

INDUCTION OF DOMINANT LETHAL EFFECTS BY X-RADIATION IN HABROBRACON

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MULLER in 1927 stated that the "partial sterility" of X-rayed males of *Drosophila* was due, at least to an appreciable extent, to dominant lethal changes induced in the sperm. It was impossible, however, to determine whether the eggs were actually "fertilized." In *Drosophila* the result would be the same; the eggs would fail to develop, whether dominant lethals were induced or the sperm were inactivated so that they could not penetrate the eggs. MULLER attributed a shift in the sex ratio by reduction in the number of females to lethals in the X chromosome.

STANCATI (1932) presented evidence that dominant lethals were induced by X-radiation of sperm in *Habrobracon*. In this wasp in which males develop by haploid parthenogenesis, any reduction in percentage of females due to inactivation of sperm should be compensated by increase in number of male offspring, "step-sons" of the treated males. The number of "step-sons" should remain constant, however, despite the decrease in females if such decrease were due to dominant lethals alone, the number of eggs fertilized remaining constant. STANCATI'S material was complicated by the presence of highly inviable biparental males which are now known to replace a variable number of females when the parents are closely related. Grouping all biparentals, males and females, together, STANCATI reported 64.8 percent of biparentals in fraternities from untreated sires, while only 24.3 percent of biparentals occurred in bisexual fraternities from treated sires. In addition to these there were 1111 sisterless males in 48 unisexual fraternities, "step-sons" of treated males. The three groups: controls, bisexual fraternities from treated and unisexual from treated males, show as average numbers of offspring per vial: 9.64, 6.16 and 4.94 respectively, indicating that decrease in biparentals is not compensated by increase in impaternal males as it is when sperm are lacking.

It has also been shown (GREB 1933 and WHITING 1935) that reduction in percentage of females occurs in *Habrobracon* if mated females are X-rayed. This may be due to a greater proportion of dominant lethal chromosomal abnormalities induced in the sperm than in the eggs.

WHITING (1936), using parental stocks that were unrelated to each other, has recently reported dominant lethals resulting from treatment of sperm with neutrons. In this case biparental males were lacking, all zygotes being potentially female-producing. The number of females was markedly decreased without any compensating increase in that of impaternal males.

The following experiments involving egg counts were undertaken in order to have a check on viability which would not be possible from counts of adults alone. Females of an orange eyed stock (11-0) were used; some were bred as virgin, others were mated to treated and to control males of an unrelated wild type stock (25). Such a cross obviates the difficulties due to differences in relative viability of females and biparental males. Only females of relatively uniform viability develop from fertilized eggs.

TABLE I

Egg counts and offspring from orange stock (11-0) females bred as virgin or mated with X-rayed and with control wild-type males, which were either unrelated (stock 25) or closely related (stock 11).

GROUPS	NO. FEMALES	DAYS	TOTAL EGGS	EGGS PER DAY	PROGENY			PERCENTAGE WITH STANDARD ERRORS OF EGGS PRODUCING		
					♂♂	+ ♂♂	+ ♀♀	♂♂	+ ♂♂	+ ♀♀
Experiment A 23-29°C										
Unmated	6	136	1511	11.1	806			53.33		
								± 1.28		
× stock 25 (untreated)	3	67	976	14.6	151		328	15.47		33.61
								± 1.16		± 1.51
× stock 25 (5000 R.)	1	14	204	14.6	29		19	14.22		9.31
								± 2.45		± 6.43
× stock 11 (untreated)	2	29	285	9.8	50	7	25	17.54	2.46	8.77
								± 2.25	± 0.92	± 1.68
× stock 11 (3750 R.)	2	66	889	13.5	254	2	30	28.57	0.23	3.37
								± 1.52	± 1.58	± 1.91
× stock 11 (5000 R.)	1	14	179	12.8	52	4	5	29.05	2.3	2.79
								± 3.39	± 1.11	± 1.23
Experiments B-C 20-24°C										
Unmated	8	87	759	8.7	189			24.90		
								± 1.57		
× stock 25 (untreated)	7	82	1005	12.3	95		215	9.46		21.39
								± 0.93		± 1.29
× stock 25 (7500 R.)	11	122	1008	8.3	54		5	5.36		0.50
								± 0.71		± 0.22
× stock 11 (untreated)	10	100	1004	10.0	105	9	110	10.46	0.90	10.96
								± 0.97	± 0.30	± 0.99
× stock 11 (5000 R.)	6	78	729	9.3	62	3	23	8.50	0.41	3.16
								± 0.10	± 0.24	± 0.65

Crosses were also made between 11-0 females and closely related stock 11 males; in this case differential maturation breaks down and male-producing zygotes, XX and YY, are formed as well as female-producing zygotes, XY. It seemed likely that X-radiation might cause a shift in ratio of homeosyngamic fertilization, X with X or Y with Y, as compared with heterosyngamic X with Y, as shown by ANDERSON (1936) for temperature differences.

Egg counts were made with a modification of the methods devised by A. R. WHITING, C. H. BOSTIAN and R. L. ANDERSON. For X-raying a Coolidge water-cooled tube with tungsten target was used at 165 KV and constant potential giving an accuracy within ten percent of the recorded dosage.

Experiment A was performed from April to May, 1936, experiments B and C from October 1936 to January 1937. Experiments B and C are summarized together in Table 1, since there was no significant difference in conditions or in results. Experiment A had a slightly higher temperature range and it is probably for this reason that the egg productivity per female per day (column 5) is slightly higher (average 12.1 —) than in Experiments B and C (average 9.6). It seems likely that stock 11-0 underwent a deterioration in viability between the times of Experiments A and B, reducing the offspring from unfertilized eggs (percentage producing orange males from unmated mothers, Column 9) from 53.3 to 24.5 percent. This reduction in viability of the impaternal males, occurring in some fraternities but not in all, makes conclusions uncertain concerning the number of eggs fertilized in Experiments B and C. Standard errors based on the total number of items (individuals) are not adequate measures of reliability when such items occur in groups (fraternities). If viability of unfertilized eggs averaged the same in all cases so that the same proportion of impaternal males developed, we could tell what proportion of eggs were fertilized and thus also determine the viability ratio of the females.

From offspring of unmated females in Experiment A, the viability of unfertilized eggs appears not far from fifty percent. Crosses with untreated individuals of the unrelated stock 25 show that about fifteen percent of eggs develop into impaternal males; therefore thirty percent were unfertilized. Of the remaining seventy percent about forty-eight percent develop into females. Female viability is therefore not greatly different from that of males.

Applying the same reasoning to Experiments B-C where viability of unfertilized eggs is only about 25 percent, we find about sixty percent of the eggs were fertilized by untreated stock 25 sperm and show thirty-three percent female viability. These conclusions are unreliable because of the occurrence of low viability factors and the small number of fraternities.

X-radiation of stock 25 sperm gives a marked decrease in female progeny, a decrease of sixty-six percent for 5000 R (Experiment A) and ninety-seven percent for 7500 R (Experiments B-C). There is no compensating increase in males and hence we are dealing with induction of dominant lethals rather than with inactivation of sperm.

In crosses with closely related stock 11 males, three classes of progeny are produced instead of two. The breakdown of differential maturation as a result of close parental relationship permits the formation of relatively inviable XX and YY combinations, a few of which develop into biparental males. The percentage of eggs producing females is significantly

lowered in both sets of experiments when stock 11 males are used, and it is further lowered by X-raying of such males. In Experiment A there appears to be an increase in impaternal males after treatment, but this statement cannot be made definitely since the number of fraternities is very small. If both sets of experiments be averaged, females develop from 10.5 percent of eggs fertilized by untreated males, 3.6 percent from those fertilized by males treated with 3750 R and 3.1 percent from those fertilized by males treated with 5000 R. The number of biparental males is too low to show any significant influence of radiation comparable to that occurring in their sisters. It can only be said that they are neither totally eliminated nor are they greatly increased.

These tests, although based on actual egg counts rather than on offspring per vial, thus far merely corroborate STANCATI'S conclusion that X-raying of sperm induces dominant lethals. Whether such treatment can inactivate the sperm, reducing the percentage of eggs fertilized, or whether it can modify the type of fertilization, changing the ratio of heterosyngamic (X with Y) and homeosyngamic (X with X or Y with Y) fertilization are still open questions.

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SUMMARY

Eggs were counted and the progeny recorded from females which were bred as virgins or were mated to unrelated or to related males. Untreated males or males treated with X-rays were used as parents.

The percentage of eggs producing progeny was not decreased in the lay of outcrossed females as compared with that of virgin females, but percentage of eggs producing daughters was greatly decreased when mothers were mated to related males as compared with those mated to unrelated males.

If crosses were made to treated males which were either related or unrelated, the percentage of eggs producing females was greatly decreased and there was no compensating increase in impaternal males. This is interpreted as an indication of the production of dominant lethals rather than inactivation of sperm and is consistent with the results of STANCATI. There was no significant effect of the treatment on production of biparental males.

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