THE OCCURRENCE OF LETHAL FACTORS IN INBRED AND WILD STOCKS OF DROSOPHILA

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TWO DIAGRAMS

Three main points are dealt with in the following account:
1) The relative frequency of sex linked lethal factors in inbred stocks of *Drosophila ampelophila* in comparison with their occurrence in wild stocks. 2) The occurrence of new lethals and their linkage relations to other sex linked characters. 3) The demonstration that an extraordinary sex ratio was due to the occurrence of two different lethal factors each carried by one of the sex chromosomes of the female that gave the ratio in question.

THE RELATIVE FREQUENCY OF LETHALS IN INBRED AND WILD STOCKS

A hundred virgin females of a stock of *Drosophila* which was caught at Falmouth, Mass., in the summer of 1912, were mated individually on November 29, 1912, with males of the same stock. The counts of the offspring from each bottle are shown in table 1.

A hundred virgin females from a stock that had been caught at Falmouth, Mass., in the summer of 1911, were mated individually to males of the same stock early in January, 1913. The results are shown in table 3.

Numbers 13, 36, 38 and 47 of table 3 show a ratio of twice as many females as males while numbers 43, 53 and 67 are doubtful.

In order to determine whether the high ratios would reappear in later generations, virgin females from several of these cultures were mated to brothers. The results are shown in table 4.

Of the four sets of tests two (viz., 36 and 38) give ambiguous results, while numbers 13 and 47 give respectively 5 high to 9

TABLE 1

FEMALES	MALES	FEMALES	MALES	FEMALES	MALES	FEMALES	MALES
97	98	96*	59	85	81	105	105
134	147	121	113	93	93	88	79
77	79	94	99	73	77	58	47
121	117	116	98	105	108	71	75
138	144	82	82	34	41	92	82
132	129	183	166	112	104	47	45
99	111	117	107	72	74	56	62
122	142	161	160	85	92	93	80
127	128	147	140	52	47	89	77
64	61	62	51	87	92	73	87
122	152	126	120	88	79	96	92
95	110	105	112	68	77	69	70
75	82	50	37	133	112	62	74
103	120	109	111	72	93	154	142
112	120	94	97	126	112	203	172
135	137	112	94	117	123	175	147
42	47	138	141	102	102	165	154
166	150	75	74	98	101	120	86
129	127	100	110	91	80	49*	28
125	112	65	62	98	101	83	72
43	50	113	109	128	122	31	21
157	160	117	105	62	59	42	34
147	115	109	106	40	42	70	49
130	111	65	70	48	68	57	52
67	56	82	88	86	72	80	70

* Two matings showed rather high sex ratios, and as this is often indicative of a lethal factor, I mated individually six of the virgin females from each bottle (twelve in all) to males from the same bottles. Since each bottle of the twelve (table 2) gave a 1 : 1 ratio it follows that the somewhat lower values noted in these two bottles was probably merely a chance deviation, or else due to the crowded condition of the bottle which prevented all of the males from hatching out. The males are known to continue hatching for some days after the females have ceased to hatch.

TABLE 2

26 F ₂		94 F ₂	
Females	Males	Females	Males
141	121	87	92
128	106	79	74
162	150	124	105
72	73	177	164
160	159	232	212
130	138	222	204

TABLE 3

NO. OF PAIR	FEMALES	MALES	SEX RATIO	NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	290	227	1.28 : 1	51	154	162	0.95 : 1
2	121	111	1.09 : 1	52	139	108	1.28 : 1
3	196	200	0.98 : 1	53	56	30	1.86 : 1
4	176	173	1.02 : 1	54	177	182	0.97 : 1
5	93	102	0.91 : 1	55	183	145	1.26 : 1
6	114	134	0.85 : 1	56	75	57	1.31 : 1
7	132	128	1.03 : 1	57	194	171	1.14 : 1
8	115	96	1.20 : 1	58	203	195	1.04 : 1
9	96	92	1.04 : 1	59	158	129	1.22 : 1
10	95	99	0.96 : 1	60	200	176	1.13 : 1
11	50	63	0.79 : 1	61	134	114	1.17 : 1
12	124	142	0.87 : 1	62	45	41	1.10 : 1
13	232	114	2.03 : 1	63	196	183	1.08 : 1
14	262	229	1.14 : 1	64	134	106	1.26 : 1
15	187	188	1.00 : 1	65	136	122	1.12 : 1
16	212	203	1.04 : 1	66	143	152	0.94 : 1
17	214	159	1.35 : 1	67	105	63	1.66 : 1
18	247	220	1.12 : 1	68	147	133	1.10 : 1
19	169	145	1.16 : 1	69	151	157	0.96 : 1
20	106	100	1.06 : 1	70	175	159	1.10 : 1
21	189	149	1.27 : 1	71	121	84	1.44 : 1
22	155	127	1.22 : 1	72	108	156	0.69 : 1
23	193	179	1.08 : 1	73	80	71	1.12 : 1
24	206	169	1.22 : 1	74	106	98	1.09 : 1
25	230	223	1.03 : 1	75	116	103	1.12 : 1
26	182	154	1.18 : 1	76	78	59	1.32 : 1
27	201	168	1.20 : 1	77	60	53	1.11 : 1
28	178	142	1.22 : 1	78	106	92	1.16 : 1
29	153	136	1.12 : 1	79	81	69	1.18 : 1
30	120	79	1.52 : 1	80	148	118	1.29 : 1
31	166	153	1.08 : 1	81	79	88	0.90 : 1
32	157	143	1.10 : 1	82	103	107	0.96 : 1
33	212	155	1.37 : 1	83	126	120	1.05 : 1
34	225	225	1.00 : 1	84	116	95	1.11 : 1
35	156	161	1.03 : 1	85	95	94	1.01 : 1
36	188	81	2.32 : 1	86	114	140	0.81 : 1
37	172	183	0.99 : 1	87	75	68	1.10 : 1
38	172	83	2.07 : 1	88	97	98	0.99 : 1
39	77	92	0.83 : 1	89	119	140	0.92 : 1
40	125	83	1.51 : 1	90	140	128	1.09 : 1
41	159	155	1.02 : 1	91	126	124	1.06 : 1
42	102	95	1.07 : 1	92	133	137	0.97 : 1
43	74	49	1.51 : 1	93	155	157	0.99 : 1
44	53	36	1.47 : 1	94	157	148	1.08 : 1
45	113	77	1.49 : 1	95	118	115	1.02 : 1
46	69	64	1.09 : 1	96	111	88	1.26 : 1
47	200	93	2.15 : 1	97	148	138	1.01 : 1
48	88	89	0.98 : 1	98	105	103	1.01 : 1
49	56	60	0.93 : 1	99	127	126	1.01 : 1
50	76	64	1.19 : 1	100	124	120	1.01 : 1

TABLE 4

13				36			
NO. OF PAIR	FEMALES	MALES	SEX RATIO	NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	194	95	2.04 : 1	1	116	128	0.91 : 1
2	123	50	2.46 : 1	2	114	124	0.92 : 1
3	123	124	0.99 : 1	3	89	63	1.41 : 1
4	131	113	1.16 : 1	4	101	107	0.94 : 1
5	164	61	2.70 : 1	5	100	74	1.35 : 1
6	108	86	1.14 : 1	6	102	124	0.82 : 1
7	143	53	2.70 : 1	7	119	96	1.24 : 1
8	82	104	0.79 : 1	8	92	94	0.98 : 1
9	193	173	1.11 : 1	9	70	49	1.43 : 1
10	148	82	1.80 : 1	10	100	80	1.25 : 1
11	159	143	1.11 : 1	11	194	153	1.27 : 1
12	87	93	0.94 : 1	12	109	47	2.32 : 1
13	53	59	0.96 : 1	13	129	105	1.23 : 1
14	119	173	1.50 : 1	14	124	105	1.18 : 1
15	165	152	1.10 : 1	15	127	116	1.10 : 1

38				47			
NO. OF PAIR	FEMALES	MALES	SEX RATIO	NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	112	56	2.00 : 1	1	137	141	0.97 : 1
2	159	139	1.14 : 1	2	150	157	0.96 : 1
3	125	78	1.61 : 1	3	140	105	1.33 : 1
4	67	73	0.93 : 1	4	85	95	0.89 : 1
5	58	46	1.26 : 1	5	115	107	1.08 : 1
6	131	90	1.45 : 1	6	127	77	1.65 : 1
7	90	79	1.01 : 1	7	185	91	2.03 : 1
8	119	129	0.92 : 1	8	201	81	2.45 : 1
9	71	78	0.91 : 1	9	119	90	1.32 : 1
10	153	86	1.78 : 1	10	149	150	0.99 : 1
11	183	153	1.19 : 1	11	201	92	2.20 : 1
12	164	117	1.40 : 1				

low 1 doubtful and 4 high to 7 low ratios where equal numbers of each kind are expected. Further tests were therefore made. Pairs were mated from 13, 1; 13, 2; 13, 5; 13, 7; 36, 12; 47, 7; 47, 8; 47, 11.

The counts from these matings are shown in table 5.

As expected, the test of 13, 1 shows the presence of a lethal since there were 6 high to 6 low ratios.

The test of 13, 2 indicates a lethal with 8 high to 11 low ratios.

The test of 13, 5 indicates a lethal with 6 high to 13 low ratios.

TABLE 5

13, 1

NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	186	103	1.80 : 1
2	118	122	0.97 : 1
3	121	128	1.06 : 1
4	116	101	1.15 : 1
5	171	81	2.11 : 1
6	138	46	3.00 : 1
7	120	116	1.03 : 1
8	107	52	2.06 : 1
9	115	110	1.05 : 1
10	104	128	0.81 : 1
11	127	68	1.86 : 1
12	174	100	1.74 : 1

13, 2

NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	159	61	2.61 : 1
2	128	146	0.88 : 1
3	105	53	2.00 : 1
4	212	94	2.36 : 1
5	139	101	1.37 : 1
6	84	74	1.14 : 1
7	135	122	1.10 : 1
8	240	100	2.40 : 1
9	225	160	1.40 : 1
10	77	79	0.98 : 1
11	91	69	1.38 : 1
12	72	87	0.83 : 1
13	109	81	1.34 : 1
14	108	84	1.17 : 1
15	175	91	1.92 : 1
16	222	116	1.91 : 1
17	88	40	2.22 : 1
18	134	104	1.29 : 1
19	145	47	3.08 : 1

Two high to 9 low ratios appear in 13, 7, which probably indicates a lethal as the parent also had a high ratio (viz., 2.7 : 1).

These four tests of 13 show beyond doubt that a lethal was present, since each of the four families tested gave some high ratios.

TABLE 5—Continued

13, 5

NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	116	139	0.87 : 1
2	103	100	1.03 : 1
3	222	109	2.03 : 1
4	140	140	1.00 : 1
5	159	58	2.75 : 1
6	150	168	0.89 : 1
7	205	210	0.98 : 1
8	107	44	2.43 : 1
9	239	140	1.71 : 1
10	164	137	1.20 : 1
11	125	117	1.07 : 1
12	148	123	1.20 : 1
13	172	156	1.10 : 1
14	107	50	2.14 : 1
15	113	115	0.98 : 1
16	100	134	0.75 : 1
17	211	150	1.41 : 1
18	116	133	0.87 : 1
19	155	62	2.50 : 1

13, 7

NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	267	229	1.17 : 1
2	180	161	1.11 : 1
3	136	123	1.10 : 1
4	208	89	2.32 : 1
5	106	106	1.00 : 1
6	162	87	2.00 : 1
7	139	131	1.06 : 1
8	119	140	0.85 : 1
9	121	119	1.01 : 1
10	109	76	1.43 : 1
11	113	83	1.36 : 1

Of the 60 females tested, half (30) should have given 2 : 1 ratios, while in fact, only 22 gave such ratios to 38 giving normal ratios. Provisionally, this deviation may be ascribed to chance.

The following tests were made of the daughters of number 12 of 36, table 4:

TABLE 5—Continued
36, 12

NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	121	72	1.7 : 1
2	151	56	2.8 : 1
3	130	109	1.2 : 1
4	159	140	1.1 : 1
5	97	115	0.8 : 1
6	177	108	1.6 : 1
7	135	88	1.5 : 1
8	144	55	2.6 : 1

In this test there were 5 high to 3 low ratios showing that 36, 12 was a lethal bearing female.

The following tests were made of the daughters of number 7 of 47, table 4.

TABLE 5—Continued
47, 7

NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	259	121	2.1 : 1
2	235	122	1.9 : 1
3	188	78	2.4 : 1
4	133	152	0.9 : 1
5	170	90	1.9 : 1
6	185	95	1.9 : 1
7	147	148	1.0 : 1
8	164	150	1.1 : 1

Here there are 5 high to 3 low ratios indicating a lethal.

In 47, 8 the 4 high to 4 low ratios indicate a lethal.

In 47, 1 there are 3 high to 7 low ratios. Of the three sets of tests of 47 of table 5 there were 12 high to 14 low ratios which establishes the presence of a lethal in this line. The general outcome of these tests leaves no doubt that a lethal was present in the original females that were tested.

Since only half of the daughters of a lethal female are heterozygous for lethal and since these females are indistinguishable

TABLE 5—Continued

47, 8

NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	146	80	1.8 : 1
2	93	94	1.0 : 1
3	201	162	1.2 : 1
4	124	58	2.1 : 1
5	147	156	0.9 : 1
6	196	69	2.8 : 1
7	150	119	1.3 : 1
8	158	57	2.8 : 1

47, 11

NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	142	79	1.79 : 1
2	168	173	0.98 : 1
3	157	171	0.92 : 1
4	159	162	0.98 : 1
5	167	124	1.34 : 1
6	247	124	2.00 : 1
7	142	127	1.12 : 1
8	190	97	1.96 : 1
9	122	146	0.90 : 1
10	163	156	1.04 : 1

from their sisters, it is by chance only that one would choose a female with a lethal factor when testing out a stock. On the other hand if a lethal female is mated to a male having a sex

TABLE 6

13, 1, 11

NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	183	156	1.11 : 1
2	138	118	1.17 : 1
3	155	70	2.22 : 1
4	158	139	1.12 : 1
5	154	82	1.90 : 1
6	142	152	0.90 : 1
7	163	152	1.01 : 1

TABLE 6—*Continued*

13, 1, 12

1	114	70	1.63 : 1
2	156	136	1.12 : 1
3	199	108	1.83 : 1
4	154	82	1.88 : 1
5	195	102	1.92 : 1
6	154	103	1.50 : 1

13, 2, 1

1	123	60	2.00 : 1
2	130	52	2.50 : 1
3	98	105	0.93 : 1
4	82	3	27.33 : 1
5	110	95	1.15 : 1
6	140	135	1.04 : 1
7	170	50	3.40 : 1
8	84	62	1.35 : 1
9	99	70	1.41 : 1

13, 2, 8

1	83	61	1.36 : 1
2	150	62	2.42 : 1
3	105	96	1.08 : 1
4	156	162	0.97 : 1
5	84	39	2.16 : 1
6	134	134	1.00 : 1
7	120	73	1.64 : 1
8	109	64	1.54 : 1
9	134	111	1.21 : 1

13, 2, 19

1	164	129	1.27 : 1
2	207	214	0.92 : 1
3	225	211	1.07 : 1
4	232	172	1.35 : 1
5	182	185	1.00 : 1
6	341	120	2.84 : 1
7	283	152	1.86 : 1
8	193	93	2.07 : 1
9	366	167	2.20 : 1
10	251	246	1.02 : 1

linked factor close to the lethal factor in question a stock may be obtained in which the lethal females may be selected with great probability. For example: If a red eyed female carrying a lethal is mated to a white eyed male half of her daughters will have the factor for red and the factor for lethal in one X chromosome and the factor for white and the factor that is the normal allelomorph of lethal in the other chromosome. If such a daugh-

TABLE 7
13, 2, 8, 2 (*four 1 : 1 ratios omitted*)

NO. OF PAIR	FEMALES		MALES		CROSSING OVER BETWEEN WHITE AND LETHALS
	Red	White	Red	White	
1	62	73	11	47	19.0
2	87	78	12	48	20.0
3	99	77	23	58	28.4
4	77	67	11	55	16.7

13, 2, 19, 6 (*five 1 : 1 ratios omitted*)

1	177	94	30	88	25.4
2	110	117	19	81	19.0

13, 2, 19, 7 (*three 1 : 1 ratios omitted*)

1	83	107	23	69	25.0
2	112	118	22	93	19.1
3	98	81	26	68	27.7
4	162	85	14	79	15.1
5	89	94	20	71	22.0
6	98	87	27	72	27.3
7	82	83	18	65	21.7

ter is mated to a white eyed male half of the female offspring will be red eyed and half white eyed. The former getting their red bearing chromosome from their mother will be the lethal bearing females since the red bearing chromosome also carried the lethal factor. By selecting the red eyed females, therefore, in each succeeding generation and breeding them to white eyed males the lethal stock can be maintained.

Virgin females from numbers 13, 1, 11; 13, 1, 12; 13, 2, 1; 13, 2, 8; 13, 2, 19; of table 5 were mated to white eyed males. The results are shown in table 6.

The tests give 19 high to 22 low ratios which is the expectation for lethals, i.e., equality is expected and is approximately realized.

Daughters from 2 : 1 cultures all of which were heterozygous for white and half of which should be heterozygous for lethal also, were again mated to white eyed males with the results in table 7.

There were 13 high to 13 low ratios shown by these daughters indicating a lethal factor. On the basis of these data the locus of the lethal is at 23.7.

It is interesting to note that the lethal factor occurred in flies that had been inbred a year and that none appeared in the stock having been inbred only two months. Miss Rawls (Biol. Bull. '13) found her lethal in a stock that had been inbred a year. The lethals described by Quackenbush (Sc. '10) and Morgan (Sc. '12; and Jour. Exp. Zool. '14) appeared in stocks that had been inbred for some time. To test whether, in general, lethals are more frequent in inbred stocks I mated 100 pairs from wild stock caught at Falmouth, Mass., and 70 pairs from wild stock caught at Harris, Minn. The results are shown in table 8.

Tables 1 and 8 show that the counts made of offspring from 270 pairs of fresh wild stocks have no unusual ratios.

THE SECOND LETHAL FACTOR

On February 10 of 1914, sixty pairs from stock collected in the summer of 1910 were mated. The results are shown in table 9.

The next to the last pair of the above table seemed to show the presence of a lethal factor. Sixty virgin daughters from this pair were mated to brothers. Nearly one-half of these gave a ratio of twice as many females as males, as shown in table 10.

Virgin females from numbers 7, 8, 12, 23 and 59 were mated to white eyed males. About one-third of the counts of the next generation show the presence of a lethal factor (table 11). Some of these lethal females were again mated to white eyed

TABLE 8 (a)
Falmouth Stock

FEMALES	MALES	FEMALES	MALES	FEMALES	MALES	FEMALES	MALES
98	111	129	111	161	132	175	182
144	132	207	216	175	176	171	174
74	78	181	154	195	187	191	190
68	86	182	193	101	118	199	223
129	120	196	205	102	85	100	88
120	117	179	187	154	162	99	106
119	138	191	175	195	190	185	180
178	174	105	97	191	198	100	84
176	175	184	181	199	202	174	194
96	103	173	138	150	150	87	128
130	109	186	150	166	183	91	90
156	141	174	169	110	123	98	86
103	88	170	197	175	177	100	108
125	152	187	222	176	180	100	93
105	95	220	182	192	171	146	136
84	92	186	157	189	172	108	110
140	188	95	110	175	193	100	92
128	151	192	200	159	173	85	102
127	139	174	171	171	159	100	101
157	193	113	111	177	173	172	160
120	145	167	119	166	184	183	189
109	106	123	120	117	81	192	189
102	100	191	210	159	163	176	180
148	125	134	129	110	107	164	170
167	155	106	102	191	199	171	175

males. It was expected that only a few of the red eyed males would appear in the second generation if red and lethal were closely linked. Results (table 11) show, however, that a great number of red males appear. Such a result indicates that a new lethal had appeared which was located some distance from the factor for white, thus giving a chance for a greater amount of crossing over.

In table 11 it will be noted that the percentage of crossovers is 46. This would place the lethal somewhere beyond the factor for sable and not far from the factor for bar eyes upon the sex chromosome.

TABLE 8 (b)
Harris Stock

FEMALES	MALES	FEMALES	MALES	FEMALES	MALES
69	166	137	142	83	95
126	126	117	96	176	167
158	139	104	104	91	86
124	121	97	105	175	130
159	216	115	125	140	139
163	132	105	98	94	76
180	170	115	79	138	120
199	196	84	87	116	115
154	155	93	81	183	185
153	153	115	89	163	135
157	167	93	75	107	78
165	135	104	105	138	120
104	117	93	82	164	161
183	179	110	136	218	229
136	142	112	110	215	210
170	156	139	129	211	196
173	161	144	132	240	244
151	133	90	87	195	236
98	98	125	93	162	165
129	99	88	82	102	98
122	116	121	119	236	230
106	95	137	117	144	154
70	90	134	135	166	167
96	79	122	96	172	165

To determine the approximate location of the lethal upon the chromosome virgin females of the fifth generation (table 11) were mated, some to sable males, and some to bar eyed males.

The counts of the second generation of crosses with sable and with bar eyed males are shown in table 12. The 1 : 1 ratios are omitted.

The data in this table show that the distance of this lethal from bar is 8.3.

If the locus of the factor for sable is 43 and that for bar is 57, the data of table 12 show that the locus of the new lethal is $43 + 23.5$ or 66.5, since the distance of lethal from the factor for bar is only 8.3. The locus of the lethal must be 'to the right' of both factors since $43 + 23.5$ or 66.5 is approximately equal

TABLE 9

FEMALES	MALES	FEMALES	MALES	FEMALES	MALES
146	151	164	161	164	169
157	168	82	125	148	131
83	79	183	136	266	239
88	99	197	193	201	216
95	104	114	93	167	160
108	103	114	111	133	129
76	78	96	106	112	140
140	138	88	86	106	86
190	213	93	120	116	97
105	85	114	95	169	173
100	79	155	230	199	185
176	152	106	111	181	205
131	155	98	103	145	154
102	84	142	119	106	96
160	133	91	64	110	96
171	153	138	110	181	197
250	188	143	135	195	178
252	216	152	135	142	162
150	163	180	149	266	108
139	105	148	134	86	55

to $57 + 8.3$ or 65.3 or at 65.6 . The locus indicated by both experiments when the data are weighted proportionately and a correction is made for double crossing over is 66.2 .

In the spring of 1914, an interesting lethal turned up in my 1910 stock. Half of the males hatched out as normal males but of the other half, though able to pass through the different stages of metamorphosis, many of them were unable to escape from the pupa case. Those that chanced to do so fell over on one side when trying to walk. I examined all the appendages carefully but noticed no abnormalities. Nevertheless, the legs did not seem strong enough to support the body, nor did they seem to move coördinately and for that reason would so often become entangled with one another that the fly could not get them separated and would die from exhaustion in a day or so. Not any of these males lived longer than two days.

Whether the first lethal of the 1910 and the lethals of the 1911 flies allow any development of the lethal bearing male at all, is still under investigation.

TABLE 10

NO. OF PAIR	FEMALES	MALES	SEX RATIO	NO. OF PAIR	FEMALES	MALES	SEX RATIO
1	211	99	2.13:1	31	112	49	2.28:1
2	197	87	2.26:1	32	56	54	1.03:1
3	161	91	1.77:1	33	176	103	1.70:1
4	123	83	1.48:1	34	46	51	0.90:1
5	201	100	2.00:1	35	143	78	1.86:1
6	64	76	0.84:1	36	44	43	1.00:1
7	277	129	2.15:1	37	205	128	1.60:1
8	253	125	2.02:1	38	49	50	1.00:1
9	63	44	1.43:1	39	68	27	2.19:1
10	112	67	1.67:1	40	26	23	1.13:1
11	96	48	2.00:1	41	73	66	1.10:1
12	244	116	2.10:1	42	28	14	2.00:1
13	155	92	1.68:1	43	160	36	4.44:1
14	69	67	1.03:1	44	124	51	2.43:1
15	72	73	1.00:1	45	109	43	2.30:1
16	119	69	1.72:1	46	45	42	1.00:1
17	168	102	1.64:1	47	50	44	1.14:1
18	71	50	1.42:1	48	173	90	1.92:1
19	38	12	3.00:1	49	115	78	1.47:1
20	90	36	2.50:1	50	44	28	1.58:1
21	213	141	1.51:1	51	64	30	2.00:1
22	70	60	1.16:1	52	58	64	0.90:1
23	208	90	2.31:1	53	164	74	2.21:1
24	117	74	1.58:1	54	73	70	1.00:1
25	64	61	1.05:1	55	27	29	0.93:1
26	85	60	1.41:1	56	103	72	1.34:1
27	69	35	1.96:1	57	56	62	0.90:1
28	88	69	1.28:1	58	191	118	1.61:1
29	231	123	1.88:1	59	193	88	2.19:1
30	217	119	1.82:1	60	148	85	1.74:1

Since no lethal has been found in the hundreds of pairs of fresh wild stock examined and since lethals have occurred in many of the inbred stocks, it may appear that inbreeding (with its constraints of confinement and homogeneous feeding) tends to cause the mutation to appear or else the removal of the flies from the competition that takes place under wild conditions makes possible the preservation and continuance of any lethal factors that may appear.

A discussion of these alternatives would involve a fuller knowledge than we have at present of the causes of mutations and the

TABLE 11

1910 Lethal	No. of Pair	♀s	♂s	No. of Pair	♀s	♂s
F ₁ ♀s ♂s (266 108)	7	(277	129)	$\times W \rightarrow$	1 (208	104)
					4 (178	76)
					7 (169	69)
	8	(253	125)	$\times W \rightarrow$	6 (229	107)
					10 (52	19)
					12 (258	127)
					13 (207	107)
	12	(244	116)	$\times W \rightarrow$	7 (146	93)
					4 (189	99)
					8 (170	94)
23	(208	90)	$\times W \rightarrow$	6 (147	93)	
				8 (228	92)	
59	(193	88)	$\times W \rightarrow$	1 (228	101)	
				10 (210	97)	
				13 (212	105)	

* The 1 : 1 ratios are omitted.

TABLE 11

No. of Pair	R ♀s	R ♂s	W ♀s	W ♂s		No. of Pair	R ♀s	R ♂s	W ♀s	W ♂s
$\left\{ \begin{array}{l} 1 (148) \\ 4 (220) \\ 6 (179) \\ 7 (160) \end{array} \right.$	75	166	123	135	$\times W \rightarrow$	$\left\{ \begin{array}{l} 1 (148) \\ 3 (128) \\ 4 (131) \\ 6 (132) \\ 7 (159) \\ 8 (158) \end{array} \right.$	56	135	77	61
							29	107	61	
							46	132	85	
							42	92	68	
							54	121	101	
							61	152	79	
$\left\{ \begin{array}{l} 2 (170) \\ 5 (140) \end{array} \right.$	80	74	90	93	$\times W \rightarrow$	$\left\{ \begin{array}{l} 1 (67) \\ 4 (88) \\ 5 (142) \\ 6 (105) \\ 8 (65) \\ 9 (119) \end{array} \right.$	27	55	37	51
							26	78	51	
							54	96	64	
							45	92	43	
							20	76	35	
							61	93	61	
$\left\{ \begin{array}{l} 6 (175) \\ 7 (120) \\ 9 (109) \end{array} \right.$	64	201	95							
	44	122	66							
	66	118	46							
$\left\{ \begin{array}{l} 1 (133) \\ 3 (183) \\ 4 (161) \\ 7 (160) \end{array} \right.$	56	135	68	97	$\times W \rightarrow$	$\left\{ \begin{array}{l} 3 (151) \\ 5 (134) \\ 6 (132) \\ 7 (130) \\ 8 (124) \\ 9 (128) \\ 10 (101) \end{array} \right.$	52	135	82	85
	76	145	89	84			59	117	85	
	64	162	89	84			47	117	73	
	57	165	84				53	126	67	
							57	112	55	
							61	137	68	
							42	80	56	
1 (138	68	146	77							
$\left\{ \begin{array}{l} 1 (113) \\ 2 (166) \\ 5 (116) \\ 10 (147) \\ 11 (153) \\ 12 (224) \\ 15 (120) \end{array} \right.$	61	118	58	91	$\times W \rightarrow$	$\left\{ \begin{array}{l} 5 (114) \\ 6 (108) \\ 9 (135) \\ 11 (124) \\ 12 (139) \end{array} \right.$	47	96	62	63
	80	170	91	146			56	103	63	
	57	212	146				53	124	74	
	57	108	83	86			52	103	56	
	67	139	86	69			60	141	72	
	83	194	86							
	60	124	69							
2 (121	45	106	72			2 (109	34	139	81	
$\left\{ \begin{array}{l} 4 (113) \\ 6 (124) \\ 9 (117) \\ 10 (173) \\ 11 (130) \\ 13 (121) \end{array} \right.$	64	115	63	62	$\times W \rightarrow$	$\left\{ \begin{array}{l} 3 (84) \\ 6 (108) \\ 7 (125) \\ 12 (135) \\ 13 (109) \end{array} \right.$	38	80	48	57
	95	124	62	56			46	90	57	
	49	131	57	59			67	112	63	
	62	96	56	69			49	78	70	
	56	109	59				42	77	58	
	54	123	69							
$\left\{ \begin{array}{l} 4 (113) \\ 6 (139) \\ 8 (117) \\ 9 (124) \end{array} \right.$	56	111	71	76	$\times W \rightarrow$	7 (76	17	51	33)	
	50	134	76	63			1405	1648		
	42	112	63							
	65	113	65							

Total no. of ♂s = 3053 No. of cross overs = 1405
 The ratio of the cross overs to all the ♂s = $1405 \div 3053 = .46$

frequency of their appearance. For the present, therefore, the fact of the occurrence of the lethals in the inbred stocks is the one important result of this examination.

THE PRESENCE OF TWO LETHALS

Number 4 of 13, 2, of table 6 yielded a ratio of 27.33 : 1. It seemed probable in this case that two different lethal factors were present, one in each chromosome. This might seem to prevent all the sons from developing since each son must get one or the other maternal sex chromosome; but the survival of the three males would be possible through the crossing over

TABLE 12 (a)

Heterozygous Bar Female × *Bar Male*

NO. OF PAIR	FEMALES	MALES		CROSSOVER PERCENTAGE
	Bar	Bar	Normal	
1	284	108	5	4.4
2	214	93	13	12.3
3	120	47	3	6.0
4	187	86	12	12.2
5	173	72	4	5.3
6	146	64	8	11.1
7	187	78	8	9.4
8	247	122	5	4.2
9	138	91	4	4.2
10	166	52	4	7.1
11	167	74	11	13.0
12	183	75	12	13.0
13	123	75	10	12.0
14	230	129	10	7.1
15	121	56	3	5.0
16	193	60	7	10.0
17	241	107	10	8.0
18	159	84	2	2.3
19	143	77	9	10.0
20	139	50	4	8.0
		1590	144	

Total number of ♂s, 1734; Crossovers = 144.

Crossover percentage = $144 \div 1734$ or 8.3.

TABLE 12 (b)
Red eyed ♀ heterozygous for sable and lethal × *sable ♂*

NÖ. OF PAIR	SABLE	NORMAL	SABLE	NORMAL	CROSSOVER PERCENTAGE
1	45	40	35	6	15.0
2	111	101	80	20	20.0
3	167	112	84	30	26.3
4	110	74	69	21	24.6
5	162	104	95	37	28.0
6	77	59	45	9	17.0
7	149	113	92	22	20.0
8	92	104	58	25	29.0
9	91	105	65	25	27.7
10	85	78	55	16	22.5
11	134	115	78	29	27.7
12	111	113	75	21	22.1
13	138	138	89	33	27.0
14	35	38	35	5	12.5
15	27	52	29	8	21.6
16	121	114	63	21	25.3
17	54	71	48	14	22.6
18	86	91	80	26	24.5
19	73	83	79	19	19.4
			1254	387	

The total number of males = 1641; Crossovers = 387.

The crossover percentage = $387 \div 1641$ or 23.5.

Therefore, the distance of lethal from sable is 23.5.

of one of the lethal factors from one chromosome in the other, thus freeing one chromosome from its lethal factor.

TABLE 13
 13, 2, 1, 4

NO. OF PAIR	FEMALES		MALES		CROSSING OVER BETWEEN WHITE AND LETHAL	SEX RATIO
	Red	White	Red	White		
1	172	174	32	116	21.6	2.34
2	217	228	30	136	18.1	2.72
3	147	174	29	126	18.7	2.07
4	215	216	28	174	13.9	2.13
5	229	194	44	124	26.2	2.52
6	228	209	30	144	17.2	2.51
7	184	201	35	139	20.1	2.21
8	214	212	25	147	14.5	2.47
9	193	155	38	138	21.6	1.97

Nine of the daughters were mated individually to white eyed males and gave the results in table 13.

All nine daughters gave a 2 : 1 ratio which is expected if their mother had two lethals.

Ten other daughters (from the very high ratio mother) were mated to their red eyed brothers¹ and gave the results in table 14.

Six red females of table 13 were tested and gave the following results:

13, 2, 1, 4, 7

NO. OF PAIR	FEMALES		MALES		CROSSING OVER BETWEEN WHITE AND LETHAL	SEX RATIO
	Red	White	Red	White		
1	59	51	4	47	7.8	2.3 : 1
2	88	84	8	59	12.0	2.6 : 1
3	87	66	12	72	15.4	1.8 : 1

13, 2, 14, 8

1	90	80	11	60	15.5	2.3 : 1
2	73	79	10	73	12.0	1.8 : 1
3	75	66	11	63	15.1	1.9 : 1

Three of the sisters by brother No. 1 failed to produce any progeny when transferred to separate bottles. Each of the other sisters, however, showed the presence of a lethal factor. Thus all 19 daughters of the female gave a 2 : 1 ratio. There can be no question but that the high sex ratio of the mother was due to two lethals. Virgin red eyed daughters of some of these females were then mated to white eyed brothers with results as shown in table 15.

Since the mothers of the females used in table 15 were all heterozygous for white and for one or the other lethal, they would, when mated to red eyed males, produce two kinds of daughters; one-half heterozygous for a lethal and the other half

¹ If the sons that came through were due to crossing over, then the X chromosome that went into each is free from lethals and consequently they must be normal males. The normality of these three males was also tested by mating them to wild females. The sex ratio was normal. The daughters of the three males were tested individually and gave normal ratios.

TABLE 14
Ten sisters by brother No. 1

NO. OF PAIR	RED FEMALES	RED MALES	WHITE MALES	SEX RATIO	CROSSING OVER BETWEEN WHITE AND LETHAL
1	105	8	41	2.14 : 1	16.7
3	224	23	108	1.80 : 1	17.6
5	64	6	18	2.70 : 1	25.0
6	90	7	36	2.09 : 1	16.3
7	35	2	7	3.88 : 1	22.2
8	38	2	6	4.75 : 1	25.0
9	36	3	12	2.40 : 1	20.0
Mass.....	428	61	136	2.18 : 1	30.9

Three sisters by brother No. 2

1	128	18	38	2.0 : 1	32.1
2	176	12	78	2.0 : 1	13.3
3	197	11	78	2.1 : 1	12.4
Mass.....	336	25	109	2.5 : 1	18.6

heterozygous for white. The females heterozygous for white when mated to white eyed males would produce equal numbers of red eyed and white eyed males and females (table 15) except where the lethal may have crossed over to the factor for white (as was the case in numbers 5 and 1, starred in table 15).² The females heterozygous for lethal when mated to the white eyed males produce the 2 : 1 ratio, also indicated in table 15.

Matings were, also, made between the three males and daughters of the sisters of the males with results as follows:

(13, 2, 1, 4; *Female by W male*)F; *Female by No. 2 male*

NO. OF PAIR	FEMALES	MALES		SEX RATIO	CROSSING OVER BETWEEN WHITE AND LETHAL
	Red	Red	White		
Mass	236	6	95	2.3 : 1	5.9
1	172	16	85	1.7 : 1	15.8
2	116	9	43	2.2 : 1	17.3
3	125	7	40	2.7 : 1	14.9
4	141	5	61	2.1 : 1	7.6

² The other class resulting from such crossing over should contain neither the white nor the lethal, and one such female is recorded in table 15.

TABLE 15
(*Sister by No. 1 male*), F_2

NO. OF PAIR	FEMALES		MALES		SEX RATIO	CROSSING OVER BETWEEN WHITE AND LETHAL
	Red	White	Red	White		
1	72	80	69	78	1.02 : 1	18.2
2	63	48	49	49	1.13 : 1	
3	18		8		2.25 : 1	
4	50		32		1.56 : 1	
5*	43	51	27	6	2.85 : 1	

(*Sister by No. 1 male*) 3 F_2

1	145		72		2.00 : 1	
2	141		75		2.00 : 1	
3	53	67	47	75	1.00 : 1	
4	30	42	32	41	1.00 : 1	
5	43	34	50	44	0.82 : 1	
6	161	34	67	44	1.76 : 1	

(*Sister by No. 2 male*), F_2

1	137		72		1.90 : 1	
2	103		107		0.90 : 1	
3	72	86	81	74	1.00 : 1	
4	164		86		2.00 : 1	
5	101		47		2.10 : 1	

(*Sister by No. 3 male*), 3 F_2

1*	101	85	64	14	2.40 : 1	19.0
2	29	24	24	20	1.00 : 1	
3	168		65		2.60 : 1	

(*Sister by No. 2 male*) Mass F_2

1	97	69	77	70	1.00 : 1	
2	78		24		3.00 : 1	
3	153		72		2.00 : 1	

The four daughters show the presence of a lethal.

Summary: The nineteen tested females of 13, 2, 1, 4 (table 6) gave a 2 : 1 ratio. Other tests showed that the three males behaved like normal males. The explanation of her high ratio (2 : 1) is that two lethal factors were present.

Table 16 gives some of the counts of the descendants of 13, 2, 1, 4 with white eyed males.

TABLE 16

FEMALES		MALES		CROSSING OVER BETWEEN WHITE AND LETHAL
Red	White	Red	White	
162	85	14	79	15.0
228	209	30	144	17.2
100	84	13	68	16.0
91	91	12	68	15.0
127	123	15	85	15.0
122	125	16	108	12.8
127	110	18	117	13.3
115	115	23	119	16.2
95	86	12	57	17.4
142	105	15	88	14.5
137	138	20	118	14.4
43	43	8	39	17.0
87	66	12	72	14.3
90	70	11	60	15.5
108	102	17	79	17.7
72	65	15	53	22.0
76	77	13	48	21.3
120	140	30	120	20.0
119	100	29	90	24.3
130	98	18	69	20.7
149	133	22	95	18.8
193	155	38	138	21.6
229	194	44	124	26.2
172	174	32	116	21.6
193	155	38	138	21.6
184	201	35	139	20.1

Numbers 5 and 1 starred of table 15 show a decided decrease in the number of white males. It looked as if the lethal factor had crossed over into the chromosome carrying the factor for white. To examine this, virgin females from number 1 were mated to white eyed miniature males as shown in table 17.

A lethal factor connected with the factor for white is evidently present since all the white eyed females gave a 2 : 1 ratio.

The red eyed sisters of the white eyed females in table 17a should bear no lethal if, as the last table indicates, crossing over

TABLE 17 (a)

White eyed granddaughters of sister and brother by a white eyed miniature male

NO. OF PAIR	WHITE FEMALES	WHITE MALES	SEX RATIO
1	79	44	1.8 : 1
2	171	71	2.4 : 1
3	176	88	2.0 : 1
4	182	90	2.0 : 1
5	187	88	2.1 : 1
6	176	63	2.8 : 1
7	139	48	2.9 : 1
8	182	72	2.5 : 1
9	170	104	1.6 : 1
10	164	68	2.4 : 1

had taken place, except when crossing over occurred again in the mother. This was tested (table 17b).

TABLE 17 (b)

Red eyed granddaughters of sister and brother by white eyed miniature male

NO. OF PAIR	FEMALES		MALES		SEX RATIO
	Red	White	Red	White	
1	48	59	20	43	1.54 : 1
2	76	78	74	58	1.16 : 1
3	82	59	50	50	1.41 : 1
4	69	68	66	62	1.07 : 1
5	76	52	67	51	1.08 : 1
6	65	63	80	61	0.90 : 1
7	88	53	29	59	1.60 : 1
8	33	34	5	27	2.09 : 1
9	42	53	6	35	2.32 : 1
10	79	65	1	44	3.20 : 1
11	64	99	7	71	2.09 : 1

Four of the red eyed females gave a 2 : 1 ratio indicating that crossing over did occur in the mother.

To determine whether this lethal is the new one or the original one whose locus was shown to be at 23.7 the white eyed females were mated to eosin³ to find the locus of the factor in the chromo-

³ Eosin is an allelomorph of white. A female that has the eosin factor in one X and the white factor in the other X can be distinguished from a pure female with eosin in both X's.

somes. If it is a crossover it should be found to have the same locus as the factor with the red.

The white eyed females mated to eosin males gave white-eosin³ long winged females (with the factor for lethal): white-eosin miniature females; white eyed miniature males; and a few white eyed long winged males as crossovers.

The white-eosin long winged females were again mated to eosin miniature males. This mating gave white-eosin long winged females with the lethal factor, eosin miniature females without the lethal factor, eosin long winged females and, white-eosin miniature females, eosin miniature males, white eyed miniature males, eosin long winged males and white long winged males. The single crossovers are the white miniature and the eosin long winged males, while the white long winged males are double crossovers. In table 18 some of the counts are given.

The crossover value of white with the lethal involved is 15.6 and that of the lethal with miniature is 19.9. Therefore the locus of this lethal is at 16.7, that is, 1.1 plus 15.6. The locus of the original lethal was shown to be at 23.7, so that this lethal with a locus at 16.7 must be the new lethal whose advent led to the production of the high sex ratio. The mother of the high sex ratio carried in one of her X chromosomes the original lethal at 23.7 and in the other X chromosome, the one derived from the father, the new lethal at 16.7.

If this female contained two lethals some of her descendants should have one and some the other; and these two kinds should be expected to give slightly different linkage values with white. If, then, the values obtained from all of her descendants be plotted they should give a bimodal curve. Diagram 1 was made from such data except that the diagram does not include the data in table 18.

In diagram 1 there is a strong mode at 15 which corresponds to the new lethal, but the mode which corresponds to the original lethal gives only a weak mode at 22; indeed the curve is not obviously bimodal, small number of determinations not being sufficient to distinguish clearly between the two lethals. The

TABLE 18

NO. OF PAIR	FEMALES				MALES				LINKAGE OF WHITE WITH LETHAL	LINKAGE OF LETHAL WITH MINIATURE
	White- eosin long	Eosin minia- ture	White. eosin minia- ture	Eosin long	Eosin minia- ture	White minia- ture	Eosin long	White long		
									W	M
1	28	32	17	10	27	4	10	0	9.8	24.4
2	34	22	24	11	32	7	7	2	18.8	18.8
3	35	24	17	18	29	9	6	0	20.5	14.0
4	39	35	14	9	29	4	9	0	9.5	21.4
5	81	62	69	36	87	15	23	1	12.7	19.0
6	66	82	42	25	74	17	20	3	17.5	20.1
7	31	11	25	7	25	4	5	0	11.8	14.7
8	34	30	26	17	41	2	9	0	3.8	17.3
9	39	42	22	10	42	5	8	0	9.0	14.4
10	48	48	51	27	59	9	18	0	10.46	20.9
11	28	40	24	15	25	5	10	0	12.5	25.0
12	47	44	19	16	48	6	15	0	8.7	21.7
13	17	23	14	17	26	6	10	0	14.3	24.3
14	44	24	21	11	35	6	10	0	11.7	19.6
15	88	62	62	31	63	12	23	0	12.2	23.4
16	93	78	37	30	100	10	30	1	8.0	22.0
17	113	120	63	80	101	25	37	1	15.6	23.1
18	104	105	70	78	83	21	33	3	17.1	23.5
19	58	42	39	34	49	15	17	3	21.4	23.8
20	87	73	51	46	78	17	18	1	15.8	16.6
21	60	60	41	38	44	9	13	1	14.9	20.9
22	60	44	38	22	47	16	18	2	21.6	24.0
23	48	45	45	22	30	9	13	1	19.0	26.5
24	48	35	38	23	58	11	17	1	13.8	20.7
25	95	76	54	26	76	26	19	3	23.4	17.7
26	58	49	39	29	56	13	14	1	16.6	18.0
27	56	35	24	37	64	21	11	3	24.2	14.1
28	63	60	49	37	69	20	16	2	20.5	17.0
29	54	44	48	33	47	4	11	2	9.4	20.3
30	52	39	38	24	55	13	19	1	15.9	22.6
31	49	38	37	25	53	5	13	0	7.0	18.3
32	53	54	29	16	49	2	9	0	3.3	15.0
33	65	45	47	30	71	14	15	1	14.8	15.8
34	107	54	67	38	100	21	26	3	16.0	19.4
35	101	54	67	29	78	21	28	0	16.4	22.0
36	69	48	52	30	63	16	23	2	17.3	24.0
37	58	24	66	25	50	8	9	3	15.7	17.0
38	57	38	47	25	57	17	17	0	18.7	18.7
39	63	45	41	33	54	18	13	1	22.1	16.2
40	28	28	19	16	39	8	12	0	13.5	20.3
41	60	36	27	26	28	6	4	2	20.0	15.0
42	64	34	51	32	71	15	23	1	14.5	21.9
43	26	32	45	25	51	8	13	2	13.5	20.2
44	52	50	46	34	57	24	10	1	27.0	12.0
	2198	2174	1780	1201	2421	524	685	48	6633	8656

determinations of table 18 are all of the crossover value white new lethal, and are expected to give a unimodal curve with the mode at 15.

SUMMARY

Lethal factors were found in inbred stock only. Fresh wild stock gave no unusual sex ratios.

The first lethal (l_{ss}) was found in stock caught in 1911 and has its locus at 23.7. One female of this stock gave an extraordinarily high sex ratio; viz., 83 females to 3 males. That this extraordinary sex ratio is due to the presence of two lethal factors, one in each X chromosome, is shown by the fact that all (not half) the daughters gave a 2 to 1 sex ratio.

The new lethal (l_{sb}) that appeared in the female with extraordinary sex ratio crossed over, in one case examined, to the X chromosome that carried the factor for white. Its locus is at 16.7. Two other lethals were found in the 1910 stock. The first (l_{sc}) has its locus at 65.2. The other (l_{sd}) differs from all other lethals in that the lethal bearing males emerge from the pupa case, and die almost immediately on becoming adult flies.