

Study on the Sex Chromosome Dependent Segregation of the Third Chromosome in *Drosophila melanogaster*

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초파리의 성 염색체의 구성이 제3염색체의 분리에 미치는 영향에 대하여

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적 요

초파리의 성 염색체의 구성 여하에 따라 그 제3염색체의 분리가 달라지는가를 조사하기 위하여 성 염색체의 구성이 다른 8가지 인자형을 만들고 제3염색체 marker로서 *e*와 *se*를 이용하여 *se*의 분리를 *k* 값으로 검토하고 아울러 성비를 조사 검토한 결과는 다음과 같다.

1. *se*의 분리 즉 *k* 값은 인자형간에 그리고 성간에 매우 유의적인 차를 보였으며 인자형과 성과의 상호작용도 유의적 차이를 보여 주었다. 이것은 분명히 *se* 제3염색체의 분리가 성 염색체의 구성에 영향을 받은 것을 말해 준다.

2. $k(\text{♀})$ 값이나 $k(\text{♂})$ 값은 다 같이 인자형간에 유의적 차이를 볼 수 없다.

3. *se*자손의 성비는 인자형간에 매우 유의적 차이를 보였으나 *e*자손에서는 뚜렷한 차이를 볼 수 없었다.

4. 평균적으로 $k(\text{♂})$ 값은 $k(\text{♀})$ 값보다 높고, *se*자손의 성비는 *e*자손의 성비보다 높았다.

5. 이러한 결과는 어떤 종류의 prezygotic selection이 작용하는 것으로 해석할 수 있는데, 즉 *e* 제3염색체와 Y염색체의 조합이 수정전에 감수되는 것으로 생각할 수 있다. 이러한 문제는 종래 초파리 등에서 실시했던 생존력 추경을 재 평가할 필요성을 말해주는 것이다.

INTRODUCTION

It has been reported in several investigations that some of the X chromosomes sampled from natural populations and laboratory stocks carried suppressor system for the segregation distorter(SD) action in *Drosophila melanogaster* such that segregation distortion in a male carrying a suppressor-X chromosome was greatly reduced (Sandler and Hiraizumi 1961, Hiraizumi and Kataoka 1965, Kataoka 1967, Chung and Kang 1969a, 1969b).

Sakai and Hiraizumi(1969) reported an instance of sex chromosome dependent segregation frequency in *Drosophila melanogaster*.

Chung(1970) designed an experiment to see if the segregation frequency of a second chromosome, which was free of SD, was changed by changing the sex chromosome constitution in males. The eight genotype males having different sex chromosome constitution and two recessive markers of the second chromosome(*cn bw*, *vg*) were used for the experiment. The result showed that the segregation frequency of the *vg* second chromosome in the male, when

made heterozygous with the *cn bw* second chromosome, was dependent upon the sex chromosome constitution.

The present study was designed to see if the segregation frequency of a third chromosome was changed by changing the sex chromosome constitution in males which were free of SD in the second chromosome.

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MATERIALS AND METHODS

The following stocks of *Drosophila melanogaster* were used in the present investigation.

- (1) *se*. A standard laboratory stock carrying a recessive marker on the third chromosome, sepia (3L-26.0).
- (2) *e*. A stock carrying a recessive marker on the third chromosome, ebony (3R-70.7).

Males of the following genotypes were constructed by appropriate matings:

$$\begin{array}{ll} \text{(A)} \frac{X'}{Y'}; \frac{e}{se}, & \text{(B)} \frac{X'}{Y''}; \frac{e}{se}, \\ \text{(C)} \frac{X''}{Y'}; \frac{e}{se}, & \text{(D)} \frac{X''}{Y''}; \frac{e}{se}, \end{array}$$

The additional four genotypes were constructed for the experiment on the sex ratio:

$$\begin{array}{ll} \text{(E)} \frac{X'}{Y'}; \frac{e}{e}, & \text{(F)} \frac{X'}{Y''}; \frac{e}{e}, \\ \text{(G)} \frac{X''}{Y'}; \frac{e}{e}, & \text{(H)} \frac{X''}{Y''}; \frac{e}{e}, \end{array}$$

The X'' , Y'' , X' , and Y' are the X and the Y chromosomes which were derived from the *se* and *e* stocks, respectively.

The method of the present experiment is same as the previous one (1970). Each genotype male

was mated to *e* female in fifty vials. The segregation frequency of the second chromosome was measured by k , the proportion of the *se* third chromosomes recovered among progeny flies of each mating. And the proportion of males among the progeny of the mating was defined as the sex ratio.

The second and the fourth chromosome pairs were almost entirely derived from the standard *e* stock by backcrossing to the *e* stock for several generations, but it might be still probable that some of them originated from the *se* stock. However, the chromosomes from the *se* stock were randomized among the four genotypes when the present experiments were carried out. Therefore, the difference in the k values in the males among genotypes had to be due to the different constitution of the sex chromosomes.

The food used was a standard corn meal, yeast, agar type with 0.5% of propionic acid as a mold inhibitor and flies were kept in the constant temperature room ($25^{\circ} \pm 1^{\circ}\text{C}$) throughout the present experiment.

RESULTS AND DISCUSSION

1. The segregation frequency of the third chromosome: The k value was calculated separately for the male [$k(\text{♂})$] and the female progeny [$k(\text{♀})$] for each vial. The average values of $k(\text{♂})$ and $k(\text{♀})$ for the four genotypes are summarized in Table 1. The analysis of variance for Table 1 are resulted in Table 2.

As Table 2 shows the k values were highly significantly different among the four genotypes and between the two sexes and the interaction of genotype and sex was significantly different.

As Table 1 shows the $k(\text{♂})$, on the average, was significantly higher than that of the $k(\text{♀})$. This suggests that some sort of selection might be operating such that the combination of the *e* third chromosome and the Y chromosome tends to be eliminated before fertilization or the gametes having the *se* third chromosome and the Y chromosome tends

Table 1. Average values of $k(\delta)$ and $k(\varphi)$ for the four genotype males shown

Genotype of male	No. males tested	Total $e_{\varphi\varphi}$	No. of $se_{\varphi\varphi}$	$k(\varphi)$	Total $e_{\delta\delta}$	No. of $se_{\delta\delta}$	$k(\delta)$	Overall
(A) $X^*/Y^* ; se/e$	49*	694	741	0.5133	753	910	0.5516	0.5312
(B) $X^*/Y'' ; se/e$	47*	688	776	0.5332	643	863	0.5768	0.5502
(C) $X''/Y^* ; se/e$	50	680	756	0.5212	631	763	0.5620	0.5416
(D) $X''/Y'' ; se/e$	43*	470	533	0.5349	436	502	0.5256	0.5337

*One mating in genotype A, three in B and seven in D were missing which were due to the accidental extinction of flies during the experiment.

Table 2. Analysis of variance of $k(\delta)$ and $k(\varphi)$ shown in Table 1

Source of variance	S.S.	d. f.	M. S.	F.
Between genotypes	0.0423	1	0.0423	7.69**
Between sexes	0.0740	3	0.0247	4.49**
Interaction	0.0625	3	0.0208	3.78*
	(0.1788)	(7)		
Error	2.0408	374	0.0055	
	(2.2196)	(381)		

*Significant, $p < 0.05$

**Highly significant, $p < 0.01$

to be produced in greater numbers than those having other combinations of the chromosomes.

The $k(\varphi)$ remains roughly constant among the four genotypes ($X^2=1.19$, d.f.=3, $0.9 > p > 0.7$). On the other hand, the $k(\delta)$ looks heterogeneous among genotypes but the X^2 test shows no significant difference ($X^2=4.29$, d.f.=3, $0.5 > p > 0.1$). The highest $k(\delta)$ is found for the X^*/Y'' (B) which is 0.5768 and the lowest, for the X''/Y'' (D) which is 0.5256. The difference in the $k(\delta)$ between X^*/Y'' (B) and X''/Y'' (D) is not significant ($X^2=3.36$, d.f.=1, $0.1 > p > 0.05$).

The results of the analysis of variance in the data of the present experiment are agreed with those of Sakai and Hiraizumi(1969) and also with those of the previous work(Chung, 1970) that the difference in k between two sexes, among genotypes and the interaction are highly significant.

The result of the present experiment that the values of the $k(\delta)$, on the average, is significantly higher than that of the $k(\varphi)$ is also agreed with those of the previous work (Chung, 1970) and the report of

Sakai and Hiraizumi(1969). Both of the $k(\varphi)$ and $k(\delta)$ are roughly homogeneous among genotypes. This is disagreed with the results of the previous work(Chung, 1970) and of the experiment of Sakai and Hiraizumi(1969) that the $k(\varphi)$ was homogenous but the $k(\delta)$ was highly heterogeneous among genotypes.

2. The sex ratio: Table 3 shows the average sex ratios in the two segregating progeny classes, e and se , for the four genotypes(A,B,C, and D). The sex ratios in the e progeny class for the additional four genotypes(E,F,G and H)are also presented in Table 3.

The sex ratio of the se progeny class was significantly heterogeneous among the four genotypes, A,B,C, and D($X^2=11.54$, d.f.=3, $p < 0.01$), the highest sex ratio was found for the genotype A(0.5808), the lowest was for the genotype D(0.4823). It was homogeneous among the four genotypes A,B, C and D for the e progeny class ($X^2=4.40$, d.f.=3, $0.5 > p > 0.1$)but it was significantly heterogenous among the additional four genotypes, E,F,G and H ($X^2=9.17$, d.f.=3, $0.05 > p > 0.025$); the highest sex

Table 3. Sex ratios (proportion of males) of the eight genotype males shown

Genotype of male	No. males tested	<i>e</i>		Sex ratio	<i>se</i>		Sex ratio	Overall sex ratio
		♀♀	♂♂		♀♀	♂♂		
(A) X'/X' ; <i>se/e</i>	49*	694	753	0.5229	741	910	0.5808	0.5308
(B) X'/Y'' ; <i>se/e</i>	47*	688	643	0.4970	776	863	0.5293	0.5147
(C) X''/Y' ; <i>se/e</i>	50	680	631	0.4830	756	763	0.5014	0.4904
(D) X''/Y'' ; <i>se/e</i>	43*	470	436	0.4753	533	502	0.4823	0.4795
(E) X'/Y' ; <i>e/e</i>	50	1914	1906	0.4976				0.4976
(F) X'/Y'' ; <i>e/e</i>	49*	1528	1706	0.5190				0.5190
(G) X''/Y' ; <i>e/e</i>	50	1185	1173	0.4990				0.4990
(H) X''/Y'' ; <i>e/e</i>	49*	1761	1722	0.4370				0.4370

*One mating in genotype A,F and H and three in B, and seven in D were missing which were due to the accidental extinction of flies during the experiment.

ratio was found for genotype F (0.5190) and the lowest was for the genotype H (0.4370). The sex ratio of *e* progeny class was also significantly heterogeneous among all of eight genotypes, A,B,C,D, E,F,G and H ($X^2=17.23$, d.f.=0.7, $0.025 > p > 0.01$); the highest and the lowest sex ratio was found for the genotype A (0.5229) and for the genotype H (0.4370), respectively.

As Table 3 shows, the sex ratio of the *se* progeny class was, on the average, higher than that of the *e* progeny class. This suggests that the combination of the *e* third chromosome and the Y chromosome tends to be eliminated before fertilization or the gamete having the combination of the *se* third chromosome and the Y chromosome tends to be produced in greater numbers than the other combinations.

Table 3 also shows that the X'' chromosome, when compared with the X' chromosome, tends to segregate with a higher frequency among the F₁ generation, resulting in a lower sex ratio (high frequency of females). The Y'' chromosome, when compared with the Y' chromosome, shows also a lower sex ratio in the F₁ generation.

Sakai and Hiraizumi(1969) examined the sex ratios in the two segregating progeny classes, *stw*³ and *cn bw* for the six genotypes corresponding to the genotypes, A,B,C,E,F and G in the present experiment. Their results showed that the sex ratio of the *stw*³ progeny class was homogeneous among the three

genotypes, A,B, and C but it was highly significantly heterogeneous for the *cn bw* progeny class and so was among the additional three genotypes, D,E and F corresponding to the genotype E,F and G, respectively in the present experiment. Their results also showed that the X'' chromosome, when compared with the X''^{bw} chromosome, tended to segregate with a higher frequency among the F₁ generation, resulting in a lower sex ratio (high frequency of females) and the Y'' chromosome, on the other hand, when compared with the Y''^{bw} chromosome, showed a higher sex ratio (low frequency of females) in the F₁ generation. These results showed to be roughly agreed with those of the previous work(Chung, 1970) in which the sex ratios in the two segregating progeny classes, *vg* and *cn bw* for the eight genotypes were examined.

The results of the present experiment are similar to those of Sakai and Hiraizumi(1919) and of Chung (1970) with the exception that (1) The sex ratio of the *e* progeny class was homogeneous among the four genotypes, A,B,C and D, (2) The Y'' chromosome, when compared with the Y' chromosome showed a lower sex ratio (high frequency of females) in the F₁ generation. One of the results of the present study that the sex ratio of the *se* progeny class was, on the average, higher than that of the *e* progeny class, is agreed with that of the previous work (Chung, 1970) in which the sex ratio of the *vg* pro-

geny class was higher than that of the *cn bw* progeny class.

The fact that the values of the $k(\hat{\ominus})$ and the sex ratio of the *se* progeny class was, on the average, higher than that of the $k(\hat{\omin�})$ and of the *e* progeny class, respectively, implying some sort of selection may be operating such that the combination of the *e* third chromosome and the Y chromosome tends to be eliminated before fertilization. The time and the mechanism of elimination are hard to know at present.

As discussed in the paper of Sakai and Hiraizumi (1969) and of Chung (1970), the viabilities of genotypes have been estimated based upon the relative frequencies of genotype recovered among the F_1 progeny of an appropriate mating in many investigations. However, the segregation frequency of the second chromosome was changed by changing the sex chromosome constitution in the study of Sakai and Hiraizumi (1969) and of Chung (1970). And in the present study the segregation frequency of the third chromosome was also changed depending upon the sex chromosome constitution. As the previous workers (Sakai and Hiraizumi 1969, Chung 1970) pointed out, this change could not be explained by the zygotic viability differences. Thus re-evaluation of many viability estimations previously made with *Drosophila* should be done.

SUMMARY

The present study was undertaken in an attempt to see if the segregation frequency of a third chromosome was changed by changing the sex chromosome which were free of SD in the second chromosome. The eight genotype males having different sex chromosome constitution each were constructed by appropriate matings and the two standard laboratory stocks of *Drosophila melanogaster*, *e* and *se* were used as the third chromosome recessive markers for the present experiment.

The results of the present investigation are given

below:

1. The k values which are the proportion of the *se* third chromosomes recovered among progeny flies from the mating of *se/e* males to *e* females were highly significantly different among the four genotypes and between the two sexes, and the interaction of genotype and sex was significantly different. Thus the segregation frequency of the *se* third chromosome in the male, when made heterozygous with the *e* third chromosome, was dependent upon the sex chromosome constitution.

2. Both of the $k(\hat{\omin�})$ and the $k(\hat{\ominus})$ remains roughly constant among genotypes.

3. The sex ratio of the *se* progeny class was highly significantly heterogeneous among the four genotypes but it was homogeneous for the *e* progeny class.

4. The values of the $k(\hat{\omin�})$ and the sex ratio of the *se* progeny class, on the average, were higher than that of the $k(\hat{\omin�})$ and of the *e* progeny class, respectively.

5. Those phenomena suggest that some sort of prezygotic selection could be operating such that the combination of the *e* third chromosome and the Y chromosome tends to be eliminated before fertilization. This tendency argues for a re-examination of the viability estimations of *Drosophila melanogaster*

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