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ABSTRACT

Individual Samarkand wildtype *D. melanogaster* males were permitted to choose between either two white-eyed or two red-eyed females or between a red-eyed and a white-eyed female. Observations of the flies were made over a period of about two hours and premating periods, intermating periods and the durations of copulations were recorded.

Approximately 82% of the males copulated first with white-eyed females and the premating and intermating periods before copulations with white-eyed females were significantly shorter than before the copulations with red-eyed females. The red-eyed females usually repelled the courtship of the males while the white-eyed females were more passive. The type of the second female present had little influence on whether or not the males would copulate a second time. However the red-eyed females were stimulated to mate sooner than the white-eyed females when a previous copulation had occurred in the vials. With each type of female, the average durations of the second copulations were longer than the first. The durations of the second copulations were positively correlated with the durations of the first. The correlations were low but very significant.

QUANTITATIVE ASPECTS OF MATING BEHAVIOR IN DROSOPHILA[o]

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INTRODUCTION

Courtship and mating behavior patterns may be of great importance in establishing sexual isolation between groups of genetically different animals and thus might have a strong influence on evolution within a species. Drosophila females when once inseminated by a male usually will not copulate again for some time. Thus as far as propagation of that species is concerned, a successful copulation with a male from her own species would be advantageous. However a copulation with a male from another species would be of little value if fertile offspring did not result, and probably would be detrimental in that the female's reproductive capacity would be reduced. Mechanisms that would permit individuals to distinguish between members of their own and alien species would then be of importance in an evolutionary sense. Similarly, differences in mating behavior caused by diverse genotypes within a species might either enhance or decrease the chances for survival of individuals having a particular genotype.

There have been several reports concerning courtship behavior in the genus Drosophila, notably those by Sturtevant (1915 and 1921), Wallace and Dobzhansky (1946), Spieth (1952), Bastock and Manning (1955), Bastock (1956), and Manning (1959). Sturtevant and also Wheeler (1947) recorded observations on the durations of copulations by Drosophila melanogaster and the numbers of copulations which male Drosophila could accomplish under varying conditions were reported by Kaufmann (1941) and Mossige (1955).

[o]This work was performed under the auspices of the U.S. Atomic Energy Commission.

It has long been known that preferences exist according to which individuals of one species more often mate with those of the same species than with even closely related ones (Dobzhansky and Koller, 1938). More detailed data on such preferences within and between species have been reported in recent years.

In Drosophila melanogaster Tebb and Thoday (1956) observed that individual females had definite preferences as to the mating partner when allowed to choose between two different types of males. Bosiger (1957) observed that males having cinnibar-colored eyes had a selective advantage over males having vermilion-colored eyes when both types of males were in the presence of females having vermilion-colored eyes. Hoenigsberg and Santibanez (1960) found that inbred males had a marked preference for their own types of females, and that certain outbred strains were indiscriminate in their preference or even preferred alien females. Santibanez and Waddington's (1958) investigations showed that white-eyed females were less acceptable to any male than were the other mutant females tested. Petit (1959a) left white-eyed or heterozygous white/Oregon-R females in the presence of white-eyed and wildtype males. Progeny tests of the females indicated that the genotype of the female did not influence the mating frequency, but that the genotype of the male did. Whether or not the white-eyed males had a selective advantage over the red-eyed males depended on the relative proportions of the two types of males in the mating chambers. The selective advantage caused by the white allele also was influenced by the rest of the genetic background. Cline (1958) determined that the gene for bar-shaped eyes reduced the mating capacity below that of the wildtype allele and also reduced the fertility of the females carrying the bar gene, thus giving the wildtype flies a selective advantage when competing with bar individuals.

Hoenigsberg, Santibanez, and Sironi (1959) investigated sexual preferences between D. prosaltans Duda and D. equinoxialis Dobzhansky and observed that the mating frequencies of males with females of their own species were much higher than with females of the other species. Ehrman (1960) found that hybrids between two subspecies of D. paulistorum had a genetic background that caused the females to repel the courtship of all males tested, mating with none. The hybrid males courted and were rejected by nearly all the females tested, including their own hybrid siblings.

The experiments reported here deal with the mating preferences in D. melanogaster when individual wildtype males were allowed the choice between two females of the same genotype or two females of different genotypes.

MATERIALS AND METHODS

Two different strains of Drosophila melanogaster provided the flies used in these experiments. Wildtype red-eyed males and females were obtained from a Samarkand stock and the second stock provided the white-eyed females. Both strains had been kept in our laboratory in mass cultures, and no attempt was made to isogenize them.

Cultures of these stocks were emptied of all flies early in the morning, and approximately 3 to 4 hr later the newly emerged offspring were collected. During this short period, after emergence of the adults, no copulations would have occurred. The etherized males were immediately placed and stored individually in 4-dr shell vials (19 mm in diameter and 65 mm deep) which contained hardened culture medium about 1 cm deep. The females were stored in similar containers in pairs--two white-eyed or two red-eyed females or one of each type. Early in the afternoon 2 days later, individual males

were shaken, without etherization, into the vials that contained the pairs of females. In each experiment approximately 100 of these vials were placed on special observation trays which were 45 cm long, 30 cm wide, and 2.2 cm deep. White paper was placed in the tray to allow better observation, and the vials were separated from each other by clear plastic rods and tubes in order to prevent the flies in any vial being influenced by the activities of flies in adjacent vials. The maximum for each tray was five rows, each containing ten vials.

The time that each male was placed with it's pair of females was recorded, and after the first flies were placed together, observations of the vials were begun at the next 5-min interval past the hour. The flies were then observed in numerical order--always starting with the first in the series--at 5-min intervals throughout the experiment. Since a successful mating usually lasts for an average of eleven or more minutes these intervals were short enough for us to observe the successful copulations, but probably some attempted copulations were missed. Records were made of the premating and intermating periods and the durations of the copulations. When a male had copulated with both females, the vial containing them was removed from the tray. If a male had not copulated with both females within two hours after being placed with them, observation of that group was discontinued.

The room temperature varied from 23.4 to 25.8° C during observations of the mating behavior, but within individual experiments the range did not vary more than 0.9°C. At all other times the flies were kept in incubators set at 25° C.

RESULTS

Mating Preferences

First Partner

When each of 294 males was given the choice between two red-eyed females as the first mating partner, 90% (264) of the males copulated at least once. When each of 282 males was permitted to choose between two white-eyed females, the frequency of males that copulated at least once was increased to 95% (264). When the individual males were given the choice between a white-eyed female and a red-eyed female, the frequency of males that copulated at least once was then increased to 98% (290/297).

When the males were permitted to choose between the two different types of females, the selection of their first mating partners was not a random choice. The first copulations occurred with white-eyed females in 82% (238/290) of the cases as opposed to only 18% with the red-eyed females.

Second Partners

After the males had copulated for the first time, the mating frequencies with the second females of the pairs were influenced very little by the type of the second female.

Among the 238 males that first copulated with white-eyed females, 81% (192) then copulated with red-eyed females. Of 52 males that copulated first with red-eyed females, 85% (44) then copulated with white-eyed females. When both females in the pair had white eyes, 83% (221) of 268 males that copulated once then copulated with the second female, and when both females of the pair had red eyes 85% (223/264) of the males that copulated once then copulated a second time.

As an indication of the level of activity, a "mating index" may be used. It is defined as the frequency of actual copulations among the possible total

of copulations. In the series in which individual males were observed with pairs of red-eyed females, there were 294 males, and if each had copulated with both females, the index would have been 2.00, which is the theoretical maximum for any of the series. However in this actual series there were 487 copulations yielding an index of 1.65. The mating index in the white-white series showed an increase to 1.73, and in the series containing a red-eyed and a white-eyed female in each pair, the mating index increased to 1.77. Table I shows the frequencies for males that did not copulate, copulated once, or copulated twice. It can be seen that even though the white-white and white-red series are similar the red-red series diverges quite sharply from both.

Premating Periods

The interval between the time that the two females and the male were placed together and the first time that the male was observed copulating with one of them is taken as the premating period. For comparisons, the copulations were grouped into those that began within the average estimated times of 5, 10, 15, 20, and greater than 20 min after the flies were placed together (Fig. 1). The male was not observed when he mounted in each case, therefore the period is a maximum estimate based on the time the male was first observed copulating.

The males copulated much sooner with the white-eyed than with the red-eyed females. More than 54% of the double copulations with white-eyed females first (WR = 54%; WW = 63%) were initiated within 5 min, but less than 25% of the double copulations with red-eyed females first (RR = 20%; RW = 25%) were begun within this same period.

Table I

Frequency of copulations.[a]
Two females and one male present in each vial.

Females present	Neither female copulated (%)	Only one female copulated (%)	Both females copulated (%)	Total males available
Two red	10	14	76	294
Two white	5	17	78	282
One white and one red	2	18	80	297

[a] $\chi^2 = 17.58$, D.F. = 4, $P < 0.01$.

Intermating Periods

The interval between the time that a male dismounted at the termination of the first copulation and mounted the other female for the beginning of the second copulation is regarded as the intermating period. The exact times that the male dismounted and mounted were not observed therefore an average estimate was calculated from the times that the male was last observed to be copulating with the first female and first observed to be copulating with the second female. The frequencies of individuals within the given intermating periods are presented in Fig. 2. In general, after the first copulation the males tended to copulate sooner with the second female of the pair if she was a white-eyed rather than a red-eyed female.

Durations of Copulations

The period between the times that a male successfully mounted and dismounted a female is considered as the duration of the copulation. As the male was not observed when he mounted and dismounted in each instance an average estimate of the durations was based on the first and the last times that a male was observed copulating with a particular female.

Singles Only

The average durations of the copulations with the white-eyed females were 13.5 min in the white-white (WW) series and 13.9 min in the white-red (WR) series. The average durations with the red-eyed females were 12.3 min in the red-red (RR) and 11.9 min in the red-white (RW) series. The ranges and distributions of the durations are presented in Table II. The results of the χ^2 analyses of these data are shown in Table III. The average durations with the white-eyed females in each case are greater than either of the averages

Table II

Durations of copulations. Percent of males that copulated for designated intervals. Two females and one male present.

Females present	Female mated first	% males copulating 5 min	10 min	15 min	20 min	Total males	Average duration
			Singles				
Two white	W	2	28	68	2	47	13.5
Two red	R	0	54	46	0	41	12.3
Red and	W	2	18	80	0	45	13.9
white	R	0	63	37	0	8	11.9
			First of doubles				
Two white	W	1	37	55	7	141	13.5
Two red	R	1	62	35	2	175	11.3
Red and	W	1	39	56	4	193	13.2
white	R	7	45	48	0	44	12.0

Table III

Homogeneity tests of differences between singles and first of doubles.

Group	χ^2	Degrees of freedom	Probability
WW	4.34	3	0.2 - 0.3
RR	2.72	3	0.3 - 0.5
WR	10.70	3	0.01 - 0.02
RW	1.20	2	0.5 - 0.7

with the red-eyed females, and although the differences appear to be small, the white-eyed females did copulate for significantly longer periods than the red-eyed (RR vs WR, $P < 0.01$; WW vs RR, $P = 0.02$ to 0.05; WR vs RW, $P = 0.02$ to 0.05). These χ^2 calculations were based on those individuals that copulated for 10 min or less compared with those that copulated for more than 10 min. In one instance (RW vs WW) the differences were not significant, the probability that the differences were caused by chance fluctuations being 0.05 to 0.1. However, not much consideration should be given to this or any other calculation involving the RW series, as it involved only eight males. There were no significant differences between the series involving white-eyed females ($P = 0.2$ to 0.3) nor those involving red-eyed females ($P = 0.9$ to 0.95) regardless of the type of the second female present.

First of the Double Copulations

In most cases the averages for the first of the double copulations were not greatly different from the single copulations within their respective mating groups, nor were the ranges and distributions much different from the singles (Tables II and III). The males copulated for longer durations with the white-eyed than with the red-eyed females; in three of the comparisons (WW vs RR, WR vs RW, and RR vs WR) the probabilities that difference in distributions between the series could be caused by chance fluctuations alone were less than 0.01, and the probability was 0.02 to 0.05 in the fourth instance (WW vs RW).

Second Copulations

The durations of second copulations were generally greater with white-eyed females than with red-eyed females (Tables IV and V). In all cases, the durations of the second copulations were significantly greater than the first of the double copulations ($P < 0.01$). The χ^2 values for white first vs

Table IV

Durations of the second copulations. Percent of males that copulated for designated periods. Two females and one male present.

Females mated		% males copulating						Total	Average
First	Second	5 min	10 min	15 min	20 min	25 min	30 min	males	duration
W	W	1	14	58	24	3	0	141	15.6
R	R	1	33	57	8	1	0	175	13.7
W	R	1	28	59	12	0	0	193	14.1
R	W	0	18	59	23	0	0	44	15.2

Table V

Homogeneity tests for (A) white second vs red second, (B) white second, and (C) red second.

	Group	χ^2	Degrees of freedom	Probability
A	WW vs RR	24.98	4	< 0.01
	WW vs WR	19.21	5	< 0.01
	RW vs RR	10.82	4	0.02-0.05
	RW vs WR	4.99	4	0.2-0.3
B	WW vs RW	2.16	4	0.7-0.8
C	RR vs WR	4.93	5	0.3-0.5

white second are (a) WW vs WW: $\chi^2 = 31.71$, D.F. = 4; (b) WR vs RW: $\chi^2 = 21.51$, D.F. = 3; (c) WW vs RW: $\chi^2 = 11.60$, D.F. = 3. For red first vs red second, the values are (a) RR vs RR: $\chi^2 = 32.68$, D.F. = 4; (b) RW vs WR: $\chi^2 = 15.89$, D.F. = 4; (c) RR vs WR: $\chi^2 = 49.46$, D.F. = 4.

The durations of the second copulations generally were positively correlated with the durations of the first copulations. A short first copulation would usually be followed by a shorter second copulation than would a longer first copulation (Table VI).

DISCUSSION

Petit (1959a) concluded that it is the genotype of the male and not of the female that influences the mating frequency. On the other hand, Tebb and Thoday and also Santibanez and Waddington attribute much of the influence on mating frequency to the female. The latter two authors found that white-eyed females were less acceptable to any of the males tested than were any of the other females. Sturtevant (1915) had observed that white-eyed females were chosen as partners more often than were red-eyed females when either red-eyed or white-eyed males were permitted to choose between them. According to Ehrman, female hybrids between two subspecies of D. paulistorum repelled the courtship of all males tested.

Apparently the mating frequencies may depend on the genotypes of both the males and females. In the experiments reported here, about 82% of the males that copulated at least once did so with white-eyed females first, and only about 18% copulated first with red-eyed females. Observations of individual males with white-eyed and red-eyed females showed that white-eyed females were less active than the red-eyed females, which in most cases would avoid the male by

Table VI

Correlations of the durations of the second copulations with the durations of the first.

Number of males	Average female copulation time (min)		Average male copulation time (min)
	White 1st	White 2nd	
1	5	10.0	15.0
53	10	14.7	24.7
77	15	16.0	31.0
10	20	18.0	38.0
	White 1st	Red 2nd	
1	5	15.0	20.0
76	10	13.2	23.3
108	15	14.8	29.8
8	20	16.2	36.2
	Red 1st	Red 2nd	
2	5	10.0	15.0
109	10	12.8	22.8
61	15	15.5	30.5
3	20	13.3	33.3
	Red 1st	White 2nd	
3	5	13.3	18.3
20	10	15.8	25.8
21	15	15.0	30.0

running or reject him by kicking. The white-eyed females showed less of this avoidance reaction toward the males and with only brief courtship would permit copulation. Frequently males would switch their courtship from the red to the white-eyed females and within seconds would have mounted the white-eyed females for the first copulation.

One small test involved 35 individual white-eyed males, each of which was permitted to choose between a red-eyed and a white-eyed female. The results were similar to those obtained when the red-eyed males were given the same choice. Among the males that copulated, about 80% did so first with the white-eyed females.

The fact that the mating index was greater in the WW and WR series than in the RR series also indicates that the genotype of the female is an important selective factor. The mating index does not distinguish between the single and the double copulations, and therefore the statistical analyses were based on the numbers of males that did not copulate, copulated only once, or copulated twice (Table I). The differences between the WW and the WR series are not great ($P = 0.2$ to 0.3), but the differences between the WR and the RR series are significant at the 5% level. The WR series has an activity level represented by a mating index of 1.77, which is much greater than that of the RR series whose mating index was 1.65 ($P < 0.01$, $\chi^2 = 16.42$, D.F. = 2).

After the males had copulated once, the types of the second females in the vials had little influence on whether or not the males would copulate a second time. Approximately 81 to 85% of the males copulated a second time regardless of the types of females with which they had copulated first, and regardless of the types of the other females in the vials. In each case the

analyses of these data yield probabilities of at least 50% that the differences could have been caused by chance fluctuations.

Premating Periods

The fact that the males copulated much sooner with the white-eyed than with the red-eyed females (Fig. 1) is a direct result of the lesser avoidance reaction of the white-eyed than the red-eyed females toward the males. When the males were permitted the choice between two white-eyed females, 63% copulated within 5 min from the time the flies were placed together, yet during the same interval, only 20% of the males allowed a choice between two red-eyed female copulated. The probability that these differences would have occurred by chance alone is less than 0.01 (χ^2 = 102.73, D.F. = 1). When the individual males were permitted to choose between a white-eyed and a red-eyed female, 54% copulated with white-eyed and only 25% with red-eyed females during this 5-min period. As in the previous analysis, the probability that chance alone would have accounted for the differences is less than 0.01 (χ^2 = 13.96, D.F. = 1). The two remaining analyses of the difference between the mating frequencies within the first 5 min also show that the males copulated sooner with the white-eyed than with the red-eyed females, and the differences are very significant (WW vs RW: χ^2 = 25.47, D.F. = 1; RR vs WR: χ^2 = 63.34, D.F. = 1).

When the males chose red-eyed females as their first partners, the type of the second female present in the vial had little influence on the frequency of copulations within the first 5 min. Twenty percent of the males in the RR series and 25% in the RW series copulated with red-eyed females within this period (P = 0.3 to 0.5, χ^2 = 0.7449, D.F. = 1). Apparently the males courted the red-eyed females only, or perhaps in these cases the

white-eyed and red-eyed females had similar avoidance reactions.

When the males chose white-eyed females as their first partners, the type of the second female present did influence the frequency of copulations within the first 5 min. During this period, there were significantly more copulations within the WW than in the WR series ($P = 0.02$ to 0.05, $\chi^2 = 4.40$, D.F. = 1). This may have been because the males unsuccessfully courted the red-eyed females before copulating with the white-eyed ones.

Intermating Periods

The average intermating periods before the copulations were shorter with the white-eyed females in each instance than with the red-eyed females (Fig. 2). The differences in distributions were found to be highly significant when the WW was compared with the RR group ($P < 0.01$, $\chi^2 = 17.76$, D.F. = 5) and when the WW was compared with the WR series ($P < 0.01$, $\chi^2 = 32.12$, D.F. = 5). In the other comparisons, WR vs RW and RR vs RW) the differences were not significant; however the RW series contained less than a quarter as many double copulations as any of the other three groups, and the statistics involving this group are not too reliable. The type of female with which the male mated first had little influence on the intermating periods, as the differences in distributions between the WW and RW series and between the RR and WR series were not significant.

The shorter intermating periods before the copulations with the white-eyed females than with the red-eyed females also are correlated with the tendency of the red-eyed females to actively repel the courtship of the male.

There is an interesting correlation between the premating and intermating periods, which is shown in Fig. 3. In the WW series, 67% of the first of the double copulations were begun within 5 min after the flies were placed together and within 5 min after the termination of the first copulations, 67% of these males had begun a second copulation (Fig. 3a). The premating periods before each of the two successive copulations follow similar distribution patterns (Fig. 3a), and based on the frequencies of copulations initiated within the first 5 min in each of these categories, the differences are not significant ($P = 0.99+$). The differences between pre-WR (56%) and inter-RW (62%) are hardly significant as seen in Fig. 3b, nor are the differences between pre-WW (67%) and inter-RW (62%). The probabilities for chance deviations accounting for the differences in the two latter cases are 0.3 to 0.5 and 0.5 to 0.7 respectively.

Apparently, whether or not a male had copulated previously had little influence in determining the durations of the periods before either the first or second copulations with white-eyed females. However, the periods before the copulations with the red-eyed females were greatly influenced by whether or not a copulation had occurred previously.

Distribution patterns for the periods before the first copulations with red-eyed females differed from the patterns for the periodo before the second copulations with red-eyed females (Fig. 3c and d). When the males had not copulated previously, only about 20% (pre-RR, Fig. 1c) to 27% (pre-RW, Fig. 3d) of the first copulations with the red-eyed females were begun within the first 5 min from the time that the flies were placed together. However, if the males had each copulated once, then about 48% (inter-WR, Fig. 3d) to 52% (inter-RR, Fig. 3c) of the second copulations

of the males were begun within 5 min after the termination of the first. In each case the distributions, based on the frequencies of copulations within the first 5-min periods of the premating as opposed to the intermating times, are significantly different from each other ($P < 0.01$, D.F. = 1; $\chi^2 = 46.88$, for pre-RR vs inter-RR, $\chi^2 = 6.93$ for pre-RW vs inter-WR). A third test, comparing the premating periods of the RR series with the intermating periods of the WR series, also yielded results that are highly significant ($\chi^2 = 35.29$, D.F. = 1).

One possible explanation why the males mated sooner with the red-eyed females after previous copulations is that a chemical released during the copulation in some way increases the mating drive of either the red-eyed female or the male. The former is more likely, because the premating and intermating times before copulations with white-eyed females hardly differed from each other. The type of female with which the male had copulated previously was not important in influencing the intermating periods, suggesting that the same chemical stimulus is produced in the copulations with each type of female. This would also suggest that the white-eyed females do not react as strongly to the stimulus as do the red-eyed females.

Mayr (1950) showed that a chemical that affects the mating threshold of the female is released, by the male. Antennae (containing olfactory organs) were removed from female *Drosophila*. Males of one or more types were placed with these females, and observations of their mating behavior were made or, in some instances, fertility of the females was used as the criterion to indicate mating activity. Petit (1959b), on the other hand, minimized the role of chemical receptors of the females. Her experiments involved excision of antennae and aristae from female *D. melanogaster* and then observing courtship behavior of these and nonoperated

females with red-eyed and white-eyed males. It was determined that it was the perception, by organs within the antennae and aristae, of differences in the patterns of the wing vibrations of the two types of males that accounted for the higher frequency of red-eyed than white-eyed males being chosen as partners. Sturtevant (1915) observed that a pair of flies would mate sooner if placed in a vial in which a copulation had just occurred than would a pair placed in a clean vial. This would indicate that olfaction and not perception of differences in wing-vibration patterns was the important factor.

The present work indicates that olfaction is important, at least in determining the frequency of second copulations within the same mating vials, but the perception of differences in wing-vibration patterns is not entirely ruled out.

Durations of Copulations

The white-eyed females generally copulated for longer periods than did the red-eyed females regardless of whether the copulation was the first, second, or only one accomplished by the male. The white-eyed females may be capable of copulating for greater durations than the red-eyed females, and it is also possible that the duration is determined by the male, either directly or indirectly. The red-eyed females might force the males to dismount, or the males might react to the copulations with the red-eyed females by dismounting earlier, even though the duration could be prolonged. Another possibility is that insemination of the red-eyed females may deplete the sperm supply faster than does the insemination of the white-eyed females thus correlating the duration of the copulation with the sperm supply.

The durations of the copulations seem to depend on the male to a large extent. Some copulate for short periods, while others copulate for greater durations. This role of the male is indicated by the fact that the average durations of the second copulations were greater than the first, regardless of the durations of the first. Scatter diagrams indicating the correlation of the durations of the second with the first copulations are presented in Figs. 4 and 5. The correlations are positive in each case, though extremely slight in the RW series (4d). In the other series, the correlation coefficients do not differ much from each other. Even though the correlation coefficients are not large, in each of the series except the RW the positive increases in the durations of the second copulations dependent upon the increases in the durations of the first were significant ($P = 0.01$). The low correlation in the RW series may be a result of the small number of individuals in the sample.

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LITERATURE CITED

Bastock, M. 1956. A gene mutation which changes a behavior pattern. Evolution, 10: 421-439.

Bastock, M. and A. Manning. 1955. The courtship of Drosophila melanogaster. Behaviour, 8: 85-111.

Bosiger, E. 1957. Sur la parade nuptiale des mâles de deux souches de Drosophila melanogaster. Compt. rendus des séances de l'Academie des Sciences (Paris), 244: 2107-2110.

Clise, R. L. 1958. Factors contributing to the low survival rate of bar-eyed Drosophila melanogaster. Proc. Tenth International Congress of Genetics, II: 54.

Demerec, M. and B. P. Kaufmann. 1941. The time required for Drosophila males to exhaust the supply of mature sperm. Am. Naturalist, 75: 366-379.

Dobzhansky, T. and P. Ch. Koller. 1938. An experimental study of sexual isolation in Drosophila. Biologisches Zentralblatt, 58: 589-607.

Ehrman, L. 1960. A genetic constitution frustrating the sexual drive in Drosophila paulistorum. Science, 131: 1381-1382.

Hoenigsberg, H. F., S. K. Santibanez, and G. P. Sironi. 1959. Intraspecific sexual preferences in Drosophila prosaltans Duda and in Drosophila equinoxiales Dobzhansky. Experientia, 15: 223-226.

Hoenigsberg, H. F. and S. K. Santibanez. 1960. Courtship and sensory preferences in inbred lines of Drosophila melanogaster. Evolution, 14: 1-8.

Manning, A. 1959. The sexual isolation between Drosophila melanogaster and Drosophila simulans. Animal Behaviour, 7: 60-65.

Mayr, E. 1950. The role of the antennae in the mating behavior of female Drosophila. Evolution, 4: 149-154.

Mossige, J. C. 1955. Sperm utilization and brood patterns in Drosophila melanogaster. American Naturalist, 89: 123-127.

Petit, C. 1959a. Les facteurs génétique de la compétion sexuelle entre une forme mutante et son allelomorph sauvage chez Drosophila melanogaster. Annals de Genetique, 1: 83-87.

1959b. De la nature des stimulations responsables de la sélection sexuelle chez Drosophila melanogaster. Compt. rendus des séances de l'Academie des Sciences, (Paris), 248: 3484-3485.

Santibanez, S. K. and C. H. Waddington. 1958. The origin of sexual isolation between different lines within a species. Evolution, 12: 485-493.

Spieth, H. T. 1952. Mating behavior in the genus Drosophila (Diptera). Bulletin of the American Museum of Natural History, 99: 399-474.

Sturtevant, A. H. 1915. Experiments on sex recognition and the problem of sexual selection in Drosophila. Journal of Animal Behavior, 5: 351-366.

Sturtevant, A. H. 1921. The North American species of Drosophila. The Carnegie Institute of Washington, 301: 1-150.

Tebb, G. and J. M. Thoday. 1956. Reversal of mating preference by crossing strains of Drosophila melanogaster. Nature, 177: 707.

Wallace, B. and T. Dobzhansky. 1946. Experiments on sexual isolation in Drosophila. VIII. Influence of light on the mating behavior of Drosophila subobscura, Drosophila persimilis and Drosophila pseudoobscura. Proc. of the Nat'l Acad. of Sciences, 32: 226-234.

Wheeler, M. R. 1947. The insemination reaction in intraspecific matings of Drosophila. The University of Texas Publication, 4720: 78-115.

FIGURE LEGENDS

Fig. 1. Premating periods showing percents of copulations begun within indicated intervals (maximum periods). Numbers of copulations are WW = 268, WR = 238, RR = 264, RW = 52.

Fig. 2. Intermating periods showing percents of second copulations by the males begun within indicated intervals (mean times used). Numbers of double copulations are WW = 212, RW = 44, RR = 215, WR = 193.

Fig. 3. Comparison of premating and intermating periods before copulations with white-eyed females (a and b) and before copulations with red-eyed females (c and d). Percents of males copulating within specified intervals are shown. Numbers of double copulations are WW = 212, RW = 44, RR = 215, WR = 193. Maximum times used for premating and mean times for intermating periods are given.

Fig. 4. Durations in minutes of first and second copulations. Here r is the correlation coefficient, and b is the regression of second copulations dependent on first. Area of the dots is approximately proportional to the numbers of individuals.

Fig. 5. Durations in minutes of first and second copulations. Total data (4a-4d). Here r is the correlation coefficient, and b is the regression of second copulations dependent on first. Area of the dots is approximately proportional to the numbers of individuals.

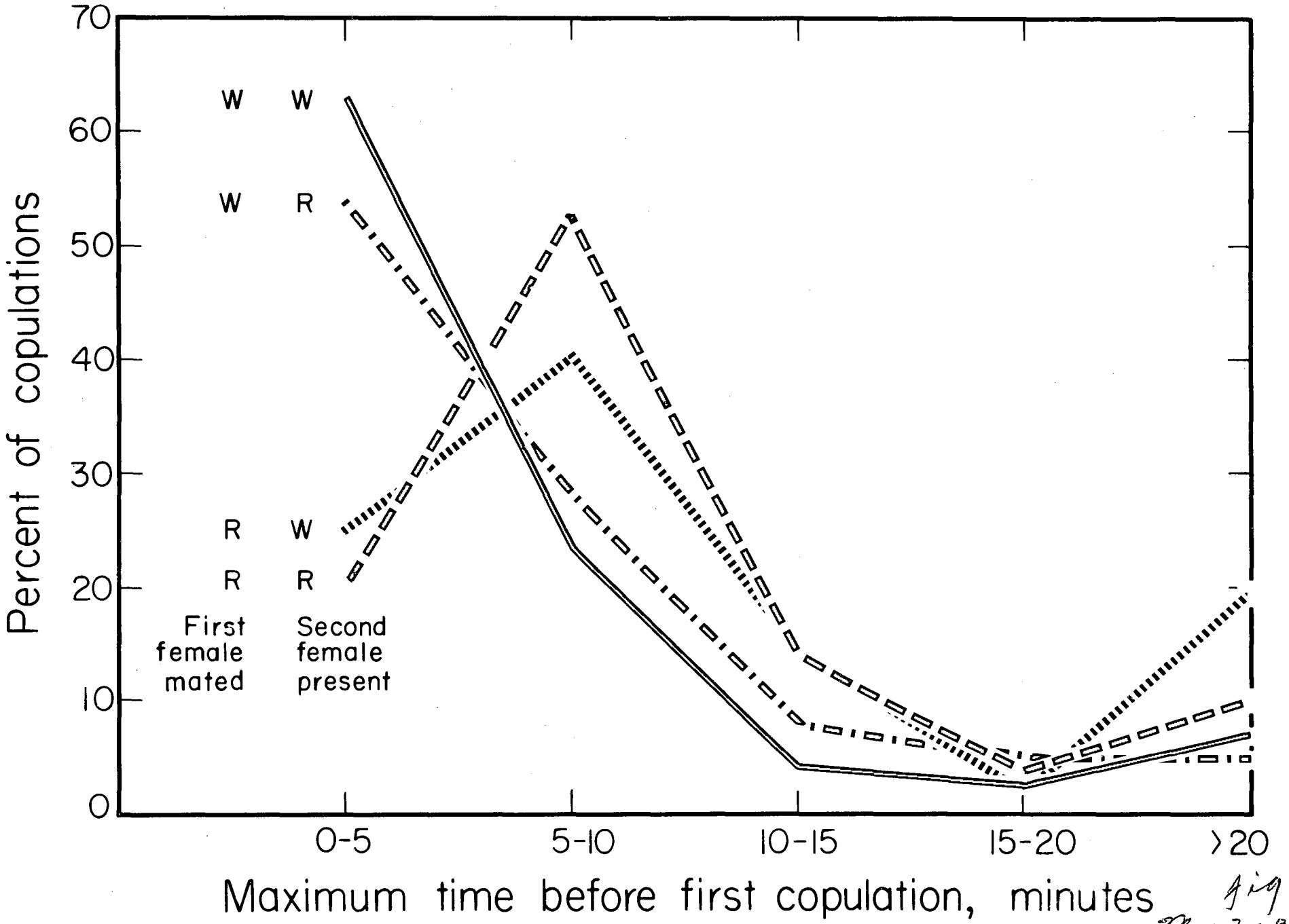
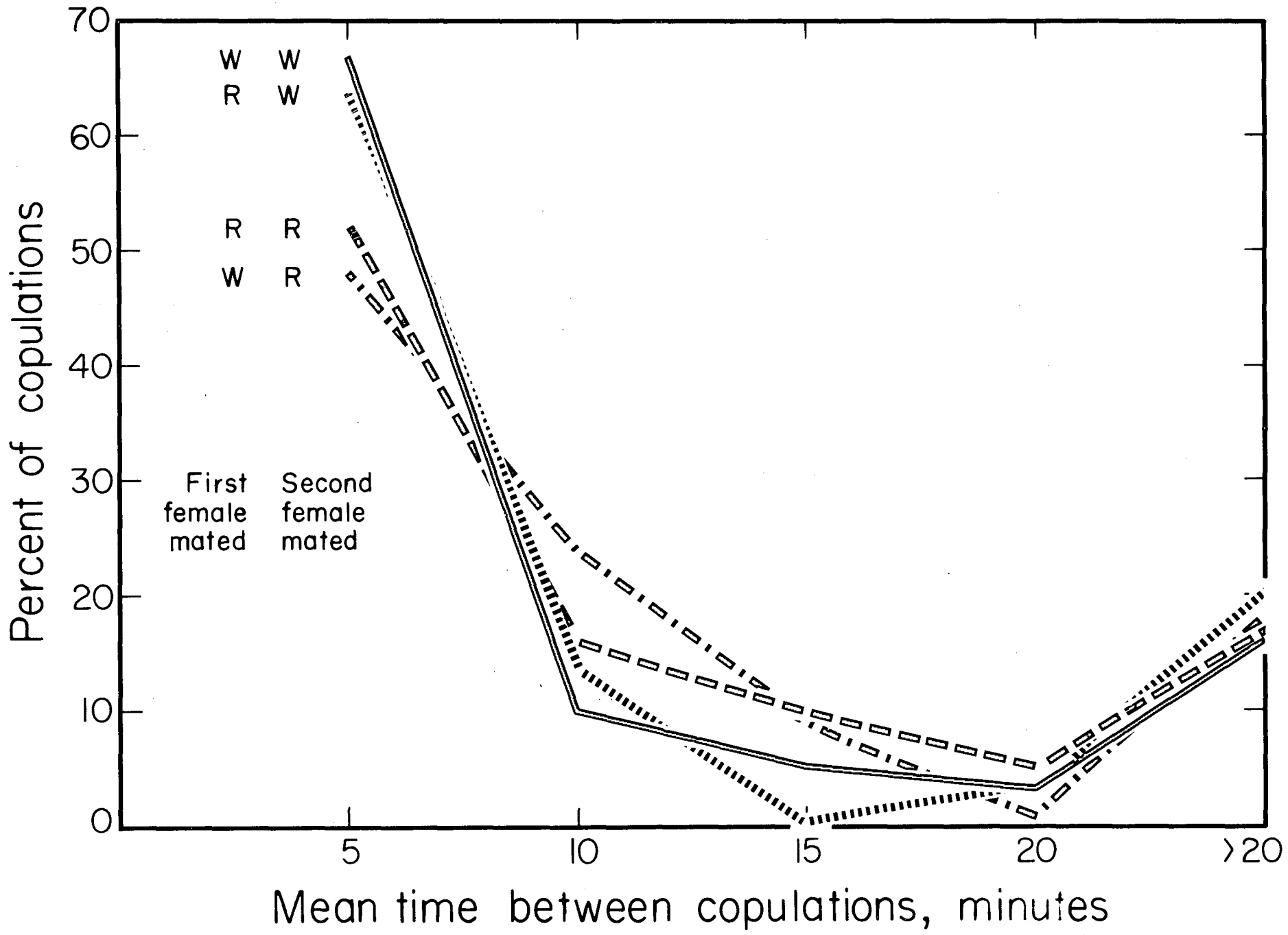


fig 1
Mw 20892


70
60
50
40
30
20
10
0
Percent of copulations
W W
R W
R R
W R
First female mated
Second female mated
5
10
15
20
>20
Mean time between copulations, minutes

Mw 20893 Fig

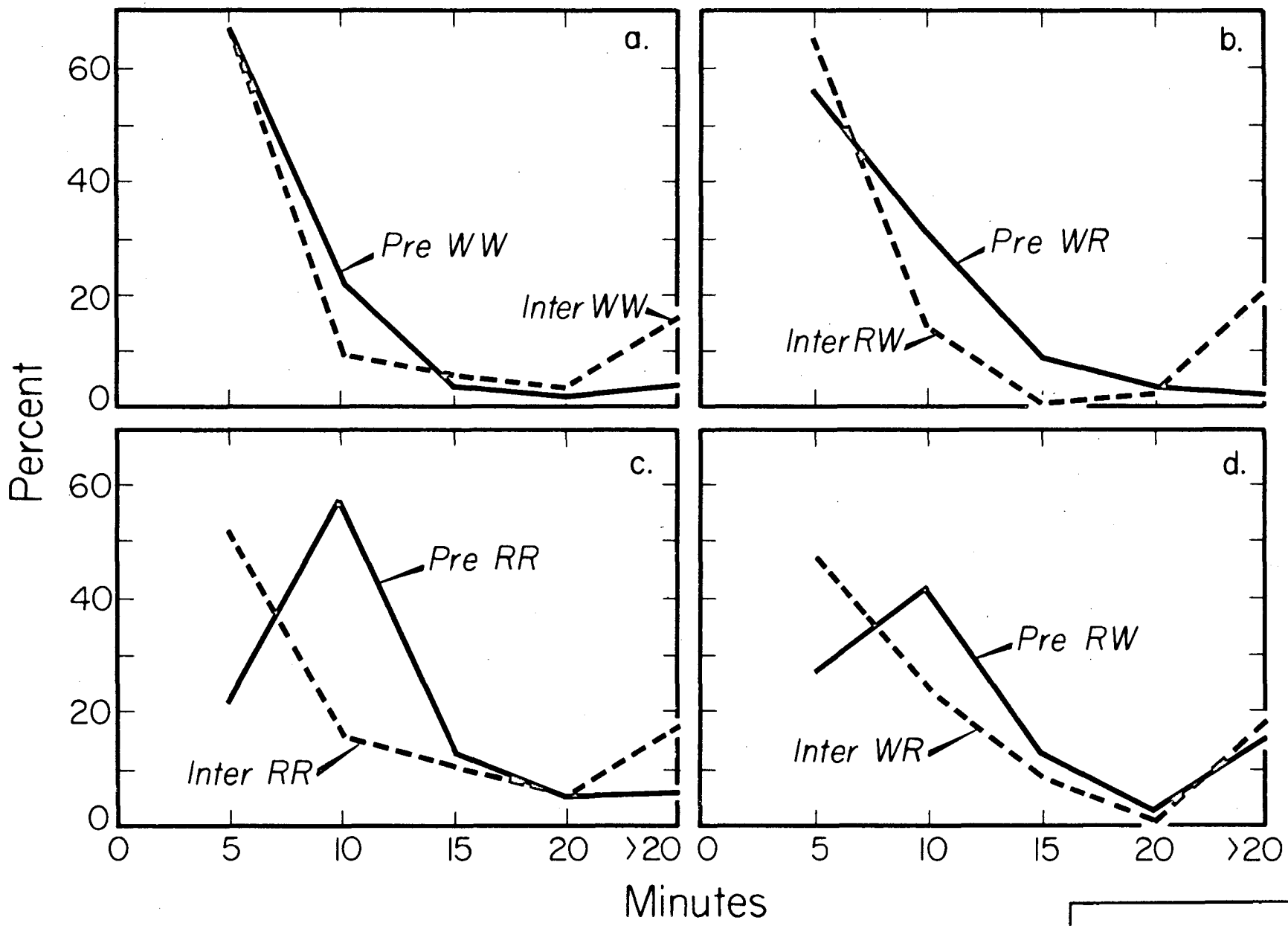
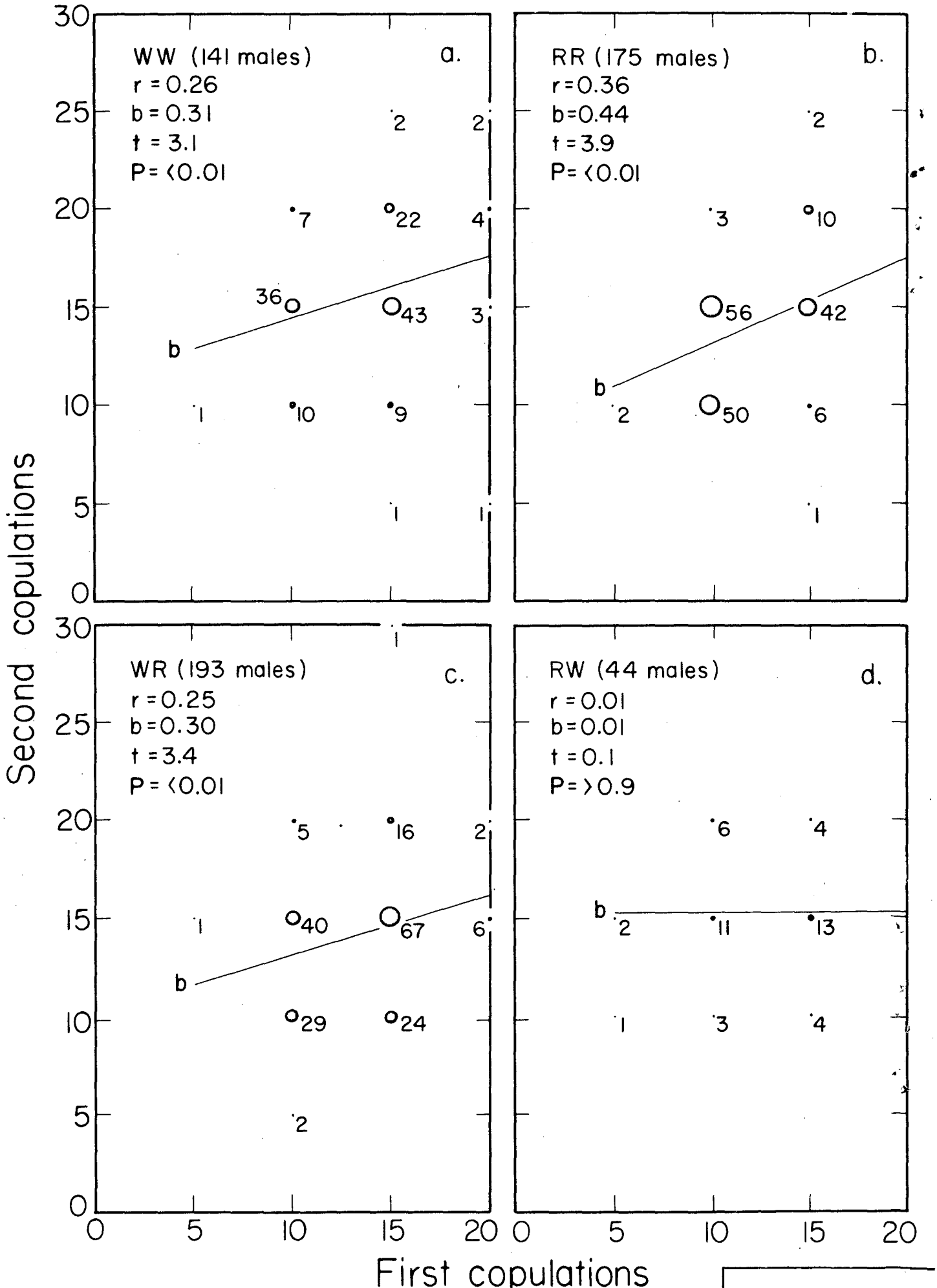
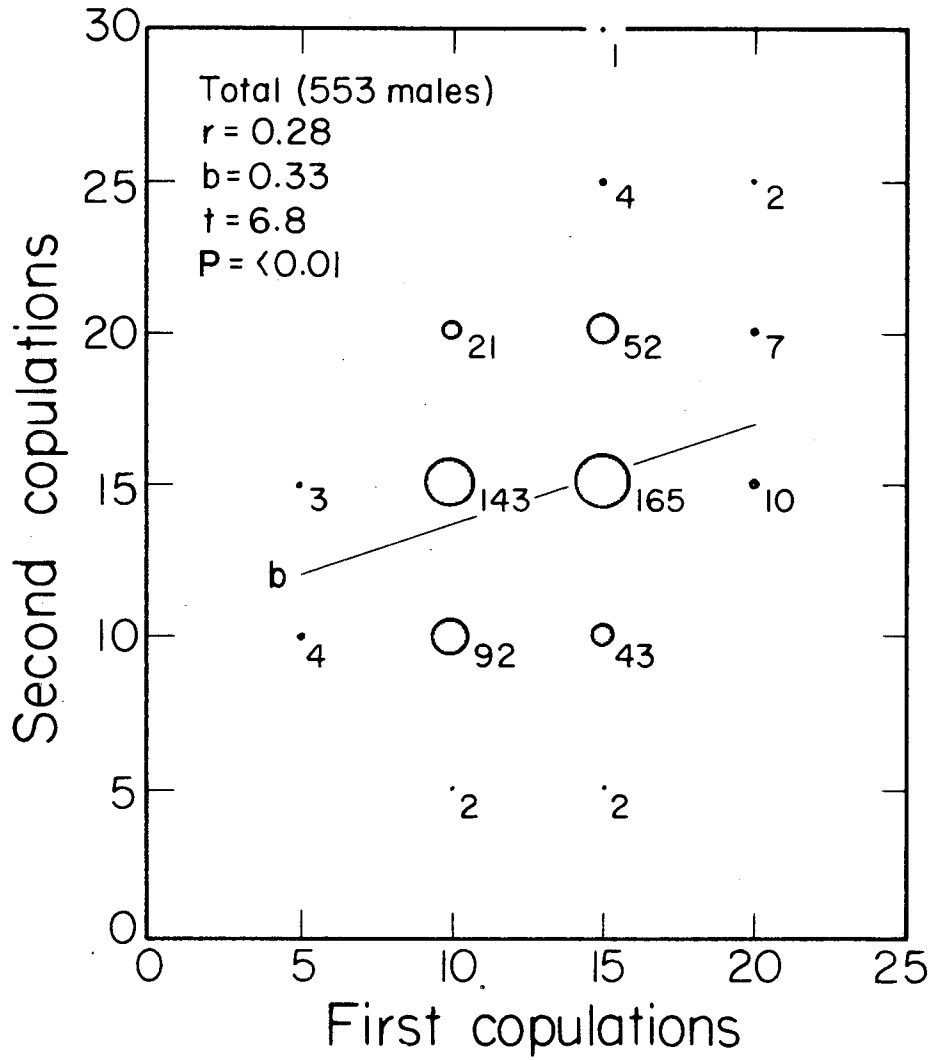


fig 3

MW 20894


WW (141 males)
r = 0.26
b = 0.31
t = 3.1
P = <0.01
a.
RR (175 males)
r = 0.36
b = 0.44
t = 3.9
P = <0.01
b.
WR (193 males)
r = 0.25
b = 0.30
t = 3.4
P = <0.01
c.
RW (44 males)
r = 0.01
b = 0.01
t = 0.1
P = >0.9
d.
Second copulations
First copulations



Mw 20896

fig 5