CHROMOSOME INTERACTIONS AFFECTING MATING SPEED IN *DROSOPHILA ROBUSTA*[1]

SATYA PRAKASH[2]

Department of Biology, Washington University, St. Louis, Missouri 63130

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GEOGRAPHICALLY central populations of *D. robusta* maintain a large amount of inversion polymorphism in their three major V shaped chromosomes *XL XR*, *2L 2R*, and *3L 3R*. In studies on a highly polymorphic population of *D. robusta* from the locality of Creve Coeur, St. Louis County, Missouri, heterokaryotypes showed no evidence of overdominance for viability in both sexes and mating speed and fertility in the male. Evidence of interactions between XR and second chromosome, affecting male mating activity was obtained. While there were no differences in the mating activity and fertility of *XR* (standard gene arrangement in the right arm of the *X* chromosome) and *XR-1* (alternate gene arrangement in the right arm of the *X* chromosome) males which are homokaryotypic in the second chromosome, *XR-1* males which are heterokaryotypic in the second chromosome have greater mating activity and fertility than the corresponding *XR* males (PRAKASH 1967a).

Experiments to be reported here were conducted with the derived strains to ascertain if interactions between second and third chromosomes affecting male mating activity exist. Four strains of $\frac{XL\ XR\ 2L\ 2R\ 3R}{XL\ XR\ 2L\ 2R\ 3R}$ and three strains of $\frac{XL\ XR\ 2L\text{-}1\ 2R\ 3R}{XL\ XR\ 2L\text{-}1\ 2R\ 3R}$ were obtained by single pair mating of homokaryotypic wild flies. Interstrain and interkaryotype crosses resulted in flies of *2L/2L*, *2L/2L-1*, and *2L-1/2L-1* karyotypes. However, no differences in the mating speed of homokaryotypes and heterokaryotypes on the 12th day of age were observed. (Table 7)

The experiments were then designed to check if $\frac{XL\ XR\ 2L\quad 2R\ 3R\text{-}1}{2L\text{-}1\ 2R\ 3R\text{-}1}$ flies show any evidence of heterosis for mating speed. PRAKASH (1967b) *has shown that a positive correlation exists among speed of mating, number of flies inseminated and fertility in* D. robusta *males*. Fast mating females did not show these correlations, but it was shown that fast mating provides the female with an advantage of having received more sperm than a slow mater. The study of mating speed then is a very important indicator of fertility.

In this paper, evidence of heterosis for mating speed of $\frac{XL\ XR\ 2L\quad 2R\ 3R\text{-}1}{2L\text{-}1\ 2R\ 3R\text{-}1}$

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[2] Present address: Department of Zoology, University of Chicago, Chicago, Illinois 60637.

flies is presented. Data which show heretofore undescribed female interactions are given. Certain homokaryotypic female combinations, in male choice experiments, raise the mating speed of the homokaryotype males so that it is nearly equal to that of the heterokaryotype males. Since different homokaryotypic female combinations differ only with respect to their cytoplasms, these female interactions show the role of cytoplasmic inheritance in mating behavior of these insects. (Table 6). No statement can be made at present regarding the physiological and behavioral mechanisms of these female interactions.

METHODS

Flies for these experiments were obtained by interstrain and interkaryotype crosses of the following selected homokaryotypic strains:

Two strains, *viz.*, a_1 and a_2 of $\frac{XL\ XR\ 2L\ 2R\ 3R\text{-}1}{XL\ XR\ 2L\ 2R\ 3R\text{-}1}$ karyotype and

two strains, *viz.*, a_3 and a_4 of $\frac{XL\ XR\ 2L\text{-}1\ 2R\ 3R\text{-}1}{XL\ XR\ 2L\text{-}1\ 2R\ 3R\text{-}1}$ karyotype.

All four strains were derived by single pair matings of F_1 homokaryotype flies which were obtained by crossing $\frac{XL\ XR\ 2L\quad 2R\ 3R\text{-}1}{XL\ XR\ 2L\text{-}1\ 2R\ 3R\text{-}1} \times \frac{XL\ XR\ 2L\quad 2R\ 3R\text{-}1}{2L\text{-}1\ 2R\ 3R\text{-}1}$ wild pairs of flies caught in August 1964 at Creve Coeur, St. Louis, Missouri. The strains had been kept in bottles in mass cultures for 5 generations before being crossed for these experiments. The experiments were conducted on flies of the 6th to the 10th generations. No change was observed in the mating activity of the flies during this period. Flies for experimental use were obtained from crosses described below.

Cross: Female	Cross: Male	Karyotype of the flies obtained from these crosses	Designation
a_1	a_2 and	$\frac{XL\ XR\ 2L\ 2R\ 3R\text{-}1}{XL\ XR\ 2L\ 2R\ 3R\text{-}1}$	A and B
a_2	a_1		
a_3	a_4 and	$\frac{XL\ XR\ 2L\text{-}1\ 2R\ 3R\text{-}1}{XL\ XR\ 2L\text{-}1\ 2R\ 3R\text{-}1}$	C and D
a_4	a_3		
a_1	a_3		
a_1	a_4	$\frac{XL\ XR\ 2L\quad 2R\ 3R\text{-}1}{XL\ XR\ 2L\text{-}1\ 2R\ 3R\text{-}1}$	e, f, g, and h, respectively
a_2	a_3		
a_2	a_4		

Hereafter, the karyotype of the flies shall be abbreviated as *2L/2L*, *2L-1/2L-1*, and *2L/2L-1*. Approximately 30 pairs of virgin flies were used as parents for each cross. Flies were changed to fresh food bottles every 4 to 5 days. Developing larvae were heavily yeasted. Newly emerged flies were collected and sexed every 24 hours. Twelve flies of one sex were left in a well-yeasted fresh food vial for a period of three days and were changed to fresh food every third day. Male choice experiments were done with ten day old virgin unetherized flies. Five males of one karyotype were allowed to mate for a period of one hour with 15 marked females, five each of the three different karyotypes, in a plexiglass chamber with wet blotting paper (PRAKASH 1967a).

Females were marked when they were seven days old by making a small circular hole near the tip of the submarginal cell of the left, right and both wings in *2L/2L*, *2L-1/2L-1*, and *2L/2L-1* females, respectively. The female combinations were randomized in the following manner: with two groups of each of the two homokaryotypes, namely, A, B and C, D, there will be four homo-

TABLE 1

Possible homo- and heterokaryotype female combinations

Homokaryotypes	Heterokaryotypes				Class
	e	f	g	h	
AC	ACe	ACf	ACg	ACh	1
AD	ADe	ADf	ADg	ADh	2
BD	BDe	BDf	BDg	BDh	3
BC	BCe	BCf	BCg	BCh	4

karyotype female combinations, that is, AC, AD, BD, and BC, which will give 16 possible female combinations with four heterokaryotype females, e, f, g, and h. (See Table 1). For convenience, hereafter, females of classes 1, 2, 3, and 4 will be referred to as AC htk, AD htk, BD htk, and BC htk, respectively.

The manner in which the mating experiments were run is given in Table 2. In order to understand this table, let us consider the ACe female combination of Class 1. Fifteen marked females, five each of the three karyotypes represented by A, C, and e, were allowed to mate with five males of the *2L/2L* karyotype of the B group. Three such independent mating runs were tested. In another mating run, 15 marked ACe females were given five males of the *2L-1/2L-1* karyotype of the D group. Three mating runs of this type were tested. In another mating run, 15 ACe females were tested with five *2L/2L-1* males of the f group and with males of the g and h groups in two other independent mating runs. As can be seen from Table 2, the females were always mated to males of different groups. This was done to avoid any preferential mating of flies which were reared in the same bottle. In other words, each female combination was tested in independent mating trials with males of *2L/2L*, *2L-1/2L-1*, and *2L/2L-1* karyotypes. Three mating runs with males of one karyotype were tested for each female combination. 240 males of

TABLE 2

Scheme of the mating experiment (For explanation, see text)

Female class	Female combinations			Males tested			
	2L/2L	*2L-1/2L-1*	*2L/2L-1*	*2L/2L*	*2L-1/2L-1*	*2L/2L-1*	
1	A	C	e	B	D	f, g, h	
1	A	C	f	B	D	e, g, h	
1	A	C	g	B	D	e, f, h	
1	A	C	h	B	D	e, f, g	
2	A	D	e	B	C	f, g, h	
2	A	D	f	B	C	e, g, h	
2	A	D	g	B	C	e, f, h	
2	A	D	h	B	C	e, f, g	
3	B	D	e	A	C	f, g, h	Subclass A
3	B	D	f	A	C	e, g, h	
3	B	D	g	A	C	e, f, h	Subclass B
3	B	D	h	A	C	e, f, g	
4	B	C	e	A	D	f, g, h	
4	B	C	f	A	D	e, g, h	
4	B	C	g	A	D	e, f, h	
4	B	C	h	A	D	e, f, g	

each karyotype and thus 720 males in total were tested with a total of 2160 females. The experiments were run between 11 AM and 5 PM. The copulatory pairs were aspirated out and each pair was left in an empty shell vial. After the mating experiment was over, the karyotype of the female was noted down by looking at the wing mark with a binocular microscope.

RESULTS

The data of mating speed of males of similar karyotypes when mated to different female combinations of the same class were pooled if the χ^2 heterogeneity test indicated no significant difference at $P = 0.05$. However, in practice, the pooled data (presented in Tables 3 to 7) indicated homogeneity at $P = 0.10$.

Mating speed of homo- and heterokaryotype males: The data were classified into four groups: (1) total mating in 10 min, (2) total mating in 10.01 to 30.00 min, (3) total mating in 30.01 to 60.00 min, (4) total not mating. χ^2 tests with 3 df were performed. In cases where no differences in the mating speed of different karyotypes were observed, the adjacent groups were pooled. The pooling results in lowering the degrees of freedom.

In all of the classes there were no differences in the mating speeds of *2L/2L* and *2L-1/2L-1* males. The two homokaryotypes were, therefore, pooled in each class. Table 3 presents the data of mating speed of homo- and heterokaryotype males with different female combinations. Heterokaryotype males show a faster mating speed than homokaryotypes when tested with the AC htk female combina-

TABLE 3

Mating speed of homo- and heterokaryotype males with different female combinations

	Percent mating in:			Number of males tested
	10 minutes	30 minutes	1 hour	
	1. AC htk female combination			
Homokaryotype	37.50	57.50	77.50	120
Heterokaryotype	56.67	83.33	91.67	60
	$\chi^2_{(3)} = 12.0$ $P < 0.010$			
	2. AD htk female combination			
Homokaryotype	64.17	81.67	86.67	120
Heterokaryotype	68.33	86.67	85.00	60
	$\chi^2_{(3)} = 5.1$ $P > 0.100$			
	3. BD htk female combination			
Homokaryotype	35.83	58.33	67.50	120
Heterokaryotype (Subclass A)	50.00	96.67	96.67	30
Heterokaryotype (Subclass B)	46.67	56.67	66.67	30
Homokaryotype *versus* heterokaryotype (Subclass A)				
	$\chi^2_{(3)} = 16.8$ $P < 0.005$			
	4. BC htk female combination			
Homokaryotype	50.00	71.67	80.00	120
Heterokaryotype	58.33	85.00	95.00	60

$\chi^2_{(1)}$ mated in 1 hour *versus* unmated $= 5.9$ $P < 0.020$, Yates' correction

tion. With the AD htk female combination, the heterokaryotypes seem to have a higher mating speed; the differences, however, are not significant. With BD htk females, the data of mating speed of heterokaryotype males were very heterogeneous and had to be classified into two subclasses, A and B (see Table 2). The heterokaryotype males in subclass A maintain a higher mating speed ($P < 0.005$) throughout the one hour period than the homokaryotypes. The differences in the mating speed of heterokaryotype males of subclass B and the homokaryotype males are not significant. The heterokaryotype males have a higher mating speed than the homokaryotype males when tested with the BC htk female combination.

In all four classes tested, the heterokaryotype males show a greater mating speed than the homokaryotypes (see Figure 1).

In order to find out if in the entire experiment the heterokaryotype males have a greater mating speed than the homokaryotypes, values of χ were calculated from χ^2 with 3 df for the differences in the mating speed of homo- and heterokaryotype males. Since in all cases the heterokaryotype males perform better, the values of χ are positive. The standardized normal deviate was then calculated. As can be seen from Table 4, the test establishes that heterokaryotypes have a faster mating speed than the homokaryotype males. Figure 2 presents the cumulative percentage curves of mating speed of heterokaryotypes and homokaryotypes. As can be seen from the figure, heterokaryotypes maintain a faster mating speed throughout the one hour period.

Mating speed of homo- and heterokaryotype females: In all female combinations, slightly more heterokaryotype females mate than homokaryotype females by the end of 10 min, 30 min, and 1 hr. There is no evidence of assortative mating. All three male karyotypes "choose" heterokaryotype females more often than homokaryotype females. Table 5 shows the number of homo- and heterokaryotype females which mated by the end of 1 hr. The mating speed of the three types of females can be summarized as *2L/2L-1 > 2L-1/2L-1 > 2L/2L.*

Female interactions: Mating speed of males which are of the same karyotype

TABLE 4

χ^2s of mating speed of homo- and heterokaryotype males in the entire male-choice experiment

Group	Female combination	$\chi^2_{(3)}$	χ
1	AC htk	12.010	+ 3.465
2	AD htk	5.102	+ 2.258
3	BD htk		
	Subgroup A	16.800	+ 4.098
	Subgroup B	2.636	+ 1.623
4	BC htk	7.430	+ 2.725
		14.169	+14.169

$\chi = 14.2$, d.f. $= 15$, Normal deviate $= \frac{}{\sqrt{15}} = 3.7$ $P \simeq 0.0004$

A positive value of χ indicates that the heterokaryotypes have a faster mating speed.

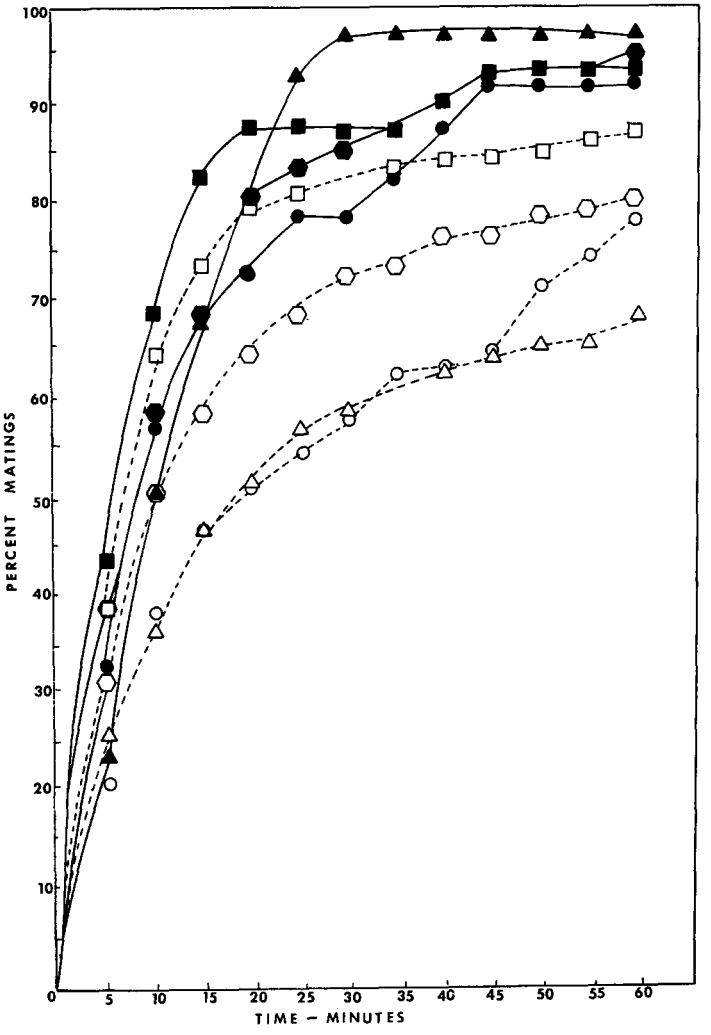

FIGURE 1.—Cumulative percentage curves for the matings of homokaryotype and heterokaryotype males (male choice experiments) during a period of one hour.

○ – – – – AC HTK ♀ × HMK ♂
● – – – – AC HTK ♀ × HTK ♂
⬡ – – – – BC HTK ♀ × HMK ♂
⬢ – – – – BC HTK ♀ × HTK ♂
△ – – – – BD HTK ♀ × HMK ♂
▲ – – – – BD HTK ♀ × HTK ♂ (Subgroup A)
□ – – – – AD HTK ♀ × HMK ♂
■ – – – – AD HTK ♀ × HTK ♂

and group was compared, when tested with different female combinations. *2L/2L* males of B group show a faster mating speed with the AD htk female combination than with AC htk (part A of Table 6). The two sets of mating runs differ only

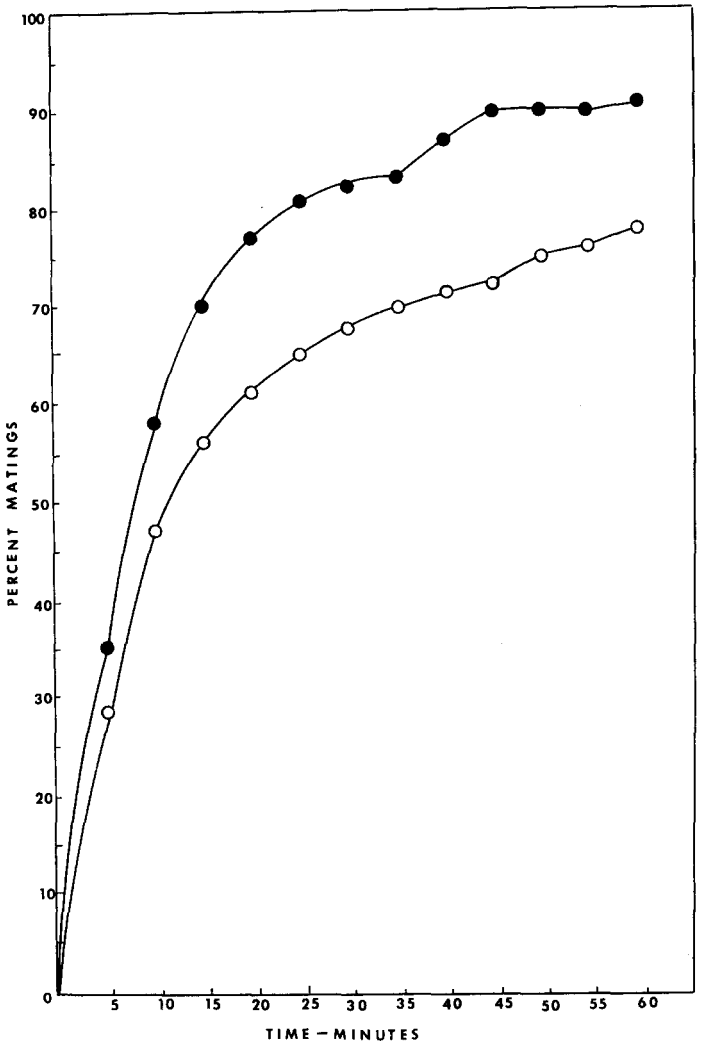

FIGURE 2.—Cumulative percentage curves for the matings of homokaryotype and heterokaryotype males (male choice experiments) during a period of one hour. These curves have been obtained by pooling the data of 480 homokaryotype males and 240 heterokaryotype males.
● = heterokaryotype males
○ = homokaryotype males

in that *2L-1/2L-1* females, *viz.*, D and C, were obtained by reciprocal crosses. Comparison of AD htk and BD htk female combinations when tested with *2L-1/2L-1* males of the C group shows that the males exhibit higher mating with the AD htk female combination (see part B of Table 6). These two mating runs differ in that *2L/2L* females, *viz.*, A and B, were obtained by reciprocal crosses, and thus differ only in their cytoplasms. There are no differences in the mating speed of heterokaryotype males when tested with these female combinations (see

TABLE 5

Mating speed of homo- and heterokaryotype females in 1 hour

Female karyotype	2L/2L	2L-1/2L-1	2L/2L-1	Total
Observed number	170	197	224	591
Expected number	197	197	197	591
	$\chi^2_{(2)} = 7.4$ $P < 0.025$			

Tables 3, 1 and 2). These results, then, lead to the conclusion that interactions between homokaryotypic A and D females are of such a nature as to raise the mating speed of homokaryotype males to a level nearly equal to that of heterokaryotype males. It should be emphasized, however, that these homokaryotypic females do not raise the mating speed of homokaryotype males by directly participating in more matings, since in the AD htk female combination, as in all others, proportionately more heterokarypotype females mate with all three karyotypes of males than the homokaryotype females. The presence of A and D females in some way, then, raises the mating speed of homokaryotypic males.

If the mating speed of *2L/2L* males of the A group with BD htk and BC htk females is compared, it is seen that males have a slightly higher mating speed with BC htk females (see part C, Table 6). Comparison of mating speed of

TABLE 6

Mating speed of homokaryotype males of the 2L/2L *or* 2L-1/2L-1 *karyotypes, each of which is from the same group, with different female combinations*

Female combination	Percent mating in: 10 minutes	30 minutes	1 hour	Number of males tested
	A. *2L/2L* males of the B group with:			
AC htk	38.33	56.67	73.33	60
AD htk	68.33	86.67	93.30	60
	$\chi^2_{(3)} = 14.8$ $P < 0.005$			
	B. *2L-1/2L-1* males of the C group with:			
AD htk	60.00	76.67	80.00	60
BD htk	38.33	61.67	75.00	60
$\chi^2_{(1)}$ mating in 10 min *versus* not mating in 10 min $= 5.6$ $P < 0.02$				
	C. *2L/2L* males of the A group with:			
BD htk	33.33	55.00	60.00	60
BC htk	48.33	65.00	75.00	60
	$\chi^2_{(3)} = 5.1$ $P > 0.10$			
	D. *2L-1/2L-1* males of the D group with:			
AC htk	36.67	58.33	81.67	60
BC htk	51.67	78.33	85.00	60
$\chi^2_{(1)}$ mating in 30 min *versus* not mating in 30 min $= 5.5$ $P < 0.025$				

2L-1/2L-1 males of the D group with AC htk and BC htk females shows that males have a faster speed with BC htk females (part D, Table 6). There are no differences in the mating speed of heterokaryotype males when tested with these female combinations. It then seems that BC female interactions raise the mating speed of homokaryotype males. Here again, the BC females themselves do not participate in more matings.

In summary, then, the mating speed of homokaryotype males is altered greatly by the homokaryotype female combinations, whereas the heterokaryotype males perform more uniformly with different female combinations.

Effect of age on mating speed: Since the male choice experiments were done on the tenth day of age, it could be that the differences in the mating speed of homo- and heterokaryotypes are due to a faster rate of sexual maturity in the heterokaryotypes. If the differences are due to early maturity of heterokaryotypes, it would be expected that at later age levels the differences in the mating speed would disappear. The mating experiments were then done at various age levels to ascertain if heterokaryotypes maintain a faster mating speed throughout life.

Mating speed of homo- and heterokaryotypes at various age levels: The flies were matured to 9, 10, 11, 12, 13, 14, 18, 21, and 25 days of age, at which ten pairs of homogamic homo- and heterokaryotypic flies were allowed to mate in a plexiglass chamber for a 1 hr period. The pairs which copulated were removed by aspiration. Groups of flies of different karyotypes were obtained by interstrain and interkaryotype crosses in the manner described in the METHODS section. Heterokaryotypes from reciprocal crosses like $a_3 \times a_1$, $a_4 \times a_1$, $a_3 \times a_2$, and $a_4 \times a_2$ were obtained. Data for reciprocal heterokaryotypes were collected on the 10th, 11th, 13th, 14th and 18th day of age. Nearly equal numbers of flies obtained from different strain crosses were tested. The data were analyzed independently for each karyotype and age level. In total 2000 pairs each of homokaryotypes and the heterokaryotypes were tested. No differences were found in the mating speed of the two homokaryotypes, but the heterokaryotypes have a faster mating speed, at all age levels, than the homokaryotypes ($P < 0.01$, except on the 18th day when the differences in the mating speed of homokaryotypes and heterokaryotypes were not statistically significant). The heterokaryotypes start mating earlier in life and continue their faster mating speed throughout the age levels tested. (Figure 3).

DISCUSSION

Table 7 presents the mating speed data of second chromosome homokaryotypes and heterokaryotypes with homokaryotypic *XR* and *3R* background. There is no evidence of overdominance. The evidence that $\frac{XL\ XR\ 2L \quad 2R\ 3R\text{-}1}{XL\ XR\ 2L\text{-}1\ 2R\ 3R\text{-}1}$ flies show overdominance for mating speed, while $\frac{XL\ XR\ 2L \quad 2R\ 3R}{XL\ XR\ 2L\text{-}1\ 2R\ 3R}$ flies show no overdominance for mating speed implies that the *3R-1* gene arrangement carries a different gene complex than does 3R. The interactions between *XR* and second

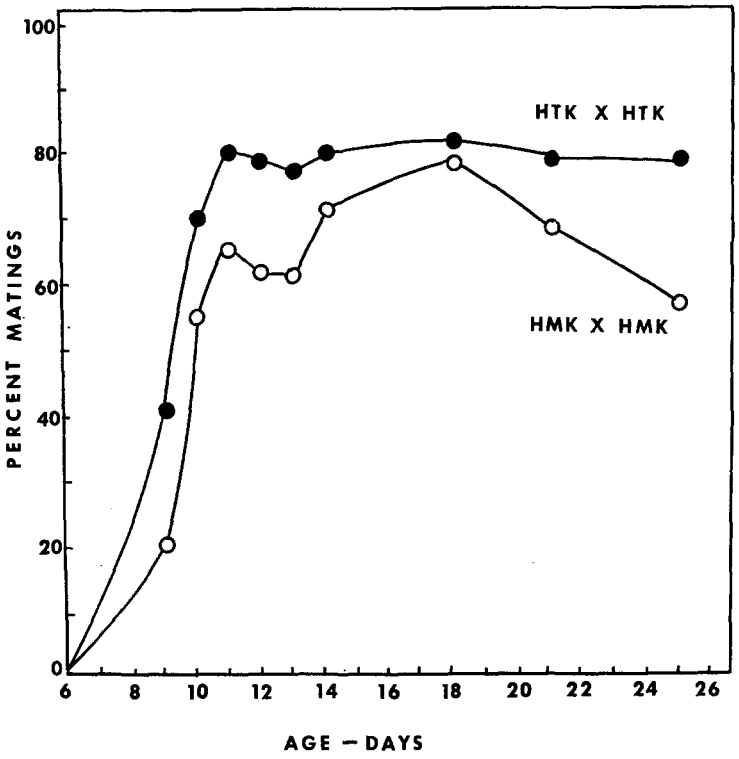

FIGURE 3.—Average percent homogamic homokaryotype and homogamic heterokaryotype matings during a one hour period with age of flies. Ten pairs of flies per mating chamber.
○ – – – – homogamic homokaryotype matings
● – – – – homogamic heterokaryotype matings.

chromosome observed by PRAKASH (1967a) also point out that *XR* and *XR-1* gene arrangements differ with respect to their gene content. In this study, it was observed that *XR-1* males which are heterokaryotypic in their second chromosome have greater mating activity and fertility than the corresponding *XR* males. This then means that the mating speed of *2L/2L-1* heterokaryotypes is greatly affected by the *XR* and *3R* karyotype and that the genes which affect

TABLE 7

Mating speed of $\frac{\text{XR 2L 2R 3R}}{\text{2L 2R 3R}}$ $\frac{\text{XR 2L-1 2R 3R}}{\text{2L-1 2R 3R}}$ *homokaryotypes and* $\frac{\text{XR 2L 2R 3R}}{\text{2L-1 2R 3R}}$ *heterokaryotypes on the 12th day of age*

Cross	Percent mating in: 10 minutes	30 minutes	1 hour	Number of males tested
HMK × HMK	27.0	43.0	50.00	120
HTK × HTK	26.0	42.0	50.00	120

mating speed are distributed on all three major chromosomes. In *D. pseudoobscura* and *D. persimilis* the third chromosome gene arrangements have been found to exert an influence on the mating propensity (SPIESS and LANGER 1964a,b). It is very likely that in these two species, as in *D. robusta*, genes for mating speed are located on all of the chromosomes.

One would like to know the kind and extent of genetic differentiation between different gene arrangements such as *XR*, *XR-1* and *3R*, *3R-1*. Obviously *XR-1* and *3R-1* gene arrangements must have at a certain proportion of their loci quite different alleles than those in *XR* and *3R* gene arrangements. The crucial question is: At what proportion of loci do the alternate gene arrangements carry entirely or mostly different alleles? In a study of two third chromosome electrophoretic loci *Pt-10* and *Amy* in *D. pseudoobscura*, it was found that the ST phylad gene arrangements are generally characterized by the alleles $Pt\text{-}10^{1.04}$ and $Amy^{1.0}$, while the SC phylad is generally $Pt\text{-}10^{1.06}$ and $Amy^{0.84}$. While in *D. pseudoobscura* the allelic frequencies for these two loci were not very different in various gene arrangements of a phylad, in *D. persimilis*, strong associations of *Amy* alleles with different gene arrangements were observed, e..g, KL gene arrangement has mainly $Amy^{1.0}$ and the WT gene arrangement has a high frequency of $Amy^{1.09}$ (PRAKASH and LEWONTIN 1968). With gene frequency values opposite to each other on the two gene arrangements, as in the *Amy* locus in *D. persimilis* the heterokaryotypes will be more heterozygous than the homokaryotypes. Given *such* associations of genes with gene arrangements and not much genetic divergence in the central and marginal populations of *D. robusta*, the central populations which are more polymorphic for the gene arrangements should also be more polymorphic at the genic level than the marginal populations. However, it is also likely that at most of the loci the differentiation between gene arrangements is of the sort observed in different gene arrangements of a phylad in *D. pseudoobscura* (PRAKASH and LEWONTIN, 1968). When the gene frequencies in the two alternate gene arrangements are different but in the same direction (e.g., if p and q are 1.0 and 0.0 in one gene arrangement and 0.80 and 0.20 in the other arrangement) then the heterokaryotypes are less heterozygous than one of the corresponding homokaryotypes. In such a case there will be no correlation between gene arrangement and genic polymorphism in the central and marginal populations of *D. robusta*. Let us, for the sake of illustration, consider that *3R* gene arrangement carries 100% of allele *A* and *3R-1* gene arrangement is segregating for the alleles *A* and *a* at frequencies of 0.80 and 0.20. The monomorphic populations for *3R* and *3R-1* gene arrangements will have, respectively, 0.0% and 32% heterozygotes at that locus, whereas the central population segregating for *3R* and *3R-1* gene arrangements at frequencies of 0.70 and 0.30 will have about 11.2% of the individuals heterozygous at that locus.

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SUMMARY

Evidence of interactions between second and third chromosome karyotypes affecting mating speed of *D. robusta* males has been presented. *XR* males heterokaryotypic in the left arm of the second chromosome which at the same time were homokaryotypic for the frequent *3R* gene arrangement showed no overdominance for mating speed; however, overdominance for mating speed was observed in *XR* males which are heterokaryotypic in the left arm of the second chromosome but at the same time homokaryotypic for the rare *3R-1* gene arrangement.

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