Lyttle, T.W. University of Hawaii, Honolulu. Segregation in XYY males and XXY females of D. melanogaster.

Grell (1958) investigated the pattern of sex chromosome segregation in the progeny of XYY males and recovered XY/Y segregation in excess of the .667 frequency predicted under non-preferential segregation. In addition, there appeared to be a deficiency of XYY males which Grell attributed to a lowered viability of such aneuploid types. This report presents data which independently supports Grell's speculation.

In the course of our work with a translocation [T(Y;2),SD L^2] in D. melanogaster which has its autosomal break in division 58 proximal to bw^+, we found it necessary to measure the amount of sex chromosome nondisjunction in X/X/T(Y;2),SD L^2/CyO females and X/Ybw^+/y^+YB^S males. Flies hyperploid for the 2R tip survive and carry all the Y fertility factors.

Table 1 shows the resulting progeny when X/X/T(Y;2),SD L^2/CyO (= Rsp^I) females are mated to y/y^+YB^S;Rsp^S cn bw (or Rsp^I-16 cn bw, kindly provided by B. Ganetzky) males. Here Rsp^S and Rsp^I denote the alleles at the Responder locus which are sensitive and insensitive, respectively, to the sperm dysfunction induced by Segregation distorter (SD).

Some progeny classes are lethal and others are confounded, but a reasonable estimate of the overall nondisjunction rate can be obtained by doubling the contribution of the three surviving nondisjunctional classes to the total, to give $\underline{m}$ = proportion of XX/Y disjunctions = 14/635 = .022. This should be compared to the somewhat higher rate of $2 \cdot (2404/54070)$ = .086 obtained by Bridges (1916, $\chi^2 = 15.4$, $p << .001$). The apparent reduction in secondary nondisjunction may be partially due to a decreased viability of y flies, or may be explained on the basis of a decreased probability of heterosynapsis owing to the interference of the bw^+ material on the Y.

Two classes of progeny males (A and B) were themselves progeny tested in matings to cn bw females in order to further determine the viability of, and segregation in, XYY flies. Tests of B Cy cn males (class A in Table 1) showed 3/21 males were XYY, and their progeny distribution is presented in Table 2. The B L males (class B, Table 1) are all XYY, but some of those (5/14) tested were carrying Rsp^S and showed segregation distortion, while the remainder were X/y^+YB^S;T(Y;2),SD L^2/Rsp^I - 16 cn bw and showed no SD activity. The progeny from these crosses are summarized in Tables 3b and a, respectively.

Several observations can be made from this somewhat heterogeneous mass of information. First, the data from Table 2 include all progeny classes and allow the best estimate of $\underline{\ell}$ = proportion X/YY disjunction (summarized in Table 4b). I give a range for $\hat{\underline{\ell}}$ because its value depends critically on whether there is a viability reduction in XYY flies, since $\hat{\underline{\ell}}_1$ = (X + YY)/TOTAL will then underestimate $\underline{\ell}$. On the other hand, $\hat{\underline{\ell}}_2$ = X/(X + Y) uses less of the available information and is therefore less precise, though perhaps moe accurate. Secondly, the presence of the SD L portion of the T(Y;2) in the B L males allows us to use Table 3a to determine whether the translocation itself affects segregation. Finally, from Table 3b we can determine whether the strength of SD is altered by the presence of the extra sex chromosome.

From Table 3a we first estimate the parameter $\underline{c}$ = proportion of X $\leftrightarrow$ SD segregations, which should be equal to 0.5 if the two chromosomes are assorting independently. Here $\underline{c}$ = 167/343 = .487 with $\chi^2_1 = .557$, $p \cong .54$, and we provisionally accept the hypothesis that the translocation is not interfering with sex chromosome disjunction.

Also in Table 3a, we attempt to measure $\underline{\ell}$ by first estimating the three missing classes by the observed numbers for their respective complementary classes (immediately right adjacent to each empty box) and summarizing the data in Table 4c. Notice that the range of $\underline{\ell}$ here barely overlaps that obtained from the data of Table 2 (see Table 4b). This is primarily because of the zero value for the XYY class in the latter data, which males $\underline{\ell}_1$ extremely low. It should be noted that the pattern of the data and the estimates of $\underline{\ell}_1$ vary very little if we ignore the missing or confounded data classes in Tables 2 and 3 and use only the even numbered columns for purposes of estimation. These alternate estimates of $\underline{\ell}$ are presented in Table 4 with asterisks.

The overall estimate of $\underline{\ell}$ in the current data may also have a slightly upward bias owing to the apparent tendency of y^+YB^S to be involved in a proportionally greater number of heterosynapses in these XYY males, perhaps due to some pairing ability of the X material on y^+YB^S. This shows up in all crosses as an increased tendency for X Ybw^+/y^+YB^S compared to X y^+YB^S/Ybw^+ segregations. The data from both Tables 2 and 3 are homogeneous in this respect, and when pooled (ignoring the SD L classes) gives an overall $\chi^2_1 = 15.63$, $p << .001$) for the contingency test for independence of the X and the type of Y chromosome present (89 XYbw^+:50 Xy^+YB^S:57 Ybw^+:84 y^+YB^S). If there is an enhanced tendency for Xy^+YB^S synapses, this will increase the proportion of recovered X $\leftrightarrow$ YY disjunctions and thus increase $\hat{\underline{\ell}}$ above the level

Table 1 - Progeny from X/X/T(Y;2)SD L^2/CyO ♀ by $y/y^+YB^S;cn\ bw$♂.

GAMETES ♂/♀	X CyO	$XYbw^+$ CyO	X SDL	$XYbw^+$ SDL	XX CyO	Ybw^+ CyO	XX SDL	Ybw^+ SDL
y;cn bw	303	cy cn♀	†	97 L♀	†	2y Cy cn	†	1 yL♂
y^+YB^S;cn bw	(A) 160	B Cy cn♂	†	(B) 61 BL♂	4 B Cy ♀	†	†	†

Table 2 - Progeny from X/y^+YB^S/Ybw^+;cn bw/CyO♂♂ by X/X;cn bw♀♀.

♂ GAMETES†	XY CyO	XY cn bw	XY^1 CyO	XY^1 cn bw	Y CyO	Y cn bw	Y^1 CyO	Y^1 cn bw	X CyO	X cn bw	YY^1 CyO	YY^1 cn bw
PROGENY	18†	28	8	10	15	9	20	22	8†	12	0	0
PHENOTYPE	Cy ♀	cn ♀	B Cy ♀	B cn♀bw	Cy ♂	Cn ♂	B Cy ♂	cn♂B bw	Cy ♀	cn bw ♀	B Cy ♀	B cn ♂

† based on partitioning 26 Cy♀ progeny according to XY cn bw: X cn bw proportions observed.

* Y = Ybw^+

Y^1 = y^+YB^S

Table 3a, b - Progeny from a) $X/\underline{y}^{+}\underline{YB}^{S};T(Y;2),\underline{SD}\ \underline{L}^{2}/Rsp^{I}$ - 16 cn bw
or b) $X/\underline{y}^{+}\underline{YB}^{S};T(Y;2),\underline{SD}\ \underline{L}^{2}/Rsp^{S}$ cn bw ♂♂ by X/X;cn bw ♀♀.

♂ GAMETES*	XY SDL	XY cn bw	XY^{1} SDL	XY^{1} cn bw	Y SDL	Y cn bw	Y^{1} SDL	Y^{1} cn bw	X SDL	X cn bw	YY^{1} SDL	YY^{1} cn bw
PROGENY a	39	42	-	26	14	33	-	42	-	30	13	6
b	71	1	-	5	73	0	-	0	-	0	12	1
PHENOTYPE	L ♀	cn ♀	+	$cn^{B}bw$ ♀	L ♂	cn ♂	+	$cn^{B}bw$ ♂	+	cn bw ♀	BL ♂	B cn ♂

* $Y = Y\underline{bw}^{+}$
$Y^{1} = \underline{y}^{+}\underline{YB}^{S}$

Table 4 - Summary of data from Grell (1958) and Tables 2 and 3.

♂GAMETES	XY	X	YY	Y	$\hat{\ell}_1$ → $\hat{\ell}_2$
PROGENY	XXY ♀	XX ♀	XYY ♂	XY ♂	
a	1153	307	207	1155	.182 - .210
b	64	20	0	66	.133 - .233 .148 - .279*
c	133	60	19	131	.230 - .314 .201 - .286*

* see text

obtained for normal XYY males. In any case, even if we ignore this potential bias, the various estimates for $\underline{\ell}$ tend to argue against nonpreferential segregation (i.e., $\underline{\ell}$ = .333), and in favor of Grell's conclusion of preferential pairing of the Y chromosomes.

Table 3b can be used to estimate $\underline{k}$ (= proportion of SD bearing sperm) in these crosses where distortion is active. The estimate obtained is $\hat{\underline{k}}$ = 156/158 = .987, indistinguishable from a control value obtained for X;T(Y;2),SD L^2/Rsp^S cn bw males of 6260/6290 = .995 (χ^2_1 = 1.94, p = .173). Therefore, I conclude that the presence of the extra Y is having no significant effect on the strength of distortion.

The low frequency of XYY males among the B Cy cn progeny tested from Table 1 (14% recovered) as well as the disparity in the X versus YY gamete recovery in all data of Table 4 indicates a reduced viability for XYY flies, best estimated from Grell's data alone as a loss of about 0.33 compared to XY males. The viability is further lowered in my data by the fact that the XYY males are often hyperploid for the 2R tip.

The estimates of $\underline{\ell}$ differ somewhat, with $\underline{\ell}_2$ being most reliable owing to the viability effect. After making allowances for the possible biases discussed, it would seem that $\underline{\ell}$ ~ .2 - .25 is a reasonable estimate. However, an important inference from the data presented here should be that marked Y chromosomes may introduce considerable bias for segregation studies in Drosophila.

References: Bridges, C.B. 1916, Genetics 1:1-52, 107-163; Grell, R.F. 1958, 10th Int. Cong. of Genet. (Proc.) p. 105.

Malogolowkin-Cohen, Ch. and M. Livni. Institute of Evolution, University of Haifa, Israel. A preliminary study on polymorphism and heterozygosity found in D. subobscura in Israel.

A genetic analysis, polymorphism and heterozygosity of 16 loci of 12 enzymes of Israeli populations of D. subobscura was initiated in our laboratory in 1976. Five collecting sites from three of the four biogeographic regions cited by Malogolowkin-Cohen (1979) and Malogolowkin-Cohen et al. (1979) are used in this study: (1) mountains - Biryah-Zefat, Carmel and Quiriat Anavim-Mevasseret; (2) foot hills - Tivon-Oranim; (3) coastal plain - Dor (Fig. 1). Males caught at the above mentioned places were pair-mated to virgin females from a stock of inversion-free chromosomes and wild impregnated females caught at the same places were permitted to oviposit in the lab, after which

Locality	$\overline{A}$ (allele frequency)	$\overline{p}$ (polymorphism)	$\overline{H}$ (heterozygosity)
Kiryat Anavim-Mevasseret	1.68	0.37	0.05
Tivon-Oranim	2.19	0.81	0.08
Biryah-Zefat	2.19	0.81	0.05
Dor	2.06	0.62	0.05
Mount Carmel	2.37	0.87	0.09

wild males and wild females were assayed for enzymes. Horizontal starch gel electrophoresis was carried out according to the techniques of Ayala et al. (1972) with modifications and additions made by Saura et al. (1973). The allele frequency, $\overline{A}$, polymorphism, $\overline{p}$, and heterozygosity, $\overline{H}$, are calculated and the results may be seen in Table 1. Polymorphism and allele frequencies are found to be higher in the center (Tivon-Oranim, Mount Carmel and Dor) and in the north (Biryah-Zefat) and lower in the western distribution area of the fly (Quiriat-Anavim-Mevasseret), while no variation is found in heterozygosity (Table 1). The estimates are based on the following loci: acid phosphatase (Acph 1, 2, and 3), aldehyde oxidase (Ao), esterase (Est), fumarase (Fum), α-glycerophosphate dehydrogenase (α-Gpdh), hexokinase (Hk), isocitrate dehydrogenase (Idh), leucine aminopeptidase (Lap), malate dehydrogenase (Mdh 2 and R), malic enzyme (Me), phosphoglucomutase (Pgm) and phosphoglucose isomerase (Pgi 1 and 2).