THE INDUCTION OF DOMINANT AND RECESSIVE LETHALS BY RADIATION IN HABROBRACON[1]

P. W. WHITING

The University of Pennsylvania, Philadelphia, Pennsylvania

Received June 15, 1938

INTRODUCTION

GENETIC literature includes much discussion of lethal factors. Texts treat the subjects of sex-linked and autosomal lethals, lethals linked with visibles, balanced lethals and semilethals. There are many studies of induction of lethals by X-radiation and other physical agents including correlation of number of lethals with dosage given. Almost without exception the lethals referred to are recessive, transmissible from one generation to another through the heterozygote.

Dominant lethals, not transmissible since zygotes receiving them die, and evident only in their mass effect, have been discussed but little. In organisms with the ordinary type of reproduction dominant lethals would be difficult to distinguish from direct inactivation of germ cells although MULLER (1927) attributed the partial sterility of X-rayed males in Drosophila to dominant lethals, pointing out that although they could not be detected individually "their number was so great that through egg counts and effects on sex ratio evidence could be obtained of them *en masse*. It was found that their numbers are of the same order of magnitude as those of recessive lethals."

In the parasitic wasp Habrobracon, in contrast to such organisms as Drosophila, the occurrence of dominant lethals in the sperm can be readily distinguished from direct killing of the male gametes, as explained below. For this reason the experiments reviewed and reported in the present paper were undertaken and the results indicate that the induction of dominant lethals by radiations can scarcely be doubted.

For an understanding of the exceptional method of reproduction and heredity in this insect the following facts should be borne in mind.

Females are diploid and develop from fertilized eggs. Normal fertile males are haploid and develop parthenogenetically from unfertilized eggs.

[1] The work reported in this paper has been greatly aided by grants from the Committee on Effects of Radiation on Living Organisms (National Research Council). Most of the recent experiments have been carried out at the University of Pennsylvania, with the breeding work done at the Zoological Laboratory, the cold rooms for storage supplied by the Department of Anatomy at the Medical School and the X-ray treatments given by Dr. Raymond Zirkle at the Department of Radiology of the University Hospital. During the summers the breeding work has been done at the Marine Biological Laboratory, Woods Hole, Mass., and the X-ray treatments have been given there.

Biparental sterile (or near-sterile) males are diploid, developing, like females, from fertilized eggs. The haploid males have been called uniparental and azygous in contrast to the biparental zygous males and females.

Unmated females produce azygous sons only. Mated females also produce azygous sons from unfertilized eggs but in smaller numbers than unmated females and zygous biparental offspring from fertilized eggs. Whether the biparental offspring shall be daughters only or both sons and daughters depends upon the relationship of the male used in the mating. If the male is from a stock unrelated to the female, all the biparental offspring are daughters but if the male comes from a related stock, biparental sons as well as daughters are produced.

In general the azygous and biparental offspring from a mated female occur in the same ratio from the different vials through which the female is transferred (a, b, c, d, etc.) until her supply of sperm is exhausted. Subsequently (vials, e, f, etc.) azygous sons only appear.

Biparental males cannot conveniently be separated from their azygous brothers unless the mother has a recessive trait and the father has the allelic dominant. Orange-eyed females crossed with wild type (black-eyed) males produce black-eyed daughters and orange-eyed azygous sons. If biparental sons are produced they may be readily separated from their azygous brothers by their black eyes.

All daughters from outcrosses appear to be similar in viability to inbred females, although the latter are in general somewhat less fecund.

Fertilized eggs may be "female-producing" or "male-producting," the latter occurring only if parents are related. "Male-producing" fertilized eggs are less likely so hatch than "female-producing." Consequently there are more "bad eggs" and fewer biparental offspring if the mating has been with a related male, since the percentage of eggs fertilized is the same whether the male is related or unrelated. Biparental male larvae are also less likely to mature than female larvae. This further reduces offspring from related parents.

Two types of male sterility may be distinguished according as the eggs are fertilized or not. If the eggs are not fertilized, the mated female breeds like an unmated female, producing a large number of azygous sons. This occurs in the case of matings with biparental males which produce diploid sperm rarely capable of fertilizing the eggs. There are also males with abortive sperm ducts or testes which may readily be mated but transmit no sperm. Recent evidence indicates that sperm may to some extent be inactivated by high dosages of X-rays, so that they are unable to penetrate the eggs.

The most striking result of X-radiation of males is, however, the pro-

duction of sterility (or partial sterility) of a second type. In this case the sperm are not inactivated but are fully capable of fertilizing the eggs. Such fertilized eggs however, do not hatch because the sperm have a dominant lethal effect. Females mated to males with this type of sterility produce azygous sons only and in numbers equal to those produced by females mated to normal males; in other words, although they produce no females, due to dominant lethal effects of the sperm which have entered the eggs, they behave like mated rather than unmated females in respect to number of azygous sons. Habrobracon, then, is especially well suited for separating dominant lethal male sterility from sterility due to inactivated sperm on the basis simply of numbers of azygous sons produced by females mated to the males to be tested.

As to the nature of dominant lethals it is probable that they are due to extensive chromosomal alterations rather than to changes in restricted regions or in single genes. A lethal effect from a single gamete may be called dominant in contrast to a condition which must be present in both gametes and hence recessive.

Since in Habrobracon an unfertilized egg provided with a single set of genes develops normally (into a male) and since the addition of a second complete set by fertilization likewise results in normal development (into a female), it might be thought that the addition of a deficient set should not be lethal to the resulting zygote. In other words, if both 1n and 2n may develop normally, why should not $1n+(n-x)$ also develop normally? The explanation is doubtless to be found in genic balance. If $n-x$ is too small to act as a recessive, containing relatively extensive deletions for example, the balance should be so disturbed that development would be prevented. Theoretically the genic set in a sperm might become so extremely deleted by X-radiation that the fertilized egg would develop as an unfertilized egg into a male. No sex intergrades have ever been found in the treated material that might be interpreted as hyperploid males or hypoploid females. The sex types surviving after X-radiation have been fully as normal as in untreated stock.

Recessive lethal (or semilethal) factors may be a cause of "bad eggs." Half of the unfertilized eggs of a female heterozygous for a recessive lethal do not hatch.

Eggs may likewise be defective in their gross morphological or non-nuclear aspects because of unfavorable cultural conditions (very low humidity) or inadequate nutriment of females (feeding with honey instead of caterpillar juice) while females of certain genetic types lay withered eggs of irregular form.

Non-hatchability may then be due to non-nuclear causes, recessive lethals, dominant lethals or "male-producing" fertilization.

Table 1 is based on part on data published by C. H. BOSTIAN (1935) who counted eggs and offspring from females of an inbred orange-eyed stock which were bred unmated, or after mating to related or to unrelated males. Eggs averaged 21 per day regardless of the type of mating. Some of the unhatchable bad eggs from unmated mothers may be so because of recessive lethals in the stock and hence there is a somewhat greater viability of offspring (of which three-fourths are females) when mothers are mated to unrelated males. Matings with related males result in many unhatchable eggs. If the difference between bad eggs from matings of related and unrelated parents be added to the biparental sons from the

TABLE 1

Offspring per day of inbred orange-eyed females (stock 11-o) bred unmated or mated with wild type males. The average daily egg production per female is 21.

TYPE OF MATING	OFFSPRING PER DAY			
	AZYGOUS. ORANGE MALES	BIPARENTAL.		BAD EGGS
		WILD TYPE FEMALES	WILD TYPE MALES	
Female unmated (or mated to male unable to transmit sperm)	14.5	—	—	6.5
Outcrossing; male of an unrelated stock	4	12	—	5
Inbreeding; male of a closely related stock	5	5.5	1.7	8.8
Dominant lethals in all sperm	5	—	—	16

former, it appears that female-producing and male-producing combinations occur in equal numbers (5.5 of each type per day). The table also gives the expectation in case of a mating with a male having dominant lethals in all sperm. Here all fertilized eggs are unhatchable and offspring are limited to five azygous sons per day.

RECESSIVE LETHALS

In a discussion of azygotic segregations from heterozygous mothers (WHITING and BENKERT 1934) deviations from equality of mutant types and wild type were explained by linkage with recessive lethals, especially when the types were otherwise of normal viability. These deviations may be very great or relatively slight indicating that the lethal may be either closely or loosely linked with the mutant locus. Not infrequently also the pedigree shows that a certain female is heterozygous for a lethal since about one-half of her daughters are lethal bearing.

WHITING (1929), in a general account of X-radiation results with Habrobracon, presented evidence that certain daughters of treated parents

were carrying recessive lethals. Very few offspring (males) were produced if such lethal-bearing females were unmated, but if mated they were able to produce many daughters. When the number of their sons was extremely reduced, it was suggested that the lethals were either very numerous or were balanced.

MAXWELL (1935) found no reduction in fecundity of F_1 females and no deviations from the 1:1:1:1 ratio of F_2 males when the wild type P_1 females were treated with X-ray dosages of 2,500 r and subsequently mated to untreated cantaloup gynoid males. In a second experiment treatment of the cantaloup gynoid males with the same dosage before mating with untreated wild-type females was however very effective, reducing the average number of sons per day per F_1 mother from 7.06 to 4.59. Males subjected to higher dosages showed still greater reduction in these averages. The 21 control F_1 females each averaged six or more sons per day, with but two exceptions, while, among the daughters of treated fathers, 31 averaged six or more while 64 averaged three or less. This bimodality indicates that about two-thirds of the daughters of treated males carried at least one lethal. Among the 105 F_2 fraternities from treated males there were significant deviations from equality for cantaloup in four and for gynoid in four. MAXWELL'S data suggest that recessive lethals are more readily induced in the sperm than in the eggs.

DOMINANT LETHALS INDUCED BY TREATMENT OF MALES

MULLER (1927) attributed the partial sterility of X-rayed males in Drosophila to dominant lethals. WHITING (1929) showed that in Habrobracon males were active and apparently uninjured after a dosage that was seven times as great as was required to induce complete sterility. With treatments below this sterilizing dosage, there was a decrease in percentage of daughters among the progeny with increasing dosages when the males were mated immediately after treatment, but there was a partial recovery of fertility as indicated by increasing percentage of females from subsequent matings on successive days.

STANCATI (1932) demonstrated dominant lethals in sperm of wild type males after treatment (2,500 r). The males were mated to females of a related stock with orange eyes, so that biparental sons were produced and could be detected. STANCATI reported numbers of offspring per vial and percentages of biparentals, including the biparental sons with the daughters. Not all matings were observed but the controls included "practically no unisexual fraternities." Among the treated, however, there were many unisexual fraternities, indicating sterilization of the males. From his figures it may be calculated that there were among the controls, 3.39 azygous sons per vial. This was increased to 4.66 among the treated

bisexual and to 4.94 among the treated unisexual fraternities. This increase might suggest inactivation of sperm, but this seems unlikely in view of later results and the low dosage. Some fraternities from unmated females may have been included among the unisexual treated. The biparental offspring, sons and daughters, are 6.25 per vial from the controls and 1.50 from the treated bisexual. This decrease is not compensated by the increase in azygous sons and hence the partial sterility of the fathers was in part at least due to dominant lethals.

WHITING (1936) showed that dominant lethals were induced in the sperm by neutrons. Treated males were mated to untreated unrelated females. While daughters decreased steadily with increasing dosages, there was no compensating increase in number of sons. Thus the sperm were not inactivated by the neutrons but were able to penetrate the eggs and prevent their development.

WHITING (1937 a and b) likewise showed a progressive increase in partial sterility due to dominant lethals when X-rayed males were mated to unrelated females. Table 2 (reprinted from WHITING 1937a) gives the data. Irregular fluctuation of sons per day may be noted. A slight increase in the 75,000 r group suggests possible sperm inactivation, but if this is significant it requires a far higher dosage than is necessary for complete sterilization by induction of at least one dominant lethal in every sperm.

TABLE 2

Offspring produced in a given number of days by untreated orange-eyed females (stock 11-o) mated to wild type unrelated males, controls and X-rayed with various dosages.
(From "The Collecting Net," Woods Hole, August 7, 1937.)

TREATMENT OF MALES	TOTAL EGG-LAYING DAYS	OFFSPRING		o ♂♂ PER DAY	+ ♀♀ PER DAY	SURVIVAL RATE
		o ♂♂	+ ♀♀			
Controls	379	459	1310	1.21	3.30	1.00
2,500 r	253	337	562	1.33	2.22	.67
5,000 r	309	419	191	1.36	.62	.19
7,500 r	361	627	57	1.74	.16	.05
10,000 r	72	62	5	.86	.07	.02
20,000 r	99	95	0	.96	0	
40,000 r	117	157	0	1.34	0	
75,000 r	515	890	0	1.73	0	
Unmated ♀♀	675	3191	0	4.73	0	

BISHOP (1937) showed by counting eggs and recording progeny that X-rayed males had fewer daughters than untreated and that there was a corresponding increase in bad eggs. Matings were between both unrelated and related parents. In the latter case biparental sons occurred but were not numerous enough to indicate decrease due to treatment.

WHITING (1938) showed that there was progressive decrease in biparentals, both sons and daughters, with increasing X-ray dosages when the treated males (wild type) were crossed with related females (orange-eyed). There was no compensating increase in number of azygous sons but this remained low as among the offspring of the mated controls.

For the four groups: controls, 2,500 r treatment, 5,000 r and 7,500 r, the daughters per day were respectively 1.83, 0.97, 0.31 and 0.06 and the biparental sons per day were 1.20, 0.59, 0.17 and 0.05. Fraternities from crosses of these stocks give a very high ratio of biparental sons, but nevertheless they fail to equal the daughters. It is of interest to note that decrease in daughters and in biparental sons is at the same rate, a fact that is taken to indicate that the radiation is no more lethal to one than to the other sex among the biparentals and that the type of fertilization (male-producing vs. female-producing) is not modified.

MAXWELL (1938) mated the same males on successive days to unrelated females. Dosages of 41,000 r and 142,000+r were administered to the two groups of treated males so that no daughters were produced by the treated. Sons per day averaged 1.05 for the controls, 1.41 for the lower treatment and 2.01 for the higher. Maxwell concludes that "Inactivation of sperm following higher dosages rather than partial exhaustion of sperm supply due to partial inhibition of spermatogenesis is indicated by the fact that there is no increase in males per day from the later matings."

DOMINANT LETHALS INDUCED BY TREATMENT OF FEMALES

Treatment of females by X-radiation was made by WHITING (1929). Mature eggs were shown to be less susceptible, while earlier stages were readily affected. Thus females fed on caterpillars and in actively laying condition had a postponed sterility since they produced offspring immediately after treatment (in vials *a*), but proved sterile thereafter. Honey-fed females, having no mature eggs, produced no offspring after equivalent dosages. In certain cases the postponed sterility was temporary for a few offspring might be produced in later life. Inviable pupae and larvae were sometimes observed after recovery, but data are not sufficient to prove that such were more numerous than usual.

In an experiment with low intensity but prolonged treatment of mated females (WHITING 1929), the percentage of daughters was decreased with increasing dosages, being 24.0−, 16.9− and 11.7− in the bisexual fraternities. No untreated controls were run. NEITA C. BOSTIAN (1931) X-rayed (3,200 to 6,400 r) inbred females mated to males of the same stock (no. 1). Offspring per female and percentage of daughters (vials *a* only) decreased with increasing dosages. When unmated females were treated (3,267 r) and subsequently mated to untreated males, offspring

per female and percentage of daughters were both higher than among the mated females treated with the lowest dosage. WHITING (1935), reporting experiments of JANE MAXWELL, ANNA R. WHITING and KATHRYN G. SPEICHER, showed that among the offspring of mated females X-rayed with dosages ranging from 3,500 to 7,000 r, the percentage of daughters decreased (38% to 7%) with increasing dosages. GREB (1933) showed that among bisexual fraternities from X-rayed mated females the average number of sons per mother was not significantly affected by a light dosage (2,000 r), although the daughters were much decreased. These experiments

TABLE 3. EXPERIMENT 11/3/37/TST

Offspring produced in a given number of days by orange-eyed females (stock 11-o), (controls and X-rayed with various dosages), which were bred unmated or were mated to unrelated untreated wild type males (stock 32) either before or after treatment.

MOTHERS	TREATMENT	DAYS FERTILE	TOTAL DAYS	o ♂♂	+ ♀♀	♂♂ PER DAY	SURVIVAL RATE	♀♀ PER DAY	SURVIVAL RATE	% ♀♀
Unmated	Controls	143	143	488		3.41+	1.00			
	1,500 r	81	81	225		2.78−	.81+			
	3,000 r	110	110	200		1.82−	.53+			
	6,000 r	20	67	28		.42−	.12+			
	12,000 r	20	103	22		.21+	.06+			
Mated	Controls	289	289	252	766	.87+	1.00	2.65+	1.00	75.25−
Mated	1,500 r	102	102	126	245	1.24−	1.42−	2.40+	.91−	66.04−
before	3,000 r	96	96	54	50	.56+	.65−	.52+	.20−	48.08−
treatment	6,000 r	12	85	13	5	.15+	.18−	.06+	.02+	27.78−
	12,000 r	20	100	4		.04	.05−			
Mated	1,500 r	86	86	49	112	.57−	.65+	1.30+	.49+	69.56+
after	3,000 r	139	139	70	250	.50+	.58−	1.80−	.68−	78.13−
treatment	6,000 r	16	70	3	15	.04+	.05−	.21+	.08+	83.33+
	12,000 r	20	106	3	20	.03−	.03+	.19−	.07+	86.96

suggest that dominant lethals are more readily induced in the sperm than recessive lethals in the eggs.

Two experiments have recently been completed in which females were X-rayed. I am indebted to DR. RAYMOND ZIRKLE and to the Department of Radiology, University of Pennsylvania Hospital, for cooperation in giving the X-ray treatments.

Females of an orange-eyed stock (11-o) were fed on caterpillars so that they were in active egg-laying condition. They were bred unmated or were mated to azygous males (collected from unmated mothers to avoid any chance of using biparental sterile males) of an unrelated wild type stock (no. 32). Thus, no biparental sons should be produced and percentage of

daughters should be relatively high. Females were subjected to X-radiation and matings were made either immediately before or immediately after treatment. Except for the controls, eggs were therefore treated in all cases, but sperm were X-rayed only when matings preceded treatments. Data are summarized separately (tables 3 and 4) since cultural conditions were much better in the second experiment resulting in larger numbers.

TABLE 4. EXPERIMENT 2/38/GS

Offspring produced in a given number of days by orange-eyed females (stock 11-o), (controls and X-rayed with various dosages), which were bred unmated or were mated to unrelated untreated wild type males (stock 32) either before or after treatment.

MOTHERS	TREATMENT	DAYS FERTILE	TOTAL DAYS	o ♂♂	+ ♀♀	♂♂ PER DAY	SURVIVAL RATE	♀♀ PER DAY	SURVIVAL RATE	% ♀♀
Unmated	Controls	225	225	1291		5.74−	1.00			
	1,500 r	86	86	382		4.44+	.90+			
	3,000 r	36	36	72		2.00	.41−			
	4,000 r	151	151	191		1.26+	.26−			
	5,000 r	88	88	109		1.24−	.25+			
	6,000 r	52	118	51		.43+	.09−			
	12,000 r	20	135	28		.21−	.04+			
	18,000 r	16	57	4		.07+	.01+			
Mated	Controls	209	209	292	953	1.40−	1.00	4.56−	1.00	76.55−
Mated before treatment	1,500 r	114	114	152	399	1.33+	.95+	3.50	.77+	72.05+
	3,000 r	124	124	154	345	1.24+	.89−	2.78+	.61−	69.14−
	4,000 r	123	123	55	70	.45−	.32+	.57−	.12+	56.00
	5,000 r	208	208	83	77	.40+	.29−	.37+	.08+	48.13−
	6,000 r	44	80	35	10	.44−	.37+	.13−	.03−	22.22+
	12,000 r	44	172	3	1	.02−	.01+	.01−	.00+	25.00
	18,000 r	20	103	11		.11−	.08−			
Mated after treatment	1,500 r	127	127	122	524	.96+	.69−	4.13−	.90+	81.12−
	3,000 r	119	119	161	510	1.35+	.97−	4.29−	.94−	76.01−
	4,000 r	186	186	106	434	.57−	.41−	2.33+	.51+	80.37
	5,000 r	150	150	108	266	.72	.52−	1.77+	.39−	71.12+
	6,000 r	80	97	22	91	.23−	.16+	.94−	.21−	80.53+
	12,000 r	28	212	18	19	.09−	.06+	.09−	.02−	51.35+
	18,000 r	20	103	8	5	.08−	.06−	.05−	.01+	38.46+

If there is no inactivation of sperm resulting from the treatment, the survival rate of sons per day (sons per day for the various treated groups divided by sons per day for the controls) (column 8, tables 3 and 4) should be the same for equal dosages in both experiments and whether mothers are unmated or mated before or after treatment. For the unmated series in both experiments where numbers of azygous sons are relatively high the rates are roughly parallel, but there is wide fluctuation in the four

mated series. In this connection it should be recalled that estimates of errors based merely on the numbers of offspring may be too small. A recessive lethal or semilethal occurring in a very few mothers may have considerable influence on averages of azygous sons. This is but one of the factors that may cause wider fluctuations than might be expected from the numbers appearing in the tables. Nevertheless it may be noted that in both experiments the groups in which sperm were treated have in general a higher rate of production of azygous sons. That this indicates sperm inactivation is doubtful in view of MAXWELL'S (1938) findings, but further tests would be of interest.

The decrease in azygous sons (as also in daughters) with increasing dosages is very marked at 6,000 r. At about this point complete sterility usually appears after vials *a*. The drop in average offspring per day is then due to the fact that the mother may live for many days subsequently without producing offspring. This postponed sterility may cause much fluctuation in averages if the length of life subsequent to the brief fertile period be greatly extended even in a single female. The "days fertile" (from time set until no more offspring were produced) are therefore lower (tables 3 and 4, column 3) for the females treated with higher dosages. In several of the 6,000 r groups (especially in experiment 2/38/GS, table 4) there were offspring in vials *a* but none in *b* followed by a few and sometimes several in *c* or *d*. This postponed temporary sterility suggests greater susceptibility of young oöcytes than of oögonia. Mature eggs seem to be but little affected and even after 18,000 r a few offspring may be produced.

Decrease in daughters per day is much more striking if matings are made before the treatment so that sperm are irradiated. Practically all daughters are eliminated by 12,000 r treatment of the sperm in the mated females. This is in agreement with the results from a closely similar treatment of the males (10,000 r) (WHITING 1937, see table 2 in this paper).

A few daughters are produced after 18,000 r treatment of eggs fertilized by untreated sperm.

The percentage of daughters drops rapidly when eggs and sperm are both treated, but if eggs alone are treated it is doubtful if there is any significant effect. The total number of offspring is very much reduced with higher dosages so that the apparent drop in percentage of daughters after treatment with 12,000 r and 18,000 r before mating (table 3) may be only a fluctuation. It was expected that a slight increase in percentage of daughters might appear on account of recessive lethals induced in the eggs. Were it possible to cause recessive lethals in all eggs escaping dominant lethal effects, the percentage of daughters might be increased up to one hundred. Further work may indicate whether this can be done, or whether eggs may be rendered unfertilizable but still able to develop normally into

males. Dominant lethals induced in the eggs should have no effect on the sex ratio.

SUMMARY

1. Dominant lethals may be induced in the sperm of Habrobracon by X-radiation of the males. At 10,000 to 20,000 r units all sperm have at least one lethal. With very high dosages, 41,000 to 142,000 r, some sperm are directly inactivated while many still remain active and able to carry dominant lethals into the eggs. Reduction of biparental sons and of daughters takes place at the same rate.

2. Recessive lethal-bearing daughters of treated males were twice as numerous as non-lethal bearing. Linkage with segregating visible mutants is sometimes indicated.

3. Treatment of females causes reduction in offspring per day, due either to the induction of dominant lethals or to direct killing of eggs. No change in sex ratio would be caused by dominant lethals in the egg.

4. If females are treated and subsequently mated, there is no appreciable reduction in male ratio, indicating that few, if any recessive lethals are induced in the egg.

5. Treatment of mated females causes a radical lowering of female ratio indicating that more dominant lethals are induced in the sperm than recessive lethals in the egg.

LITERATURE CITED

BISHOP, D. W., 1937 Induction of dominant lethal effects by X-radiation in Habrobracon. Genetics **22**: 452–456.

BOSTIAN, C. H., 1935 Biparental males and hatchability of eggs in Habrobracon. Genetics **20**: 280–285.

BOSTIAN, NEITA C., 1931 Sex ratios and mutants from X-rayed adult females of Habrobracon. Anat. Rec. **51**: 121.

GREB, RAYMOND J., 1933 Effects of X-radiation on production of mosaic males and on sex ratio in Habrobracon. Amer. Nat. **67**: 88–93.

MAXWELL, JANE, 1935 Recessive X-ray lethals in Habrobracon. Amer. Nat. **69**: 70.

1938 Inactivation of sperm by X-radiation in Habrobracon. Biol. Bull. **74**: 253–255.

MULLER, H. J., 1927 Artificial transmutation of the gene. Science **66**: 84–87.

STANCATI, M. F., 1932 Production of dominant lethal genetic effects by X-radiation of sperm in Habrobracon. Science **76**: 197–198.

WHITING, P. W., 1929 X-rays and parasitic wasps. J. Hered. **20**: 268–276.

1935 Recent X-ray mutations in Habrobracon. Proc. Penna. Acad. Sci. **9**: 60–63.

1936 Dominant lethal genetic effects caused by neutrons. Science **84**: 68.

1937a A convenient test of physical agents as producers of dominant lethals. The Collecting Net (Woods Hole) **12**: 129–130.

1937b Habrobracon as a means of testing the effectiveness of physical agents in causing mutations. Proc. Penna. Acad. Sci. **11**: 50–52.

1938 Decrease in biparental males by X-raying sperm in Habrobracon. Proc. Penna. Acad. Sci. **12**: 74–76.

WHITING, P. W., and BENKERT, LYSBETH HAMILTON, 1934 Azygotic ratios in Habrobracon. Genetics **19**: 237–267.