ON THE MODELS OF SEGREGATION DISTORTION IN *DROSOPHILA MELANOGASTER*[1]

DIANA W. MARTIN AND YUICHIRO HIRAIZUMI[2]

Department of Zoology, The University of Texas at Austin, Texas 78712

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ABSTRACT

The Segregation Distorter system of *Drosophila melanogaster* consists of two major elements, *Sd* and *Rsp*. There are two allelic alternatives of *Rsp*—sensitive (*Rsp*^{s}) and insensitive (*Rsp*^{i}); a chromosome carrying *Rsp*^{i} is not distorted. According to the model proposed by HARTL (1973), these two elements interact to cause segregation distortion. For a sperm to complete the maturation process, it is assumed that the *Rsp* locus has to be complexed with the product of the *Sd* locus. This product is assumed to be a multimetric regulatory protein. Three kinds of regulatory multimers may be distinguished: *Sd*+/*Sd*+, which is assumed to complex with both *Rsp*^{s} and *Rsp*^{i}; *Sd*+/*Sd* heteromultimers, which complex preferentially with *Rsp*^{i}; and *Sd*/*Sd* homomultimers, which complex with neither *Rsp*^{s} nor *Rsp*^{i}. Most of the regulatory protein in the *Sd*+/*Sd* heterozygous male is assumed to be the *Sd*+/*Sd* heteromultimer. ——Some modifications of HARTL's model were made by GANETZKY (1977). Rather than the binding of a product of *Sd* at the *Rsp* locus being a necessary condition for normal spermigenesis, this binding causes sperm dysfunction. It is assumed that the product of *Sd* complexes more readily with *Rsp*^{s} than with *Rsp*^{i} and that the amount of *Sd* product is limited with respect to the number of binding sites available. No function is ascribed to the *Sd*+ locus. In order to explain reduced male fertility of some genotypes, GANETZKY further assumes that the *Sd* product, when not competed for by an *Rsp*^{s} locus, can bind to an *Rsp*^{i} *locus*.——Two consequences of these models were criticically examined: according to these models (1) an *Sd Rsp*^{s}/*Sd*+ *Rsp*^{s} male should not show any segregation distortion, and (2) an *Sd Rsp*^{s}/*Sd Rsp*^{s} male should show much reduced fertility, if not complete sterility.——The results of the present study bear on these two points. (1) *Rsp*^{s} locus seems to consist of multiple alleles, each having a different degree of ability to interact with the product of the *Sd* locus. An *Sd Rsp*^{s}/*Sd*+*Rsp*^{s} male shows a certain degree of segregation distortion when the two *Rsp*^{s} alleles are different, but it shows a normal Mendelian segregation ratio when the *Rsp*^{s} alleles are homozygous. The first prediction of the models is supported by actual observation when the two *Rsp*^{s} alleles are the same. (2) There is a suggestion of slight reduction in fertility, but generally *Sd Rsp*^{s}/*Sd Rsp*^{s} males are quite fertile. Thus, the second prediction is not supported by actual observation. The mechanism of segregation distortion is still open for future studies.

THE Segregation Distorter (*SD*) system of *Drosophila melanogaster* has had a long history since it was first discovered, in 1956, in a natural population

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[2] To whom reprint requests or any information relating to this report should be addressed.

in Madison, Wisconsin (SANDLER, HIRAIZUMI and SANDLER 1959). Many interesting and important discoveries about this system have since been made by many workers. These were reviewed and summarized by HARTL and HIRAIZUMI (1976); only the more basic aspects of the system relevant to the present study will be outlined below.

When a heterozygous SD/SD^+ male is backcrossed to a normal SD^+/SD^+ female, they produce progeny containing the *SD* element in a great excess over the expected 50%—usually 80% or more. This distorted transmission frequency is due to dysfunction of sperms containing the normal SD^+ element (HARTL, HIRAIZUMI and CROW 1967; NICOLETTI, TRIPPA and DEMARCO 1967). For simplicity, let k be the frequency of *SD* recovered among progeny of the above backcross mating. When the transmission ratio is Mendelian, $k = 0.5$, but in the above backcross mating, $k = 0.8$ or more.

The *SD* system consists of two major elements that are separable by recombination. One element, *Sd* for *S*egregation *d*istorter, is located in the left arm of chromosome *2*, close to the centromere. The other element, *Rsp* for *Resp*onder, is located in the right arm of chromosome *2*, to the left of the *cn* locus (*2R*,57.5), close to the centromere (HARTL 1974). GANETZKY (1977) mapped more precise positions for these elements, locating *Sd* to the left of, but very close to, the *pr* locus (*2L*,54.4), while locating *Rsp* within the centromeric heterochromatin of the right arm of chromosome *2*, proximal to the *stw* locus (*2R*,55.1). There are two allelic alternatives of *Rsp*—sensitive (Rsp^s) and insensitive (Rsp^i); a chromosome carrying Rsp^i is not distorted by *SD*.

According to the model proposed by HARTL (1973), these two elements interact to cause segregation distortion. He assumed that, as a necessary condition for sperm maturation, the *Rsp* locus must be complexed with the product of the *Sd* locus. This product is further assumed to be a multimeric regulatory protein. Three kinds of regulatory multimers may be distinguished: Sd^+Sd^+, which is assumed to be capable of interaction with both Rsp^s and Rsp^i; Sd^+/Sd heteromultimers, which complex preferentially with Rsp^i; and Sd/Sd homomultimers, which can complex with neither Rsp^s nor Rsp^i. Most of the regulatory protein in the Sd^+/Sd male is assumed to be Sd^+/Sd heteromultimers.

A few years later, GANETZKY (1977) proposed a model of segregation distortion similar to that of HARTL (1973), but with the following modification. Rather than the binding of a product of *Sd* at the *Rsp* locus being a necessary condition for normal spermiogenesis, this binding causes sperm dysfunction. It is assumed that the product of *Sd* complexes more readily with Rsp^s than with Rsp^i and that the amount of *Sd* product is limited with respect to the number of binding sites available. No function is ascribed to the Sd^+ locus. In order to explain reduced male fertility of some genotypes, GANETZKY further assumes that the *Sd* product, when not competed for by an Rsp^s locus, can bind to an Rsp^i locus.

Both of the models predict the following consequences: (1) an *Sd* Rsp^s/Sd^+ Rsp^s male should not show any segregation distortion, and (2) an *Sd* Rsp^s/Sd Rsp^s homozygous male should show very much reduced fertility, if not complete sterility. The main purpose of the present investigation is to critically examine whether these two predictions can be supported by actual observations.

MATERIALS AND METHODS

The second chromosome lines employed in the present study are listed below.

Original lines

cn bw: a standard chromosome *2* line marked with two recessive eye color mutants, *cn* (cinnabar eye color, *2R*, 57.5) and *bw* (brown eye color, *2R*, 104.5).

al dp b pr sp: a chromosome *2* line carrying five recessive mutants, *al* (aristaless, *2L*, 0.01), *dp* (dumpy wing, *2L*, 13.0), *b* (black body color, *2L*, 48.0), *pr* (purple eye color, *2L*, 54.4), and *sp* (speck, *2R*, 107.0). This chromosome line is associated with a recessive lethal gene.

lt stw^3: a chromosome *2* line carrying two mutants, *lt* (light eye color, *2L*, 55.0) and *stw*^{3} (an allele of *stw*, straw body color, *2R*, 55.1). This chromosome line is associated with a recessive lethal gene.

Tokyo: a wild-type second chromosome line originally isolated from a Tokyo, Japan, population.

In(2LR) SM5: a multiply inverted chromosome *2* balancer. This chromosome carries the mutant markers *al*^{2}, *Cy* (Curly wing, *2L*, 6.1), *lt*^{v}, *cn*^{2} and *sp*^{2}. In this report, this chromosome will be referred to as *SM5*.

R(SD^{cn})-14: a chromosome *2* line showing a moderate degree of segregation distortion when made heterozygous with the *cn bw* chromosome in the male. This chromosome carries the marker *cn*, and so far no structural abnormality has been found. For the origin of this chromosome, see HIRAIZUMI and NAKAZIMA (1967). For simplicity, this chromosome will be abbreviated as *cn-14* throughout this study. This chromosome carries a recessive lethal gene (or genes) independent of the *SD* system.

SD-72: a second chromosome line isolated in 1956 from a natural population in Madison, Wisconsin. This chromosome shows a strong degree of segregation distortion against the *cn bw* chromosome. This chromosome carries one para- and one pericentric inversion.

All of the second chromosome lines listed above have been kept in this laboratory by backcrossing, through heterozygous males, to the standard *cn bw* females for at least 20 generations. Therefore all the genetic backgrounds associated with these lines were, except for the second chromosome, derived from the *cn bw* stock.

The *k* values for the lines listed above are summarized in Table 1.

As can be seen in Table 1, all of the three "normal" chromosome lines (Tokyo, *lt stw3*,

TABLE 1

A list of the k *values and male fertility for several combinations of basic second chromosome lines*

Genotypes of male parents	*k*	No. of progeny per male	% of sterile males
cn bw/al dp b pr sp	0.505	46.35	0.00(17)
cn bw/lt stw^3	0.507	53.45	0.00(55)
cn bw/Tokyo	0.529	41.75	0.00(20)
Average of control	0.514	47.18	0.00
al dp b pr sp/cn-14	0.856	34.38	4.17(24)
cn bw/cn-14	0.922	42.75	0.00(20)
lt stw^3*/cn-14*	1.000	42.62	4.76(21)
Tokyo/*cn-14*	1.000	37.80	0.00(10)
cn bw/SD-72	1.000	44.50	0.00(20)

The genotype of female parents was, in all cases, *cn bw*. The age of the male parents was 0.5 to 1.5 days when the mating was initiated, and the parents were allowed to produce progeny for three days. The *k* values were computed for the right-hand side chromosomes shown under "Genotypes of male parents." The number of replications is shown within parentheses.

and *al dp b pr sp*), when made heterozygous in males with the standard *cn bw* chromosome, show *k* values that are slightly larger than the theoretical 0.5. After adjustment for differential viabilities between the *cn bw* and wild phenotypes, these *k* values can be considered equal to 0.5. It can also be seen that the Tokyo and the *lt stw*^{s} chromosomes, compared with the standard *cn bw* chromosome, are "super-sensitive" to the action of Segregation Distorter. The *al dp b pr sp* chromosome line, on the other hand, has a slightly reduced sensitivity when compared to the standard *cn bw* chromosome, but the reduction is very small. This line may be classified as having a weak suppressor of *SD*, or as slightly insensitive to *SD* action.

Recombinant chromosome lines

Many independent recombinant chromosome lines were generated in the *cn-14/al dp b pr sp* females by crossing over between the *pr* and *cn loci*. A total of 13,263 progeny were examined, among which 64 were found to be *pr*+ *cn*+, and another 64 were *pr cn* recombinant types. The recombination frequency between these two loci, 0.0097 or about 1%, is comparable to the value observed by others.

Procedures

The mating types employed in this study can be summarized as one mating type: two *cn bw* ♀ × 1 *x*/*y* ♂, where *x* and *y* are the second chromosomes carrying either one, both, or neither of the *Sd* and *Rsp*^{i} elements. In the preliminary experiments designed to characterize the recombinant chromosomes for the *Sd* and *Rsp*^{i} elements, the age of the male was three to seven days, and the parents were kept in a vial for seven days, and then discarded. The fly counts were completed on the 19th day from the date when the mating was initiated. Unless otherwise indicated, the *k* value was computed for each male separately, and then an unweighted average of *k* was computed for each line.

SANDLER and HIRAIZUMI (1961) showed that the *k* value was somewhat dependent upon the age of the parental *SD* heterozygous male. In order to minimize such an aging effect, the age of the males in the later experiments was more strictly regulated (0.5 to 1.5 days) and the parents were kept in a vial for only three days, and then discarded. The number of progeny per mating was naturally reduced because of the short period during which the parents were allowed to produce progeny; nevertheless, about 40 to 50 flies could be obtained from a control mating. Under these experimental conditions, the number of progeny produced per male is not an accurate measure of the number of functional sperm produced, since the inseminated females were discarded before they used all of the sperm they received. Although these conditions may not be sensitive enough to allow detection of slight changes in male fertility (the number of functional sperm), any large reduction in the number of functional sperms per male would be observed. Note that, in Table 1, the average number of progeny per control male was 47.18, and although there was a general tendency toward fewer progeny for the *cn-14* and *SD-72* male matings, the decrease was much smaller than that expected, based upon the *k* value. When the *k* value is close to one, one expects about a 50% reduction in the number of functional sperms.

RESULTS

Characterization of the recombinant chromosomes

A method very similar to that employed by HARTL (1974) was used to characterize each of the recombinant chromosomes for the *Sd* and *Rsp*^{i} elements. Two mating types were examined first, as shown below.

(1) *cn bw* ♀ × *R*/*cn bw* ♂ matings, where *R* is one of the recombinant chromosomes (between the *pr* and *cn* loci) generated by the *cn-14/al dp b pr sp* females. A total of 18 *pr*+ *cn*+ (these will be referred to as *R*(+ +)) and 25 *pr cn* (these will be abbreviated as *R*(*pr cn*)) recombinant chromosomes was tested.

(2) *cn bw* ♀ × *R/SD-72* ♂ matings. Before these matings were made, all of the *R*(+ +) recombinant lines were marked by placing *bw* on the right arm of the second chromosome, so that the *SD-72* and *R*(+ +) chromosomes could be distinguished by the phenotypes of the progeny. These marked recombinant chromosomes were used throughout the following experiments, and they will be designated as *R*(+ +) *bw* lines.

The results are summarized in Table 2 for the *R*(+ +) or *R*(+ +) *bw*, and in Table 3 for the *R*(*pr cn*) recombinant lines.

In Table 2, the distribution of the *k* values among lines within Mating type 1 appears to be continuous, but the results of Mating type 2 clearly indicate the presence of two distinct classes—those that are distorted by *SD-72* (Group A) and those that are not (Group B). The lines in Group B clearly show *k* values larger than 0.5 in Mating type 1, indicating that they are distorting the *cn bw* chromosomes. The overall average *k* value for the lines in this group, 0.750, is considerably smaller than the average *k* value of 0.922 for the *cn-14/cn bw* males. This reduction might be partly due to a weak suppressor originally located

TABLE 2

A list of k *values for various* R(++) *and* R(++) bw *recombinant chromosomes*

Group	Line No.	Mating 1	Mating 2*
	7	0.519(22)	0.888(14)
	9	0.542(21)	0.897(12)
A	1	0.543(22)	0.894(14)
	10	0.549(22)	0.855(13)
	2	0.581(18)	0.920(14)
	11	0.599(18)	0.897(14)
Unweighted average		0.556	0.892
	16	0.654(22)	0.471(14)
	6	0.696(22)	0.435(14)
	12	0.699(22)	0.545(14)
	8	0.708(20)	0.576(14)
B	17	0.714(20)	0.479(14)
	20	0.737(18)	0.522(14)
	15	0.743(21)	0.519(14)
	14	0.763(22)	0.375(14)
	19	0.799(22)	0.484(14)
	5	0.800(22)	0.561(13)
	13	0.813(22)	0.472(12)
	3	0.871(20)	0.514(12)
Unweighted average		0.750	0.496

Mating 1: *cn bw* ♀ × *cn bw/R*(++) ♂. Mating 2: *cn bw* ♀ × *R*(++)*bw/SD-72* ♂. The *k* values were computed for the right-hand side chromosomes shown above in the male genotypes and the number of replications is shown within parentheses. The age of the males was three to seven days when the mating was initiated, and the parents were allowed to produce progeny for seven days.

* Male fertility of this mating type was generally low (especially for Group B), and therefore the *k* values were computed based upon the total progeny produced by the number of males indicated within parenthesis.

TABLE 3

A list of k *values for various* R(pr cn) *recombinant chromosome lines*

Group	Line No.	Mating 1	Mating 2
	4	0.500(22)	0.504(16)
	5	0.505(22)	0.486(14)
	8	0.511(18)	0.486(13)
	13	0.512(19)	0.526(14)
A	17	0.512(21)	0.530(20)
	15	0.526(22)	0.449(16)
	12	0.531(20)	0.477(22)
	7	0.537(22)	0.501(15)
	2	0.541(20)	0.473(12)
Unweighted average		0.519	0.492
	23	0.476(13)	0.934(8)
	20	0.485(21)	0.955(14)
	14	0.487(20)	0.914(13)
	24	0.492(17)	0.954(14)
	3	0.493(20)	0.954(15)
B	16	0.506(21)	0.963(21)
	25	0.507(19)	0.984(12)
	22	0.509(18)	0.921(14)
	6	0.510(22)	0.977(14)
	11	0.516(18)	0.991(14)
	18	0.523(20)	0.953(16)
	9	0.527(20)	0.984(14)
	26	0.528(21)	0.978(22)
	1	0.533(23)	0.970(21)
	10	0.534(21)	0.985(13)
	19	0.555(16)	0.984(21)
Unweighted average		0.511	0.962

Mating 1: *cn bw* ♀ × *cn bw/R(pr cn)* ♂. Mating 2: *cn bw* ♀ × *R(pr cn)/SD-72* ♂. The *k* values were computed for the right-hand side chromosomes shown in the male genotypes above, and the number of replications is shown within parenthesis. The age of the males was three to seven days when the mating was initiated, and the parents were allowed to produce progeny for seven days.

on the *al dp b pr sp* chromosome, but this is not sufficient to explain the observed reduction in the *k* value. It seems likely that the *R*(++) lines lost an *SD* enhancer, which was originally located on the *cn-14* chromosome. In any event, the suppressor and enhancer are not the major elements of the *SD* system.

The *k* values of lines in Group A of Mating type 1 are somewhat ambiguous. The average *k* of 0.556 seems higher than the average *k* value normally observed for the control, non-*SD* chromosome matings. Usually *k* is 0.51–0.52—a little larger than 0.5 because of the viability differences between the *cn bw* and the wild phenotypes. However, for simplicity, we shall tentatively assume that the chromosome lines in Group A do not distort *cn bw* chromosomes. We may then categorize the recombinant lines in Gruop A as either Sd^{+} Rsp^{s} or *Sd* Rsp^{s}, and the lines in Group B as *Sd* Rsp^{i}.

Let us now turn to Table 3 for the *R(pr cn)* recombinant lines. In Mating type 1, each of the 25 lines showed a *k* value essentially equal to 0.5, but in Mating type 2, there were two distinct groups, designated A and B. The recombinant lines in Group A were not distorted by *SD-72*, and those in Group B were distorted by *SD-72*. The former may be categorized as carrying Sd^+ Rsp^i, and the latter Sd^+ Rsp^s. The overall average *k* value for the *SD-72* chromosome in Group B, 0.962, appears somewhat smaller than that characteristic for the *SD-72/cn bw* male matings, *i.e.*, 0.99 to 1.00. This reduction could perhaps be due to a weak suppressor located on the original *al dp b pr sp* chromosome.

From Table 2 and 3 we then have the following four classes of recombinant chromosomes:

Table 2-A:	*R(++) bw; Sd* Rsp^s or Sd^+ Rsp^s.	Number of lines found = 6
-B:	*R(++) bw; Sd* Rsp^i.	Number of lines found = 12
Table 3-A:	*R(pr cn);* Sd^+ Rsp^i.	Number of lines found = 9
-B:	*R(pr cn);* Sd^+ Rsp^s.	Number of lines found = 16

Distinction between the *Sd* Rsp^s and Sd^+ Rsp^s genotypes was made following HARTL's (1974) procedure. The recombinant lines in Group A of Table 2 were made heterozygous in males with some of the recombinant lines in Group A of Table 3, and these males were mated to *cn bw* females. The results are summarized in Table 4.

TABLE 4

A list of k *values to demonstrate "suicide" distortion*

Genotype of males	*k*	No. of replications
R(pr cn)-2/*R(++) bw-1*	0.297	15
4/1	0.301	10
5/1	0.327	24
2/2	lethal	
4/2	lethal	
5/2	lethal	
2/7	0.323	17
4/7	0.305	12
5/7	0.392	13
2/9	0.371	11
4/9	lethal	
5/9	0.271	5
2/10	0.300	9
4/10	lethal	
5/10	0.311	23
2/11	0.344	3
4/11	0.221	2
5/11	0.208	3
Unweighted average	0.306	

The mating type is *cn bw* ♀ × *R(pr cn)*/*R(++) bw* ♂. The *k* values were computed for the *R(++) bw* recombinant chromosome lines. The age of males was three to seven days when the mating was initiated, and the parents were allowed to produce progeny for seven days.

It can be seen in Table 4 that the "suicide" distortion first observed by SANDLER and HIRAIZUMI (1960), and later shown in more detail by HARTL (1974), is reproduced in these data. It is interesting to note that the overall average k of 0.306 is reasonably close to $1 - 0.750 = 0.250$, where 0.750 is the overall average of k among recombinant lines that are assumed to be *Sd Rsp*^{i} (see Group B of Table 2).

Because of the recessive lethals common between the *R*(+ +) *bw-2* and the *R*(*pr cn*)*-2*, *4* and *5* chromosome lines, no k value could be estimated for the *R*(+ +) *bw-2* line, but the five remaining *R*(+ +) *bw* lines showed "suicide" distortion. These lines can now be categorized as being *Sd Rsp*^{s}. For reasons to be discussed later, the *R*(+ +) *bw-2* line can also be classified as *Sd Rsp*^{s}.

These results are consistent with the notion that there are two distinct elements in the *SD* system that can be separated by recombination. Summing up the results presented thus far, we have shown that the results of SANDLER and HIRAIZUMI (1960) and those of HARTL (1974) are precisely repeatable. Thus, the chromosome lines employed in the present study can be considered to be essentially the same as those used by both SANDLER and HIRAIZUMI (1960) and HARTL (1974).

Segregation distortion in Sd Rsp^s/Sd$^+$ Rsp^s *males*

Further analyses were performed for several representative recombinant chromosome lines for each of the four classes. In Table 2, the recombinant chromosome lines in Group A were all tentatively assumed to have no distorting effect on the *cn bw* chromosomes. In order to verify this, the same matings were repeated, but with regulation of the age of the parental males. In addition, those six recombinant chromosomes were each made heterozygous with the Tokyo and *lt stw*^{s} chromosome lines, and the k values were examined. Both the Tokyo and *lt stw*^{s} chromosomes were "super-sensitive" to the action of *SD*; *cn-14/cn bw* males, giving an average k value of about 0.9, while *cn-14*/Tokyo and *cn-14/lt stw*^{s} males give a k value of 1.000 (see Table 1). The results are shown in Table 5 with the results for three recombinant lines from Group B of Table 2.

It is quite clear that all six lines in Group A distort the Tokyo and *lt stw*^{s} chromosomes; they appear to distort even the *cn bw* chromosome—the average k value of 0.561 is too high to be explained by viability differences between the *bw* and *cn bw* phenotypes.

Similarly, the *R*(*pr cn*); *Sd*$^+$ *Rsp*^{s} and *R*(*pr cn*); *Sd*$^+$ *Rsp*^{i} lines were tested for their k values against the *cn bw*, Tokyo and *lt stw*^{s} chromosomes. Results are shown in Table 6.

It is clear that there is no segregation distortion associated with these recombinant chromosome lines.

These results suggest that *Sd* by itself may be capable of causing segregation distortion even in the absence of *Rsp*^{i}, but *Rsp*^{i} alone can not induce segregation distortion. We shall discuss this point in more detail later.

TABLE 5

A list of k *values for several male genotypes to demonstrate that* Sd, *without* Rsp^i, *can cause segregation distortion*

Group	Line No.	Mating 1	Mating 2	Mating 3
	1	0.553(10)	0.668(5)	0.758(6)
	2	0.623(9)	0.733(7)	0.787(6)
A	7	0.524(10)	0.813(6)	0.648(10)
	9	0.599(10)	0.792(6)	0.679(8)
	10	0.525(10)	0.760(4)	0.674(8)
	11	0.542(10)	0.747(6)	0.716(7)
Unweighted average		0.561	0.752	0.710
Average No. of progeny per male		49.58	42.84	50.41
% of sterile males		0.00	0.00	0.00
	3	0.915(10)	0.996(10)	0.976(11)
B	5	0.643(10)	1.000(9)	0.994(8)
	6	0.652(10)	0.995(10)	0.984(7)
Unweighted average		0.737	0.997	0.985
Average No. of progeny per male		49.70	47.12	28.40
% sterile males		0.00	0.00	6.06

Mating 1: two *cn bw* ♀ × one *can bw*/*R*(++) *bw* ♂. Mating 2: two *cn bw* ♀ × one Tokyo/*R*(++) *bw* ♂. Mating 3: two *cn bw* ♀ × one *lt* stw^3/*R*(++) *bw* ♂. The age of the male was 0.5 to 1.5 days when the mating was initiated and the parents were allowed to produce progeny for three days. The *k* values were computed for the *R*(++) *bw* chromosomes, and the number of replications based on which the *k* value was calculated is shown within parentheses.

TABLE 6

A list of k *values for several genotype males as shown below*

Group	Line No.	Mating 1	Mating 2	Mating 3
	2	0.499(10)	0.482(6)	0.493(4)
A	4	0.435(10)	0.496(8)	0.474(8)
	5	0.505(10)	0.535(6)	0.494(8)
Unweighted average		0.480	0.504	0.487
Average No. of progeny per male		47.00	44.42	53.13
% of sterile males		0.00	0.00	0.00
	3	0.511(10)	0.502(5)	0.438(5)
B	6	0.534(10)	0.456(8)	0.477(7)
	9	0.519(10)	0.527(6)	0.532(6)
Unweighted average		0.521	0.495	0.482
Average No. of progeny per male		45.60	40.60	57.72
% of sterile males		0.00	0.00	0.00

Mating 1: two *cn bw* ♀ × one *cn bw*/*R*(*pr cn*) ♂. Mating 2: two *cn bw* ♀ × one Tokyo/*R*(*pr cn*) ♂. Mating 3: two *cn bw* ♀ × one *lt* stw^3/*R*(*pr cn*) ♂. The age of the males was 0.5 to 1.5 days when the mating was initiated, and the parents were allowed to produce progeny for three days. The *k* values were computed for the *R*(*pr cn*) chromosomes, and the number of replications, based on which the *k* value was computed, is shown within parentheses.

Fertility of Sd/Sd *homozygous males*

As mentioned earlier, according to either HARTL's (1974) or GANETZKY's (1977) models, the number of functional sperm produced by an *Sd* homozygous male should be very much reduced, perhaps resulting in almost complete sterility. The simplest genotype to test this prediction is *Sd Rsp^s/Sd Rsp^s*, where the two *Sd*'s (and the two *Rsp^s*'s) are of the same origin. Each of the six recombinant chromosome lines in Group A of Table 2 carries *Sd* elements from the *cn-14* line and *Rsp^s* elements from the *al dp b pr sp* line. These six lines were combined in all possible ways, and the male fertility of each combination was examined. The mating scheme was as follows: Each of the six lines was made heterozygous with the *SM5* chromosome, and from the matings of *x/SM5* ♀ × *y/SM5* ♂, F_1 non-*SM5* progeny males of the genotype *x/y* were obtained, where *x* (or *y*) stands for either one of the six lines. These males, at 0.5 to 1.5 days of age, were then mated to two (two- to four-day-old) *cn bw* females and kept in a vial for three days, then discarded. Results, with those of the control male matings, are summarized in Table 7.

TABLE 7

The male sterility (percent of sterile males, and the number of progeny produced per male) for various combinations of lines of the genotype, R(++) bw; Sd Rsp^s

Genotype of males *i/j*	% of sterile males	No. of progeny produced per male
1/1	0.00	44.10(10)
1/2	0.00	42.00(5)
1/7	0.00	34.00(7)
1/9	0.00	46.60(10)
1/10	0.00	26.40(10)
1/11	0.00	49.20(10)
2/7	10.00	28.00(10)
2/9	0.00	38.67(6)
2/10	11.11	20.78(9)
2/11	0.00	38.50(10)
7/7	0.00	55.00(6)
7/10	0.00	34.10(10)
7/11	0.00	47.30(10)
9/11	0.00	48.89(9)
10/11	0.00	50.50(10)
Unweighted average	1.41	40.27
Control genotype		
cn bw/Tokyo	0.00	41.75(20)
cn bw/lt stw^2	0.00	53.45(55)
cn bw/al dp b pr sp	0.00	46.35(17)
Unweighted average	0.00	47.18

The mating was two *cn bw* ♀ × one *R(++) bw; Sd Rsp^s-i/R(++) bw; Sd Rsp^s-j* ♂, where *i* and *j* represent line numbers. The age of the males was 0.5 to 1.5 days when the mating was initiated, and the parents were allowed to produce progeny for three days. The number of replications is indicated within parentheses.

It is shown in this table that, although there is in fact a slight reduction in fertility, the reduction is rather small. Considering the probable homozygosity for some portion of the chromosome segments among the six recombinant lines, we may conclude that the *Sd* homozygous males are quite fertile. Certainly they can not be classified as sterile.

DISCUSSION

The results presented in the previous sections can be summarized as follows. (1) The *Sd* element, without Rsp^i, appears to cause segregation distortion. (2) *Sd* Rsp^s/*Sd* Rsp^s homozygous males are fertile, although there is a tendency toward a slight reduction in fertility.

As mentioned earlier, the six recombinant lines of the genotype *R*(+ +) *bw*; *Sd* Rsp^s clearly distort the Tokyo and *lt* stw^s chromosomes, and they were judged to distort even the *cn bw* chromosome, resulting in an average *k* value of 0.561. Although this *k* value appears to be too large to be accounted for by the differential viabilities between the *bw* and the *cn bw* phenotypes, the amount of deviation from the expected 0.5 is not large, and one may still suspect that this deviation could simply be due to differential viabilities. In order to make this point clear, the same matings were repeated with the age of males more strictly regulated. Virgin males, *R*(+ +) *bw*; *Sd* Rsp^s/*cn bw*, 1.0 to 1.5 days of age, were individually mated to two young *cn bw* females. Parents were kept together in a vial for only one day before the male parent was discarded. The inseminated female parents were allowed to lay eggs for seven days; then they were discarded. Seven replications were made for each of the six lines. All but one of the males were fertile. The average *k* values for the *R*(+ +) *bw*; *Sd* Rsp^s*-1*, *-2*, *-7*, *-9*, *-10* and *-11* were 0.629, 0.600, 0.613, 0.532, 0.563 and 0.597, respectively, giving an overall average *k* value of 0.589. This value seems large enough to conclude that segregation distortion in fact takes place in *R*(+ +) *bw*; *Sd* Rsp^s/*cn bw* males.

There is one important point to be considered here. Thus far we have assumed that the Rsp^s alleles located in the *cn bw*, *al dp b pr sp*, Tokyo and *lt* stw^s chromosomes were the same. They may, however, differ from each other, constituting a multiple allelic series of Rsp^s. HARTL (1977) showed that there was genetic variation among Rsp^i's in nature; if such variation is also present among Rsp^s's, the present results, with some assumptions, can be explained by HARTL's (1973) model. The Rsp^s locus on each of the six recombinant chromosome lines was originally located on the *al dp b pr sp* chromosome. Hence, we may simply assume that the Rsp^s locus on the *al dp b pr sp* chromosome has a little higher probability of being complexed with the Sd/Sd^+ protein than does the Rsp^s locus on the *cn bw* chromosome. On the other hand, the Rsp^s locus on the Tokyo (or *lt* stw^s) chromosome may be an allele that has a much smaller probability of being complexed with the protein than does the Rsp^s locus on the *cn bw* chromosome. This hypothesis of multiple alleles of Rsp^s is, in fact, very attractive, since it may provide some understanding of the nature of sensitivity of the normal chromosomes to the activity of Segregation Distorter. This can easily be tested by examining the *k* value of a *R*(+ +) *bw*; *Sd* Rsp^s/*al dp b pr sp* male, in which

both homologues carry the same *Rsp*^{s} allele. Accordingly, the males of this genotype, 0.5 to 1.5 days old, were individually mated to two *cn bw* females. Parents were kept in a vial for three days, then discarded. The results are summarized in Table 8. The results for three *R*(+ +) *bw*; *Sd Rsp*^{i} lines are also included in this table.

The three *R*(+ +) *bw*; *Sd Rsp*^{i} lines showed *k* values distinctly larger than 0.5, indicating that they can distort the *al dp b pr sp* chromosome. The overall average *k* value of 0.582 appears to be somewhat smaller than the *k* value of 0.737 found when the lines were tested against the *cn bw* chromosome, but this can be accounted for, at least qualitatively, by the assumption mentioned above, *i.e.*, that the *Rsp*^{s} allele on the *al dp b pr sp* chromosome has a somewhat higher probability of being complexed with the *Sd*/*Sd*$^+$ protein than does the *Rsp*^{s} allele located in the *cn bw* chromosome.

The six *R*(+ +) *bw*; *Sd Rsp*^{s} chromosome lines, on the other hand, gave an overall average *k* value of 0.494, indicating that they are not capable of distorting the *al dp b pr sp* chromosome. In fact, this *k* value is what we would expect based upon the differential viabilities between the *bw* and the wild-type phenotypes when $k = 0.5$.

Based upon these observations, it seems reasonable to conclude that *Sd Rsp*^{s}/*Sd*$^+$ *Rsp*^{s} males show no segregation distortion when the two *Rsp*^{s} alleles are the same, although it may show a certain degree of segregation distortion when the two *Rsp*^{s} alleles are different. The two models can not explain, however, the results of male fertility presented in Table 7, *i.e.*, that *Sd* homozygous males are quite fertile. If we insist on explaining these results by HARTL's (1973) model, we must assume that the *Rsp*^{s} locus, when *Rsp*^{i} is absent in a genome, can complex readily with the *Sd*/*Sd* homomultimeric protein. This is very difficult to

TABLE 8

A list of k *values for several* R(++) bw; Sd Rsp^s *and* R(++) bw; Sd Rsp^i *lines*

Genotype of males		*k*
al dp b pr sp/*R*(++) *bw*; *Sd Rsp*^{i}	-3	0.596(10)
	-5	0.579(9)
	-6	0.570(10)
Unweighted average		0.582
al dp b pr sp/*R*(++) *bw*; *Sd Rsp*^{s}	-1	0.507(10)
	-2	0.493(10)
	-7	0.459(10)
	-9	0.506(10)
	-10	0.515(10)
	-11	0.483(9)
Unweighted average		0.494

The mating type was two *cn bw* ♀ × one *x*/*al dp b pr sp* ♂, where *x* is either *R*(++) *bw*; *Sd Rsp*^{s} or *R*(++) *bw*; *Sd Rsp*^{i} chromosome. The age of the males was 0.5 to 1.5 days when the mating was initiated, and the parents were allowed to produce progeny for three days. The number of replications is indicated within parentheses.

accept without any further, perhaps complicated, assumptions. Certainly, the mechanism of segregation distortion is not yet fully understood, and is still open for future studies.

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Corresponding editor: D. HARTL