Behavior Genetics, Vol. 5, No. 2, 1975

Relative Mating Activity of the Sexes in Homokaryotypes of *Drosophila persimilis* from a Redwoods Population

Eliot B. Spiess[1] and Hui-Fang Yu[1]

Received 4 Apr. 1974—Final 3 June 1974

Previous tests for mating activity of Drosophila persimilis *homokaryotype KL (Klamath) and MD (Mendocino) chromosomal arrangements (northern California population: Redwoods) had shown KL to mate faster on the average than MD in homogamic tests. A strain (double-cross hybrid of four KL lines from the same population) with reliable high mating activity was developed for testing the sexes separately. Five pairs of KL-MD homokaryotype strains were chosen to be tested by the criterion that each pair had been derived from a separate wild KL/MD progenitor. Strains were crossed within arrangements in a diallelic design (20 inter- and five intrastrain crosses tested in 16 replicates per cross) to provide mating activity indices of four sets: KL females, KL males, MD females, MD males. Mating tests employed ten virgin experimental flies with ten tester (double-cross hybrid) flies of the opposite sex in 30-min observation periods. All flies were matured for 5 days at 25°C before testing. Among parental strains, females were consistently higher in mating activity than males for both KL and MD arrangements. Most interstrain hybrids were heterotic, with KL and MD females not significantly different. However, hybrid MD males displayed greatest variation and had lowest mating activity, while KL males were the least variable and highest in mating activity. With heterosis in the hybrids, there was no predictability (additivity) from performance of parental strains to hybrid offspring. Mating activities of the two sexes were uncorrelated, indicating either that the sexes have independent genetic systems controlling mating activity or that the*

Work supported in part by National Science Foundation Grant GB 34206.

[1] Department of Biological Sciences, University of Illinois at Chicago Circle, Chicago, Illinois.

expression of the same genetic system is influenced by sex. Since the hybrid males of the two karyotypes displayed different courtship activity while the females were at about an equal level of receptivity, intrasexual selection among males is likely to be important in nature.

KEY WORDS: mating activity; *Drosophila persimilis*; chromosomal variants, homokaryotypes; heterosis for mating activity; populational variation in mating activity.

INTRODUCTION

In a series of studies with both *Drosophila pseudoobscura* and *D. persimilis*, we have found mating activity and frequencies of chromosomal variants in certain natural populations to be correlated (see review by Spiess, 1970). Extensions of this work have been (1) control of mating activity by third chromosome arrangements and polygenic background in *D. pseudoobscura* investigated by Sherwin and Spiess (1973) and (2) analysis of female receptivity, the "switch-on" component proposed by Manning (1966, 1967, 1968) in *D. persimilis* from a redwoods population (Yacher and Spiess, 1973; Spiess and Stankevych, 1973).

In most of our previous observations, we had tested matings within lines or within cultures, i.e. homogamically, leaving us the problem of discriminating between the sexes as to control of the mating event and determining whether genetic variation was expressed in one or both sexes. In some extreme cases observed in the past where mating activity was very slow or very fast (slow PP vs. fast AR in *D. pseudoobscura* cultured at 25°C or slow KL vs. fast WT in *D. persimilis* from the high Sierras cultured at 15°C), it was easy to demonstrate that females of slow mating strains were not receptive although males from slow mating strains were usually also less sexually active than males from fast strains. But when we began studying the redwoods population of *D. persimilis* (Spiess *et al.*, 1971), we found no clear way to ascertain the relative activity of each sex: for that population there was only a statistical difference between levels of mating activity of karyotypes. KL had a higher average index of mating than MD, but there was considerable overlap when flies matured to 6 days of age were used.

We have therefore designed experiments to solve the following basic problems: (1) Do the sexes have equivalent levels of mating activity as determined by a representative sample of naturally occurring genetic variation from this population? By "equivalent levels" we mean to ask whether each sex is equivalent to the other within strains in having a relatively high or low threshold for its appropriate response to the opposite sex in achieving mating. (2) How much do the chromosomal arrangements affect

mating activity of each sex? (3) Is the inbred lines' activity predictive for their progenies following outcrossing; that is, can we observe significant additivity among F_1 hybrids or is there considerable nonadditivity for this trait?

To make comparisons between the sexes, we developed a tester strain of uniformly high mating activity (low threshold). Each female tester accepts courting males readily, while each male tester persistently courts most females. To make comparisons between the Klamath (KL) and Mendocino (MD) homokaryotypes, strains were chosen solely on the basis that they had been derived as KL-MD strains descended as pairs via sib matings from single wild heterokaryotype (KL/MD) females caught in nature. We term these pairs of strains "kinlines," referring to their descent from a common wild progenitor. Such kinlines of KL-MD have not been made isogenic. We expected that by pairing lines descended together from a single wild parental pair, reduction of a portion of the genetic background variation would be accomplished as compared to the amount of variation from random pairs of KL and MD lines independently derived. That is, kinlines would be expected to be derived from a maximum of four genomes, while random pairs would be derived from a maximum of eight genomes. Differences measured between KL and MD within kinlines then would be more likely to be accounted for by third chromosome arrangement blocks than by any special background differences.

MATERIALS AND METHODS

Strains of Klamath (KL) and Mendocino (MD) arrangements used in this experiment were descendents of inseminated females collected from the redwoods forest area of Humboldt County, California, in 1964. Strains were made homokaryotypic by single-pair mating and salivary gland analysis for about four to eight generations until 1966. Each strain has been maintained by mass mating for a least 50 generations since that time.

Five pairs of KL-MD strains ("kinlines") were chosen because each pair was derived from a separate wild progenitor of KL/MD karyotype. The five strains of each karyotype were crossed in a diallelic design (homokaryotype only) to produce 20 inter- and five intrastrain combinations. All flies were tested for mating propensity (in ten pairs per test) against the opposite sex of a reliable fast-mating tester strain which had been developed as a KL double-cross hybrid from four lines not among the experimental lines but from the same population. A total of four sets (sexes and two arrangements) comprised of 20 intrastrain and 80 interstrain subsets were tested in 16 replicates each, for a total of 16,000 pairs of flies.

Since environmental variables can affect the expression of behavior via developmental change, it is very important to maintain a uniform environment both in rearing the flies and in testing them. The flies were crossed in a predetermined randomized sequence so that any change was not likely to affect solely the cross involving one line.

To obtain flies for each mating test, 20 pairs of virgin parental flies were introduced into a half-pint bottle provided with a plastic spoon of yeasted food. After 48 hr of egg laying, each spoon, with an egg density between 100 and 200, was inserted into a food bottle. All flies were cultured on cornmeal–agar–molasses–yeast–propionic acid food medium and kept in a constant-temperature chamber (25°C) with 12 hr light–12 hr dark cycle. On emergence, adults were sexed, separated, and kept in vials with yeasted food. The vials were stored in the same chamber for 5 or 6 days before the mating tests. This period for storage of adults is adequate to insure that all individuals normally should have matured and be at peak sexual response. All the mating tests were carried out between 11 a.m. and 4 p.m.

Mating tests were made in the manner previously described (Spiess *et al.*, 1966). Ten pairs of flies were introduced into a plastic chamber (5 by 10 by 4 cm) without etherization at room temperature (23 $\pm$ 1°C) and observed under fluorescent light of about 20 watts for 30 min. When mating occurred, time was recorded and pairs in copulation were removed by aspirator to prevent males from repeated matings. Courtship of male testers and receptivity of female testers were carefully watched. If tester flies showed low mating propensity, they were replaced by more sexually active individuals from storage vials.

Mating activity was measured by our "mating index" (Spiess *et al.*, 1966), which combines the speed of mating in 30 min of observation with the number of mating pairs in 5-min intervals (weighted average reciprocal of time $\times$ 100 to give a maximum of 200 if 10 pairs mate in 5 min or a minimum of 10 if no matings occur in 30 min). Frequency of mating and this mating index are highly correlated (Spiess *et al.*, 1971); we have omitted the data on frequency of mating for brevity since they do not add any new information for the results presented.

RESULTS

Mean Mating Activity

Figures 1 and 2 are bar graphs of average mating indices for parent (kinline) strains and interstrain hybrids, respectively. In Fig. 2, reciprocals are indicated together and all in the same order, with the left-hand bar representing the progeny from the female parent strain and the right-hand

bar those from the male parent strain. Standard errors of these means are omitted for brevity: for kinline inbreds the average standard error was ± 5.3 (ranging from a low of ± 1.80 to ± 7.07 for 20 inbred means), while for interstrain hybrids the average standard error was ± 5.2 (ranging from ± 2.98 to ± 7.62 for the 80 hybrid means). The mating index tends to be about normally distributed within each genetic subset.

Overall average mating indices are given in Table I, presented as four sets by sex and homokaryotype arrangement (KL or MD) tested. In each set, interstrain average indices are in the first two columns ($\bar{X}_{i.}$ and $\bar{X}_{.i}$), which are the kinline means for female parent strain outcrossed to the other four kinlines and for male parent to the other four kinlines, respectively. The third column in each set gives the within-kinline (inbred) average indices.

It is apparent that MD males, both inbred and hybrid, displayed the lowest mating activity on the average (although one line, No. 3 MD males, was about equal to average KL males), with the greatest amount of variation beteen lines and the greatest heterosis for the four sets of sexes and arrangements. (We use the term "heterosis" here in its original sense from Shull, 1948, that the hybrids' mating activity lies outside the range of the parents in a consistent direction.) KL males also showed heterosis from low

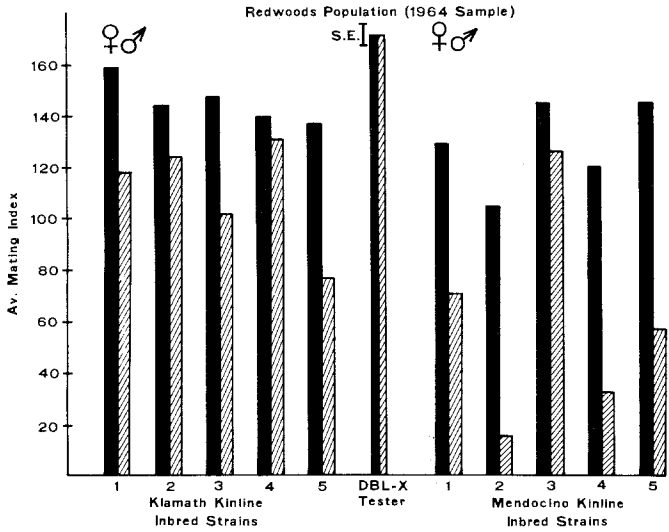

Fig. 1. Bar graphs for average mating indices of five kinline parent ("inbred") strains of KL and MD, with double-cross hybrid tester average in center. Female indices solid, male indices crosshatched.

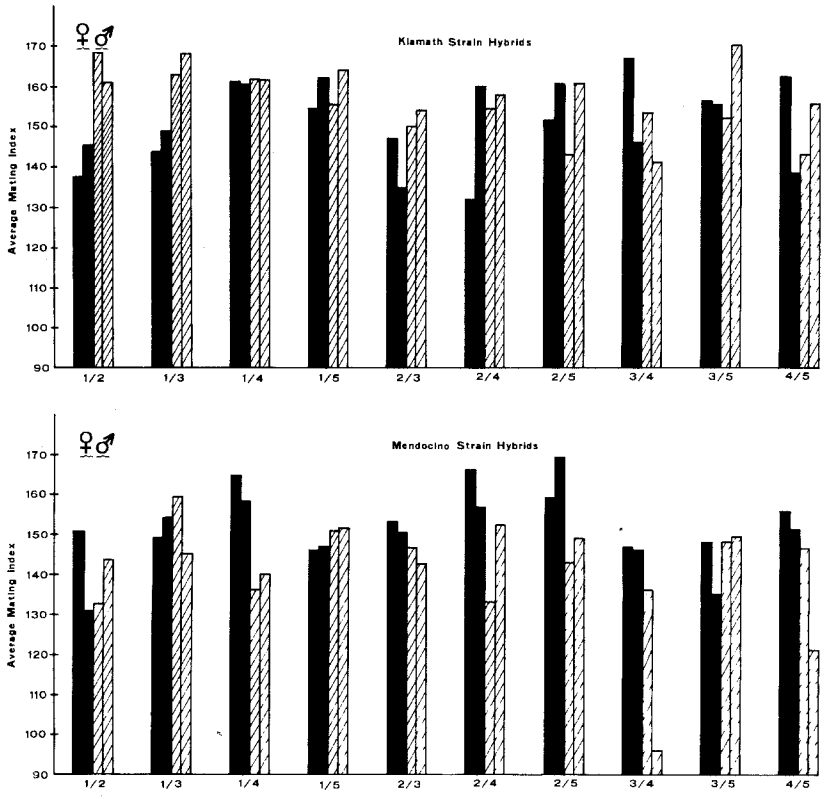

Fig. 2. Bar graphs for average mating indices of 20 KL and 20 MD interstrain hybrids. Reciprocal crosses alongside each other, with female parent strain progeny to left of male parent strain progeny.

inbred activity to highest among their hybrids. Hybrid females did not differ significantly between arrangements, but inbred MD females were lower than KL females. There was no significant heterosis for hybrid KL females since the inbred KL female averages were consistently high.

Analysis of variance data for subsets (genetic strains or strain crosses) within the sets are omitted for brevity. Among inbred kinlines, all the "between-subset" F ratios were highly significant except for KL females ($F = 2.3$ n.s. for KL females, but $F = 9.1$ for MD females, 13.9 for KL males, and 74.6 for MD males, all with $P < 0.001$). Among hybrids, all the "between-subset" F ratios were significant ($P < 0.001$), with F ranging from a low of 2.5 for KL hybrid males to a high of 6.6 for MD males. It is noteworthy that variation among kinline inbred males was far greater than among kinline inbred females. MD hybrid males are the most variable of the four groups of interstrain flies.

Table I. Mean Mating Indices for Hybrids ($\bar{X}_{i.}$ and $\bar{X}_{.i}$) and Inbreds ($\bar{X}_{ii}$)[a]

Kinline No.	$\bar{X}_{i.}$	$\bar{X}_{.i}$	$\bar{X}_{ii}$	$\bar{X}_{i.}$	$\bar{X}_{.i}$	$\bar{X}_{ii}$
	KL females			KL males		
1	154.41	149.39	159.12	163.78	162.50	117.75
2	148.20	144.11	143.69	160.41	152.20	124.37
3	148.09	151.80	148.12	156.11	156.94	101.87
4	149.61	159.16	139.87	156.39	150.77	130.81
5	156.20	154.06	136.94	148.36	162.64	77.06
Overall mean	151.30		145.55	157.01		110.37
	MD females			MD males		
1	147.56	152.80	128.94	145.19	144.83	70.44
2	156.81	152.52	104.44	144.31	141.83	15.87
3	146.08	150.05	144.75	138.11	143.36	125.75
4	157.41	154.33	119.56	132.00	134.08	33.37
5	152.58	150.75	144.81	147.59	143.11	57.31
Overall	152.09		128.50	141.44		60.55

[a] $\bar{X}_{i.}$, Means for female parent crossed with the four other lines; $\bar{X}_{.i}$, means for male parent crossed with the four other lines; $\bar{X}_{ii}$, means for inbred lines.

In order to contrast the four major sets of data, an orthogonal treatment of the variance is presented in Table II: first between the arrangements within the sexes, and then between the sexes as the most meaningful contrast. It is clear that the only significant contrast is between males. With KL males averaging above both female karyotypes and MD males far below, the sex difference becomes nullified. In effect, then, the particular arrangement and sex (MD males) account for nearly all the variation over the entire array of interstrain hybrids.

Finally, the double-cross hybrid line, which was developed as the tester for measuring the mating activity of each sex separately, was run in homogamic tests for a check. More than 80% of these flies mated in the first 5 min and have a mean mating index of 166.5 $\pm$ 4.4, a value in the upper 10% of all tests done on the experimental flies (see the center column of Fig. 1). Sexual activity of these tester flies was always watched during the mating tests to reduce any bias caused by failure of these testers: if any female tester continued to repel experimental courting males, she was replaced by another more receptive female from the storage vials, and if a male tester failed to court, a more active male was substituted. In such a way, the experimental flies were given equal and maximum opportunity to express whatever mating activity they could.

Table II. Analysis of Variance for Hybrids with Orthogonal Contrast Between Four Major Groups

Source	df	MS	*F*
Between four major groups, contrasts:	3		
KL females vs. MD females	1	98.44	< error
KL males vs. MD males	1	38,781.76	21.35[a]
Females vs. males	1	1,952.78	1.08 (n.s.)
Between 20 crosses within major groups	76	1,816.35	
For total groups	79		
Within crosses	1200	464.06	
Total	1279		

[a] $P < 0.001$.

Correlations

It can be noted from Table I at a glance that between kinline parent values and those of their hybrid offspring there is little corelation; for example, the MD No. 2 males, which had the lowest mating activity, did not produce progenies with lowest values nor did the highest KL produce the highest hybrid male progenies. Heterosis made the hybrid mating activities unpredictable from the parent kinline values.

Correlations beteen the sexes' mating indices and between the chromosomal arrangements within kinlines might be of importance. First, if the two sexes were derived from the same kinline, we might expect them to have equivalent levels of mating activity with some genotypic identity. Nonsignificant positive correlation coefficients were obtained between corresponding strain crosses of opposite sexes, for both intra- and interstrain data. (Highest correlation was for intrastrain MD female vs. MD male, $r = +0.802$, but with only 3 df, $p = 0.08$.) This outcome suggests that the mating activity level of one sex cannot be predicted by the performance of the opposite sex of the same genotype. In other words, the mating activity is likely to be controlled by sex-influenced genetic systems which affect the sexes independently, at least for their performance at maturity (5 days of age).

Between the two karyotypes, the correlation between paired genotypes would be an indication of the genetic background influence, since each pair of KL-MD parental strains was derived from a single wild pair (within kinlines). The correlations for female KL-MD are not significant, although the hybrid males of the two karyotypes have a positive correlation approaching

the significance level ($r = +0.38$, df = 18, $P = 0.08$). There may be a slight tendency for KL and MD male hybrids' mating activity to be determined by common genetic modifiers within kinlines.

Diallelic Analysis of Mating Activity Among Hybrids

The diallelic intercrosses were analyzed using the method devised by Griffing (1956*a,b*), which determined the relative magnitudes of the genetic and environmental variances. The inbred lines were excluded in order to obtain an unbiased estimate of these components of variance. Since the genotypic variance components are significant in every subgroup, the variance can be partitioned into additive and nonadditive components of variance: general combining ability (g.c.a.), special combining ability (s.c.a.), and reciprocal effects (r.e.).

Since the parental lines were derived from wild pairs randomly sampled from a natural population about which inferences are to be made, it is quite reasonable to use Model II, a random-effects model, to analyze the data here. In Table III, the combining ability analysis of variance for the

Table III. Four Diallelic Sets of Hybrids Analyses of Variance

	g.c.a.	s.c.a.	r.e.	E'[a]
KL females				
df	4	5	10	300
MS	126.943	86.112	108.942	27.556
F	1.47	3.12[b]	3.95[c]	
KL males				
df	4	5	10	300
MS	139.671	47.748	57.237	28.653
F	2.92	1.67	2.00[d]	
MD females				
df	4	5	10	300
MS	146.736	131.145	42.942	31.638
F	1.12	4.15[c]	1.36	
MD males				
df	4	5	10	300
MS	271.363	184.854	154.829	28.168
F	1.47	6.56[c]	5.50[c]	

[a] Mean square error divided by replicate number ($n = 16$).
[b] $0.01 > P > 0.001$.
[c] $P < 0.001$.
[d] $0.05 > P > 0.01$.

four subgroups is given. *F*-tests show that the general combining ability (g.c.a.) of no subgroup is significant. This result implies that no parental strain affected F_1 hybrids' activity in any consistently additive respect; that is, the value of the hybrids cannot be predicted solely from the knowledge of the value of the parents or from the average performance of the progeny from any one strain.

The variance components of specific combining ability (s.c.a.) are highly significant for both sexes with MD chromosomal arrangement, while the KL arrangement displays only slightly significant s.c.a. in females and none in males. The relatively low s.c.a. variance components associated with the KL arrangement indicate that the parents with KL karyotype more uniformly transmit their mating ability to all their progenies.

The variance components due to reciprocal effect are significant for the KL females and MD males and only slightly significant for the KL males and not significant for the MD females. The reciproal differences encountered in KL females and MD males could not be traced to the progenies of any particular parental lines: they were sporadically distributed throughout the F_1 families of all parental lines. Such a phenomenon is very difficult to explain simply by overall maternal effects or sex-linkage effects, and for the time being we presume that a portion of them represent the unpredictability inherent in the phenotype we are measuring.

DISCUSSION

A survey of mating propensity for KL and MD karyotypes from a redwood population of *Drosophila persimilis* has previously shown KL to mate faster and in greater numbers than MD on the average in homogamic mating tests but with some overlap in particular strains (Spiess *et al.*, 1971). By developing a special tester (double-cross hybrid of four fast-mating KL strains), it has been possible to test each sex separately in inbred lines and their first generation hybrids.

Five pairs of KL-MD strains were chosen solely because each pair was derived from a separate KL/MD progenitor. The F_1 intercrosses were expected to possess genetic variation similar to that of the natural population and to permit efficient estimation of the population parameters for each sex and homokaryotype mating activity.

Manning (1968) has shown that the two sexes have different responses to artificial selection. However, such differences were not analyzed quantitatively. It is necessary to use an experimental design and analytical methods of biometrical genetics to obtain the detailed information on the components of variance of a polygenic character such as mating propensity.

Parsons (1964) had used a diallelic analysis to study the mating activity in *D. melanogaster*. From his tests of inbred lines, he found that the strain of male was more important for speed of mating (early matings) while total mating over the 40-min observation period was more a function of the female's strain. Similar dependence on the male as determiner of early mating in *D. pseudoobscura* was observed by Kaul and Parsons (1965). An efficient technique for quantitative analysis has been used by Fulker (1966) in *D. melanogaster*, although only the performance of males was reported. Since it is apparent from our results that the sexual activity of one sex at maturity has little predictive value for the activity of the other sex, mating activity measured without considering the performance of females is certainly ambigious. The method employed in the present experiment has proved itself to be an efficient technique for the study of total mating activity.

The results here with *D. persimilis* indicate that the mating activity level of matured females is superior to that of the males. Many of the inbred males from certain strains, especially MD, suffered from aberrant courtship, while inbred females displayed a relatively high mating propensity. Such nonequivalent sexual activity of the two sexes with the same genotypes suggests that the two sexes differ with respect to the genetic control of mating activity, or that the expression of the genotype is influenced by sex. It is very possible that the genetic system controlling the courtship behavior of males conceals a higher genetic load than that controlling female receptivity. Inbreeding increases homozygosity and manifests the concealed genetic load. The fitness (mating propensity) decreases proportionally to their concealed genetic load and the amount of inbreeding achieved. It appears that MD males express more of such a load in mating activity than any of the other groups tested.

The primary purpose in choosing paired parental strains was to reduce the variation of genetic background between the two karyotypes. It would be expected that genetic background within pairs should correspond to some extent; however, the correlation coefficient between each corresponding genotype is not significant. The results might be due to either or both of the following reasons: (1) The third chromosomal arrangements have such strong epistatic control over mating propensity that the influences of genetic background are covered up, as had been demonstrated by Sherwin and Spiess (1973) in *D. pseudoobscura*. (2) The original wild progenitors were highly heterozygous so that when the derived paired strains are isolated they may easily contain discrete sets of genotypes not shared between them, as had been discussed by Parsons *et al.* (1967).

A more refined genetic analysis would be to use a marker technique which could simplify the situation here and make the genetic background

isogenic. However, while there are still not enough marker stocks available for *D. persimilis* for a complete chromosome isogenation, the method of choosing "paired" strains as parents seemed to be the most efficient technique to reduce variation of genetic background between the two different karyotypes.

The diallelic analysis reveals some of the genetic architecture for the control of mating propensity. It is noteworthy that the general combining ability, or additive effect, is not significant. Regardless of the performance of the parental strains, the average mating propensity of the hybrid progeny for each strain is not significantly different from that of the other strains. Since mating activity is a very important component of fitness, the nonsignificant additive genetic effects were not unexpected. Robertson (1955) has pointed out that fitness traits, as distinct from traits more neutral to selection, are not likely to have much additive variance available in natural populations. Parsons (1964) and Fulker (1966) used diallelic crosses to analyze the mating activity in *D. melanogaster*. In contrast to the results in this survey, they found significant additive effects in mating activity. In agreement with ours, Parsons' data (early matings) showed considerable heterosis for five out of six sets of hybrids over their inbred parents, and Fulker's hybrids indicated heterosis throughout all crosses. The contrast in additivity between their data and ours might be attributable to one or all of the following at least:

1. The *D. persimilis* strains used here were derived from a random sample of a coadapted genetic system which is likely to display special phenotypic nonadditive effects. All the *D. melanogaster* wild-type strains used by Parsons and Fulker were independently derived from diverse origins and presumably did not represent a populational coadapted system.

2. The techniques for testing activity were different. Parsons employed homogamic mating to measure activity of both sexes simultaneously. His results are related to the behavioral interactions of particular pairs of genotypes only, and generalization to other possible genotypic combinations cannot be made with assurance. In Fulker's experiments, a "standard set" consisting of six virgin females was used and only the mating frequency of the males was measured.

3. Parsons' and Fulker's frequency-of-mating data do indicate additivity (hybrid values intermediate between parental values), while ours do not consistently show additivity to any degree because our hybrids displayed much dominance and overdominance. Yet we have evidence that there is considerable genetic additivity available for significant selection response, at least with KL strains (Spiess and Stankevych, 1973). While the additive component of variance in Table III was not statistically significant under the random Model II (s.c.a. used for error), it was nevertheless

sizable in some cases (MD males), and we might consider that in view of our small number of degrees of freedom for s.c.a. we should contemplate their significance based on the within-crosses mean square for error (Model I). Under the assumption that this interpretation is in fact more realistic, we have estimated the variance components to give the estimates of heritability in the narrow sense (diallele hybrids only) (Table IV). Both types of males have greater h^2 estimates than the two types of females, and these values are similar in magnitude to those estimated by Fulker (h^2_{est} = 0.36) and by Parsons for his total mating frequencies (h^2_{est} = 0.27).

Yacher and Spiess (1973) studied the onset of females' receptivity and males' courtship of *D. persimilis* collected from the same redwoods population with respect to the KL and MD chromosomal arrangements. They found that KL females "switched on" significantly earlier than MD females, while the onset of males' courtship started 24 hr after eclosion for both kinds of males. This switch-on of receptivity is determined by juvenile hormones, according to Manning. The other element controlling females' receptivity is "courtship summation" (Manning, 1967, 1968), which has been shown in this present experiment not be be variable significantly among females of these two karyotypes. Once the concentration of juvenile hormone has reached a critical amount by 5 days after eclosion, the females, regardless of their karyotype, respond to courtship by acceptance of males. Although the onset of courtship is about the same between these two kinds of males, the mating propensity of mature males with KL arrangement is higher than that of males of MD arrangement. Since physiological determination in controlling males' courtship behavior in *D. persimilis* has not been studied, it is very difficult to assess the mechanisms through which these chromosomal systems affect the courtship activity. It is very clear that the KL arrangement acquires selective advantages in earlier switch-on of females' receptivity and higher sexual activity in males.

Since males with the less frequent arrangement MD (20%) display a

Table IV. Estimated Variance Components and Estimated Heritabilities According to Model I

Set No.	Additive variance component	Total phenotypic variance	h^2_{est}
KL females	13.62	111.15	0.122
KL males	30.64	83.13	0.368
MD females	5.20	92.24	0.056
MD males	28.84	198.69	0.145

great deal of variation for courtship and are on the average lower than KL, intrasexual selection must occur and may be an important factor in maintaining the balanced chromosomal polymorphism in the natural population; that is, the males provide a diversity of variation from which females do the selecting.

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