MULTIPLE MEIOTIC DRIVE SYSTEMS IN THE
DROSOPHILA MELANOGASTER MALE

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ABSTRACT

The behaviour of two "meiotic drive" systems, *Segregation-Distorter (SD)* and the sex chromosome sc^4sc^8 has been examined in the same meiocyte. It has been found that the two systems interact in a specific way. When the distorting effects of *SD* and sc^4sc^8 are against each other, there is no detectable interaction. Each system is apparently oblivious to the presence of the other, gametes being produced according to independence expectations. However when the affected chromosomes are at the same meiotic pole an interaction occurs; the survival probability of the gamete containing both distorted chromosomal products is *increased*, rather than being decreased by the combined action of two systems.

THE *Segregation-Distorter (SD)* "meiotic drive" system in the Drosophila male, discovered originally by SANDLER, HIRAIZUMI and SANDLER (1959), has been extensively studied and recently reviewed (ZIMMERING, SANDLER and NICOLETTI 1970). HARTL, HIRAIZUMI and CROW (1967) demonstrated genetically that the SD/SD^+ genotype operates by "gamete dysfunction," so that the SD^+ chromosome is generally recovered in very low frequency in the offspring of an SD/SD^+ male, and the *SD* homologue appears among the progeny in excess of 99%.

Other lines of inquiry have further specified the mechanism of the SD system.

By means of electron microscope studies, NICOLETTI (1968), as well as TOKU-YASU, PEACOCK and HARDY (1972), have provided cytological insights into the dysfunction hypothesis. The latter authors have shown that a maximum of half of the sperm of SD/SD^+ males can exhibit developmental abnormalities, and they have inferred that the irregularities in sperm development are confined to the SD^+ class. The statistical approach of MIKLOS and SMITH-WHITE (1971) has been generalised to provide a framework in which the *SD* system can be visualized in standard quantitative genetic terms (MIKLOS 1971, 1972). Many previous problems in the genetic interpretation of *SD* data have stemmed from the way in which the observed progeny classes have been analysed. The use of k value (the ratio of *SD* gametes to the total recovered) has introduced complexities which have been avoided by MIKLOS and SMITH-WHITE (1971), who used the

standard deviation of the normal distribution as a unit of measurement.

The conclusions which emerge from the cytological and statistical approaches are that SD^+ sperm are eliminated during gametogenesis, and that the mechanisms causing elimination are due to a normally distributed underlying variable or summation of variables.

Another "meiotic drive" system which has been analysed both genetically and by means of the light microscope is the $In(1)sc^{4L}sc^{8R},y/y^+Y$ genotype studied by SANDLER and BRAVER (1954), ZIMMERING (1963) and PEACOCK (1965). This genotype, which has an X chromosome partially deficient for a portion of the heterochromatin, shall be denoted the sc^4sc^8X/Y system, and a sc^4sc^8 male shall refer to an $In(1)sc^{4L}sc^{8R},y/y^+Y$ male. In this system the sex chromosomes undergo nondisjunction. The unpaired chromosomes exhibit nonrandom movement, such that *nullo* and X/Y cells are produced from meiocytes in which the chromosomes were not paired at meiosis I. There are thus two populations of meiocytes, disjunctional and nondisjunctional; in disjunctional ones the sc^4sc^8X and the Y chromosome are paired, separate regularly, and sc^4sc^8X and Y-bearing cells are produced in equal frequency at the end of meiosis. In nondisjunctional meiocytes, the sc^4sc^8X and the Y remain as univalents, both proceed to one anaphase pole, and *nullo* and sc^4sc^8X/Y cells in equal proportion, are the virtually exclusive meiotic products.

An analysis of the progeny of sc^4sc^8 fathers however, reveals that the sc^4sc^8X is recovered approximately twice as frequently as the Y, and that the *nullo* is recovered about twenty times more frequently than the sc^4sc^8X/Y gamete. To be more precise, the frequency of nondisjunction in sc^4sc^8 males is related in a specific way to gametic recovery. The higher the nondisjunction, the higher is both the recovery of the sc^4sc^8X as well as the *nullo* (MIKLOS and PEACOCK, in manuscript).

It is the purpose of this paper to investigate the similarities between the SD/SD^+ and sc^4sc^8X/Y systems, and to present the results and conclusions of the synthesis of "double drive" systems, in which the SD/SD^+ and sc^4sc^8X/Y chromosomes exist in the same meiocyte.

DESCRIPTION OF THE SYSTEMS

Segregation-Distorter: There are a number of previously established tenets which form the basis of this paper, and for SD they are as follows:

(1) Only SD^+ sperm from an SD/SD^+ male undergo extinction; the SD sperm are all potentially capable of fertilization.

(2) Distortion is measured by use of the normal distribution.

(3) SD^+ gametes with different sex-chromosome constitutions undergo differential extinction with increasing distortion. For example, at a given distortion level, a *nullo*; SD^+ gamete is more susceptible to extinction than Y; SD^+, X; SD^+ or attached XY; SD^+ gametes. Furthermore, the probability that a given gamete will "dysfunction," depends also on whether it came from a "disjunctional" or "nondisjunctional" primary meiocyte (DENELL and MIKLOS 1971).

sc^4sc^8: In this system, distortion in the disjunctional class is expressed as the ratio $X/(X + Y)$ and in the nondisjunctional class as $nullo/(nullo + X/Y)$. The frequency of nondisjunction has been given as $(nullo + X/Y)/(\text{Total gametes})$, (PEACOCK 1965). The relationship between these three ratios is shown in Figure 1. These curves are derived from data to be published in more detail elsewhere (MIKLOS and PEACOCK, in manuscript).
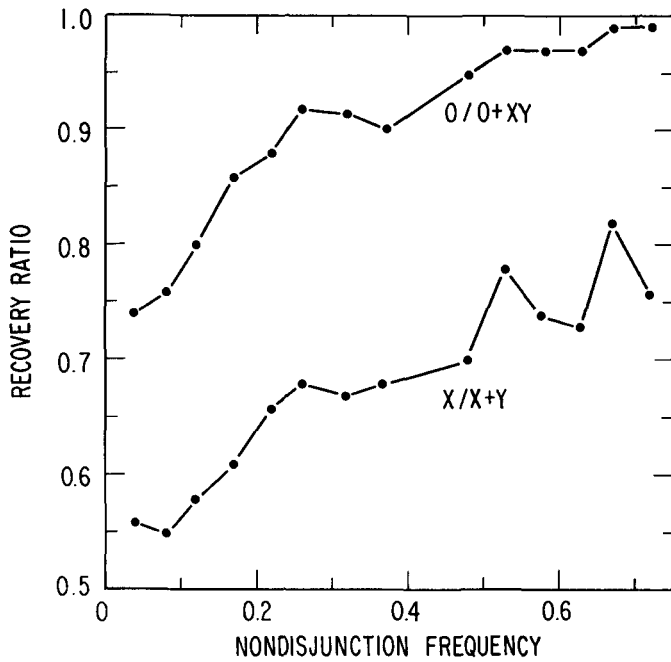
FIGURE 1.—This figure shows the relationships between the recovery ratios $X/(X+Y)$, and $nullo/(nullo + X/Y)$, expressed as functions of the nondisjunction frequency, $(nullo + X/Y)/$ $Total$. (Data from MIKLOS and PEACOCK, in manuscript.)

These authors have argued, both from the curves of Figure 1 as well as from light microscope observations of putative sperm breakdown, that the sc^4sc^8 case can be interpreted in terms of "gamete dysfunction," where the sc^4sc^8X and $nullo$ gametes suffer negligible elimination, and the Y and X/Y ones undergo different levels of extinction. Secondly, a statistical analysis has revealed extra binomial between-male variance in the three ratios of the sc^4sc^8 system. This is similar to the situation in the $SD/SD+$ case, and is an indication that the two "meiotic drive" systems probably share common features.

The sc^4sc^8 system can be described in the following way:

(1) Disjunctional meiocytes produce only sc^4sc^8 X and Y gametes of which only the Y-bearing ones suffer "gamete dysfunction."

(2) Nondisjunctional meiocytes produce solely $nullo$ and X/Y gametes, of which only X/Y-bearing ones undergo "gamete dysfunction."

(3) The distortion in both the disjunctional and nondisjunctional gametic classes is related in a special way to the nondisjunction frequency, and conforms to the curves drawn in Figure 1.

It will be shown that this approach, when combined with the knowledge of $SD/SD+$ systems, provides a useful exploratory avenue for the investigation of "double drive" systems.

MATERIALS AND METHODS

"Double drive" males are of the constitution $In(1)sc^{4L}sc^{8R},y/y+Y$; SD-$72/cn\ bw$. The SD-72 chromosome is a standard strongly distorting system; its homologue is marked with the mutants cinnabar eye (cn) and brown eye (bw).

"Control" males are of the following four genotypes: (1) $In(1)sc^{4L}sc^{8R},y/y+Y$; SD-$72/$ $In(2LR)Cy$; (2) $X/y+Y$; SD-$72/In(2LR)Cy$; (3) $In(1)sc^{4L}sc^{8R},y/y+Y$; $cn\ bw/In(2LR)Cy$; and (4) $X/y+Y$; $cn\ bw/In(2LR)Cy$. Details of markers are in LINDSLEY and GRELL (1968).

"Double drive" males and "controls" were mated to γ; $cn\ bw$ virgin females under standard conditions at 25°C. The experiments are denoted E1, E2, E3 and E4.

RESULTS

The data are presented in Table 1. The data of E2 were comparable to the data of the other experiments, but it appeared to contain two distinct populations of

TABLE 1

1A. *The relative gametic frequencies from* sc⁴sc⁸X/Y; SD/SD⁺ *males*

| | | SD class | | | | SD⁺ class | | | Total |
	X	Y	Nullo	X/Y	X	Y	Nullo	X/Y	progeny
E1	0.283	0.143	0.128	0.012	0.221	0.176	0.022	0.016	5997
E2(a)	0.185	0.071	0.294	0.013	0.230	0.143	0.037	0.028	945
E2(b)	0.387	0.277	0.022	0.008	0.132	0.166	0.002	0.006	2494
E3	0.227	0.090	0.262	0.012	0.196	0.145	0.054	0.039	5326
E4	0.409	0.180	0.236	0.016	0.058	0.068	0.001	0.032	5441

1B. *The relative gametic frequencies from* "control" *males carrying* SD

Genotype									
X/γ⁺Y; SD/Cγ	0.236	0.257	——	——	0.257	0.250	——	——	3362
sc⁴sc⁸X/γ⁺Y; SD/Cγ	0.247	0.127	0.119	0.012	0.262	0.125	0.096	0.013	1211

1C. *The relative gametic frequencies from* non-SD *"control" males*

X/γ⁺Y; cn bw/Cγ	0.254	0.234	——	——	0.261	0.250	——	——	6809
sc⁴sc⁸X/γ⁺Y; cn bw/Cγ	0.213	0.131	0.098	0.015	0.252	0.147	0.124	0.019	4196

TABLE 2

Individual male data from "double drive" males of E2

| | SD class | | | | SD⁺ class | | | Total |
X	Y	Nullo	X/Y	X	Y	Nullo	X/Y	progeny
125	56	8	0	97	89	0	0	375
146	88	5	4	44	59	0	6	352
30	31	4	1	28	28	3	0	125
199	191	14	4	14	35	0	2	459
151	104	8	1	88	130	1	1	484
198	153	15	5	13	19	0	3	406
117	68	1	4	45	54	0	4	293
16	15	39	2	25	15	5	1	118
8	0	19	1	11	11	0	1	51
14	4	18	0	2	4	1	1	44
8	2	20	1	27	7	9	2	76
44	18	22	3	51	25	2	0	165
16	5	27	2	41	13	12	2	118
16	5	41	2	3	7	0	7	81
16	3	28	1	25	14	3	3	93
18	4	26	0	12	16	0	2	78
8	6	15	0	14	8	3	1	55
11	5	23	0	6	15	0	6	66

males with grossly disparate nondisjunction frequencies, probably attributable to a segregating modifier. E2 has thus been divided into two parts on the basis of nondisjunction frequency, and the raw data have been presented in their entirety in a separate table (Table 2).

<center>DISCUSSION</center>

The experimental results, and the hypotheses to be drawn, can be visualized by examining the meiotic configurations which yield the final gametic arrays. These are drawn in Figure 2.

In meiocyte I, the SD and sc^4sc^8 systems operate in the same "direction", so that the sc^4sc^8 X; SD gametes suffer no extinction, whereas the Y; SD^+ ones are affected. Similarly, in meiocyte III, $nullo$; SD gametes escape elimination and sc^4sc^8 X/Y; SD^+ ones do not.

In meiocytes II and IV, the SD and sc^4sc^8 systems work against each other, so that all the gametes, Y; SD, sc^4sc^8 X; SD^+, sc^4sc^8 X/Y; SD and $nullo$; SD^+ undergo some degree of extinction.

The data will be examined in two ways; firstly by analysing the gametic array in the SD class, and then by examining meiocytes I to IV on an individual basis.

The SD *class:* An examination of the sc^4sc^8X; SD, Y; SD, $nullo$; SD and sc^4sc^8X/Y; SD gametic frequencies is in fact an investigation of the "drive" of the sc^4sc^8 system in meiocytes II and IV, since in the SD class, it is only the Y; SD and sc^4sc^8X/Y; SD gametes which have been affected. The X; SD and $nullo$; SD gametes have remained unaffected by the extinction mechanisms.

From the SD class it is possible to estimate the frequency of nondisjunction as well as the distortion amongst disjunctional and nondisjunctional gametes. It is then possible to compare these figures with the curves of Figure 1, which are observations from independent experiments with the sc^4sc^8 genotype. For example, in E1 the frequency of nondisjunction is $(0.128 + 0.012)/(0.283 + 0.143 + 0.128 + 0.012)$, that is 0.25, and the distortion in the disjunctional and nondisjunctional classes is $(0.143)/(0.283 + 0.143)$ and $(0.128)/(0.128 + 0.012)$, that is 0.66 and 0.91. An examination of Figure 1 shows that at 0.25 nondisjunction, the expected distortions from a sc^4sc^8 system are 0.65 and 0.90; in excellent agreement with the figures observed here.

The nondisjunction frequencies and recovery ratios have been calculated for experiments E1 to E4 and they have been compared to the recovery ratios from Figure 1. These comparisons are given in Table 3.

For all "double drive" experiments, the recovery ratios are in excellent agreement with the recovery ratios from sc^4sc^8 experiments at every level in the nondisjunction spectrum. Hence when the two "meiotic drive" systems are at opposite poles of the meiocyte, and "drive" against each other, so that in meiocytes II and IV simultaneous elimination of SD and SD^+ gametes occurs, there is no detectable complex interaction of the systems which would lead to levels of gametic death that are inconsistent with the curves of Figure 1.

Examination of meiocytes I and III: In these meiocytes the SD and sc^4sc^8 systems "drive" in the same direction and the different classes of data enable an answer to each of the following questions: Is the survival probability of the Y;
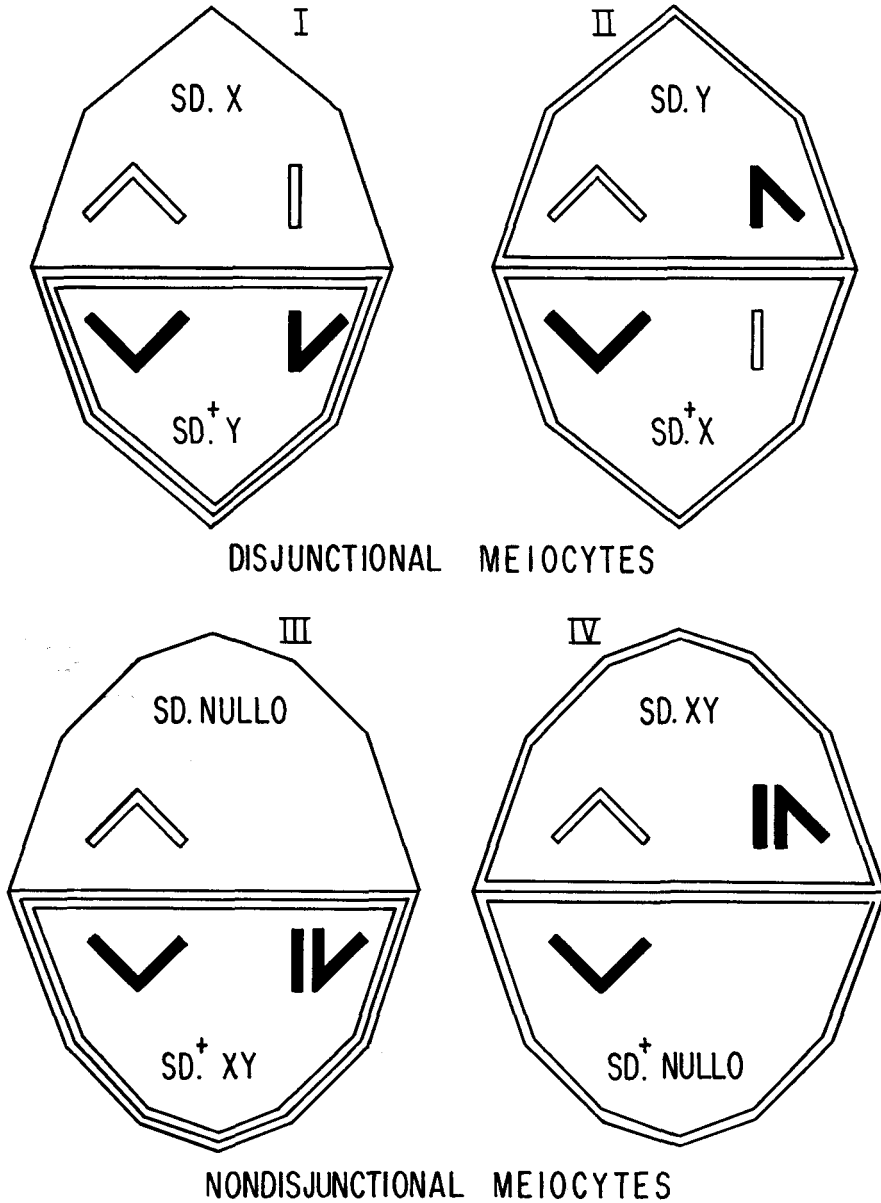
FIGURE 2.—This figure is a schematic representation of the four types of meiocytes discussed in the text; its value is purely illustrative and implies nothing about the time of action or the mechanisms involved in distortion. In meiocyte I, the Y and $SD+$ chromosomes are subjected to perturbations by both meiotic drive systems and distortion is "unidirectional"; both chromosomes being affected are to be found at one pole of the primary spermatocyte. Distortion in meiocyte II is "bidirectional," since the Y and $SD+$ chromosomes are at opposite ends of the primary spermatocyte. Similarly in nondisjunctional meiocytes, both systems distort in the "same direction" in meiocyte III, and in an "opposite direction" in meiocyte IV.

TABLE 3

A comparison of the recovery ratios estimated from the SD *gametic class of "double drive" males, and the same ratios estimated from a simple* sc⁴sc⁸ *system*

	Observed $X/(X+Y)$ from "double drive"	Observed $X/(X+Y)$ from the sc⁴sc⁸ system	Observed nullo/(nullo + X/Y) "double drive"	nullo/(nullo + X/Y) from the sc⁴sc⁸ system	Frequency of nondisjunction
E1	0.66	0.65	0.91	0.90	0.25
E2(a)	0.72	0.74	0.96	0.95	0.55
E2(b)	0.58	0.53	0.73	0.73	0.04
E3	0.72	0.71	0.96	0.95	0.46
E4	0.69	0.67	0.94	0.92	0.30

SD^+ and sc^4sc^8X/Y; SD^+ gametes the product of the survival probability of each system? Does either of the systems "drive" at the expense of the other, or is there an interaction, such that each system "drives" at at intermediate level? The answers are given below.

The distorting effect of SD in the disjunctional class can be estimated from the relative frequencies of the SD and SD^+ gametes which contains the sc^4sc^8X chromosome. The effect of SD in the nondisjunctional class is obtained from the frequencies of *nullo; SD* and *nullo; SD⁺* gametes. The magnitude of action of the sc^4sc^8 system can be measured from the survival probabilities of the $Y; SD$ and $sc^4sc^8X/Y; SD$ gametes in meiocytes II and IV. Hence all the survival estimates which shall be used to examine the behaviour of the two systems in meiocytes I and III, have been independently obtained from meiocytes II and IV.

The evaluation of the data is facilitated if Table 1A is re-expressed in survival probabilities, that is if the frequencies of $Y; SD$, $Y; SD^+$ and $sc^4sc^8X; SD^+$ are given relative to the $sc^4sc^8X; SD$ class which has remained intact. Similarly, *nullo; SD⁺*, $sc^4sc^8X/Y; SD$ and $sc^4sc^8X/Y; SD^+$ are expressed relative to the frequency of the *nullo; SD* class. This reconstruction is shown below in Table 4.

The discussion now concerns only the survival probability of the $Y; SD^+$ and $sc^4sc^8X/Y; SD^+$ gametes, since these are the only gametes which suffer elimination under the combined action of both systems. For example, in E1, the observed probability of survival of the $Y; SD^+$ gametes is 0.62. From meiocyte II, the distorting effect of SD alone is such as to permit a survival probability of the

TABLE 4

The gametic frequencies from sc⁴sc⁸X/Y; SD/SD⁺ *males expressed relative to the* sc⁴sc⁸X; SD *and* nullo; SD *classes*

	SD class				SD⁺ class			
	X	Y	Nullo	X/Y	X	Y	Nullo	X/Y
E1	1.00	0.51	1.00	0.09	0.78	0.62	0.17	0.12
E2(a)	1.00	0.38	1.00	0.04	1.00	0.77	0.13	0.10
E2(b)	1.00	0.72	1.00	0.36	0.34	0.43	0.09	0.27
E3	1.00	0.40	1.00	0.05	0.82	0.64	0.21	0.15
E4	1.00	0.44	1.00	0.07	0.14	0.17	0.00	0.14

$sc^4sc^8X; SD^+$ gamete of 0.78, and the distortion of sc^4sc^8 alone is such as to permit a survival probability of the $Y; SD$ gamete of 0.51. Hence, if in meiocyte I the SD and sc^4sc^8 systems independently eliminated their homologues, the survival probability of the $Y; SD^+$ gamete would be 0.78 × 0.51, *viz.* 0.40. If either system "shuts down" in the presence of the other so that only SD drives, or only sc^4sc^8 drives, then the survival of the $Y; SD^+$ would be either 0.78 or 0.51. None of these three estimates corresponds to the observed survival probability of 0.62—however, the *average* survival probability under both systems is 0.65.

The calculations for the nondisjunctional gametic class of $sc^4sc^8X/Y; SD^+$ are similarly performed and the observed survival probability is found to be 0.12. The probability of survival under the action of SD alone is 0.17, under sc^4sc^8 alone is 0.09, under independent elimination is 0.02, and under *average* elimination is 0.13.

Table 5 summarises the results of experiments E1 to E4 when examined in the previous way. It is clear that the $Y; SD^+$ and $sc^4sc^8X/Y; SD^+$ gametes are not eliminated as an independent combination of two systems. Furthermore, the hypothesis that either system "shuts down" also does not seem to provide a satisfactory fit. However, the *average* survival probability hypothesis does present a reasonable approximation, except perhaps in experiment E4.

The control experiments (Tables 1B and 1C), were all performed at the same time as E4, and the results need little comment. The control males were regular in all respects. The SD/Cy genotype is a non-distorting one, and there is no detectable interaction between it and the "driving" sc^4sc^8 system.

It should also be noted that the distorting effect of the SD chromosome has been appreciably reduced in the presence of the sc^4sc^8 system. However, we have not attempted a genetic analysis to define the basis of the modification of the reduction in distortion. A further point of interest concerns the raw data of Table 2.

TABLE 5

Observed and expected survival probabilities of the Y;SD+ *and* sc⁴sc⁸X/Y; SD+
gametes under differing hypotheses

	Observed survival of $Y; SD^+$	If *average* distortion	Expected If SD only distorts	If sc^4sc^8 only distorts	If independent survival probability
E1	0.62	0.65	0.78	0.51	0.40
E2(a)	0.77	0.69	1.00	0.38	0.38
E2(b)	0.43	0.53	0.34	0.72	0.24
E3	0.64	0.61	0.82	0.40	0.33
E4	0.17	0.29	0.14	0.44	0.06
	Observed survival of $sc^4sc^8X/Y; SD^+$				
E1	0.12	0.13	0.17	0.09	0.02
E2(a)	0.10	0.09	0.13	0.04	0.01
E2(b)	0.27	0.23	0.09	0.36	0.03
E3	0.15	0.13	0.21	0.05	0.01
E4	0.14	0.04	0.00	0.07	0.00

It is clear that an examination of the SD class reveals that males with extremely low nondisjunction values appear far more fertile than those whose nondisjunction values are high. We have noted similar trends in other unrelated experiments and shall discuss them fully in another paper (MIKLOS and PEACOCK, in manuscript).

The results of the "double drive" males may be summarised thus. In meiocytes II and IV, where SD and sc^4sc^8 drive "against" each other, each system drives with a characteristic resultant extinction probability. In meiocytes I and III, where SD and sc^4sc^8 drive together, the $Y; SD^+$ and $sc^4sc^8X/Y; SD^+$ gametes do not survive with the simple expectation of the multiplicative survival probability of each system. There is *less* gametic death under the combined action of these two systems than if the systems interacted independently.

Interpretation of the data: There are at least two ways in which these results can be interpreted, but since a distinction between these hypotheses seems unlikely at this time, both will be discussed.

Hypothesis 1. The SD and sc^4sc^8 systems do not function simultaneously when both are at the same meiotic pole. It could be that in half of meiocytes I and III SD "drives" alone, and in the remainder, sc^4sc^8 "drives" by itself. This hypothesis would produce a gametic survival probability for $Y; SD^+$ and $sc^4sc^8X/Y; SD^+$ gametes which would be an exact average of the survival probability of each meiotic drive system. A more general variant of this hypothesis would be that one system functions in a given proportion of meiocytes, and the other functions in the remainder.

Hypothesis 2. There is a compensatory interaction of both systems when they are at the same meiotic pole, so that *each* system then distorts *less* than it would if it were alone. In this way, the survival probability of $Y; SD^+$ and $sc^4sc^8X/Y; SD^+$ gametes could still be the multiplicative survival probability of each system, with each genotype distorting less efficiently. This second hypothesis is effectively one of competition for a common substrate, whereas the former is non-competitive in the loose sense that only one system functions at a time.

At the moment, a distinction between these alternatives does not seem practical. However, the important point revealed by the data is that the systems interact differently depending on whether they are at the opposite, or at the same end of the primary spermatocyte. It seems unlikely that the systems compete for a diffusible substance which exists throughout the meiocyte, because then they should interact independently of whether they are at the same or different meiotic poles. If there is competition, it could be pole specific: that is, the meiotic poles may differ in some ways. This suggestion has been put forward by PEACOCK and ERICKSON (1964) and YANDERS et al. (1968), who demonstrated the existence of an intracellular gradient in the primary spermatocytes of sc^4sc^8 males.

Alternately, the poles may be identical as regards the meiotic drive system, but there may only be one available "site" for distortion, and both systems compete for that "site". On this scheme, the more meiotic drive systems that are placed in a meiotic cell, the higher should be the survival probability of the gamete being affected in those cells where all systems distort in the same direc-

tion. In the only other multiple meiotic drive system investigated to date, the "$T(1;Y;4)$ plus SD/SD^+" genotype investigated by Novitski and Peacock (1970), this is precisely what is found. The gamete with the highest survival probability is the one that has been effected by all the "driving" components of the system.

There are some aspects of the treatment of the data which need further comment. Although we cannot estimate the survival probability of the y^+Y; SD^+ gamete under the distorting action of SD alone, we do know that regular X; SD^+ and Y; SD^+ gametes have very similar susceptibilities to the distorting effect of SD, particularly at low and intermediate distortion values (Denell and Miklos 1971). Consequently we have assigned the same survival probability to sc^4sc^8X; SD^+ and y^+Y; SD^+ gametes.

Similarly in the nondisjunctional class, the same survival probabilities were assigned to a nullo; SD^+ as to a sc^4sc^8X/Y; SD^+ gamete, since nullo; SD^+ and X/Y; SD^+ exceptions have reasonably similar susceptibilities to SD.

The data of the nondisjunctional class are not inconsistent with the general proposition that the susceptibility of SD^+ gametes to distortion by SD depends not only on the sex chromosome complement that the sperm carries, but also depends on whether the gamete arose from a disjunctional or nondisjunctional meiocyte.

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