AGING EFFECT ON THE PHENOMENON OF SEGREGATION DISTORTION IN *DROSOPHILA MELANOGASTER*¹

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SEGREGATION Distorter (*SD*) is an element located in the centromeric region of chromosome 2 of *Drosophila melanogaster*. When a male carries *SD* in heterozygous condition, it transmits *SD* to its progeny in a great excess over the theoretical frequency of 50%. The *SD* system consists of three major elements: the *SD* locus itself which is the element causing segregation distortion; Activator of *SD*, *Ac(SD)*, which is located to the right and close to the *SD* locus and is necessary, in coupling, for *SD* to function; and Stabilizer of *SD*, *St(SD)*, which is located at the tip of the right arm of chromosome 2 and has a function, either in coupling or in repulsion phase, to stabilize, or enhance the *SD* action. For further information on *SD*, the reader may refer to the following papers: SANDLER, HIRAIZUMI and SANDLER (1959), SANDLER and HIRAIZUMI (1960a, b), SANDLER and HIRAIZUMI (1961), PEACOCK and ERICKSON (1965), HIRAIZUMI and NAKAZIMA (1967), HARTL, HIRAIZUMI and CROW (1967).

In 1961, SANDLER and HIRAIZUMI reported that when a *SD* heterozygous male was aged the intensity of segregation distortion was remarkably reduced: if k is the proportion of *SD* progeny flies recovered in the F_1 generation of the mating, $SD^+/SD^+ \text{ } \varphi \text{ } \varphi \times SD/SD^+ \text{ } \delta \text{ } \delta$, k decreased when the *SD* males got old. However they were unable to show which of the three elements, *SD*, *Ac(SD)*, or *St(SD)*, was responsible for the aging effect nor were they able to show whether the decrease in k was due to an increase in the number of SD^+ , or due to a decrease in the number of *SD* progeny.

The purpose of the present study is (1) to present data for the aging effect on k values of males carrying various elements of the *SD* system and (2) to show that the decrease in k with increasing age of the male is in fact due to an increase in the number of SD^+ progeny, but that the number of *SD* progeny is independent of the aging effect.

MATERIALS AND METHODS

- (1) *cn bw*: Standard mutant stock carrying cinnabar and brown eye color recessive mutants. *cn bw* gives white eye color.
- (2) *Tokyo*: Standard wild stock, which was originally isolated from a natural population in Tokyo, Japan, more than 10 years ago.

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- (3) *SD Ac(SD) St(SD)*: SD-72, SD^{NH}-2. These are the Original-SD chromosome lines carrying *SD*, *Ac(SD)*, and *St(SD)*, isolated from a natural population in Madison, Wisconsin, and in Odate, Japan, respectively. Distorting effect is very strong, showing average *k* values of practically 1.
- (4) *SD Ac(SD)*: R(SD-36)-1, R(R-1)-cn-14, R(SD^{NH}-1)-1. These Recombinant-SD chromosome lines carry *SD* and *Ac(SD)*. *St(SD)* was removed by recombination. The first two lines were derived from an Original-SD chromosome found in Madison (= SD-36), and the third from that found in Odate (= SD^{NH}-1). Segregation distortion is slightly reduced showing average *k* values of about 0.80–0.95.
- (5) *SD*: R(R-1)-cn-2, R(R-1)-cn-5. These chromosome lines carrying *SD* were derived from the R(SD-36)-1 chromosome line. *Ac(SD)* was removed by recombination. Segregation distortion is very weak showing average *k* values of approximately 0.6.
- (6) *Ac(SD)*: R(R-1)-pr-3, R(R-1)-pr-7. These chromosome lines carrying *Ac(SD)* were derived from the R(SD-36)-1 line by recombination.
- (7) *St(SD)*: R(SD^{NH}-1)-2, R(SD-72)-103. These chromosome lines carrying *St(SD)* were derived by recombination from SD^{NH}-1, and SD-72, respectively.
- (8) *X^{stw}*: An X-chromosome line extracted from the *stw^s* (straw) laboratory stock. This X chromosome is known to suppress segregation distortion.

Before the present experiments were done, the genetic background other than the second (other than the X for line 8) chromosome had been replaced by those of the standard, *cn bw*, stock. This was done by backcrossing through males to the standard *cn bw* females for more than 10 generations.

All of the males tested throughout the present study were heterozygous for the standard *cn bw* second chromosome and for simplicity "*Tokyo/cn bw* heterozygous male," for example, has been abbreviated to "*Tokyo* male." Mating schemes are briefly summarized as follows:

Experiment 1: Some of the results of this experiment were reported by HARTL, HIRAIZUMI and CROW (1967). Males of various genotypes less than 1 day old were mated individually to two or three *cn bw* virgin females for 3 days, then 4 days, alternating thus until all of the males became sterile. The fertilized females were allowed to deposit eggs for a total of 7 days.

Experiment 2: Males less than 2 hrs old were individually mated to seven *cn bw* virgin females for 24 hrs, then each of the males was removed and was mated to seven fresh, new *cn bw* virgin females for another 24 hrs. This procedure was repeated until all of the males became sterile. The inseminated females were transferred to fresh vials once a day during the first 6 days, then once every two days. This transfer of the inseminated females was continued until none of the females were fecund. Some of these females were then tested for fertility by supplying young males; they produced hundreds of progeny so that the loss of fecundity was due to exhaustive utilization of the stored sperm, but not due to sterility caused by the old age of the females.

Experiment 3: The brothers of the males used in experiment 2 were kept in groups in vials without any supply of females for 3 weeks, then were mated to seven *cn bw* females individually for 24 hrs. They were separated from the females and kept for 6 additional days, then were mated individually to seven *cn bw* females for the second time. This procedure was repeated until all of the males became sterile. The interval between 4th and 5th matings was 16 days. The inseminated females were transferred to the fresh culture vials in the same way as in experiment 2.

Experiment 4: The R(SD-36)-1 brothers of the males used in experiment 2 were used in this experiment. Eight R(SD-36)-1 males less than one day old were mated individually to seven *cn bw* females for 24 hrs, then separated from the females for 9 days, then mated again to seven fresh *cn bw* females for 24 hrs for the second time. This procedure was repeated until all of the males became sterile. The inseminated females were transferred to fresh culture vials in the same way as in experiment 2. Fly counts were made in each transferred culture vial separately.

RESULTS

Experiment 1: Since many of the *SD Ac(SD) St(SD)* and the *SD Ac(SD)* males became sterile after reaching the age of 20 days, the data from older males

TABLE 1
Change in k values with increasing age of males of various genotypes shown

The average number of progeny per fertile male per age period was approximately 80

Age in days	<i>SD Ac(SD)</i>		<i>SD Ac(SD)</i> [†] ($k \geq 0.98$)		<i>SD Ac(SD)</i>		<i>SD</i>		$\bar{X} \pm s$; <i>SD Ac(SD)</i>		<i>St(SD)</i>		<i>Ac(SD)</i>	
	Mean k	Number of σ^7 fertile	Mean k	Number of σ^7 fertile	Mean k	Number of σ^7 fertile	Mean k	Number of σ^7 fertile	Mean k	Number of σ^7 fertile	Mean k	Number of σ^7 fertile	Mean k	Number of σ^7 fertile
2.5	0.996	25	0.996	8	0.916	24	0.626	24	0.547	54	0.547	23	0.534	24
6.0	0.991	25	0.965	8	0.849	23	0.555	24	0.522	55	0.539	21	0.534	23
9.5	0.990	24	0.940	8	0.802	23	0.547	23	0.523	55	0.535	23	0.524	24
13.0	0.974	17	0.903	7	0.727	22	0.534	21	0.529	54	0.537	22	0.517	23
16.5	0.982	9	0.923	3	0.725	15	0.526	21	0.505	50	0.527	23	0.525	22
20.0	0.970	7	0.925	2	0.715	8	0.526	18	0.513	49	0.525	19	0.524	20
$r^{\ddagger}$	-0.193*		-0.446**		-0.445**		-0.405**		-0.239**		-0.097		-0.070	

* ** $P < 0.05$ and $P < 0.01$, respectively.

[†] Males selected for k values of more than, or equal to 0.98 at the 2.5 days old period.

[‡] Correlation coefficient between age of male and k value.

were not included. Results are summarized in Table 1. The decrease in k with increasing age of the males is pronounced in the $SD\ Ac(SD)$ line; this tendency can be also seen in the $SD\ Ac(SD)\ St(SD)$ and the SD lines. The correlation coefficients between the k values and the age of the males are also given in Table 1. In calculating correlation coefficients, the k values of the $SD\ Ac(SD)\ St(SD)$ and the $SD\ Ac(SD)$ lines were subjected to an arcsin transformation.

Table 2 shows the decrease in k for the males which were fertile for at least 20 days. Decrease in k is again clearly demonstrated. All of the genotypes except $Ac(SD)$ and $St(SD)$ showed a significant decrease in k values as the parental males got old. The amount of decrease, however, differed among genotypes. It is interesting to point out that $St(SD)$ not only stabilizes SD action, but also somehow prevents the aging effect. If we choose the $SD\ Ac(SD)$ males which showed k values of 0.98 or more in the first 2.5 day old period, the rate of decrease in k is found to be much larger than that in the $SD\ Ac(SD)\ St(SD)$. This is presented in Tables 1 and 2 under the genotype, $SD\ Ac(SD)$ ($k \geq 0.98$). The average k value for this selected group in Table 1 was 0.996, which is exactly the same as that of $SD\ Ac(SD)\ St(SD)$ at the same age period, but the rate of decrease in k was much more pronounced.

$Ac(SD)$, on the other hand, seems to have little effect on the aging effect. Note that in Tables 1 and 2 the relative values of k between the $SD\ Ac(SD)$ and the SD genotypes remain nearly constant with increasing paternal age.

The X^{stw} ; $SD\ Ac(SD)$ male showed practically no segregation distortion, but showed a significant aging effect suggesting, perhaps, that although the k value was greatly reduced by the presence of the suppressor X^{stw} , it still showed very weak distortion, thus was subjected to the aging effect.

Although the results presented in Tables 1 and 2 clearly show a general tendency in the aging effect, only a fraction of the sperm were sampled in this experiment. Therefore, to avoid any ambiguity, and to obtain more exact information, it is desirable to conduct experiments in such a way that as many sperm as possible will be sampled. Accordingly, experiment 2 was carried out.

Experiment 2: The results are summarized in Table 3. Practically no aging effect was seen in SD^{NH-2} , but the decrease in k was quite clear in the $R(SD-36)-1$ line. From this table it is seen that the relative average number of non-*cn bw* progeny remains nearly the same among the three genotypes in each age period, while the number of *cn bw* progeny of the $R(SD-36)-1$ males relative to that of the Tokyo males increases as the males get old.

Since the distribution function of the number of progeny flies was not known, a statistical analysis was done in the following way. Let a_x and b_x be the number of non-*cn bw* progeny of a SD^{NH-2} male and the average number of non-*cn bw* progeny of the Tokyo males at age x , respectively. As is shown in Table 3, three SD^{NH-2} males were tested and, therefore, there are three a_x 's at a given age x . Let $c_x = b_x \times 1343.0/1474.0$ and let p_x be the proportion of the a_x 's which are larger than a corresponding value of c_x . The values 1343.0 and 1474.0 (average number of non-*cn bw* progeny produced by the SD^{NH-2} and the Tokyo males, respectively, during their whole fertile period) were chosen arbitrarily to make the expectation

TABLE 2
Change in k values with increasing age of males of various genotypes which were fertile for at least 20 days
The average number of progeny per male per age period was approximately 80

Age in days	$SD\ Ac(SD)$		$SD\ Ac(SD)$ ($k \geq 0.98$)		$SD\ Ac(SD)$		SD		$\chi^2_{stc}; SD\ Ac(SD)$		$SI(SD)$		$Ac(SD)$	
	Mean k	Number of σ fertile	Mean k	Number of σ fertile	Mean k	Number of σ fertile	Mean k	Number of σ fertile	Mean k	Number of σ fertile	Mean k	Number of σ fertile	Mean k	Number of σ fertile
2.5	1.000	7	0.995	2	0.923	8	0.627	18	0.552	50	0.544	19	0.533	20
6.0	0.994	7	0.945	2	0.850	8	0.555	18	0.523	51	0.539	17	0.539	19
9.5	0.993	7	0.885	2	0.769	8	0.546	18	0.524	51	0.532	19	0.530	20
13.0	0.972	7	0.895	2	0.685	8	0.531	18	0.525	51	0.536	18	0.520	20
16.5	0.977	7	0.895	2	0.725	8	0.519	18	0.505	50	0.525	19	0.528	20
20.0	0.970	7	0.925	2	0.715	8	0.526	18	0.513	49	0.525	19	0.524	20

TABLE 3

The mean k values and the average number of progeny flies produced by the SD Ac(SD) St(SD), SD Ac(SD) and the control Tokyo males at successive age periods

Age in days	SD Ac(SD) S/(SD) SDNH ₂ -2					SD Ac(SD) R(SD-36)-1					Control Tokyo				
	Mean k	Number of male fertile	Mean number <i>cn bw</i>	Mean number SD	p^*_x	Mean k	Number of male fertile	Mean number <i>cn bw</i>	Mean number SD	q^*_x	s^*_x	Mean k	Number of male fertile	Mean number <i>cn bw</i>	Mean number Tokyo
0.5	1.000	3	0.0	30.0	0.00	0.907	3	5.3	51.5	0.75	0.00	0.570	3	54.3	72.0
1.5	1.000	3	0.0	114.7	1.00	0.856	4	23.0	137.0	0.75	0.25	0.541	3	71.1	83.7
2.5	0.999	3	0.3	86.7	0.33	0.678	4	50.5	106.5	0.25	0.25	0.516	3	131.7	140.3
3.5	1.000	3	0.0	158.7	0.67	0.732	4	61.5	168.3	0.50	0.50	0.532	3	148.7	169.3
4.5	1.000	3	0.0	91.0	0.67	0.783	4	28.5	103.0	0.50	0.25	0.546	3	99.7	119.7
5.5	1.000	3	0.0	115.3	1.00	0.756	4	34.3	106.3	1.00	0.75	0.509	3	56.7	58.7
6.5	1.000	3	0.0	73.0	0.33	0.719	4	35.0	89.5	0.25	0.25	0.518	3	82.0	89.3
7.5	1.000	3	0.0	119.3	1.00	0.680	4	55.0	116.8	0.50	0.75	0.521	3	116.0	126.0
8.5	1.000	3	0.0	65.7	0.33	0.659	4	50.5	97.5	0.75	0.50	0.497	3	97.3	96.3
9.5	1.000	3	0.0	127.3	1.00	0.633	4	56.3	97.3	0.50	0.50	0.492	2	113.7	110.0
10.5	1.000	3	0.0	83.7	1.00	0.573	4	67.5	90.5	0.75	0.75	0.467	2	58.3	51.0
11.5	1.000	2	0.0	63.3	0.33	0.597	4	70.0	103.5	0.75	0.75	0.495	2	72.7	71.3
13.0	0.995	2	0.3	60.3	0.33	0.626	3	53.8	90.0	0.50	0.75	0.522	2	95.0	103.7
Older	0.998	.	0.3	154.0	...	0.723	.	16.0	43.0	...	...	0.535	.	158.7	182.7
Total	1.000	1.0	1.0	1343.0		0.698	607.2	1400.7				0.521		1355.9	1474.0

* See text for explanation.

of p_x closer to 0.5. This kind of adjustment is preferred when the difference in the average number of progenies between two genotypes is large.

In the same way q_x was defined for non-*cn bw*, and s_x for *cn bw* progeny comparisons between the R(SD-36)-1 and the Tokyo lines. The values of p_x , q_x and s_x were then subjected to arcsin transformation. Let p'_x , q'_x and s'_x be the transformed values of p_x , q_x and s_x , respectively. The regression coefficients of p'_x and q'_x on x were computed to be +1.13 and +0.06, respectively; none of them was statistically significant ($t = 0.51$, $df = 11$, $0.6 < P < 0.7$ for p'_x ; $t = 0.05$, $df = 11$, $P > 0.9$ for q'_x). The regression coefficient of s'_x on x , +4.54, however, was highly significant ($t = 3.42$, $df = 11$, $P < 0.01$.) This amount of increase corresponds to roughly 0.07–0.08 per day under the s_x scale), and was significantly larger than that of q'_x ($t = 2.35$, $df = 22$, $P = 0.025$). In calculating the regression coefficients, data from the males older than 13 days were excluded, since the average number of progeny flies per male per day was remarkably reduced after this age period.

The results of the analyses described above indicate that the decrease in k with increasing age of the *SD* male is mainly caused by an increase in the number of *cn bw* progeny relative to that of the control Tokyo male, while the number of non-*cn bw* progeny is of lesser consequence.

Experiment 3: This experiment was done to see the aging effect without supply of females. Table 4 summarizes the results. As is clearly seen in this table, the average k values are lower for the three genotypes than those presented in Table 3, thus the aging effect can occur in males which are kept without a supply of females. Note that, in Table 4, the aging effect took place not only in R(SD-36)-1, but also in Tokyo males. The overall average k value of each genotype in experiment 2 was 1.000, 0.698 and 0.521 for *SD^{NH}-2*, R(SD-36)-1, and Tokyo, respectively, while it was, respectively, 0.990, 0.658 and 0.507 in experiment 3, thus showing, though not significantly, reduced overall k values in experiment 3. Taking the k values of R(SD-36)-1 and Tokyo at the youngest age group in Table 4 and comparing them with those in Table 3, we will see that, roughly speaking, the sperm, corresponding to the first 5 days period in experiment 2 were wasted or missing in experiment 3.

The average k 's in experiment 2 after 6 days old are 0.656, and 0.511 for the R(SD-36)-1 and Tokyo respectively, which are in good agreement with those in experiment 3.

Experiment 4: This experiment was done to see a possible change in k with increasing age of sperm when stored in the female. In experiment 3, the fly counts were also made in each vial separately, and the data in both experiments were pooled and are presented in Table 5. In Table 5, data are arranged according to the k value intervals of the parental males. It is clearly seen in this table that as the sperm stored in the female body get old, the k values increase slightly, but consistently.

The correlation coefficients between k and the age of sperm in the female body ($= r$) are computed to be +0.345 ($P = 0.02$), +0.298 ($P = 0.02$), +0.312 ($P < 0.01$), and -0.036 ($P > 0.10$) for the high, intermediate, low k group of

TABLE 4
Aging effect on k values when males are kept for three weeks without females

Age in days	<i>SD Ac(SD) St(SD)</i>				<i>SD Ac(SD) R(SD-36)-1</i>				Control Tokyo			
	Mean <i>k</i>	Number of male fertile	Number <i>cn bw</i>	Number <i>SD</i>	Mean <i>k</i>	Number of male fertile	Number <i>cn bw</i>	Number <i>SD</i>	Mean <i>k</i>	Number of male fertile	Number <i>cn bw</i>	Number Tokyo
21.5	0.996	5	5	1,222	0.678	6	561	1,179	0.509	6	1,028	1,066
28.5	0.971	5	15	497	0.616	6	533	853	0.526	6	606	673
35.5	0.996	2	1	233	0.682	6	358	767	0.489	5	645	617
42.5		0	.	...		0	...	...	0.517	4	308	329
58.5		0	.	...		0	...	...	0.474	2	163	147
Total	0.990		21	1,952	0.658		1,452	2,799	0.507		2,750	2,832

TABLE 5
Relation between k value and the age of sperm when stored in female body

Age of sperm in days	Culture vial transferred	R(SD-36)-1												Control	
		High k , $n^*=10$ $k \geq 0.80$			Intermediate k , $n=14$ $0.80 > k \geq 0.70$			Low k , $n=19$ $0.70 > k$			Tokyo, $n=23$				
		Mean k	Mean number of <i>cn bw</i>	SD	Mean k	Mean number of <i>cn bw</i>	SD	Mean k	Mean number of <i>cn bw</i>	SD			Mean k	Mean number of <i>cn bw</i>	Tokyo
0.5	1st	0.783	11.5	38.0	0.723	18.9	49.5	0.583	23.3	33.8	0.504	27.3	27.7		
1.5	2nd	0.819	7.6	31.9	0.712	12.2	31.4	0.566	16.9	21.8	0.501	21.3	21.4		
3.0	3rd-4th	0.849	7.1	35.9	0.750	11.3	33.2	0.617	17.3	27.6	0.507	22.2	22.8		
6.0	5th-7th	0.855	8.4	45.7	0.784	13.9	45.1	0.612	18.1	28.6	0.526	23.0	25.5		
13.0	8th-12th	0.890	4.6	36.2	0.772	10.6	31.4	0.664	19.6	33.9	0.500	25.8	25.8		

* Number of males included in this group.

R(SD-36)-1 line, and for the Tokyo line, respectively. In computing correlation coefficients, arcsin transformation was applied to the k values of high and intermediate k groups.

Thus, the control Tokyo line showed little change in k with increasing age of the sperm, while the R(SD-36)-1 line showed a consistent increase. The regression coefficients for the high, intermediate, and the low k group were computed to be $+0.536$ (this corresponds to approximately $+0.0065$ in k scale), $+0.334$ (approximately $+0.0050$ in k scale), and $+0.0068$, respectively, thus all three groups showed nearly the same rate of increase in k .

DISCUSSION

HARTL, HIRAIZUMI and CROW (1967) presented evidence supporting a dysfunctional sperm formation model as a mechanism of segregation distortion. Their model was also supported by an independent study of NICOLETTI (personal communication). In their study, however, only a fraction of the sperm was sampled, and it appeared desirable to obtain additional evidence by sampling all of the sperm produced during the whole fertile period of the male. The results presented in Table 3 provide clear evidence for this. The average number of non-*cn bw* progeny for the overall fertile period was 1343.0, 1400.8, and 1473.9 for SD^{NH}-2 ($k = 1.000$), R(SD-36)-1 ($k = 0.698$), and Tokyo ($k = 0.521$) lines, respectively, thus showing nearly the same amount of non-*cn bw* sperm production instead of the apparent difference between the genotypes as expressed in the k values. The number of *cn bw* progeny flies, however, was clearly different among the three genotypes: it was 1.0, 607.2, and 1,355.9 for the SD^{NH}-2, R(SD-36)-1, and the Tokyo line, respectively. On the average, approximately 3,000 progeny were produced by a Tokyo male. Considering that the hatchability of eggs produced by the *cn bw* female is approximately 50%, the number 3,000 corresponds to about 6,000 sperm sampling per male. If a fraction I of the *cn bw* sperm are effectively functional in fertilization, then, $k = 1/(1 + I)$, or $I = (1 - k)/k$, thus the expected number of *cn bw* progeny is proportional to $(1 - k)/k$. The correlation coefficient between $(1 - k)/k$ and the number of *cn bw* flies for the three genotypes is computed to be $+0.99964$, which, with only one degree of freedom, is significant ($0.02 > P > 0.01$).

The k value significantly increased when sperm from the SD males were aged in the female body. Perhaps this is because of a reduced viability of the *cn bw* sperm produced in the SD males although other possibilities cannot be ruled out at present; for example, on the average, *cn bw*-bearing sperm may function sooner.

It is interesting to point out that the control Tokyo males also showed a decrease in k as the males got old. The rate of decrease was rather small, but it was statistically significant. In our laboratory, the same tendency was also found in some of the other genotypes studied for other purposes. ZIMMERING and BARBOUR (1961) reported an aging effect in the Bar-Stone system, and YANDERS (1965) reported a sex ratio change associated with the age of the males from a wild-type

stock of *Drosophila melanogaster*. These altogether suggest that the phenomenon of aging effect of the male on the segregation frequency is not an unique phenomenon of the *SD* system.

Finally, it is worth mentioning that in Table 3, both the R(*SD*-36)-1 and the Tokyo males showed a decrease in *k* for the first several days, then an increase. A similar tendency is also found in some of the genotypes presented in Tables 1 and 2. The reason for this is not yet known.

SUMMARY

When a segregation distorter (*SD*) heterozygous male gets old, the intensity of segregation distortion (measured by *k*: the proportion of recovery of *SD* in the progeny) decreases. This phenomenon is called an "aging effect." The present study established the following points: (1) Of the three major elements in the *SD* system, *SD* (and possibly *St*(*SD*)) showed an aging effect but *Ac*(*SD*) was of little consequence for the aging effect. (2) The aging effect is not due to a change in the number of *SD* sperm produced, but due to increased production of the *SD*⁺ sperm as the male gets older. (3) A model of dysfunctional sperm formation as a mechanism of segregation distortion was re-confirmed by sampling all of the sperm covering the whole life span of the males.

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