions p are comparatively small the factor $n q_1 \ldots q_k$, which is seen to be the expected frequency of insects carrying no dominant, may be evaluated from the sum of the frequencies of the dominants, with corrective terms derived from the sums of their products, two, three or more at a time. For

$$n q_1 \ldots q_k = n(1 - p_1) \ldots (1 - p_k)$$
$$= n\{1 - \Sigma(p) + \Sigma\Sigma(pp') - \Sigma\Sigma\Sigma(pp'p'') + \ldots\}.$$

Now if a_1 stand for the sum of the frequencies of all the dominants observed, evidently

$$n\Sigma(p) = a_1,$$

and if a_2, a_3 stand for the sums of the products of the frequencies, two, three or more at a time,

$$nq_1 \ldots q_k = n - a_1 + \frac{a_2}{n} - \frac{a_3}{n^2} + \frac{a_4}{n^3} \ldots.$$

In the present case the third coefficient provides sufficient accuracy, but the method may be easily used when further terms are required.

The expected number of insects carrying no dominant is therefore

$$n - a_1 + \frac{a_2}{n} - \frac{a_3}{n^2} + \frac{a_4}{n^3},$$

as far as the fourth correction.

For the number expected with one dominant we must evaluate

$$\sum_{i=1}^{k} p_i(1-p_1) \ldots (1-p_{i-1})(1-p_{i+1}) \ldots (1-p_k),$$

in which every product r at a time occurs, with sign $(-)^{r-1}$, r times, giving

$$a_1 - \frac{2}{n}a_2 + \frac{3}{n^2}a_3 - \frac{4}{n^3}a_4 + \ldots.$$

For the number expected with two dominants, we have

$$n \sum_{i=1}^{k} \sum_{j=1}^{k} p_i p_j (1-p_1) \ldots (1-p_k),$$

where $(1-p_i)$ and $(1-p_j)$ are omitted from the product, and $i \neq j$. Evidently every product of r terms may be found $\frac{1}{2}r(r-1)$ times, giving

$$\frac{1}{n}a_2 - \frac{3}{n^2}a_3 + \frac{6}{n^3}a_4 - \ldots.$$

The method is evidently applicable directly to combinations of any number of dominants, and the law of distribution is now clearly of the form

No. of dominants	Frequency
0	$n - a_1 + \dfrac{a_2}{n} - \dfrac{a_3}{n^2} + \dfrac{a_4}{n^3}$
1	$a_1 - \dfrac{2a_2}{n} + \dfrac{3a_3}{n^2} - \dfrac{4a_4}{n^3}$
2	$\dfrac{a_2}{n} - \dfrac{3a_3}{n^2} + \dfrac{6a_4}{n^3}$
3	$\dfrac{a_3}{n^2} - \dfrac{4a_4}{n^3}$
4	$\dfrac{a_4}{n^3}$

where $a_2, \ldots$ are the sums of products of the observed frequencies.

4. NUMERICAL TEST

Using the sample from Tynan, Texas, the frequencies of the fifteen dominants other than **D** are shown in the second column of Table III, with their sum and sums of products of two, three and four at a time developed in the columns following. In writing each line of the table the entries in the previous line are each multiplied by the frequency of the new factor, and the product added to the next entry on the right. If the work is done mentally it is well to start with the larger frequencies. If the process is applied to data with many repeated values, it can be easily adjusted to introduce each set of these in one set of operations.

Table III. *Calculation of elementary symmetric functions*

Factor	Frequency				
J	(21)	21			
H	(18)	39	378		
θ	(24)	63	1314	9072	
E	(33)	96	3393	52434	299376
B	(21)	117	5409	123687	1,400490
P	(16)	133	7281	210231	3,379482
C	(8)	141	8345	268479	5,061330
N₁	(9)	150	9614	343584	7,477642
N	(10)	160	11114	439724	10,913481
Cof	(7)	167	12234	517522	13,991549
S	(7)	174	13403	603160	17,614203
I	(3)	177	13925	643369	19,423683
F	(1)	178	14102	657294	20,067052
L	(5)	183	14992	727804	23,353522
K	(4)	187	15724	787772	26,264738

The use of sums of products a is, of course, algebraically equivalent to the use of the sums of powers s, these different symmetric functions being connected by the combinatorial equations

$$a_1 = s_1,$$
$$a_2 = \tfrac{1}{2}(s_1^2 - s_2),$$
$$a_3 = \tfrac{1}{6}(s_1^3 - 3s_2 s_1 + 2s_3),$$
$$a_4 = \tfrac{1}{24}(s_1^4 - 6s_2 s_1^2 - 3s_2^2 + 8s_3 s_1 - 6s_4),$$

or, in general,

$$a_\omega = \sum_P \frac{(-)^{\omega-\rho}}{p_1^{\pi_1} p_2^{\pi_2} \dots \pi_1! \pi_2! \dots} S(P),$$

where P is any partition of the partible number w into ρ parts specified by

$$P = (p_1^{\pi_1} p_2^{\pi_2} \dots),$$

and $S(P)$ stands for $s_{p_1}^{\pi_1} s_{p_2}^{\pi_2} \dots$. The direct calculation of a is, however, in this work much quicker than the use of formulae in sums of powers.

The values of $a_2, a_3, \dots$ are now divided by n (i.e. 1219), n^2, ..., giving the distribution as shown in Table IV.

Table IV. *Frequency distribution expected*

Number of dominants				
0	1	2	3	4
1219 − 187 12·899 − 0·530 + 0·014	187 − 25·798 + 1·590 − 0·058	12·899 − 1·590 0·087	0·530 − 0·058	0·014
1044·383	162·734	11·396	0·472	0·014

We are now in a position to compare the frequencies observed with those expected in the absence of counter-selection against the compounds of two or more dominants. The non-occurrence of compounds of three or more proves nothing since the expectation is less than half an individual; we may therefore without loss of precision put all compounds together in one class (Table V).

Table V. *Comparison with observations*

	Expected (m)	Observed ($m+x$)	Difference (x)	x^2/m
0 1 2 or more	1044·383 162·734 11·882	1037 177 5	− 7·383 + 14·266 − 6·882	0·052 1·251 3·986
	1218·999	1219		5·289

The measure of discrepancy, χ^2, is 5·289. There is only one degree of freedom, since the total number of observations and the total number of dominants are both introduced into the expectation. Consequently, the discrepancy must be judged significant. The apparent selective aversion among the fifteen dominants other than **D**, like that of **D** with the aggregate of the others, is greater than could reasonably be explained by errors of random sampling.

Had we wished to include **D** as a sixteenth dominant in the comparison effected above, the difficulty that **D** is not of rare occurrence like the other fifteen, could be got over by performing the calculation for the fifteen rarer dominants with the result obtained above. The dominant **D** is present in 158 individuals out of 1219, or 12·961444 %; if this fraction of the class with no dominants is moved into the class with 1, and the same with the other classes, we shall have the distribution of number of dominants, including **D**, as shown in Table VI, giving $\chi^2 = 17·18$ for one degree of freedom, and showing an even more clearly significant departure from expectation.

5. CONFIRMATION FROM OTHER SAMPLES

The slightly smaller sample from Irish Creek, Cuero, Texas, taken on 12 July confirms each of the conclusions drawn from the Tynan sample, although the proportions of the several dominants are not the same. The 2×2 table showing the frequency of **D** in com-

Table VI. *Comparison with observations, including* **D**

	Expected (m)	Observed (m + x)	Difference (x)	x^2/m
0	909·016	888	− 21·016	0·486
1	277·008	317	39·992	5·774
2	31·012	14 ⎫	− 18·976	10·920
3 or more	1·964	0 ⎭		
				17·180

bination with other dominants (Table VII) shows only ten compounds, where about twenty-seven would be expected, a clearly significant deficiency. Of the compounds of these other dominants among themselves, there are only two in the sample (**HΘ** and **JS**) where twelve are to be expected in a proportionate distribution.

Table VII

	+	**D**	Total
+ Others	747 169	150 10	897 179
Total	916	160	1076

The sample from Canvassback Lake, Texas, has fourteen compounds with **D**, where about twenty-nine would be expected (Table VIII).

Table VIII

	+	**D**	Total
+ Others	495 120	153 14	648 134
Total	615	167	782

The compounds of the other dominants among themselves number only three in this sample (**BF**, **BI** and **HP**), showing a deficiency, which, while less clearly significant by itself than those in the larger samples, clearly confirms them. While of the three smaller samples from Kerrville (Texas), Tamos (Mexico) and Topila (Mexico), totalling 569 insects, it is sufficient to say that in all they contain seven compounds with **D**, and only two (**JΘ** and **IS**) between the other dominants. The feature of a general mutual aversion of all the dominants of this species is thus confirmed from all the sources available. The conclusion is supported both by the internal tests of significance on the three largest samples, and by the corre-spondence in the deviations found in the different samples.

6. FREQUENCIES EXPECTED WHEN COMBINATIONS IN COUPLING ARE COMPLETELY ABSENT

The extreme genetic effect of selection directed against insects bearing more than one dominant would be to eliminate completely all cases in which the two dominants are coupled. Owing to the very close linkage found in *Paratettix texanus* quite small selective intensities would suffice to maintain the frequency of coupled pairs at so low a level that the frequencies in nature should be indistinguishable from those of a population showing variation in only a single series of multiple allelomorphs.

The theoretical relationship which holds among the frequencies in such a system may be deduced by equating the frequency of the recessive gamete to the square root of the frequency of the recessive zygote. In the sample from Canvassback Lake, for example, there are 495 recessive insects out of a total of 782. Consequently, if p is the frequency of gametes recessive in all factors we should have, apart from errors of random sampling, $495 = 782p^2$, or

$$\sqrt{(495)} = p\sqrt{(782)}.$$

Next, taking any particular dominant, such as **D**, we note that there are 153 insects carrying this dominant only, and therefore 648 recessive for all factors except **D**; hence, if q is the frequency of gametes bearing **D** only, $p+q$ is the frequency of gametes recessive for all factors but **D**, and the equation corresponding to that written above is

$$\sqrt{(648)} = (p+q)\sqrt{(782)}.$$

A similar equation will be available for each of the thirteen dominants present in the sample. Now the sum of p, q, and the other frequencies of gametes bearing single dominants must, in a multiple allelomorphic system, add up to unity. Consequently, we may test this hypothesis by adding the thirteen quantities corresponding to the left-hand side of the last equation and subtracting

$$12\sqrt{(495)} + \sqrt{(782)}.$$

The difference, if positive, indicates that the dominant compounds observed are less frequent than they should be, even in the complete absence of combinations in coupling. The arithmetical procedure for the sample from Canvassback Lake is illustrated in Table IX.

Evidently the seventeen compounds observed in this sample were somewhat fewer than might have been expected, even on the assumption of the complete absence of combinations in coupling. The deficiency may be calculated by squaring the difference $295\cdot05 - 266\cdot98$, or $28\cdot0669$, giving $787\cdot7509$, which exceeds 782 by $5\cdot751$. Evidently about six more compounds would be needed, in conjunction with the numbers of recessives and single dominants observed, to produce perfect agreement with theory.

The sample of 1219 from Tynan gives a difference, also positive, of $0\cdot1276$, showing that the fourteen compounds observed are $8\cdot928$ fewer than might have been expected. The sample of 1076 from Irish Creek, Cuero, gives a positive difference $0\cdot1864$, showing that the twelve compounds observed are $12\cdot261$ short of expectation. The sample of 295 from Kerrville gives a positive difference $0\cdot2337$, showing that the six compounds observed are

Table IX. *Calculation for the absence of combinations in coupling*

Dominant	No. observed with no other dominant	Square root
D	648	25·4558
J	518	22·7596
H	517	22·7376
B	509	22·5610
N	505	22·4722
Cof	504	22·4499
C	503	22·4277
θ	503	22·4277
P	502	22·4054
E	501	22·3830
S	500	22·3607
N_1	499	22·3383
L	496	22·2711
		295·0500
		$12\sqrt{(495)} = 266·9831$
		$\sqrt{(782)} = 27·9643$
		Difference 0·1026

8·110 short of expectation. Only the two small samples from Tamos and Topila in Mexico, in both of which the proportion of dominants is small, show negative differences. For the sample of 146 from Tamos the difference is $-0·0264$, showing that the two compounds observed were about 0·637 more than would be expected. While the sample of 126 gives an even smaller negative difference $-0·0181$, showing that the one compound observed also exceeds expectation. It appears, therefore, that the four larger samples show consistent and substantial deficiencies of dominant compounds compared even with the hypotheses that coupling is completely absent.

If we ascribe the absence of coupling to the selective elimination of dominant compounds it is easy to see the reason for the deficiency of insects of these types in the samples of adults taken. This deficiency indicates not only that selection in the past has left its mark on the species by eliminating chromosomes containing more than one dominant, but in the actual generation sampled has eliminated a large proportion of the double heterozygotes in repulsion which must be formed afresh by chance in each generation.

The consistent deficiency of insects carrying more than one dominant, as compared even with expectation based on the supposition that combinations in coupling are completely absent, is thus of great importance. Let us assemble the comparisons for the six samples (Table X). The number observed, 52, is only just over 60 % of the expectation. On no genetic view, therefore, can much less than 40 % of all dominant compounds be eliminated in a single generation between zygosis and the age of collection.

Actually, the estimate obtained above for the differential elimination of the dominant compounds must be to some extent an underestimate, for it is based on the extreme possibility of the complete absence of combinations in coupling.

Table X. *Comparison of numbers expected and observed*

	Total insects	Compounds	
		Expected	Observed
Tynan	1219	22·928	14
Irish Creek	1076	24·261	12
Canvassback Lake	782	22·751	17
Kerrville	295	14·110	6
Tamos	146	1·363	2
Topila	126	0·594	1
		86·007	52

Now, if any of the 306 pairs of dominants produced a genotype either advantageous or not appreciably less well fitted than the recessive (though it might still be considerably less well fitted than either singly dominant type) there is nothing to prevent the accumulation of chromosomes carrying both dominants, so that nearly as many compounds of such types would be in the coupling as in the repulsion phase.

This seems to be the case with the combination **DJ**, involving the two dominants most generally common. In the Tynan sample there are 888 recessive, 149 **D**, 18 **J** and 3 **DJ**. The number of **DJ** expected is

$$(\sqrt{(1037)} + \sqrt{(906)} - \sqrt{(888)})^2 - 1055 = 1\cdot444,$$

showing that the number observed is in excess of expectation. Taking the evidence for all samples I obtain the results shown in Table XI.

Table XI

	DJ Expected	**DJ** Observed
Tynan	1·444	3
Irish Creek	0·248	4
Canvassback Lake	3·278	7
Kerrville	2·307	0
Tamos	0·194	0
Topila	0·064	0
	7·535	14

It therefore looks very much as though the particular combination **DJ**, unlike the majority of dominant combinations, existed nearly as frequently in coupling as in repulsion. The same may be true of some other rarer combinations. If this is so, the elimination of the majority of the other dominant compounds must be as high as 50 %. It might be thought that gametes bearing **DJ** cannot be present without producing some triple dominants, and these are completely absent in all the samples. The expected frequency of such triples is not, however, sufficient to exclude a small proportion of coupling gametes.

For example, the highest frequency of the combination **DJ** is shown by seven out of 782 from Canvassback Lake. If half of these are in coupling, the frequency of **DJ** gametes would be about one in 400. Now, only 104 insects in the sample contain dominants other than **D** and **J**, so that the expectation of triples, even in this chosen favourable case, is only about one-quarter of a unit.

7. EQUILIBRIUM OF SINGLE FACTORS

The extremely heavy elimination in the wild population of compounds of two dominants is of great importance in the equilibrium of each single factor. We must, therefore, reconsider the evidence from breeding experiments in culture conditions obtained with *Apotettix eurycephalus*. For this species the samples obtained from nature are, unfortunately, small, 619 from Tamos and eighty-two from Topila, but, since these also show a significant deficiency of double dominants, the available data should throw some light on the situation in *Paratettix texanus*. The most important point to note is that the breeding data, in which viability may be measured by deviations from expected frequencies, do not show any such large elimination of double dominants as must occur with *P. texanus*, at least in wild conditions. Had they done so the conclusions drawn as to the viability of homozygotes in my previous paper (Fisher, 1930) would require to be greatly modified, for in measuring the viability of homozygotes relative to heterozygotes, matings of the type $P/Q \times P/Q$ were used, since in these the homozygotes form distinguishable classes. They gave in all 4309 homozygotes against 4617 heterozygotes, a significant deficiency, indicating an average elimination of about 7 %. It should now be specifically noted, what did not previously appear to be of importance, that the heterozygotes with which comparison is made all carry two and sometimes more different dominants. They are, in fact, the class which have been eliminated to the extent of at least 40 % in the wild *P. texanus* collections. If this elimination were ascribed to physiological inviability we should have to ascribe an even lower viability to most genotypes of the homozygous class, and this in turn would imply that it should be balanced by much higher selective tendencies in favour of single heterozygotes.

Matings, however, of the type $+/P \times +/Q$ provide the opportunity of comparing, in conditions of culture, recessives, single heterozygotes and double heterozygotes simultaneously. As Table V of my previous paper shows, the recessives are actually in defect, being in all 1732 against 5476 for the three classes of heterozygotes. In that table the classes of single and double heterozygotes were not separated, and some matings of parents doubly and triply heterozygous in coupling were included. It will, therefore, be of interest to consider a more complete enumeration, according to the numbers of dominants in the parents (Table XII).

If we compare the numbers observed with those expected in each class, on the supposition of equal survival, it is seen that the agreement is very close. The respective ratios are 96·1, 101·8, 100·7, 102·8, 101·3, 98·7, 93·4. Evidently there is in *Apotettix eurycephalus* in culture no such drastic elimination of the double dominants as takes place in *Paratettix texanus* in

Table XII. *Frequencies in culture with varying numbers of dominants*

Parents	No. of dominants							Total
	0	1	2	3	4	5	6	
1, 1	39	89	35	——	——	——	——	163
2, 1	236	250	247	292	——	——	——	1025
3, 1	649	685	——	656	683	——	——	2673
2, 2	215	——	465	——	223	——	——	903
3, 2	457	——	474	468	——	458	——	1857
3, 3	136	——	——	314	——	——	137	587
Total	1732	1024	1221	1730	906	458	137	7208
Expected	1802	1006	1213	1682	894	464	147	——

nature. The cause of elimination is thus probably not lack of physiological viability, which in a double heterozygote would in any case be anomalous, but some cause such as elimination by predators, which is inoperative in conditions of culture.

Table XIII shows, for the three large samples, the percentage of the genes for different dominants which in each generation find themselves in a double dominant combination. Since about 40 % of the bearers of these genes are eliminated, the loss is, in different cases, from about 3·3 % to about 8·3 %. The selective intensities in favour of the heterozygotes must be at least as great as these. They must, indeed, be greater, to an extent balanced by the selective elimination of the homozygotes, in order to give stability to the proportions of different competing dominants.

Table XIII. *Percentage of genes of different factors occurring*
in double heterozygotes

	Tynan	Irish Creek	Canvassback Lake
D	8·25	9·21	9·88
J	11·49	16·76	18·91
H	11·54	16·10	18·99
θ	11·30	15·86	20·09
E	10·96	16·54	20·25
B	11·44	16·76	19·62
P	11·74	16·16	20·17
C	11·98	16·10	20·09
N_1	11·93	15·78	20·41
N	12·03	16·60	19·94
Cof	12·03	16·82	19·98
S	12·03	16·82	20·33
I	12·23	16·82	20·73
F	12·33	16·76	20·73
L	12·18	17·09	20·65
K	12·18	17·04	20·73

Without an exact analysis it would be rash to dogmatize, but it is difficult to see how stability can be maintained unless the homozygotes are at a selective disadvantage, at least as great as are the heterozygotes for two dominants. If this is so the least possible average selective advantages for dominant heterozygotes over the general recessive are 6·58 %

for Tynan, 10·44 % for Irish Creek and 14·16 % for Canvassback Lake. These are, of course, average values representative of what is perhaps in reality a very complex system of selection.

Although selective intensities of this order must certainly exist in the wild population, it is a question to some extent of conjecture whether they are to be ascribed to physiological causes, differences in relative viability, or to selection of the colour patterns by the action of predators. As has been shown, there is a small deficiency of homozygotes in the breeding experiments. In wild conditions a difference in inherent viability might much more strongly affect the numbers surviving. The great contrast between heterozygotes and homozygotes of any one factor may safely be ascribed to this cause, since these are phenotypically alike.

On the other hand, the breeding experiments give no reason to suspect a difference in viability between single and double heterozygotes. Since their survival in nature is in a ratio nearly as high as 2 : 1, this large difference is evidence of very powerful ecological selection.

8. Summary

Six samples of *Paratettix texanus* taken in different places in the United States and Mexico agree in demonstrating a mutual avoidance of different dominant variants. "Compounds" of different dominants are less frequent than they should be on any purely genetical theory.

The genetical situation least favourable to the production of such compounds would be the complete absence of chromosomes carrying two or more of such dominant genes; as this condition would be brought about by the selective elimination of double dominants, it has been used as the basis of calculation.

On this basis the elimination of double dominants in wild conditions is estimated to be not less than 40 % in each generation.

Equilibrium in the gene ratios between different competing dominants then requires that the survival of the homozygotes should in general be equally low.

The minimal average selective intensities in favour of the heterozygotes for single dominant factors in the three largest samples are 6·6, 10·4 and 14·2 % in each generation.

Comparison with breeding data in *Apotettix eurycephalus* suggests that the selection in wild conditions between homozygotes for any one factor and the heterozygotes of the same factor may be largely due to inherent differences in viability. On the contrary the large selective advantage of single against double heterozygotes points to powerful and variable ecological causes of elimination.

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