EVIDENCE FOR RARE MALE MATING ADVANTAGE IN A NATURAL POPULATION OF *DROSOPHILA MELANOGASTER*

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SUMMARY

Drosophila melanogaster flies were collected from nature each two months for one year. Only chromosomal inversions of *D. melanogaster* second chromosome were used in this study. A standard stock (St) of *D. melanogaster* which was free of any inversions on this chromosome was prepared. Two paracentric inversions, *(2L)Cy* and *(2R)NS*, were found only in heterozygous condition in captured flies. Crosses were conducted between the captured males and the St females and between the captured females and the St males. Standard karyotypes were more frequent in males, females and their offspring whereas the heterozygous karyotypes were less frequent in the three genotypes. The frequencies of gene arrangements in the larval offspring differed significantly from those in the captured parental adults. The pooled estimates of karyotypic frequencies showed that as for the homokaryotypic *(2R)NS*, Δp_m (the change of frequency due to differences in male mating success) was highly significant. The significant value of Δp_m for the rare karyotype showed that rare male karyotypes, as a group, have a significant higher mating success than common karyotypes. The relative mating success of the rare karyotypes was estimated to be 1.33, nearly once and one third of the common karyotypes. This gives the evidence that rare male karyotypes showed a large advantage in mating success over the common karyotypes.

Keywords: Drosophila – melanogaster – population genetics – rare male advantage.

INTRODUCTION

Fluctuations in gene frequencies are causing by several factors including selection. Some kinds of selection were found to be difficult to test for in nature. The rare male mating advantage of *Drosophila* species is a case in point (Salceda and Anderson, 1988).

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Rare male mating advantage is a kind of sexual selection, which, in turn, is a component of fitness known to play an important role in selection on *Drosophila* genotype (Prout, 1971; Anderson and Watanabe, 1974; Anderson *et al.*, 1979 and Som and Singh (2005)). The mechanisms of this mating advantage are behavioral, including such aspects of the mating process as female preferences; recognition of male types by olfactory, auditory and tactile cues; and vigor of male and female types (Petit and Ehrman, 1969; Ehrman and Parsons, 1981; Spiess, 1987; Knoppien, 1985 and Partridge and Hill, 1984).

The mating success of the male genotypes determines the frequencies of gene arrangement in the sperm carried by females. Hence, one test for selective differences in male mating success is to compare gene arrangement frequencies in male with those in larvae produced by females collected at the same time (Anderson, 1989). This reasoning of measuring gene arrangements to test for selective differences in male mating success is based on the assumption that other components of fitness do not confound this analysis, and in particular that karyotypic frequencies in adult males and females are alike, or nearly so. Selection by differences in female fecundity could be ruled out in this kind of experiments, because each female contributes equally to the larval frequencies. Since almost all females from nature were inseminated, there was little possibility of selection among females by differential mating success. Viability differences between male and female karyotypes could lead to different frequencies of the inversion types in reproducing adults of the two sexes, and hence to differences between males and their larval offspring. This differential viability in the sexes seems to be the most important factor that could complicate the analysis for selection by male mating success (Anderson *et al.*, 1979).

It has been known for many years that *Drosophila* males mate repeatedly, and recently, evidence has been advanced that females do so as well (Anderson, 1974 and Levine *et al.*, 1980). Sperm displacement has been shown for *D. melanogaster* in the laboratory (Lefevre and Johnson, 1962). This evidence will ensure that captured natural females are carrying only the sperms of selected rare male.

The objectives of this study were to test and document the occurrence of rare male advantage in a natural population of *D. melanogaster*.

MATERIALS AND METHODS

1. Collection of flies:

Drosophila flies were captured from nature at the Faculty of Agriculture Farm at Kafr EL-Sheikh, Egypt. These flies were collected each two months started with January. Females were separated from males as soon as they were collected (this procedure eliminated mating among the flies after capture, so that the only sperm stored in females would have been deposited during matings in nature). After that, males of *D. simulans* were separated from those of *D. melanogaster* and discarded. Progeny tests were conducted to select for *D. melanogaster*.

2 Experimental procedure:

Standard flies, free of inversions in the second chromosome, were aimed to use in this study to test for chromosomal inversions in natural flies. In order to produce the standard stock, the balancer stock of *Curly Lobe/Plum* (*CyL/Pm*) was used. Males, which were free of inversions on the second chromosome, were first mated to virgin females of the *CyL/Pm* stock. After three matings, homozygous second chromosome flies that don't carry any inversion, the standard stock, can be obtained (Figure 1).

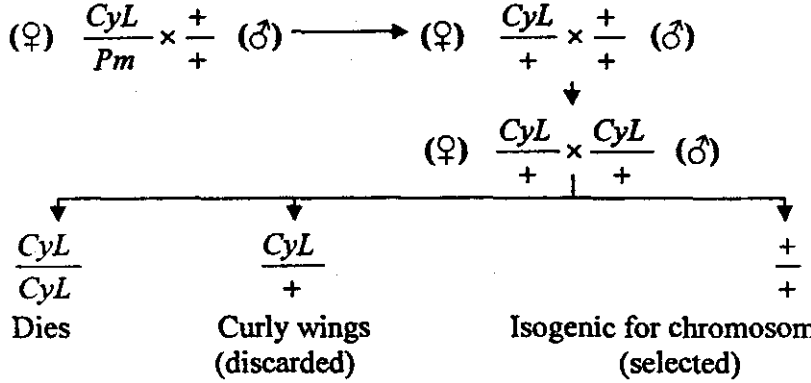


Figure 1. The crossing pattern of generating stocks of isogenic flies that are entirely for of *D. melanogaster* second chromosome using the balancer stock of *CyL/Pm* containing *Curly* wing (*Cy*), *Lobe* eye (*L*) and *Plum* eye (*Pm*) markers (Spiess, 1977).

In order to estimate the rare male contribution to its offspring the next crosses were applied. Each wild captured male was mated to a virgin female from a laboratory strain homozygous for the standard (St) gene arrangement; the standard stock. The second cross was assumed to be done in nature between wild type males and wild type females. To collect the outcome of these matings, each wild captured female was placed in a separate vial without male and was allowed to lay eggs from their mating in nature for two weeks. During that time they were allowed to be cleared from natural sperms by storage at 5°C for a month and transferred to a fresh vial every few days. After the month, the third cross was conducted as cleared wild type females were mated to standard males from the same standard strain.

1st cross	♀ *Standard*	×	*Wild type* ♂
2nd cross	♀ *Wild type*	×	*Wild type* ♂
3rd cross	♀ Wild type (cleared)	×	Standard ♂

3. Cytological studies:

The gene arrangement frequencies in males, females and the offspring of females were determined. The resulting larvae were reared in near optimal condition of temperature (15°C), nutrition and density. They were provided daily by one drop of yeast suspension. Salivary chromosomes of ten larvae from each culture were identified. Chromosomes were studied in squash preparation of salivary glands dissected from third instar larvae and stained with aceto-lactic orcein (2 gm orcein, 50 ml glacial acetic acid, 30 ml glacial lactic acid and 20 ml distilled water). The preparations were regularly examined after two days of staining. Estimations of inversion frequencies were based on cytological analysis of ten larvae for each adult male, and adult females captured from nature, and also in the offspring of the females by their mates in nature.

4. Data analysis:

4-a- Chi-square test for contingency table was conducted to test for the viability difference between the males and females according to Ott (1988).

4-b-Estimation of mating success and rare male:

The change of frequency (Δpm) due to differences in male mating success and the percentage of the change in frequency were computed according to Salceda and Anderson (1988) (Table 1). The

calculation of mating success of the rare male karyotypes was computed according to Anderson and Brown (1984) and Salceda and Anderson (1988) (Table 2).

Table 1. A model for estimation of the karyotypic frequencies during the breeding cycle of *D. melanogaster* from a natural population: estimation of frequencies (as %) in sperm stored in females and Δpm, the change in frequency among males due to differential male mating success.

	Cy/St	*Cy/NS*	*St/NS*
1-Frequencies in offspring	x	y	z
2-Contribution of female parents to offspring	$x_f/2$	$y_f/2$	$z_f/2$
3-Contribution of male parents to offspring = (row1-row2)	$x-(x_f/2)$	$y-(y_f/2)$	$z-(z_f/2)$
4-Male contribution scaled to 100 % = frequencies in sperm stored in females = (2×row3)	$2[x-(x_f/2)]$	$2[y-(y_f/2)]$	$2[z-(z_f/2)]$
5-Frequencies in adult males from nature	x_m	y_m	z_m
6-Δpm due to differences in male mating success = (row4-row5)	$2[x-(x_f/2)]-x_m$	$2[y-(y_f/2)]-y_m$	$2[z-(z_f/2)]-z_m$
7-% change in frequency = 100×(row6/row4)	$100\{2[x-(x_f/2)]-x_m\}/2[x-(x_f/2)]$	$100\{2[y-(y_f/2)]-y_m\}/2[y-(y_f/2)]$	$100\{2[z-(z_f/2)]-z_m\}/2[z-(z_f/2)]$

Where:

-Line I represents the karyotypic frequencies in larval offspring.

-Line II shows the contribution of female parent to offspring which is the same frequencies of karyotypes in the female parent. Female parent would contribute by 50% to its offspring as well as the male parent.

-Row 3 shows the male parent contribution which can be obtained by subtracting female parent contribution in row 2 from the offspring frequencies in row 1.

In order to compare the male parent contribution with the frequencies found in adult males, this contribution of male parent

should be scaled to 100% by multiplying the estimate in row 3 by 2 to give the scaled male parent contribution (row 4) which in turn will be compared with the adult male frequency (row 5).

-Row 6 gives the change in karyotypic frequencies due to male mating success. This change in karyotypic frequency can be obtained from the difference between chromosomal frequency in adult male (row 5) and the frequency of these chromosomes that the adult parent contributed to the next generation (row 4).

-Row 7 gives the percentage of the change in chromosomal frequency due to male mating success relative to the chromosome frequency of male contribution.

Table 2. A model for estimating the mating success of the rare male karyotypes relative to that of the common karyotypes.

	Rare karyotype (p)	Common karyotype (q)
-Initial male frequencies	a	b
-Frequency of offspring fathered	A	B
-Relative mating success	M	1

Hence the relative mating success of rare males is estimated according to the model as M=bA/(aB).

4-c- *t* test:

1- The change of frequency (Δpm) of these rare chromosomes, between adult males and their contribution to offspring, can be tested by the *t* test (Spiess, 1977) as follows:

$$t = \frac{\Delta p_m}{\sqrt{\overline{pq}\left(\frac{1}{2N_m} + \frac{1}{2N_L}\right)}}$$

Whereas the variance of (Δpm) can be calculated from its component frequencies.

2- The rare male mating advantage can be tested by *t* test (Spiess, 1977) as follow:

$$t = (A - a)/\sqrt{(\mathrm{var}A + \mathrm{var}a)}$$

To test the hypothesis A=a, where: var = $\frac{pq}{2N}$.

RESULTS AND DISCUSSION

Karyotypes of males from nature were deduced by identifying and computing the frequencies of karyotypes in the offspring of each wild male when it was crossed with the St/St females. In a similar manner, the karyotypic frequencies of each wild female were deduced from those of the karyotypes found in the offspring it produced after remating with the St/St males.

In this study, the other components of fitness don't confound this analysis. Since the viability does not differ in the sexes in all the months under study. Also, selection by differences in female fecundity could be ruled out in these experiments. Since almost all adult females were inseminated in nature, there was a little possibility of selection among female by differential mating success. Karyotypic frequencies in the males and females collected in nature and in the offspring produced by each female from her mating in nature in March are presented in Table 3.

Karyotypic frequencies were compared in the males and females, since a significant difference between them would suggest that viabilities differed in the sexes. The sexes did not differ significantly in karyotypic frequencies. The χ^2 for homogeneity was 5.36 with 2 degrees of freedom, and the associated probability was < 0.01.

The data showed that the chromosomes which did not carry any inversions were more frequent in males, females and their offspring whereas the heterozygotes were less frequent in the three genotypes.

Table 4 presents the frequencies of chromosomes contributed by males to their offspring and the change in chromosome frequency due to male mating success in March. These results showed that both homokaryotype frequencies increased, especially *(2R)NS*. The frequency of chromosomes that don't carry any inversion in adult males is close to 50%. The heterokaryotype (*Cy/NS*) frequency was very low (8.40) and can be attributed as rare karyotype.

Under the null hypothesis that there was no selection, the karyotypic frequencies in males and larvae should be the same and Δpm should be zero. The *t* test estimate for *(2R)NS* is 18.68 and its degrees of freedom 912 is significantly different from zero at probability level 0.01. The estimate of Δpm for the heterokaryotype

is 7.64 and the percentage change in its frequency due to selection for rare male is 47.63. The *t* test estimate for this change is 8.13 which is highly significant with 912 degrees of freedom.

Table 3. Karyotypic frequencies (as %) in *D. melanogaster* adults from a natural population and in their offspring during March.

Type	*Cy/St*		*Cy/NS*		St/NS		*St/St*		Tot. no. of chromosome s examined	χ^2
	n	%	n	%	N	%	n	%		
Male	69	18.7	31	8.40	86	23.31	183	49.59	369	
Female	9	3.41	9	3.41	48	18.18	198	75.00	264	5.36
Offspring	63	11.56	53	9.72	176	32.29	253	46.42	545	

n, The observed number of karyotypes. χ^2, difference between the males and females for karyptypic frequencies.

Table 4. Karyotypic frequencies during the breeding cycle of *D. melanogaster* from a natural population: estimation of frequencies (as %) in sperm stored in females and Δpm.

	Cy/St	*Cy/NS*	St/NS	St/St	Total %	n
1-Frequencies in offspring	11.56	9.72	32.29	46.42	100	1090
2-Contribution of female parents to offspring	1.70	1.70	9.09	37.50	50	528
3-Contribution of male parents to offspring = (row1-row2)	9.86	8.02	23.20	8.92	50	
4-Male contribution scaled to 100 % = frequencies in sperm stored in females = (2×row3)	19.72	16.04	46.40	17.84	100	
5-Frequencies in adult males from nature	18.70	8.40	23.31	49.59	100	738
6-Δpm due to differences in male mating success = (row4-row5)	1.02	7.64	23.09	-31.75	0	
7-% change in frequency =100×(row6/row4)	5.17	47.63	49.76	-177.97		
t	0.91	8.13**	18.68**	-	-	-

n.=Number of chromosomes on which frequencies are based. ** $P < 0.01$

In contrast, Anderson and Brown (1984) found that both homokaryotypes of *ST/ST* and *CH/CH* in *D. pseudoobscura* showed a male mating advantage, relative to that of the heterokaryotype

ST/CH. While, in this particular situation, our data show that there is a case of protected polymorphism, since protected polymorphism requires a rare male advantage for the heterokaryotype (Anderson, 1989).

Table 5 shows the karyotypic frequencies in the males and females collected in nature and in their offspring. The results revealed that karyotypic frequencies in the two sexes did not differ significantly at *P* level of 0.01 science χ^2 was 2.93.

The results declared also that the homokaryotypic frequencies of *(2L)Cy* and *(2R)NS* in adult males were low (13.11and 14.08, respectively), whereas the heterokaryotypes were less in frequency (2.91).

Table 5. Karyotypic frequencies (as %) in *D. melanogaster* adults from a natural population and in their offspring for different collections.

Type	*Cy/St*		*Cy/NS*		*St/NS*		*St/St*		Tot. no. of chromosomes examined	χ^2
	n	%	*n*	%	*n*	%	*n*	%		
Month	May									
Male	27	13.11	6	2.91	29	14.08	144	69.90	206	
Female	19	11.31	15	8.93	36	21.43	98	58.33	168	2.93
Offspring	32	7.78	23	5.60	123	29.93	233	56.69	411	
Month	July									
Male	76	16.74	27	5.95	107	23.57	144	53.74	454	
Female	34	11.07	23	7.49	72	23.45	178	57.98	307	1.13
Offspring	54	9.80	13	2.36	124	22.50	360	65.33	551	
Month	September									
Male	72	14.14	64	12.57	111	21.81	262	51.47	509	
Female	56	14.28	34	8.67	107	27.29	195	49.74	392	1.30
Offspring	58	13.33	37	8.50	108	24.83	232	53.33	435	
Month	November									
Male	62	15.05	35	76	18.45	18.45	239	58.01	412	
Female	50	16.02	25	51	16.35	16.35	186	59.61	312	0.14
Offspring	79	18.33	44	145	33.64	33.64	163	37.82	431	
Month	January									
Male	46	9.62	36	7.53	96	20.08	300	62.76	478	
Female	46	8.35	28	5.08	113	20.51	364	66.06	551	0.42
Offspring	85	17.31	53	10.79	135	27.49	218	44.40	491	

Table 6 shows the frequencies of chromosomes (in percentage) contributed by males to their offspring and the change in

chromosome frequency (Δpm) due to male mating success in different months.

The data illustrated that, in May, the homokaryotype *(2R)NS* increased in frequency (24.36) while the frequencies of homokaryotype *(2L)Cy* and the heterokaryotype decreased (-8.85 and -0.63, respectively). Thus, the homokaryotype *(2R)NS* could be treated as rare chromosomes because it started in adult males with low frequency. Under the null hypothesis that there was no selection, the karyotypic frequencies in males and larvae should be the same and Δpm should be zero. The *t* estimate for *(2R)NS* is 22.44 which is highly significant at the 0.01 probability level.

The χ^2 used to compare karyotypic frequencies in the males and females was 1.13, in July, which did not differ significantly at $p < 0.01$ (Table 3). This Table showed that the *St* chromosomes were high while the heterozygotes were low in frequencies in all genotypes.

The chromosomes which are free of inversion increased in frequency in July (18.94) while the frequencies of both homokaryotypes and heterokaryotypes decreased (Table 6).

The inversion polymorphisms in *D. melanogaster* are subjected to physical and biological components of environment which in turn affect their frequencies. These fluctuations in frequency may lead to loss of gene arrangements (Anderson *et al.*, 1975). In this month the data could not give a good evidence for male mating success. In this respect, Anderson *et al.* (1979) reported their evidence that adult males and zygotes of the next generation sometimes differ in gene arrangements frequency, and sometimes do not. It is likely that this selection is not constant, but changes continually, both in direction and intensity, in response to a changing environment and to the changing genetic constitution of each population (Anderson *et al.*, 1986).

There was no evidence for selection for rare-males for the month of September. The selection did not favor any one of the homokaryotypes *(2L)Cy* or *(2R)NS* (-1.76 and 0.57, respectively) or even the heterokaryotypes *Cy/NS* (-4.23). Whereas the *t* estimate for *(2R)NS* is 0.52 which is insignificant at the 0.01 probability level.

Table 6. Karyotypic frequencies during the breeding cycle of *D. melanogaster* from a natural population: estimation of frequencies (as %) in sperm stored in females and Δpm.

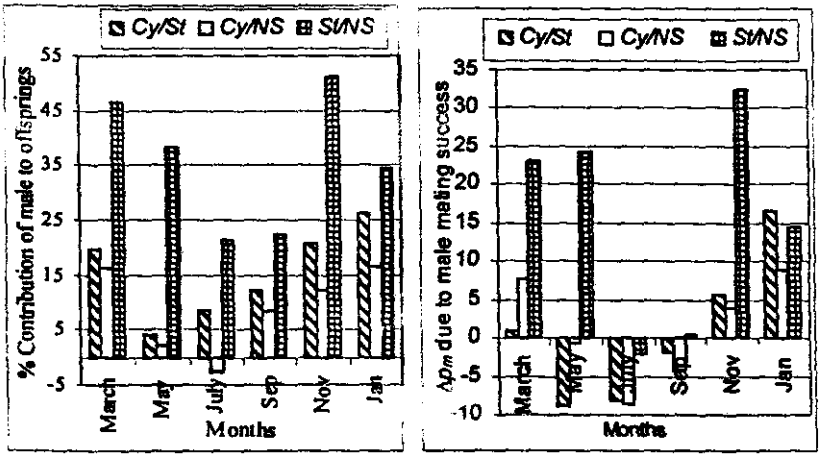
Month		*Cy*/St	*Cy*/*NS*	St/*NS*	St/St	Total %
May	1-Contribution of male parents to offspring	2.13	1.14	19.22	27.53	50
	2-Male contribution scaled to 100 %	4.26	2.28	38.44	55.06	100
	3-Δpm due to differences in male mating success	-8.85	-0.63	24.36	-14.84	0
	4-% change in frequency = 100×(row3/row2)	-207.75	-27.63	63.37	-26.95	
	t	-8.85**	-0.39	22.44**	-	-
July	1-Contribution of male parents to offspring	4.27	-1.38	10.78	36.34	50
	2-Male contribution scaled to 100 %	8.54	-2.76	21.56	72.68	100
	3-Δpm due to differences in male mating success	-8.20	-8.71	-2.01	18.94	0
	4-% change in frequency = 100×(row3/row2)	-96.02	315.58	-9.32	26.06	
	t	-9.63**	-2.24*	-	-	-
September	1-Contribution of male parents to offspring	6.19	4.17	11.19	28.46	50
	2-Male contribution scaled to 100 %	12.38	8.34	22.38	56.92	100
	3-Δpm due to differences in male mating success	-1.76	-4.23	0.57	5.45	0
	4-% change in frequency= 100×(row3/row2)	-14.22	-50.72	2.55	9.57	
	t	-1.77*	-4.64**	0.52	-	-
November	1-Contribution of male parents to offspring	10.32	6.21	25.47	8.02	50
	2-Male contribution scaled to 100 %	20.64	12.42	50.94	16.04	100
	3-Δpm due to differences in male mating success	5.59	3.93	32.49	-41.97	0
	4-% change in frequency= 100×(row3/row2)	27.08	31.64	63.78	-261.66	
	t	4.72**	4.03**	25.61**	-	-
January	1-Contribution of male parents to offspring	13.14	8.25	17.24	11.37	50
	2-Male contribution scaled to 100 %	26.28	16.50	34.48	22.74	100
	3-Δpm due to differences in male mating success	16.66	8.97	14.40	-40.02	0
	4-% change in frequency= 100×(row3/row2)	63.39	54.36	41.76	-175.99	
	t	17.41**	10.69**	13.66**	-	-

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

In November, the χ^2 test was estimated to compare karyotypic frequencies in the males and females and its value was

0.14 which gives the statistical evidence that these frequencies in the two sexes did not differ significantly at the 0.01 probability level.

Table 6 and Figure 2 show the frequencies of chromosomes contributed by males to their offspring (row 1) and the change in chromosome frequency due to male mating success in November (row 3). These data revealed that both homokaryotype frequencies increased, especially *(2R)NS* (32.49) as well as the heterokaryotype frequency. Under the null hypothesis that there was no selection, the karyotypic frequencies in males and larvae should be the same and Δpm should be zero. The *t* test estimate for *(2R)NS* is 25.61 which is highly significant at *P* level at 0.01. Also the *t* estimate for the heterokaryotype is 4.03 which is also highly significant at $P < 0.01$. These changes in karyotypes especially the heterokaryotypes since it started with very low frequency in the adult males, give an evidence for rare-male selective advantage.



(a) (b)

Figure 2: The percentile contribution of male to their offsprings (a) and the comparisons between the estimates of Δp_m (b) for the three gene arrangements during the six months.

These results agree with those of Salceda and Anderson (1988) who stated that chromosome frequencies in *Drosophila* population undergo cycles, and selection by male mating success is strong enough to account for a major part of the changes in chromosome frequency. Anderson *et al.* (1979) also mentioned that male mating success seemed to be the only component of fitness that

may play a major role in bringing about the large frequency difference they found between eggs and sperm. In our study this difference is estimated by -2.10 (female frequency-male frequency) in favoring male, which gives a supportive evidence for male mating success.

The two sexes did not differ significantly in karyotypic frequencies in January (Table 5), where the value of χ^2 test for homogeneity between sexes was 0.42.

The frequencies of homokaryotype *(2L)Cy* and heterokaryotype (*Cy/NS*) were found to be very low in the wild adult males (9.62 and 7.53, respectively), these chromosomes could be considered as rare karyotypes.

The frequencies of chromosomes contributed by males to their offspring in January (row 1) and, follow that, the change in chromosome frequency due to male mating success (row 3) are presented in Table 6. It is clear that both karyotypic frequencies of *(2L)Cy* and *Cy/NS* increased, especially *(2L)Cy*. The change in *(2L)Cy* frequency due to rare-male contribution is 63.39%, whereas this change in the heterokaryotype (*Cy/NS*) is 54.36%. These changes in both karyotypes give an evidence for the rare-male advantage and selection was acting for the advantage of these two karyotypes when they were rare.

The *t* test estimates can be calculated to test the null hypothesis that there was no selection. The karyotypic frequencies in males and larvae should be the same and Δpm should be zero. The *t* test estimate for *(2L)Cy* is 17.41 and for *Cy/NS* 10.69. These two estimates are highly significant at $P < 0.01$. The calculations for similar changes were also reported by Salceda and Anderson (1988). They found that the highest values of change in chromosomal frequencies were for the rare gene arrangement and their analysis showed that rare male karyotypes as a group have a significantly higher mating success than common karyotypes.

Table 7 shows the pooled estimates of karyotypic frequency in the adult males and females captured from nature and in their offsprings. The value of χ^2 of homogeneity between the sexes was 0.46 with 2 degrees of freedom and the associated probability was < 0.01, thus the karyotypic frequencies in the two sexes did not differ significantly.

Table 7. The pooled estimates of karyotypic frequencies (as %) in *D. melanogaster* adults from nature and in their offspring over the six months period.

Type	Cy/St		Cy/NS		St/NS		St/St		Tot. no. of chromosomes examined	χ^2
	n	%	N	%	n	%	n	%		
Male	352	14.50	199	8.20	505	20.80	1372	56.51	2428	
Female	214	10.73	134	6.72	427	21.41	1219	61.13	1994	0.
Offspring	371	12.95	223	7.79	811	28.32	1459	50.94	2864	46

The karyotypes are divided naturally into three types, two homokaryotypes of *(2L)Cy* and *(2R)NS* and heterokaryotype (*Cy/NS*) which exhibited the least frequency among these karyotypes.

Table 8 reveals how much is the contribution that males can give to their offsprings for the three karyotypes. For the homokaryotype *(2L)Cy*; row 6 gives an estimate of 0.68 for the frequency change (Δpm) which is due to male mating success. This change (Δ*pm*) can be expressed as a function of male contribution (row 4), which in turn was found to be 4.48%. The estimate of *t* test for Δ*pm* in this case is equal 1.65 which is significant at *P* level < 0.05.

For the heterokaryotype *Cy/NS*, the estimate of Δ*pm* is 0.66 with a 7.45% change in larvae frequency due to male contribution. The value of *t* test is equal to 1.93 which is significant at *P* level < 0.05. As for the homokaryotype *(2R)NS*, the value of Δ*pm* is 14.44 with a percentage change of 40.98% due to male contribution. The *t* test estimate for Δ*p* is 32.05 which is highly significant.

The data, when pooled, give an evidence for rare-male mating advantage. Selection was found to favor certain karyotypes when they were rare. As mentioned before selection acted upon the heterokaryotypes in certain months when they were rare. These results can be interpreted as convincing evidence for an important role for male mating success as a component of selection in nature. The significant values of Δ*pm* for the rare karyotypes show that rare male karyotypes, as a group, have a significant higher mating success than common karyotypes.

Hartl and Clark (1997) in their book "Principles of Population Genetics" stated that in reality, a genotype may have different fitnesses depending on many aspects of the environment, including food or light availability, population density, and the relative frequencies of other genotypes (frequency dependent

selection). They added that any rare genotype will have the greatest number of potential successful mates. On the other hand, many authors gave evidence for mating success in *Drosophila* especially *D. pseudoobscura*, where rare male sometimes seems to be at an advantage (Ehrman, 1970; Spiess, 1968, 1970; Petit and Ehrman, 1969; Anderson, 1969; Anderson *et al.*, 1979; Anderson and Brown, 1984; Anderson *et al.*, 1986; Salceda and Anderson, 1988 and Brockett *et al.*, 1996).

Table 8. The pooled estimates of karyotypic frequencies of *D. melanogaster* natural population: estimation of frequencies (as %) in sperm stored in females and Δpm.

	Cy/St	*Cy*/*NS*	St/*NS*	St/St	Total %	n.
1-Frequencies in offspring	12.95	7.79	28.32	50.94	100	5728
2-Contribution of female parents to offspring	5.36	3.36	10.70	30.56	50	3988
3-Contribution of male parents to offspring = (row1-row2)	7.59	4.43	17.62	20.38	50	
4-Male contribution scaled to 100 % = frequencies in sperm stored in females = (2×row3)	15.18	8.86	35.24	40.76	100	
5-Frequencies in adult males from nature	14.50	8.20	20.80	56.51	100	4856
6-Δpm due to differences in male mating success = (row4-row5)	0.68	0.66	14.44	- 15.75	0	
7-% change in frequency = 100×(row6/row4)	4.48	7.45	40.98	- 38.64		
t	1.65*	1.93*	32.05**	-	-	-

The present study provides and for the first time ever, a convincing evidence for the rare-male advantage in *D. melanogaster*. The homokaryotype *(2R)NS* is the only rare karyotype occurring frequently enough to cause concern about contribution from homokaryotypic adult males (Figure 3). The homokaryotype *(2R)NS* is the only rare chromosome found among the 2428 males and 1994 females collected from nature in this study. Since karyotypic frequencies in the two sexes did not differ significantly. We can use the pooled adult data to estimate the homokaryotype *NS* chromosomes. A total number of 1265 *NS* chromosomes was observed in the 4422 adults from nature; from

them 932 occurred in homokaryotypes. Thus we apportion the male contributions of homokaryotype *NS* Chromosomes as follow: $\frac{932}{1265}$ =0.7368.

In Table 8, line 4, the frequency of homokaryotype *NS* in the sperm stored within females at capture has been already calculated (the male contribution to offspring) and it was 35.24%. Hence the male parental contribution of *NS* homokaryotypes is estimated to 0.3524 x 0.7367 = 0.2596, the estimated total frequency of chromosomes contributed by rare male karyotypes. Since each chromosome contributed by a male equal one offspring fathered, the fraction of offspring fathered by rare male karyotypes is estimated to be 0.2596.

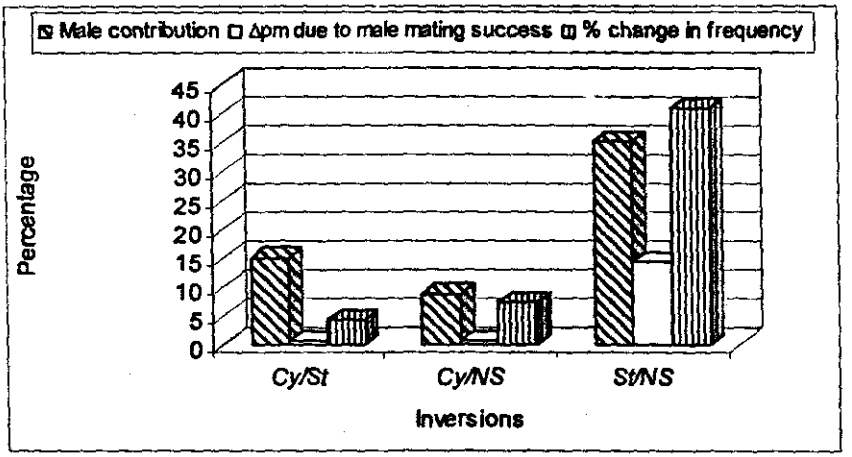


Figure 3: The change in gene arrangements due to male contribution.

The model, in Table 2, for estimating the mating success of the rare male karyotypes relative to that of the common karyotypes is outlined in Table 9. Applying this model to our data, the relative mating success of the rare karyotype, *(2R)NS*, can be estimated to be 1.33, nearly one and one third of the common karyotypes, *(2L)Cy*, *Cy/NS* and *St/St*.

The *t* test estimates can be used to test the rare male mating advantage whereas the null hypothesis that the fraction of offspring that they fathered, its frequency is equal to the frequency of rare karyotypes in adult males (A=a). The *t* estimates is 6.28 which is highly significant. The fraction of offspring fathered by the

karyotypes of rare males is significantly higher than the frequency of rare karyotypes among the adult males collected in nature.

Table 9. Calculations of rare male mating advantage in nature.

	Rare Karyotype	Common karyotype
% frequencies in adult males	20.80	79.20
% of offspring fathered	25.96	74.04
Relative mating success	1.33	1
t	6.28**	-

** $P < 0.01$

In common, the results of this study give the evidence that rare male karyotypes showed a large advantage in mating success over the common karyotypes. Salceda and Anderson (1988) showed that the effect of this component of selection will be to increase the frequencies of rare gene arrangements. Rare gene arrangements would not be rare if their frequencies continued to be increased under selection. In this study, the homokaryotypes were favored by selection when they were rare in certain months, but selection worked in favor of the homokaryotype *(2R)NS*. In cases that selection favor the rare karyotype for a long period of time, Salceda and Anderson (1988) mentioned that it seems more likely that the increased mating success of the rare karyotypes favors the retention of rare gene arrangements in the face of opposing forces such as genetic drift.

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الملخص العربي

اثبات لميزة القدرة التزاوجية النادرة في عشيرة برية لحشرة *الدروسوفيلا ميلانوجاستر*

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تم تجميع حشرات دروسوفيلا ميلانوجاستر كل شهرين خلال عام واحد . استخدمت في هذه الدراسة الأنقلابات الكروموسومية الموجودة على الكروموسوم الثاني فقط. و قد تم اعداد سلالة قياسية من دروسوفيلا ميلانوجاستر خالية من أي انقلاب على

هذا الكروموسوم. وجد اثنين من الأنقلابات هما *(2L)C* و *(2R)NS* في حالة خليطة في الحشرات البرية . تم عمل تهجين بين الذكور البرية المأخوذة من الطبيعة و الاناث القياسية الخالية من الأنقلابات على الكروموسوم الثاني و أخر بين الاناث البرية مع ذكور قياسية. أيضا أظهرت البيانات أن تكرار الانقلابات في نسل اليرقات يختلف معنويا عن الأباء المأخوذة من الطبيعة.

من الواضح أن التركيب الكروموسومى الخالي من الانقلابات كان اكثر تكرارا في الذكور و الاناث و في نسلهم بينما التركيب الكروموسومى الخليط كان اقل تكرارا في الثلاثة تراكيب الوراثية وذلك في الستة اشهر تحت الدراسه. أظهرت التقديرات المجمعة لتكرار التركيب الكروموسومي المتماثل *(2R)NS* أن تقدير اختبار *t* بالنسبة لـ Δp_m كان عالي المعنوية. القيمة المعنوية لـ Δp_m بالنسبة للتركيب الكروموسومي النادر أظهرت أن التراكيب الكروموسومية للذكر النادر، كمجموعة، لها معنوية لنجاح التزاوج أعلى من التراكيب الكروموسومية الشائعة. أوضحت هذه الدراسة أن التركيب الكروموسومى المتماثل *(2R)NS* هو الوحيد النادر و الذي وجد بتكرار كافي ليعطي أهمية لمساهمة التركيب المتماثل للذكور النادرة. و لقد قدر نجاح التزاوج النسبي للتركيب النادر بـ 1.33، تقريبا مرة و ثلث المرة للتراكيب الشائعة. و هذا يعطي دليل على أن تراكيب الذكور النادرة تظهر ميزة انتخابية أعلى في نجاح التزاوج عن التراكيب الشائعة.