THE EFFECT OF SELECTION UPON THE SEX-RATIO IN DROSOPHILA AMPELOPHILA.

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It is a well-known fact that sex-ratios in most animals approximate equality. The ratio is seldom one of exact equality, however, and the preponderance may be in favor either of the males or the females. The variation from equality is fairly constant for the species. For man the ratio has been found to be 100 females to 105 males; for the horse, 100 to 98; for the cow, 100 to 107; for the sheep, 100 to 97; for the pig, 100 to 111; for the dove, 100 to 105; and for the hen, 100 to 94. These variations are so constant that they cannot be attributed to chance and they are irregularities for which our present theories of sex determination offer no adequate explanation.

The writer has attempted to determine the sex-ratio of the fruit fly, *Drosophila ampelophila*. The determination was made from three unrelated stocks in which the best possible environmental conditions were provided. All matings were in single pairs. Over 35,000 flies were examined and the ratio was found to be 100 females to 95 males.

Moenkhaus tested the effect of selection upon the sex-ratio of *Drosophila ampelophila* and decided that the sex-ratio in this species is "amenable to selection." If it be true that the relative number of males and females in a strain can be varied by selection, the present theories of sex determination must be somewhat modified. Although this fact would not necessarily disprove the theories of sex determination, it would necessitate the assumption of an hypothesis of selective fertilization or of differential mortality or viability of the determining elements.

In view of the vital bearing of Moenkhaus's findings upon the theories of sex determination, it has been deemed worth while to repeat his work.

[1] Contribution No. 159.

Methods and Material.

The selection experiments were carried out upon three unrelated stocks. The stock for the first experiment was collected in Bloomington, Ind.; for the second, in Saratoga, Ind.; and for the third, in Warsaw, Ind. In the first two cases the experiments were started as soon as the stocks were collected from nature but the Warsaw stock was inbred in the laboratory for about six months before the experiment was started. At all times the greatest care was exercised to prevent contamination. The flies were provided with an abundance of food and care was taken to examine all the offspring of each pair. All matings were single pair matings.

Each experiment was conducted upon the offspring of a single pair of flies, that is, for the first experiment, a virgin female was selected from the Bloomington stock and mated to a brother. From among the offspring of this pair of flies, the parents of the two strains were obtained. The one strain in which there was selection for a relatively high number of females in comparison to the number of males, has been called the "high" strain and the one in which the selection was in the opposite direction, has been called the "low" strain. Before selection was started, a sufficient number of flies were examined to obtain a fair estimate of the sex-ratio of the stock under consideration. Moenkhaus's high and low strains were not offspring of a single pair of flies but were obtained by selecting from nature, pairs which had unusual ratios in the desired direction. Furthermore, he knew nothing of the original sex-ratio of his strains before selection began.

In each generation an attempt was made to examine the offspring of ten pairs in each strain. Unsuccessful matings, usually due to poor food conditions, sometimes prevented this. In each generation, the pair which gave the most extreme ratio in the desired direction was used as the parent of the succeeding generation. At times, technical difficulties prevented the most extreme pair being used and in these cases the next best was used. Pairs showing extreme ratios but producing a small number of offspring were not used. Since it was not possible to know which pair had the most desirable ratio till all of the offspring of all the pairs in a generation were examined, the technique of the experiment was made somewhat difficult. This might have been overcome by isolating some males and females from each mating and then, after the counts for that generation were completed, mating the offspring of the pair giving the most extreme ratio. This would have prolonged the experiment, so to avoid delay, at about the eighth or ninth day after the young had begun to emerge, fifteen pairs were mated from among the offspring of each mating which was being examined. In this way, by the time one generation was finished, the next was almost ready to begin to emerge. Since ten matings in each strain were examined, this necessitated the mating of about300 pairs of flies in each generation. A control was also carried in each experiment in which a few hundred flies were examined each generation.

Preliminary Experiment.

This experiment was to test whether the age of the parents would in any way influence the relative number of males and females produced. Several matings were made and the adults

Table I.

Showing Results of Experiment to Test the Effect of Age of Parent Upon the Sex-Ratio.

Culture Number.	Original Mating 1 Day Old.		First Transfer 11 Days Old.		Second Transfer 18 Days Old.		Third Transfer 26 Days Old.		Fourth Transfer 34 Days Old.		Fifth Transfer 42 Days Old.		Sixth Transfer 50 Days Old.		Seventh Transfer 58 Days Old.		Eighth Transfer 62 Days Old.		Totals.	
	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.
202A$_2$.	56	68	112	110	105	111	51	40											324	329
203A$_2$.	93	92	110	128	60	89	126	124	172	152	49	60							610	645
203A$_3$.	156	162	135	150	58	60	78	89	136	123	91	93							654	677
204A$_1$.	232	194	140	146	20	24													392	364
204A$_2$.	223	234	155	156	157	151	115	115											650	656
204A$_3$.	134	128	46	70	38	37													218	235
205A$_2$.	214	202	109	114	86	104	115	110	12	12									536	542
205A$_3$.	187	161	140	130	103	113	114	107											544	511
206A$_1$.	68	58	80	55	75	77	78	76	94	89	72	95	126	118	45	45	10	5	648	618
206A$_2$.	149	152	173	176	79	126	135	106	152	130	34	23							722	713
206A$_3$.	173	164	179	207	141	134	129	162	156	159	183	203	71	91					1032	1120
207A$_1$.	90	87	153	143	81	90	100	100											424	420
207A$_2$.	120	118	129	123	86	83	84	69											419	393

were transferred to new bottles every eight days as long as they both lived. The age of the parents does not influence the sex-ratio as is shown by the results given in Table I.

Selection Experiment I. (Bloomington Stock.)

From a stock of flies collected in Bloomington, a virgin female was selected and mated to a male from the same stock. From the offspring of this pair of flies the high and low strains were started. Before selection was begun, 2,936 flies were examined for sex. The ratio was 1,456 males to 1,480 females, or 1 male to 1.06 females. The ratio here is stated in just the reverse order from the customary form but since Moenkhaus used the reverse order, the ratios in the present discussion will be stated likewise to make the two experiments more comparable. Table II. gives the history of the origin of the high and low strains.

Table II.[1]

Showing Origin of the "High" and "Low" Strains of the Bloomington Stock.

206 (Original pair)

206 A_1	206 A_2	206 A_3
68–58	149–152	173–164

206 B_1	206 B_2
185–176	175–166

206 C_3	206 C_4	206 C_5	206 C_7	206 C_8	206 C_{11}	206 C_{12}
15–30	84–74	63–52	108–130	93–100	152–140	91–121
		Low				*High*

Tables III. and IV. give the history of the high and low strains. There is no indication of the ratios having changed in the direction of the selection. In fact, in the high strain where there was selection for a relatively high number of females, the totals show a relatively lower number of females than in the low strain. The totals for the high strain were 8,837 males to 8,942 females or a ratio of 1 male to 1.012 females while in the low strain there were 8,368 males to 9,091 females or a ratio of 1 male to 1.086 females.

[1] In all tables where two numbers are expressed with a dash between them, as 68–58, the number to the left of the dash always represents the male count and the number to the right, the female count.

TABLE III.

Showing Summary of the "High" Strain of the Bloomington Stock. Experiment I.

Generation.											Totals.
A	91 ♂–121 ♀ (*1 : 1.33*) (From Mating 206C12)										
B	2	4	5	6	7	8	9	10	11	13	
	145–150	200–224	216–229	188–198	179–177	229–183	154–162	99–85	111–116	121–140	1642–1664
	1 : 1.03	*1 : 1.12*	*1 : 1.06*	*1 : 1.05*	*1 : .99*	*1 : .80*	*1 : 1.05*	*1 : .85*	*1 : 1.05*	*1 : 1.16*	*1 : 1.013*
C	1	3	4	5	6	8	10	12		13	
	78–65	106–118	153–148	167–179	53–53	176–165	143–136	127–115		42–69	1045–1048
	1 : .83	*1 : 1.11*	*1 : .97*	*1 : 1.07*	*1 : 1*	*1 : .94*	*1 : .95*	*1 : .91*		*1 : 1.64*	*1 : 1.003*
D	2	3	5	6	7	9	10	11	12	14	
	201–233	83–83	115–110	92–90	221–204	117–125	95–104	37–35	139–160	284–254	1384–1399
	1 : 1.16	*1 : 1.0*	*1 : .96*	*1 : .99*	*1 : .92*	*1 : 1.07*	*1 : 1.09*	*1 : .95*	*1 : 1.15*	*1 : .89*	*1 : 1.01*
E	1	2	3	4	5	6	7	10	12	13	
	117–99	184–176	223–225	194–173	302–279	179–180	252–278	93–111	195–194	36–31	1775–1746
	1 : .85	*1 : .96*	*1 : 1.01*	*1 : .89*	*1 : .92*	*1 : 1.01*	*1 : 1.1*	*1 : 1.19*	*1 : .99*	*1 : .86*	*1 : .984*
F	1	2	3	4	5	7	9	12	13	14	
	179–177	208–188	79–70	98–128	188–154	124–142	149–159	158–154	113–139	52–61	1348–1372
	1 : .988	*1 : .90*	*1 : .89*	*1 : 1.31*	*1 : .82*	*1 : 1.15*	*1 : 1.07*	*1 : .97*	*1 : 1.241*	*1 : 1.18*	*1 : 1.018*
G	1	2	5	6	8	10	11	12	14	15	
	85–96	166–168	31–55	164–174	219–223	125–135	144–143	70–80	111–119	86–96	1201–1289
	1 : 1.13	*1 : 1.01*	*1 : 1.77*	*1 : 1.06*	*1 : 1.02*	*1 : 1.08*	*1 : .99*	*1 : 1.143*	*1 : 1.07*	*1 : 1.12*	*1 : 1.073*
H	3			4		8	9	10			
	95–101			116–103		64–57	50–35	117–128			442–424
	1 : 1.06			*1 : .89*		*1 : .89*	*1 : .70*	*1 : 1.09*			*1 : .959*

Grand Total........8837–8942
1 : 1.012

TABLE IV.

Showing Summary of the "Low" Strain of the Bloomington Stock. Experiment I.

Generation.

A 63 ♂–52 ♀ (*1 : .83*)
(From Mating $206C_5$)

Generation											Totals.
B	1	3	4	5	7	8	9	10			
	164–228	227–248	109–113	138–146	190–187	35–88	185–184	191–197			1239–1391
	1 : 1.39	*1 : 1.09*	*1 : 1.04*	*1 : 1.06*	*1 : .98*	*1 : 2.51*	*1 : .99*	*1 : 1.03*			*1 : 1.123*
C	1	4	5	7	8	9	10	11			
	123–135	51–53	291–327	105–119	120–114	60–44	176–181	52–71			978–1044
	1 : 1.1	*1 : 1.04*	*1 : 1.12*	*1 : 1.13*	*1 : .95*	*1 : .73*	*1 : 1.03*	*1 : 1.37*			*1 : 1.067*
D	2	6	7	9	10	11	12	13	14	15	
	175–207	153–128	136–160	130–126	133–158	192–196	85–104	225–261	135–158	181–199	1545–1697
	1 : 1.18	*1 : .84*	*1 : 1.18*	*1 : .97*	*1 : 1.19*	*1 : 1.03*	*1 : 1.22*	*1 : 1.16*	*1 : 1.17*	*1 : 1.2*	*1 : 1.098*
E	1	2	4	5	8	9	10	11	12	15	
	176–141	125–123	138–131	141–135	151–151	139–142	285–277	167–141	193–234	180–180	1695–1655
	1 : .8	*1 : .98*	*1 : .95*	*1 : .96*	*1 : 1*	*1 : 1.02*	*1 : .97*	*1 : .84*	*1 : 1.21*	*1 : 1*	*1 : .976*
F	1	2	3	4	6	7	9	11	12	14	
	275–252	174–167	145–179	115–105	173–190	194–180	164–264	246–266	219–215	181–202	1886–2020
	1 : .92	*1 : .96*	*1 : 1.23*	*1 : .91*	*1 : 1.10*	*1 : .93*	*1 : 1.61*	*1 : 1.08*	*1 : .981*	*1 : 1.11*	*1 : 1.071*
G	1		6		9	11	14	15			
	114–134		84–180		89–83	205–190	37–30	84–132			613–749
	1 : 1.18		*1 : 2.14*		*1 : .93*	*1 : .93*	*1 : .81*	*1 : 1.57*			*1 : 1.221*
H	1	4	5	7	8	10	12	13	14	17	
	52–64	56–72	59–87	48–70	38–47	47–53	8–14	9–9	45–61	50–58	412–535
	1 : 1.23	*1 : 1.29*	*1 : 1.47*	*1 : 1.46*	*1 : 1.24*	*1 : 1.13*	*1 : 1.75*	*1 : 1*	*1 : 1.36*	*1 : 1.16*	*1 : 1.298*

Grand Total........8368–9091
1 : 1.086

Selection Experiment II. (Saratoga Stock.)

In the first experiment, a much larger number of flies were examined than were examined by Moenkhaus. But since opposite results were obtained, a criticism might be offered that the writer, by chance, selected a stock which was not affected by selection. So the second experiment was made upon a new and unrelated stock. This stock was collected at Saratoga, Indiana. Fifty matings were made from among the offspring of a single pair. The extremes of these fifty were used as parents of the high and low strains. The counts of these fifty pairs are given in Table V. There were 21,019 flies examined before selection began and the stock showed a ratio of 1 : 1.0512, or 10, 247 males to 10,772 females.

Table V.

Showing the Origin of the "High" and "Low" Strains of the Saratoga Stock.

♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.
264	**235**[1]	202	222	252	241	213	248	179	149
157	165	246	236	157	190	187	168	266	263
208	230	290	280	163	202	241	235	224	234
285	256	192	232	214	237	232	257	109	129
137	160	218	223	176	188	245	205	184	171
173	190	187	217	243	282	75	106	226	206
193	187	251	222	160	189	245	225	195	233
155	168	192	207	200	280	188	171	183	168
252	236	**181**	**307**[2]	212	275	129	175	226	222
288	271	183	187	200	225	235	247	234	220
Grand Total..............................						10,247 ♂'s to 10,772 ♀'s			

The results of the selection in this experiment are given in Tables VI. and VII. In this stock there were greater individual variations from the normal sex-ratios in each direction but they did not breed true. The totals show the high strain to have a higher relative number of females than the low strain. They are as follows: for the high strain, 7,377 males to 8,365 females, or a ratio of 1 : 1.134; for the low strain, 10,923 males to 11,246 females or a ratio of 1 : 1.029. Considering these totals, it might seem that something had been accomplished by selection but when the totals are considered generation by generation the results do not seem so conclusive. If selection has been the factor which

[1] From this mating originated the "low" strain.

[2] From this mating originated the "high" strain.

Table VI.

Showing Summary of the "Low" Strain of the Saratoga Stock. Experiment II.

Generation.													Totals.
A		264 ♂–235 ♀ (*1 : .89*)											
B		1	2	3	4	5	6	7	8	9	10		
		146–150	159–202	199–152	199–213	131–129	83–91	81–78	109–119	108–100	107–121		1322–1355
		1 : 1.03	*1 : 1.27*	*1 : .76*	*1 : 1.07*	*1 : .99*	*1 : 1.10*	*1 : .96*	*1 : 1.09*	*1 : .926*	*1 : 1.13*		*1 : 1.024*
C		1	2	3	4	5	6	7		8	10		
		144–161	135–143	210–208	132–130	138–149	157–138	224–251		45–44	90–84		1275–1308
		1 : 1.12	*1 : 1.06*	*1 : .99*	*1 : .98*	*1 : 1.08*	*1 : .88*	*1 : 1.12*		*1 : .98*	*1 : .93*		*1 : 1.0259*
D		1	2	3	4	5	6	7	8	9	10		
		270–294	212–242	174–135	193–217	223–211	256–246	67–81	219–215	308–308	267–263		2189–2212
		1 : 1.09	*1 : 1.14*	*1 : .78*	*1 : 1.12*	*1 : .95*	*1 : .96*	*1 : 1.21*	*1 : .98*	*1 : 1*	*1 : .985*		*1 : 1.0105*
E		1	2	3	4	5	6	7	8	9	10		
		137–136	106–115	50–65	146–169	115–130	153–153	109–138	206–188	32–39	160–149		1214–1282
		1 : .99	*1 : 1.08*	*1 : 1.3*	*1 : 1.16*	*1 : 1.13*	*1 : 1*	*1 : 1.27*	*1 : .91*	*1 : 1.22*	*1 : .931*		*1 : 1.056*
F		2		3		4		5	6				
		166–176		199–213		72–84		171–210	62–37				670–720
		1 : 1.06		*1 : 1.07*		*1 : 1.17*		*1 : 1.23*	*1 : .60*				*1 : 1.0746*
G		1	2	3	4	5	6	7	8	9	10		
		43–41	101–97	130–137	124–121	79–90	154–170	90–103	148–156	68–67	205–213		1142–1195
		1 : .95	*1 : .96*	*1 : 1.05*	*1 : .98*	*1 : 1.14*	*1 : 1.10*	*1 : 1.14*	*1 : 1.05*	*1 : .985*	*1 : 1.039*		*1 : 1.0464*
H		1	2	3	4	5	6	7	8	9	10		
		199–197	172–169	144–152	169–179	151–152	124–141	92–101	210–225	163–185	114–107		1538–1608
		1 : .99	*1 : .98*	*1 : 1.06*	*1 : 1.06*	*1 : 1.01*	*1 : 1.14*	*1 : 1.10*	*1 : 1.07*	*1 : 1.135*	*1 : .938*		*1 : 1.0455*
I		1	2	3	4	5	6	7	8	9	10		
		184–178	182–183	164–137	184–180	74–97	111–110	187–216	136–116	177–168	174–181		1573–1566
		1 : .967	*1 : 1.005*	*1 : .835*	*1 : .978*	*1 : 1.31*	*1 : .991*	*1 : 1.155*	*1 : .853*	*1 : .949*	*1 : 1.04*		*1 : .996*

Grand Total........10,923–11,246
1 : 1.029

Table VII.

Showing Summary of the "High" Strain of the Saratoga Stock. Experiment II.

Generation.

A 181 ♂–307 ♀ (*1 : 1.696*)

Generation											Totals.
B		1	2	3	4	5	6	7	8	9	10	
	149–163	145–152	147–212	208–194	201–178	172–198	143–149	240–240	22–22	207–231	1634–1739
	1 : 1.09	*1 : 1.05*	*1 : 1.442*	*1 : .932*	*1 : .885*	*1 : 1.151*	*1 : 1.04*	*1 : 1*	*1 : 1*	*1 : 1.116*	*1 : 1.064*
C	2		4		6	8	9	10			
	72–81		122–109		163–158	117–118	106–148	144–136			724–750
	1 : 1.125		*1 : .893*		*1 : .969*	*1 : 1.008*	*1 : 1.396*	*1 : .944*			*1 : 1.036*
D	1	2	3	4	5	6	7	8	9	10	
	171–192	132–157	119–203	189–324	191–221	175–212	140–222	127–189	97–169	136–149	1477–2038
	1 : 1.123	*1 : 1.189*	*1 : 1.706*	*1 : 1.714*	*1 : 1.157*	*1 : 1.211*	*1 : 1.586*	*1 : 1.488*	*1 : 1.742*	*1 : 1.096*	*1 : 1.3798*
E	1	2	3	4	5	6	7	8	9	10	
	107–143	111–180	152–144	93–109	88–104	207–181	70–106	168–228	98–99	33–43	1127–1337
	1 : 1.34	*1 : 1.62*	*1 : .95*	*1 : 1.17*	*1 : 1.18*	*1 : .874*	*1 : 1.51*	*1 : 1.36*	*1 : 1.01*	*1 : 1.30*	*1 : 1.186*
F	2	3	4	5	6	7	8	9		10	
	258–276	50–37	118–107	119–102	260–221	81–104	33–28	163–206		49–56	1131–1137
	1 : 1.07	*1 : .74*	*1 : .907*	*1 : .86*	*1 : .85*	*1 : 1.284*	*1 : .85*	*1 : 1.264*		*1 : 1.14*	*1 : 1.0053*
G	1	2	3	4	5	7	8	9			
	33–84	82–111	152–138	32–41	78–94	42–38	27–30	89–91			536–627
	1 : 2.55	*1 : 1.35*	*1 : .91*	*1 : 1.28*	*1 : 1.21*	*1 : .88*	*1 : 1.11*	*1 : 1.022*			*1 : 1.1698*
H	2		3	4	5	6		9			
	74–79		154–151	108–129	40–28	99–89		37–42			512–518
	1 : 1.068		*1 : .9805*	*1 : 1.19*	*1 : .70*	*1 : .899*		*1 : 1.135*			*1 : 1.0117*
I	1		3		4	6		8			
	63–81		22–15		60–56	68–49		23–18			236–219
	1 : 1.28		*1 : .68*		*1 : .93*	*1 : .72*		*1 : .78*			*1 : .928*

Grand Total........7,377–8,365
1 : 1.134

has made the difference between the two strains, the difference should be most evident in the later generations of the experiment. This is not true, for a moment's calculation will show that the last three generations in each strain do not show as extreme an average ratio in the desired direction as those which preceed tehm. Although the difference between the totals of the two strains may be sufficiently large to be considered significant, it seems more probable that it is a chance variation, especially since the first experiment showed a similar variation in the direction opposite selection.

Selection Experiment III. (Warsaw Stock.)

In order to make the work still more conclusive, selection was attempted upon a third stock. This stock was collected at Warsaw, Indiana, and kept as a stock culture in the laboratory for about six months before the experiment was started.

Here forty-two pairs were mated from among the offspring of a single pair and the extremes of these matings were used as the parents of the high and low strains.[3] There were 11,190 flies examined before the selection began, 5,448 males to 5,742 females, a ratio of 1 : 1.0539. The counts of these matings are given in Table VIII.

Table VIII.

Showing Origin of the "High" and "Low" Strains of the Warsaw Stock.

♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.
38	43	91	82	125	106	226	220	255	247
66	72	106	101	155	150	110	114	136	143
133	169	135	156	**235**	**238**[2]	80	72	84	77
192	208	41	39	102	105	74	93	94	100
85	75	105	128	48	61	114	129	187	200
147	**187**[1]	178	189	186	186	195	203	89	79
170	192	91	102	127	142	179	199	175	171
105	113	101	104	187	220	158	156		
125	119	106	114	112	138				

Grand Total.................................. 5,448 ♂'s to 5,742 ♀'s

[1] From this mating originated the "high" strain.

[2] From this mating originated the "low" strain.

[3] It will be seen in Table VIII. that the pair used as the parents of the low strain did not produce the most extreme ratio in that direction. This mistake was due to a mathematical error which was not checked up until it was too late to rectify the experiment.

In the latter part of this experiment there was a diveation from the usual methods. The element of time was sacrificed to be able to make a larger number of matings in each generation. A number of males and females were isolated from each mating, being examined, and held to be mated after all of the counts for the generation were finished. By this method it was necessary to make matings only from the cultures which had given the most desirable ratios but in so doing a considerable amount of time was lost between each generation.

This third attempt to modify, by selection, the sex-ratio did not result in bringing about any very significant difference between the two strains. (Tables IX. and X. give the results of selection upon this stock.) The ratios computed from the totals in each strain showed a slight difference in the desired direction but this was so slight that it might be due to chance. Therefore it seems that no definite conclusions can be drawn from this experiment. In the low strain the totals were 9,673 males to 9,951 females, or a ratio of 1 : 1.0287 and in the high strain 12,327 males to 12,898 females, or a ratio of 1 : 1.0463.

Conclusion.

Since three distinct and unrelated stocks of flies show no significant effect of selection, it seems safe to conclude from these data that Moenkhaus's conclusion concerning the amenability of the sex-ratio in *Drosophila ampelophila* will not hold.

Discussion of Moenkhaus's Work.

Moenkhaus concludes from his work on the effect of selection on sex-ratios in *Drosophila ampelophila* that sex-ratios are "strongly transmissible and amenable to the process of selection." From his paper it is somewhat difficult to tell whether Moenkhaus intended to say that he had developed by selection, strains characterized by high and low female ratios or that by selection, he simply maintained a high and low strain which he found in nature. His results are given in the discussion which follows.

By way of explanation it might be said that Moenkhaus called the strain in which he selected for a relatively higher female ratio the "female" strain, and the one in which he selected in

Table IX.

Showing Summary of the "Low" Strain of the Warsaw Stock. Experiment III.

Generation.													Totals.
A	235 ♂s–238 ♀s (1 : 1.013)												
B	2	3	4	5	6	7	9	10					
	183–171	266–256	141–144	150–155	112–139	227–216	224–254	155–125					1458–1460
	1 : .934	1 : .962	1 : 1.02	1 : 1.033	1 : 1.24	1 : .951	1 : 1.13	1 : .806					1 : 1.0013
C	1	2	3	4	5	6	7	8	9	10			
	222–207	234–252	231–242	105–112	211–254	164–193	247–246	158–160	96–115	111–109			1779–1890
	1 : .932	1 : 1.077	1 : 1.048	1 : 1.067	1 : 1.204	1 : 1.177	1 : .996	1 : 1.013	1 : 1.198	1 : .982			1 : 1.062
D	1	2	3	4	5	6	7	8	9	10			
	163–151	226–238	141–153	139–125	206–227	204–209	200–297	142–177	193–187	188–196			1802–1960
	1 : .926	1 : 1.053	1 : 1.085	1 : .899	1 : 1.10	1 : 1.025	1 : 1.49	1 : 1.246	1 : .969	1 : 1.04			1 : 1.087
E	1	2	3	4	5	6	7	8					
	51–46	96–111	37–45	125–119	84–89	56–48	101–101	73–68					
	1 : .902	1 : 1.156	1 : 1.216	1 : .952	1 : 1.059	1 : .857	1 : 1	1 : .93					
E	9	10	11	12	13	14	15						
	88–92	101–112	86–78	88–86	71–94	63–84	53–62						1173–1235
	1 : 1.045	1 : 1.109	1 : .907	1 : .977	1 : 1.324	1 : 1.33	1 : 1.169						1 : 1.053
F	1	3	4	5	6	7	8	9	10	11			
	151–123	100–72	192–158	135–152	113–96	121–110	117–129	41–32	97–80	99–123			
	1 : .815	1 : .72	1 : .823	1 : 1.126	1 : .849	1 : .909	1 : 1.102	1 : .78	1 : .83	1 : 1.242			
F	12	13	14	15	16	17	18	19	20	21			
	95–123	154–153	44–33	68–96	209–202	59–57	169–189	70–73	55–52	51–43			2140–2096
	1 : 1.295	1 : .99	1 : .75	1 : 1.41	1 : .966	1 : .97	1 : 1.118	1 : 1.043	1 : .945	1 : .843			1 : .979
G	1	2	4	7	9	10	12	13	15	16	18	19	
	64–64	103–97	51–72	25–27	28–38	39–26	59–79	36–34	42–27	79–83	33–39	34–22	
	1 : 1	1 : .94	1 : 1.41	1 : 1.08	1 : 1.36	1 : .67	1 : 1.34	1 : .94	1 : .64	1 : 1.05	1 : 1.18	1 : .647	
G	20	21	22	23	24	25	26	27	28	30	31		
	19–37	55–46	29–29	88–78	34–34	89–69	104–108	75–79	65–71	115–112	55–39		1321–1310
	1 : 1.95	1 : .84	1 : 1	1 : .89	1 : 1	1 : .78	1 : 1.04	1 : 1.05	1 : 1.09	1 : .974	1 : .709		1 : .9916

Grand Total........9673–9951
1 : 1.0287

Table X.

Showing Summary of the "High" Strain of the Warsaw Stock. Experiment III.

Generation.

A 147 ♂s–187 ♀s (*1 : 1.272*)

Generation.											Totals.
B	1	2	3	4	5	6	7	8	9	10	
	126–115	195–210	52–42	53–76	119–127	138–143	191–188	194–196	206–189	208–253	1482–1539
	1 : .913	*1 : 1.08*	*1 : .81*	*1 : 1.43*	*1 : 1.07*	*1 : 1.04*	*1 : .98*	*1 : 1.01*	*1 : .92*	*1 : 1.22*	*1 : 1.039*
C	1	2	3	4	5	6	7	8	9	10	
	76–95	168–202	209–204	80–85	228–242	59–66	154–170	183–176	160–179	181–149	1498–1568
	1 : 1.25	*1 :·1.20*	*1 : .98*	*1 : 1.06*	*1 : 1.06*	*1 : 1.12*	*1 : 1.10*	*1 : .962*	*1 : 1.12*	*1 : .82*	*1 : 1.047*
D	1	2	3	4	5	6	7	8	9	10	
	43–43	69–78	79–90	141–152	149–141	147–139	194–190	195–202	193–181	146–152	1356–1368
	1 : 1	*1 : 1.13*	*1 : 1.14*	*1 : 1.08*	*1 : .946*	*1 : .946*	*1 : .979*	*1 : 1.04*	*1 : .94*	*1 : 1.04*	*1 : 1.009*
E	1	2	3	4	5	6	7	8			
	28–39	36–41	74–93	59–70	112–116	123–128	107–121	94–91			
	1 : 1.39	*1 : 1.14*	*1 : 1.26*	*1 : 1.19*	*1 : 1.04*	*1 : 1.04*	*1 : 1.13*	*1 : .97*			
E	9	10	11	12	13						
	92–105	52–62	84–82	67–121	105–126						1033–1195
	1 : 1.14	*1 : 1.19*	*1 : .976*	*1 : 1.806*	*1 : 1.2*						*1 : 1.157*
F	1	2	3	4	5	6	7	8	9	10	
	145–146	214–245	249–246	28–65	168–179	169–162	154–162	77–63	133–146	79–74	
	1 : 1.007	*1 : 1.15*	*1 : .988*	*1 : 2.32*	*1 : 1.07*	*1 : .96*	*1 : 1.05*	*1 : .82*	*1 : 1.098*	*1 : .94*	

TABLE X.—*Continued.*

	11	12	13	14	15	16	17	18	19	20		
F	100–102	214–228	195–226	182–199	177–149	208–214	194–207	121–135	148–157	93–86		
	1 : 1.02	*1 : 1.07*	*1 : 1.16*	*1 : 1.09*	*1 : .842*	*1 : 1.03*	*1 : 1.07*	*1 : 1.12*	*1 : 1.06*	*1 : .93*		
	21	22	23	24	25	26	27	28				
F	132–127	75–98	115–149	114–122	192–206	113–130	118–136	173–156				4080–4315
	1 : .96	*1 : 1.31*	*1 : 1.3*	*1 : 1.07*	*1 : 1.07*	*1 : 1.15*	*1 : 1.15*	*1 : .902*				*1 : 1.0576*
	1	2	3	4	5	6	7	9	10	11	12	
G	57–69	58–56	85–91	49–56	33–27	84–72	26–46	44–49	90–94	112–122	92–83	
	1 : 1.21	*1 : .97*	*1 : 1.07*	*1 : 1.14*	*1 : .82*	*1 : .86*	*1 : 1.77*	*1 : 1.11*	*1 : 1.04*	*1 : 1.09*	*1 : .90*	
	13	14	15	16	17	18	19	20	21	22	23	
G	65–67	46–51	128–109	73–75	53–49	73–86	41–44	62–49	34–32	68–76	63–98	
	1 : 1.03	*1 : 1.11*	*1 : .85*	*1 : 1.03*	*1 : .93*	*1 : 1.18*	*1 : 1.08*	*1 : .79*	*1 : .94*	*1 : 1.12*	*1 : 1.56*	
	24	25	26	27	28	29	30	31	32	33	34	
G	36–27	39–60	80–69	53–33	52–62	134–108	42–35	50–48	49–39	103–113	71–87	
	1 : .75	*1 : 1.54*	*1 : .86*	*1 : .62*	*1 : 1.19*	*1 : .81*	*1 : .83*	*1 : .96*	*1 : .796*	*1 : 1.097*	*1 : 1.23*	
	35	36	37	38	39	40	41	42	43	44	45	
G	113–109	58–57	84–94	32–27	29–32	60–50	61–64	27–36	67–70	152–126	50–66	2878–2913
	1 : .97	*1 : .98*	*1 : 1.12*	*1 : .84*	*1 : 1.10*	*1 : .83*	*1 : 1.05*	*1 : 1.33*	*1 : 1.05*	*1 : .829*	*1 : 1.32*	*1 : 1.0122*

Grand Total........12,327–12,898
1 : 1.0463

the opposite direction the "male" strain. This terminology will be used throughout this discussion. As the starting point of his female strain, he selected from nature a pair of flies which produced 52 males and 135 females and in his male strain he started with a pair which produced 84 males and 75 females.

Considering first the effect of selection upon his female strain we find here no conclusive evidence of any progressive change in the direction of the selection. (His data for this strain are given in Table XI.) To be sure, there is a slight increase in the relative number of females in his second and third generations over his first generation, but this fluctuation could easily be attributed to the small number of individuals examined. The greatest difficulty in assuming the effectiveness of selection here, is the fact that his last two generations are the ones in which he obtained the lowest relative number of females. Moenkhaus explains these low ratios of the last two generations in that he possibly made a poor selection in the preceding generation, but if we consider selection as having a cumulative effect (as Moenkhaus seems to consider it) it is difficult to see how one could lose by one poor selection all that he had accomplished in the previous selections. It must be admitted that by using as parents of each succeeding generation, pairs which threw the most extreme ratios in favor of the females, Moenkhaus was able to maintain a strain which on an average gave a relatively high number of females. But this was probably not due to any cumulative effect of selection but to the isolation of a peculiar type of female which will be discussed more fully later.

As to the male strain (Table XII)., Moenkhaus admits that the effect of his selection here has been slight and after examining his data carefully it is difficult to see how it could be assumed that there has been even a slight effect of selection. He started with a ratio (84 males to 75 females) which was only slightly different from normal and this slight difference was not transmitted to the first generation nor any succeeding one. So it seems that he had here a normal strain which would have given the same ratio regardless of the direction of the selection.

The female strain is the unusual one and is in need of an explanation. It throws some very exceptional ratios in favor of

Table XI.

History of Moenkhaus's "Female" Strain.

206 (52 ♂s : 135 ♀s)

Generation.												Totals.
	1	2	3	4	5	6	7	8	9	10	11	
1	21–37	42–68	71–164	76–71	108–125	51–80	43–67	51–46	53–103	8–56	55–102	578–969 *1 : 1.67*
						7	8	9	10			
2						21–49	41–94	55–70	98–178			215–391 *1 : 1.82*
				3	4	5	7					
3				15–37	18–54	25–37	35–71					93–201 *1 : 2.17*
	1	2	3	5	7	8	10					
4	26–47	39–56	33–52	64–67	53–93	85–162	54–106					354–483 *1 : 1.36*
					4	5	6	7	8			
5					121–139	32–32	93–101	40–114	86–132			372–518 *1 : 1.39*
	2	3	5	6	7	10	13					
5	51–44	67–53	41–47	74–78	120–130	102–136	41–47					496–535 *1 : 1.07*

Table XII.

History of Moenkhaus's "Male" Strain.

207 (*84* ♂s : *75* ♀s)

Generation												Totals.
1		2 79–68	5 99–121	6 71–88	7 67–73	8 60–57	10 72–71	11 86–100				536–579 *1 : 1.08*
2					3 44–50	5 133–140	7 25–21	9 18–21				220–223 *1 : 1.00*
3	1 71–98	2 115–101	3 76–84	4 51–73	5 42–37	6 45–48	7 36–39	8 61–52	9 84–108			581–640 *1 : 1.10*
4						1 10–14	5 41–41	6 38–38	7 45–47			142–147 *1 : 1.04*
5	1 40–32	3 45–144	5 46–35	6 26–26	7 146–144	8 72–98	9 64–74	11 79–84				518–607 *1 : 1.17*
6	1 30–50	2 94–116	4 58–67	5 32–51	7 55–75	8 85–92	9 64–104	10 43–99				561–654 *1 : 1.42*
6	1 118–109	2 99–107	3 164–198	4 141–157	5 61–85	6 56–63	7 24–27	8 116–109	9 42–40	10 73–67	11 50–35	944–997 *1 : 1.05*

the females and these exceptional individual ratios caused the relative number of females in the female strain to be higher than normal. These unusual ratios can be readily explained by assuming that the female which Moenkhaus selected as the mother of his female strain carried a recessive sex-linked lethal factor and it will be pointed out later that all of Moenkhaus's data substantiate, very precisely, this assumption. The existence of such factors has been conclusively demonstrated by the recent work of Morgan and his students. A recessive lethal factor is any factor that brings about the death of the individual in which it occurs, provided its effect is not counteracted by the action of its normal allelomorph. Then if a lethal is sex-linked, all males which get it will die for they cannot carry its normal allelomorph since they possess but one X-chromosome. Since all males receiving the lethal factor die, this factor is never transmitted by the male and as a consequence the female can never be homozygous for it. Therefore the lethal factor has no effect on the female but she, by transmitting it to half of her sons, causes their death. Since half of the males die, a 2:1 ratio will result. A female carrying a lethal will transmit it to half of her daughters and they will always be heterozygous for it since they cannot receive it from their father.

Then the female which Moenkhaus used as the mother of his female line was probably a lethal female. It should be said that Moenkhaus is not to be criticised for not considering lethals in his paper, for lethals were not known till two years after his work was published. The original female gave a ratio which was an approximate 2:1 ratio. As mothers of the succeeding generations, Moenkhaus probably selected lethal bearing females (excluding female 5 of generation 4). These females should transmit the lethal factor to half their daughters and this expectation is realized, for from the 31 matings made in the female strain (excluding the offspring of female 5 of generation 4), fifteen 2:1 ratios resulted. Those considered 2:1 ratios are matings 3, 9 and 11 of generation 1; 7, 8 and 10 of generation 2; 3, 4 and 7 of generation 3; 1, 7, 8, and 10 of generation 4; and 7 and 8 of generation 5. So the number of 2:1 ratios obtained would justify the assumption of the presence of a lethal factor.

Another indication of the presence of a lethal factor is the fact that in generation 4, when he used female 5 which gave a normal ratio, as mother of the next generation, all of her daughters also threw normal ratios. This female did not carry the lethal factor and none of her offspring showed abnormal ratios.

A third indication of a lethal factor is the fact that Moenkhaus found in crossing his male and female strains that the female is almost wholly responsible for the transmission of the sex-ratio. For he found if females from a strain possessing a high female ratio be mated with males from a strain possessing a low female ratio or vice versa, the offspring will show a sex-ratio which is wholly or very near that of the strain from which the females were taken. If his female strain carried a lethal factor and if his male strain was a normal strain, as it appears to be, the above result would be the expected one. For, if a lethal bearing female is mated to a normal male, she will transmit the lethal factor to half her daughters but a male from the lethal strain cannot transmit the lethal factor because all of the lethal bearing males die. Therefore the end result would be as Moenkhaus found, that the offspring will show sex-ratios like that of the strains from which the females came.

Of course, the only sure way of testing for a sex-linked lethal factor is to cross the suspected female to a male carrying another sex-linked factor and the resulting F_2 will be characterized by a deficiency in the class of normal males. So it is not possible to determine beyond doubt whether the unusual ratios in Moenkhaus's female strain were due to a lethal factor. But since several lethals have already been found and all of his data substantiate this assumption, it seems that this explanation is probably the correct one.

Discussion.

The writer's three attempts to modify by selection, the sex-ratio in the fruit fly have resulted in no clear-cut evidence that it was modifiable. In each experiment, the work covered more generations and many more individuals than the work of Moenkhaus. Since Moenkhaus's results could not be obtained in any one of the three experiments, it leads one to question Moenkhaus's conclusions or, at least, to question the general application of his findings. The fact that the difference which Moenkhaus found between his two strains can be readily explained to be due to a cause entirely independent of the cumulative effect of selection, makes his work support, rather than oppose the findings of the writer. It must be admitted that negative results in secletion work can never be conclusive, for the criticism may always be offered that selection over a greater period might have yielded different results. But, nevertheless, we feel justified in concluding from the data here presented that the sex-ratio in *Drosophila ampelophila* is not readily, if at all, modifiable by selection.

Lethals.

Since the offspring of over 700 pairs of flies were examined for sex in these experiments, and since extreme ratios were sought, it would not be surprising to find a sex-linked lethal mutation. In fact, there is fairly good evidence that one such mutation occurred. This was mating number of 6 generation G of the low strain of the Bloomington stock (Table IV.). This gave an approximate 2:1 ratio (84 males to 180 females). Four matings were made from among the offspring of this mating and three out of the four gave 2 to 1 ratios while the fourth was doubtful. If a sex-linked lethal mutation had occurred, half of the four should have given 2 to 1 ratios and the other half normal. Since so few matings were made, it is possible that all the females chosen were lethal bearers. The stock was lost by accident at this time and further tests were not possible. But since the unusual ratio was transmitted it is probable that a mutation occurred here. In the high series of the Saratoga stock, there were several ratios which approximate a 2 to 1 ratio but none of the flies showing it transmitted this tendency to their offspring. Also in the high strain of the Warsaw stock, generation E mating 12 gave a 2 to 1 ratio. A large number of matings were made among the offspring of this pair but this unusual ratio was not transmitted to any of the progeny.

In all of the matings examined there were comparatively few ratios found which were two to one or more.[1] These extreme

[1] The unusual ratios more frequently occurred where the counts were very small. These cases were considered to have been due to some unfavorable environmental condition.

ratios were more frequently in favor of the females and in only one case was there any evidence that a sex-linked lethal mutation had occurred.

In conclusion, I wish to express my thanks to Professor Fernandus Payne for the suggestion of this problem and also for many helpful suggestions and criticism while the work was in progress. I am also greatly indebted to my wife, Elmira Shierling Warren, for help, both in the carrying out of the experiment and in the preparation of the manuscript.

Summary.

1. The sex-ratio in *Drosophila ampelophila* is 100 females to 95 males.

2. The age of the parent has no effect upon the sex-ratio of its offspring.

3. The difference which Moenkhaus found between his two strains, and which he attributed to selection, was probably due to the fact that his male strain was a normal one and his female strain was a lethal bearing one.

4. The sex-ratio in *Drosophila ampelophila* is not readily, if at all, modifiable by selection.

5. There was probably one sex-linked lethal mutation in the writer's selection stocks.

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