The Effect of Temperature on the Viability of Superfemales in Drosophila melanogaster

Th. Dobzhansky

PNAS 1928;14;671-675
doi:10.1073/pnas.14.8.671

THE EFFECT OF TEMPERATURE ON THE VIABILITY OF SUPERFEMALES IN DROSOPHILA MELANOGASTER

BY TH. DOBZHANSKY*

COLUMBIA UNIVERSITY

Communicated June 20, 1928

The superfemale is an individual having three X-chromosomes and two sets of autosomes. It has also many external characteristics by means of which it can be easily distinguished both from the normal sexes and from other sexual forms, i.e., intersexes and supermales. The superfemales arise in several kinds of genetical experiments concerned with abnormal chromosomal situations, such as in the progeny of the attached X-chromosome female, of the triploid female and in cases of non-disjunction of the X-chromosomes. But the frequency of superfemales found in cultures is always very much below that which might be expected theoretically on the basis of a knowledge of the genetic situation in a given case. Therefore, the superfemale can be considered as a typical semilethal form, which only relatively rarely reaches the imago stage.

Another fact, which can easily be noticed in working with the cultures producing superfemales, is the considerable variability of their frequency in the progeny of flies of like genetical constitution. This variability may be explained by the effect of some external influences on the viability of superfemale individuals. The preliminary results of Dr. A. H. Sturtevant (unpublished) suggested that a change of temperature really affects the frequency of the superfemales. The purpose of the present investigation is to check up this point more definitively.

The easiest way to obtain superfemales is to breed attached-X females (described by L. V. Morgan, 1922; T. H. Morgan, Bridges, Sturtevant, 1925). Such a female contains in its cells two X-chromosomes attached by their ends to each other, and in addition one Y-chromosome and two sets of the autosomes. In maturation of gametes two kinds of eggs are formed; one containing two attached X-chromosomes, and the other only the Y-chromosome, both having one set of the autosomes. Fertilized by the X-containing sperm of a normal male these eggs give two kinds of zygotes: XXX, which is the superfemale, and XY, which is normal male. In a similar way the Y-containing sperm gives XXY female, which is like the mother, and YY zygotes, which presumably never survive. If, as in the strain used by the author, the mother has the genes for the yellow recessive body color in both of its attached X-chromosomes, and the father is wild type with respect to sex-linked genes, all the daughters will be yellow and all the sons wild type in appearance. The superfemales in this

case must also be wild type because of the dominance of one wild type over two yellow allelomorphs.

Females from the attached-X stock were crossed to sooty males in order to prevent the possible harmful effect of the inbreeding on the viability of the flies. Sooty is a recessive autosomal gene and its presence in the culture does not affect the accuracy of classification of the sexes or of the yellow body color. The progeny of this cross was bred in pairs and placed in common half-pint bottles provided with a standard amount of the cornmeal-molasses food. The flies were raised at four different temperatures: 30½°, 24½°, 20° and 16°C. The accuracy of the temperature control was ±¼° at 30½° and 20°, and ±½° in the other two series. The flies were allowed to lay eggs until pupae of the next generation appeared, i.e., over a longer period in low and a shorter one in high temperature. The hatching flies were counted once every two days until the end of hatching. The summary of all counts is given in table 1. The percentage of superfemales is shown in table 2.

TABLE 1

THE PROGENY OF ATTACHED-X FEMALES AT DIFFERENT TEMPERATURES

			DETACHMENT		EDUCATIONAL EXCEPTIONS			
T°	YELLOW FEMALES	WILD TYPE MALES	SUPER-FEMALES	WILD TYPE FEMALES	YELLOW MALES	IN THE MALE	INTER-SEXES	TOTAL
30½	1749	1878	1	5	1	.	1	3635
24½	3262	3645	101	2	1	.	.	7011
20	3013	3340	351	1	.	.	.	6705
16	2635	2630	8	5	3	2	.	5283
Total	10659	11493	461	13	5	2	1	22634

TABLE 2

THE PERCENTAGE OF SUPERFEMALES AND THE SEX RATIO AT DIFFERENT TEMPERATURES

T°	SUPERFEMALES	FEMALE:MALE RATIO	DETACHMENT, %
30½	0.03±0.03	1:1.07	0.17
24½	1.44±0.14	1:1.12	0.04
20	5.23±0.27	1:1.11	0.01
16	0.15±0.05	1:1.00	0.15

In the cultures raised at 30½° there were found only 0.03±0.03% of superfemales. This means practically a complete non-occurrence of this kind of individuals. At 24½° the superfemales were not rare (1.44±0.14%) and usually could be found in each culture bottle. At 20° the highest frequency of the superfemales was observed (5.23±0.27%). The differences between these three figures are indubitably significant from the statistical standpoint. Below 20° the frequency of the superfemales diminishes again and at 16° only 0.15±0.05% of individuals found in the cultures are superfemales. This percentage is nearly as low as that observed at 30½° and the difference between these two values is below the limit of certainty.

The results obtained may be illustrated in a different way. Assuming that the attached-X female produces XX and Y gametes in equal numbers, and that all the XXX zygotes may survive to the imago stage, a frequency 33.3% of the superfemales may be expected in the cultures. The frequencies actually observed are only fractions of that. At 30½° only 1 of 1111.1 of the superfemales survives. For the temperatures 24½°, 20° and 16° this ratio is 1:23.1, 1:6.4 and 1:222.2, respectively.

Two hypotheses can be advanced for the explanation of these facts. First, the temperature may affect the frequency of production of XX and Y gametes in the attached-X mother. If more XX are produced at 20° and at 30½° and 16° more Y gametes, then the superfemales must be rarer in the last two temperatures and more frequent at 20°. But in such a case the sex ratio must also be affected. At 20° must be found a very considerable excess of females, and at 30½° and at 16° an excess of males. A disturbance of the sex ratio due to production of different numbers of XX and Y gametes in the attached-X female was described by T. H. Morgan, (Morgan, Sturtevant, Bridges, 1927). As table 2 shows, in my case the sex ratio is nearly equal at all the temperatures used, or even slightly changed toward the male side at 20° and 24½°. Since no correlation is observed between the sex ratio and the frequency of the superfemales also in the separate cultures, this hypothesis is untenable.

TABLE 3

THE NUMBER OF OFFSPRING OF ONE ATTACHED-X FEMALE AT DIFFERENT TEMPERATURES

T°	MEAN VALUE	δ	LIMITS
30½	86.6±6.2	40.2	18–175
24½	188.8±10.5	33.8	9–295
20	203.5±4.1	23.3	151–241
16	159.8±6.1	34.8	27–217

Second, the temperature may affect the viability of the superfemales themselves. The XXX zygotes may be absolutely lethal at 30½° and at 16°, but some of them may survive at 20 or 24½°. There is some independent evidence in favor of this hypothesis. The superfemales hatched at 24½° and at 16° are extremely weak, they very often have misshaped legs, shriveled wings and defects in the arrangement of the abdominal tergites. Some individuals break their pupa-cases but can not get out and die half emerged. The superfemales hatched at 20° are stronger and the defects just mentioned are seldom observed. Dead half-emerged pupae were never found at 20°.

Many dead pupae can be observed in the bottles kept at all the temperatures used, but at 30½° and at 16° they seem to be more frequent than at 24½° and especially at 20°. The fact that these dead pupae contained

superfemales was several times tested directly by means of dissection: inside of the pupa-cases fully formed dead flies were found. Li (1927) has shown also that approximately 25% of the eggs laid by an attached-X mother die without development (these are presumably the YY eggs), and another 25% die in old larval or pupal stages (superfemales).

To what extent the temperature affects the viability of the superfemales directly or indirectly cannot be decided at present. It is possible that the effect of temperature is partially due to changing of the physico-chemical condition of the food. These conditions may be the most favorable at 20° for all the flies and for the superfemales in particular. Comparing the average numbers of flies produced per bottle at different temperatures (Table 3) with the percentage of the superfemales (Table 1), it can be seen that there is some correlation between these values. But the average number of flies per bottle depends upon both egg-laying rate and laying duration. Therefore no conclusion can be drawn on the basis of this correlation. No correlation exists between the number of individuals hatched in a separate bottle and the percentage of the superfemales in the same bottle (at 20° the coefficient of correlation is equal to $+0.07 \pm 0.18$).

As seen from the table 1, some exceptional wild type females and yellow males are present in the cultures. The yellow males and most of the wild type females (giving some yellow sons if crossed to wild males) are the result of breaking apart of the attached pair of the X-chromosomes in the gametogenesis of their mother. Two wild type females have given no yellow males in their progeny when tested. Their origin is due probably to the equational non-disjunction of the X-chromosomes in the spermatogenesis of their father.

The percentage of the exceptional individuals due to the detachment of the attached X-chromosomes seems to be higher at both $30^1/_2°$ and 16°, than at $24^1/_2°$ and 20°. This means probably that the high and the low temperature increase the frequency of breakage of the attached-X pair. This fact in the case of high temperature was already stated by Bridges and Gabritschevsky (1928). But in my case the low temperature seems to produce the same effect as the high.

Summary.—The viability of the superfemales is much affected by the temperature; the optimum lies near 20°. At $30^1/_2°$ and at 16° no, or very few, superfemales hatch from the pupae. Both high and low temperature increase the breaking apart of the attached X-chromosomes.

* Fellow of the International Education Board.

Bridges, C. B., and E. Gabritschevsky, "The Giant Mutation in Drosophila Melanogaster. I. The Heredity of the Giant," *Zeitschr. indukt. Abstamm. Vererb.*, **46**, 231–47 (1928).

Li, J. C., "The Effect of Chromosomal Aberrations on Development in Drosophila Melanogaster," *Genetics*, **12**, 1–58 (1927).

Morgan, L. V., "Non-criss-cross Inheritance in Drosophila Melanogaster," *Biolog. Bull.*, **42**, 267–74 (1922).

Morgan, T. H., C. B. Bridges and A. H. Sturtevant, "The Genetics of Drosophila," *Bibliographica Genetica*, **2**, 1–262 (1925).

Morgan, T. H., A. H. Sturtevant and C. B. Bridges, "The Construction of the Germ Material in Relation to Heredity," *Carnegie Inst. Year Book*, **26**, 284–8 (1927).

PRELIMINARY NOTE ON THE ELASTIC HYSTERESIS OF THE HUMAN AORTA

BY A. V. BOCK, P. S. BAUER AND J. H. MEANS

MEDICAL LABORATORY OF THE MASSACHUSETTS GENERAL HOSPITAL AND CRUFT LABORATORY, HARVARD UNIVERSITY

Communicated July 13, 1928

Introduction.—As a result of a study of blood pressure changes occurring during muscular exercise[1] an attempt has been made to determine the rôle played by the arch of the aorta under conditions producing an increase in

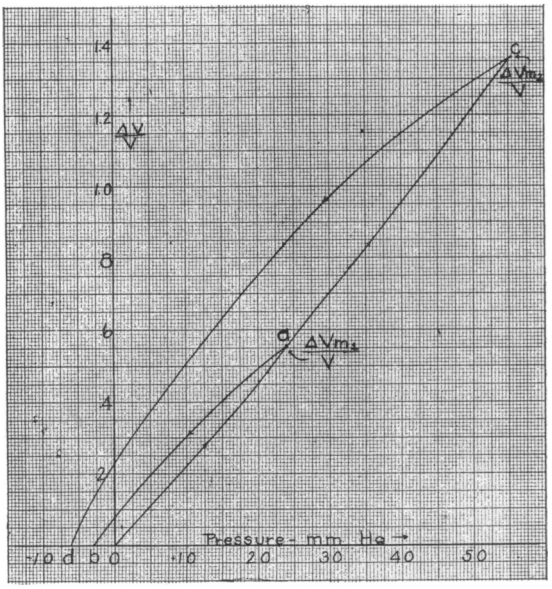

FIGURE 1

Typical curve illustrating elastic hysteresis of human aorta.

systemic blood pressure. Experimental results with reference to changes in blood pressure during exercise in different subjects suggested the possibility that variations in the elastic properties of the arch of the aorta