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SEX-LIMITED EFFECT AND ADAPTEDNESS IN EXPERIMENTAL POPULATIONS OF *Drosophila melanogaster**

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ABSTRACT

The adaptedness of experimental populations of homozygous females and hemizygous males for different X chromosomes of *Drosophila melanogaster* was measured by average population size and productivity. The X chromosomes extracted from wild flies were 4 subvital, 4 normal and 4 supervital for female sex-limited effect on viability. The sex-limited effect was measured by the ratio of the numbers of wild-type females and males in the extraction crosses. For each chromosome two populations were founded, respectively with 25% and 75% of females. The adaptedness of the populations of the same chromosome, with different female initial frequency, was not significantly different. A significant positive correlation was observed for the viability sex-limited effect and population size or productivity, but the viability of the flies in the populations was not significantly correlated with that in the extraction crosses.

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INTRODUCTION

Only neutral variants or genetic factors which express themselves differently in the two sexes could accumulate in the X chromosome, owing to its frequent passage through the hemizygous state in the males (Dobzhansky *et al.* 1942).

In X chromosomes of *Drosophila melanogaster*, Kerr and Kerr (1952) have shown concealed variability due to genes or gene combinations, with sex-limited effect on female viability. Viability is a character influenced by a broad spectrum of genes, ranging from complete lethality to semilethal, subvital, normal, and occasionally supervital genotypes (Strickberger, 1976).

Gene effects limited to the female sex were first reported in Hymenoptera populations, particularly the Apidae, by Kerr (1951; see also Kerr and Laidlaw, 1956 and Kerr, 1969).

Evidence of female sex-limited effect genes, also for X chromosomes of *D. melanogaster*, was later obtained by Drescher (1964), Magalhães (1969), Gallo (1978), Gallo and Salceda (1974, 1978) and Renesto (1976, 1977). In a recent study of release of genetic variability through recombination, Gallo (1981) found, among 138 recombinants of normal wild X chromosomes of *D. melanogaster*, 52% with semilethal or subvital synthetic sex-limited effect on female viability. Female sex-limited effect on viability was also detected in autosomes of *D. melanogaster* (Tedeschi and Magalhães, 1967; Vartanian, 1974; Gallo and Salceda, 1978).

Such effects have been studied by means of special crosses' sequences with marked strains and wild flies, producing homozygous females and hemizygous males for different wild X chromosomes. The deviations from the expected ratio of the numbers of wild-type females and males in the progeny of the crosses are used as measures of sex-limited effect of the wild X chromosomes on the viability of the homozygous females.

All the studies mentioned were restricted to the crosses' sequences to obtain the homo-hemizygosis of the wild X chromosomes. This paper is a report on experimental populations of *D. melanogaster* carrying subvital, normal or supervital X chromosomes, searching for a relationship between the sex-limited effect and the adaptedness of the populations.

MATERIALS AND METHODS

The experiment was carried out with 12 strains of *D. melanogaster*, each homozygous for one different wild X chromosome. The homozygosis was obtained by crossing males Muller-5 with F_1 females from females collected in nature (São José do Rio Preto, SP). The crosses followed the sequence given by Gallo (1978) and the strains used were 4 subvital, 4 normal and 4 supervital, for the sex-limited effect on female viability.

For each strain two populations were founded with 240 flies, one with 25% of females, the other with 75%. The populations were maintained in bottles (240 ml) for about seven months, at 25°C, by the serial transfer technique described in Dobzhansky and Pavlovsky (1961). In short, adult flies are introduced in a bottle (corn and wheat flour-agar medium); a piece of toweling paper partially pressed into the medium provides additional surface for the flies. Once a week the flies are transferred to new bottles. When the flies begin to emerge in the bottles where the eggs were laid, they are collected and added to the new bottle, together with the adult survivors of the previous census. Each bottle is discarded after five weeks. A population consists of five bottles: one contains the adults (population size) and the other four contain eggs, larvae, pupae and newly emerged flies (population productivity). In each census adult survivors and newly emerged flies were counted by sex.

RESULTS

Sex-limited effect on viability is estimated on the basis of the sex ratio of a certain phenotype, expressed as the number of females per 100 males. Table I shows the flies sex ratio in the extraction crosses, which vary from 66 up to 148. Among each class of four chromosomes, three have nearly the same sex ratio: subvitals 2, 3 and 4 and normals and supervitals 1, 2 and 3. The mean sex ratios for subvital, normal and supervital chromosomes are 74, 106 and 131, respectively. The increase of the ratio means a decrease of the viability sex-limited effect, detrimental for the females.

Table II gives the means for population size and productivity of the flies carrying the subvital, normal or supervital X chromosomes. The initial frequency of females (25% or 75%) did not affect the adaptedness of the populations (the t Student values are all nonsignificant). It is apparent from Table II that the populations homozygous for the wild X chromosomes differ from each other in their adaptedness to the experimental environment. The mean population size ranges from 463 (chromosome N-3) to 776 flies (chromosome SV-4) and the productivity ranges from 184 (chromosome N-3) to

Table I - Number of females and males for subvital (sV), normal (N) and supervital (SV) X chromosomes obtained in the crosses' sequence (sex ratio = females/100 males).

Chromosome	Females	Males	Sex ratio
sV – 1	72	109	66
sV – 2	89	119	75
sV – 3	52	67	78
sV – 4	71	90	79
N – 1	17	17	100
N – 2	29	28	104
N – 3	59	56	105
N – 4	67	59	114
SV – 1	83	67	124
SV – 2	45	36	125
SV – 3	63	50	126
SV – 4	46	31	148

595 flies (chromosome SV-3). In fact, the homogeneity of the means of the 24 populations is rejected both for population size ($F_{23,566} = 2.92$, $P < 0.005$) and productivity ($F_{23,542} = 5.57$, $P < 0.005$).

The sex ratio means for population size and productivity, given in Table III, are higher than the respective sex ratio in the extraction crosses. All the ratios correspond to normal or mostly to supervital viability. In 7 populations (29%) the sex ratio means for population size and productivity differ significantly, meaning a difference in young-adult viability of both sexes, higher for the females in 3 cases, lower in the other 4. All the 7 cases are among subvital or supervital chromosomes. When the means of the populations of each chromosome type are compared (Table III), only three differences are significant: population size sex ratio of populations N-3 ($t_{30} = 2.448$, $P < 0.05$) and productivity ratio of populations sV-2 ($t_{29} = 2.192$, $P < 0.05$) and N-1 ($t_{28} = 3.463$, $P < 0.01$). Again, it is apparent from Table III that the populations differ from each other as to the sex ratio: those of population size range from 116 (chromosome N-1) to 175 (chromosome sV-4) and those of productivity range from 115 (chromosome sV-1) to 177 (chromosome N-2). The F values for heterogeneity of the means either for productivity ($F_{23,342} = 2.96$) or population size sex ratio ($F_{23,342} = 8.37$) are significant at the 0.005 level.

Table II - Means and standard errors for population size and productivity of the populations of subvital (sV), normal (N) and supervital (SV) X chromosomes, starting with 25% or 75% of females.

Chromosome	Population size			Productivity		
	25%	75%	t	25%	75%	t
sV – 1	503 ± 42	525 ± 39	0.384	321 ± 44	322 ± 39	0.017
sV – 2	584 ± 43	568 ± 49	0.305	318 ± 46	343 ± 42	0.408
sV – 3	587 ± 44	545 ± 48	0.643	485 ± 53	488 ± 57	0.039
sV – 4	571 ± 57	607 ± 56	0.450	439 ± 62	387 ± 45	0.679
N – 1	616 ± 53	651 ± 37	0.547	395 ± 43	376 ± 43	0.310
N – 2	620 ± 57	626 ± 69	0.068	458 ± 48	424 ± 53	0.476
N – 3	463 ± 39	469 ± 43	0.103	228 ± 37	184 ± 26	0.959
N – 4	604 ± 60	583 ± 50	0.268	505 ± 58	490 ± 54	0.188
SV – 1	495 ± 37	514 ± 29	0.402	523 ± 51	548 ± 42	0.378
SV – 2	656 ± 60	696 ± 50	0.510	585 ± 65	584 ± 47	0.012
SV – 3	713 ± 62	699 ± 50	0.177	595 ± 48	549 ± 54	0.637
SV – 4	776 ± 64	752 ± 60	0.273	549 ± 46	539 ± 47	0.152

The number of measurements was approximately 25; t for the differences between means.

The average population size, productivity and sex ratio of the eight populations of each class of chromosome are given in Table IV. Except for population size sex ratio, the F values indicate heterogeneity of the means. It can be seen that population size increases in the order of the subvital, normal and supervital populations. Also, the supervital populations have the highest productivity. The difference between the sex ratios of population size and productivity, significant for the supervital chromosome populations, indicates higher viability for females than for males.

The correlation coefficient between productivity and population size of the 24 populations is $r = 0.650$ ($t_{22} = 4.012, P < 0.001$). This positive correlation means that the populations which produce more flies tend also to have larger population size. However, the correlation is far from complete. Populations of the chromosome SV-1 have high productivity for one of the lowest population sizes.

Table III -Means and standard errors of the sex ratio of population size and productivity of the populations of subvital (sV), normal (N) and supervital (SV) X chromosomes, starting with 25% or 75% of females.

Chromosome	25%			75%		
	size	productivity	t	size	productivity	t
sV – 1	109 ± 4	138 ± 8	3.256**	115 ± 3	140 ± 8	2.790**
sV – 2	143 ± 6	151 ± 8	0.809	130 ± 5	131 ± 5	0.138
sV – 3	119 ± 8	117 ± 7	0.196	129 ± 7	124 ± 8	0.463
sV – 4	175 ± 9	137 ± 5	3.627**	160 ± 11	135 ± 8	1.831
N – 1	148 ± 16	116 ± 7	1.869	141 ± 8	150 ± 7	0.848
N – 2	157 ± 11	150 ± 8	0.467	177 ± 13	169 ± 11	0.479
N – 3	128 ± 5	152 ± 14	1.629	154 ± 9	159 ± 12	0.328
N – 4	145 ± 5	150 ± 10	0.437	163 ± 12	148 ± 10	0.977
SV – 1	120 ± 5	122 ± 4	0.302	117 ± 5	130 ± 4	2.082*
SV – 2	133 ± 8	128 ± 5	0.513	155 ± 9	124 ± 5	3.098**
SV – 3	163 ± 7	136 ± 4	3.353**	163 ± 7	126 ± 4	4.752**
SV – 4	153 ± 6	138 ± 6	1.888	154 ± 8	135 ± 7	1.802

The number of measurements was approximately 15; t for the differences between means; *: $P < 0.05$; **: $P < 0.01$.

The most interesting results are those concerning correlation analyses. The r values between the crosses' sex ratio (Table I) and those in the populations (Table III) are both nonsignificant: for population size $r = 0.323$ ($t_{22} = 1.601$, $P > 0.05$) and for productivity $r = -0.048$ ($t_{22} = 0.225$, $P > 0.05$). Also nonsignificant is the correlation between the adult (population size) and young (productivity) flies' sex ratio ($r = 0.358$, $t_{22} = 1.798$, $P > 0.05$). Figure 1 shows the correlation between population size or productivity means (Table II) and the sex ratio of the crosses (Table I). The correlation coefficient for population size is $r = 0.580$ ($t_{22} = 3.340$, $P < 0.01$) and that for productivity is $r = 0.622$ ($t_{22} = 3.726$, $P < 0.01$). These correlations are also incomplete. However, the r value for population size rises to 0.915 ($t_{18} = 9.622$, $P < 0.001$), if populations N-3 and SV-1 are excluded and the productivity r value rises to 0.824 ($t_{20} = 6.504$, $P < 0.01$) excluding the N-3 populations.

Table IV - Average mean population size, productivity and sex ratio, with their standard errors, of the populations of subvital (sV), normal (N) and supervital (SV) X chromosomes.

Populations	size	productivity	Sex ratio		
			size	productivity	t_{14}
sV	561 ± 12	388 ± 26	135 ± 8	134 ± 4	0.112
N	579 ± 26	382 ± 42	152 ± 5	149 ± 5	0.267
SV	663 ± 37	559 ± 9	145 ± 7	130 ± 2	2.165*
$F_{2,21}$	4.34*	12.10**	1.53	6.71**	

F for homogeneity; t for the difference between means; * : $P < 0.05$; **: $P < 0.01$.

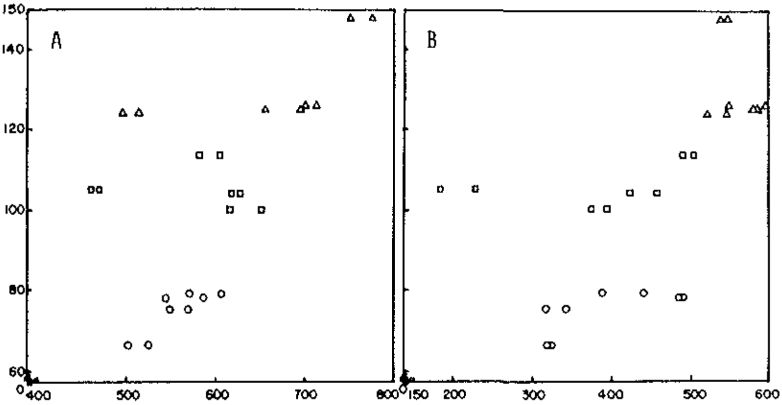

Figure 1 - Correlation between population size in A or productivity in B (abscissa) of populations of subvital (circles), normal (squares) and supervital (triangles) X chromosomes and sex ratio (ordinate) in the crosses' sequence.

DISCUSSION

Adaptedness is a state of being adapted and refers both to survival and to reproduction (Dobzhansky, 1968). The adaptedness of a genotype or a group of genotypes is conditioned by the ability to survive and reproduce in a given environment. Population size and productivity, as measurable results of a population's ability to transform the available food and energy into living matter of its own kind, have been used to estimate the adaptedness of experimental populations of *Drosophila* species (*e.g.* Ayala, 1968; Mourão *et al.*, 1972; Vartanian, 1975; Benado *et al.*, 1976).

The adequacy of the genetic load as a measure of the adaptedness of populations has been questioned. According to Wallace (1968) the genetic load is a rigorously defined quantity, although it is not a concept that necessarily serves as a measure of the well-being of a population. Genetic load, by itself, tells very little about a population's ability to continue from one generation to the next.

Together with average Darwinian fitness, the genetic load was pointed out by Mourão *et al.* (1972) as a measure that cannot be taken as a general index of how well adapted a population is to its environment.

The adaptedness of the populations studied proved to be positively correlated with the sex-limited effect measured in the extraction of the chromosomes. The extraction sex ratio was greatly modified in populations, denoting an improvement of female viability. The incomplete positive correlations found between sex-limited effect and population size or productivity seem to contradict the observations of Wallace (1968) and Mourão *et al.* (1972). The sex ratio in the crosses proved to be a strong predictive element of the adaptedness of the populations. The results also indicate the possibility of a role of subvital sex-limited effect genes in the adaptedness of the populations. The sex-limited effect genes may be a part of the concealed genetic variability, which in homozygous condition may increase female viability and produce a high adaptedness of the population, as a benefit of the genetic load.

The subvital chromosomes, more than the normal and supervital ones, have produced, in homozygous condition in the populations, an increase in female viability. When comparing the means for the sex ratio in the crosses (Table I) with those in the populations as an average of population size and productivity (Table IV), the latter are found to be nearly 2.0, 1.5 and 1.0-fold the former, respectively, for the subvital, normal and supervital chromosomes.

The viability genes have then two faces that might be met in natural populations. While the heterozygosis of normal chromosomes may release an enormous amount of detrimental effects through recombination (Gallo, 1981), the homozygosis of genes of the subvital chromosomes may strongly improve female viability. This subject requires further study.

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RESUMO

O estado-de-ser-adaptado de populações experimentais de *Drosophila melanogaster,* de fêmeas homozigotas e machos hemizigotos para diferentes cromossomos X, foi medido pelo tamanho e produtividade das populações. Os cromossomos, extraídos de moscas da natureza, eram 4 subvitais, 4 normais e 4 supervitais quanto ao efeito na viabilidade das fêmeas. Esse efeito, limitado ao sexo, foi medido pela proporção entre fêmeas e machos selvagens nos cruzamentos de extração dos cromossomos. Para cada cromossomo foram fundadas duas populações, respectivamente com 25% e 75% de fêmeas. As populações de mesmo cromossomo não diferiram significativamente quanto ao estado-de-ser-adaptado. Observou-se uma significativa correlação positiva entre o efeito limitado ao sexo dos cromossomos e o tamanho ou produtividade das respectivas populações, mas não foi observada correlação significativa entre a viabilidade das moscas, nas populações e nos cruzamentos.

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