classes were examined by routine gel electrophoresis. Parental strains of D. pseudoobscura were homozygous for the + allele while the individuals from D. persimilis strains were homozygous for the - allele. On examination of progeny of F_1 females backcrossed to males of D. persimilis, fifty percent of the female progeny were homozygous for the - allele while the remaining fifty percent were +/-. Conversely, all the progeny of F_1 females backcrossed to D. pseudoobscura males were of the + phenotype. This result suggests that the enzyme activity at the acid phosphatase-6 locus is not disrupted in the backcross individuals. This work was carried out at the Museum of Comparative Zoology, Harvard University, and was supported by NIH Grant GM-21179 to Professor R.C. Lewontin.

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Gene dosage compensation in the X chromosome of D. melanogaster: transcription levels in metafemales and metamales and the amount of 6-phosphogluconate dehydrogenase in metafemales.

Studies of transcription activity and protein amounts encoded by X-chromosome genes in D. melanogaster suggest that the X chromosome of males is twice as active as the X chromosome of females (Khesin & Leibovitch 1976; Lucchesi 1977; Stewart & Merriam 1980). All authors agree that the activity of the X chromosome crucially depends on the ratio of the number of X chromosomes to the number of autosome sets (X:A ratio), i.e., the sex index. Yet various groups have come out with different assessments of the relationship between X-chromosome activity and the sex index. Lucchesi et al. have shown the activity of the X chromosome, measured by the incorporation of ^{3}H-uridine in polytene chromosome RNA and by the activity of the enzymes encoded by X-chromosome genes, to be higher in metamales (1X3A) than in diploid males (1X2A) (Lucchesi et al. 1974) and lower in metafemales (3X2A) than in diploid females (2X2A) (Lucchesi et al. 1977). This amounts to a gradual dependence of X-chromosome activity on the value of sex index. By contrast, we have shown (Faizullin & Gvozdev 1973; Ananiev et al. 1974) by similar methods that the transcription activity of the X chromosome is the same in metamales and males and is half that level in the X chromosomes of females and metafemales, as assessed by transcription intensity and the activity of 6-phosphogluconate dehydrogenase

Table 1. Transcription activity of X chromosomes in metafemales, intersexes and metamales.

Sex	Method of analysis: incorporation	Number of grains over X	Number of grains over autosomes	X/A[a)]	1X/1A[b)]	Number of nuclei
Metafemales	of ^{3}H-uridine	5487	17245	0.35±0.04	0.22±0.01	8
(3X2A)	of ^{3}H-NTP	5000	14176	0.35±0.02	0.23±0.01	24
Metamales	of ^{3}H-NTP	6241	34490	0.18±0.01	0.55±0.03	28
(1X3A)						
Intersexes	of ^{3}H-NTP	4164	16821	0.25±0.01	0.38±0.02	20
(2X3Z)						
Females	of ^{3}H-uridine[c)]	-	-	0.24	0.25	-
(2X2A)	of ^{3}H-NTP[d)]	-	-	0.24	0.24	-
Males	of ^{3}H-uridine[c)]	-	-	0.24	0.48	-
(1X2A)	of ^{3}H-NTP[d)]	-	-	0.26	0.52	-

a) = ratio of the number of grains over all X chromosomes to the number of grains over all autosomes; b) = ratio of the number of grains over one X chromosome to the number of grains over one autosome set; c) = data from (7); d) = data from (8). The Table lists mean values ± standard error.

Table 2. Relative amounts (%) of 6-phosphogluconate dehydrogenase antigen in metafemales and females[a)]

Experiment No.	Genotype		
	females		metafemales
	+/+	+/Df(1)Pgd-kz	+/+/+
1	100	57	119
2	100	64	100
3	100	53	115
4	100	52	97
5	100	not determined	100
6	100	not determined	90
7	100	54	115
8	100	67	100
9	100	65	97

Mean ± standard error.
a) = metafemales were obtained by crossing C(1)RM,ywf/Y females to Swedish b6 males.

(6PGD). Thus our results suggest a threshold-wise rather than gradual dependence of X-chromosome activity upon the value of sex index. The equally low levels of transcription activity in females and metafemales were confirmed by measurements of ^{3}H-nucleoside triphosphate (^{3}H-NTP) incorporation during the transcription of fixed X chromosomes with E. coli RNA polymerase (Khesin & Leibovitch 1976; Leibovitch et al. 1976).

In view of the above contradictions, we have re-investigated the matter in the present study by measuring RNA synthesis via ^{3}H-uridine incorporation in living cells or ^{3}H-NTP incorporation using E. coli RNA polymerase in chromosome preparations from metafemales, metamales and intersexes (2X3A). The activity of the Pgd gene in the X chromosome was assessed by the amount of antigen (6PGD) in females and metafemales in a reaction of complement fixation with a specific antiserum (Levin 1967; Gvozdev et al. 1981). The method allows a direct evaluation of the number of enzyme molecules. Metafemales were obtained by crossing C(1)RM,ywf/Y females to wild-type Swedish b6 males; metamales and intersexes were obtained by crossing wild-type Oregon RG females to y^2;C(2L)dp;C(2R)px; C(3L)g;C(3R)+ males. The larval karyotype was checked by the brain ganglion metaphases. RNA synthesis in living cells was studied according to Ananiev et al. (1974); RNA synthesis in fixed chromosomes by E. coli RNA polymerase was studied according to Khesin & Leibovitch (1974). The transcription activity measurements are summarized in Table 1.

The Table demonstrates that metamales and males have about the same transcription activity of X-chromosome which is twice as high as that of diploid females and metafemales, irrespective of the method used. Intersexes have an intermediate transcription activity, as has been found earlier (Khesin & Leibovitch 1976; Lucchesi 1977; Stewart & Merriam 1980). Thus we have corroborated the results which we had previously obtained for individuals from other crosses. The transcription intensity of the X chromosomes does depend on the sex index in a threshold-wise manner. This relationship might reflect some important changes in the chromatin structure depending on the concentration of hypothetical positive regulators of autosome origin (Lucchesi 1977; Stewart & Merriam 1980; Ananiev et al. 1974).

The assessment of the amount of product of the X-chromosome Pgd gene has yielded a different kind of result (Table 2).

The Table demonstrates that the amount of antigen relative to the protein amount in the extract (the amount of antigen in female extracts is 100%) is the same in females and metafemales. In the control of experiments we determined the amount of 6PGD in females with a single dose of the Pgd gene (carrying a deletion in one of the X chromosomes, Df(1)Pgd-kz). As might have been expected, such females had about 59% of the normal antigen amount. The results show that the amount of the Pgd gene product per one X chromosome is 1.5 times smaller in metafemales than in females. This is consistent with the dat of Lucchesi et al. (1977). We cannot evaluate the transcription activity of the Pgd gene but a comparison of these results with the results in Table 1 suggests that the amount of the final product of X-chromosome genes might well be regulated at the posttranscription stage as well.

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