EFFECTS OF GENETIC BACKGROUND ON THE COMPETITION BETWEEN THE *asc* AND *FM6* CHROMOSOMES OF *DROSOPHILA MELANOGASTER*

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Abstract

The *asc* and *FM6* chromosomes of *D. melanogaster* were studied in competition in two differing genetic backgrounds, that of the *FM6* strain and that of the combined *Ore-R* and *FM6* strains.

The competition between the *asc* and *FM6* chromosomes led to a selection against the *FM6* chromosome in favour of the *asc* chromosome for both sexes in both backgrounds. Varying the genetic background not only changed the rate of selection but also tended to increase the population size and number of recombinants for the combined background. A tendency was observed towards the occurrence of a seeming or apparent "balanced polymorphism" in the *FM6* background compared with "complete" elimination of the *FM6* chromosome in the combined background.

The reasons for selection against the *FM6* chromosome are: the relative fitness of *asc* versus *FM6* in that *asc* appears to be the more "fit" of the two; the fact that homozygous *FM6* females are sterile and therefore contribute nothing to the population in the way of future offspring; the fact that *FM6* males are poorer maters due to the presence of the recessive mutation *y* (yellow body colour); and background effect.

The evidences of background effect are: the larger population size of the combined background compared with the *FM6* background; a greater number of recombinants in the combined background versus the *FM6* background; the establishment of a balanced polymorphism with the *FM6* but not with the combined background; and selection rates in the *FM6* versus the combined background. The background effect is brought out through heterozygosis, inversional differences, and recombination effects in *asc*/*FM6* heterozygotes.

An appropriate statistical method is presented which can be used to analyse for the presence of background effect involving selection between sex-linked variants that have overlapping generations.

I. INTRODUCTION

Reed and Reed (1950) and Merrell (1953) showed that "selective mating" could lead to a reduction in chromosome frequency and the possible elimination of homozygous phenotypes. Furthermore, when dealing with sex-linked variants this chromosomal reduction could proceed more rapidly than the reduction of autosomal chromosomes comparable in effect. Also, Petit (1958), Ehrman (1965), and Ehrman

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et al. (1965), using sex-linked variants, showed that when two kinds of males are present in a population the mating success of each type of male may depend upon its frequency relative to the other kind. They reported that "rare" males seem to mate more frequently than the "common" males. This implies that when one type of chromosome becomes rare due to selection there might be a slight increase in its frequency until a "balanced polymorphism" is obtained.

The purpose of the study reported herein was to determine whether either of these factors could act upon a single population of sex-linked variants at the same time and whether altering the genetic background for the autosomes had any influence on these factors. In this investigation, two complex *X* chromosomes (*asc* and *FM6*) were put into two different genetic backgrounds, *FM6* and combined *Ore-R*+*FM6*. By competing *asc* against *FM6* chromosomes in different genetic backgrounds it can be determined whether the autosomes exert some type of influence on the nature of the competition between the *asc* and *FM6* chromosomes.

II. Materials and Methods

The strains of *Drosophila melanogaster* used were as follows (Lindsley and Grell 1967):

asc/*asc*; *SM1*/*Pm*; *TM2*/*CSb*
FM6/*Ext*; +/+; +/+
wild type *Ore-R*, designated as *R*/*R*; *R*/*R*; *R*/*R*

To obtain the desired genetic background stocks (*asc* in *FM6* background and *asc* and *FM6* in *Ore-R* background) crosses were made as shown in Figure 1, using 500 male and 500 female flies of the appropriate strains.

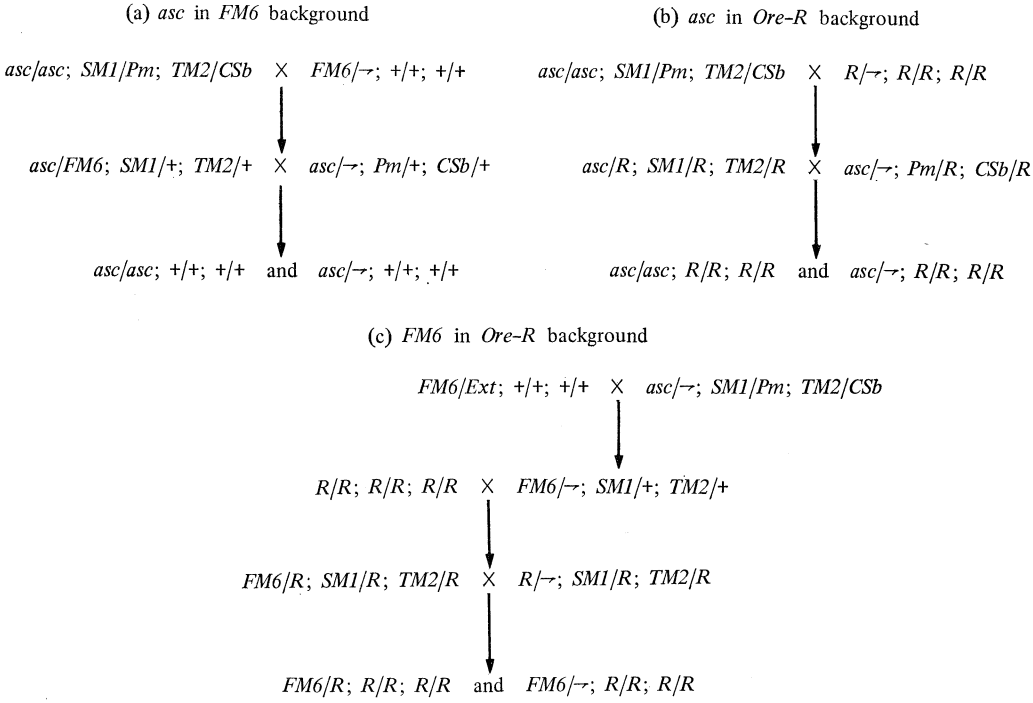

Fig. 1.—Details of the crosses which were made to establish stocks with genetic backgrounds suitable for the competition experiments.

The initial cage populations were established as shown in Figure 2, using 500 virgin *FM6/asc* heterozygous females and 250 *asc* and 250 *FM6* males of the appropriate background population stocks. After a period of 7 days the adults were removed from the cages and either used to initiate another cage or discarded; the vial rotation was started at this time. Random sampling was then performed every 2 weeks, the first sampling occurring 2 weeks after the cage was started (one generation=2 weeks), and approximately one-eighth of the total adult population was scored as to phenotype (*asc/asc*, *asc/FM6*, *FM6/FM6* females and *asc/Y*, *FM6/Y* males) for the determination of chromosome frequencies. Each type of background was run in triplicate.

asc versus *FM6* in *FM6* background

$$asc/asc;\ +/+;\ +/+ \times FM6/{\rightarrow};\ +/+;\ +/+ \longrightarrow FM6/asc;\ +/+;\ +/+ \text{ and } asc/{\rightarrow};\ +/+;\ +/+$$

$$FM6/Ext;\ +/+;\ +/+ \times asc/{\rightarrow};\ +/+;\ +/+ \longrightarrow asc/FM6;\ +/+;\ +/+ \text{ and } FM6/{\rightarrow};\ +/+;\ +/+$$

asc versus *FM6* in combined (*FM6* and *Ore-R*) background

$$asc/asc;\ R/R;\ R/R \times FM6/{\rightarrow};\ +/+;\ +/+ \longrightarrow asc/FM6;\ R/+;\ R/+ \text{ and } asc/{\rightarrow};\ R/+;\ R/+$$

$$FM6/R;\ R/R;\ R/R \times asc/{\rightarrow};\ +/+;\ +/+ \longrightarrow asc/FM6;\ R/+;\ R/+ \text{ and } FM6/{\rightarrow};\ R/+;\ R/+$$

Fig. 2.—Details of the crosses which were made to establish cage populations in the experiments on competition between the *asc* and *FM6* chromosomes.

Cage triplication was considered to be adequate as the number of offspring obtained from the experimental run was near 5000 adult flies, giving a pooled total population of 15,000 adult flies. The results of χ^2 and Student's *t*-tests clearly showed that averaging the data from the three cages was appropriate for comparisons of the genetic backgrounds as no evidence of significant differences between replicates was found.

The construction, design, usage, and maintenance of the population cages was as described by Bennett and Ostrowski (1969), with the following modifications:

1. there were spaces for five rows of six vials with medium,
2. there were four side holes allowing for control of humidity, and
3. a hole-saw was used to obtain a tight grip by gasket on the vial.

For the duration of the experiment the population cages were kept in an incubator at a temperature of 25 ± 1°C.

III. Results

The data indicated that there was extreme selection against the *FM6* chromosome in each of the genetic backgrounds.

To facilitate comparisons theoretical expectations were calculated according to the Hardy–Weinberg Law extension for sex-linked variants (Li 1967) using the following assumptions:

1. The population was panmictic and infinitely large.
2. The population was randomly and uniformly distributed.
3. Mutation and migration did not occur.
4. The gene frequencies were the same in both sexes.
5. The fitness (*asc/asc*)=fitness (*asc/FM6*)=1.

6. The fitness $(FM6/FM6)=0$.
7. The fitness $(asc/Y)=$fitness $(FM6/Y)=1$.
8. There was no background effect.

Figure 3 shows that in the beginning there was a heterotic effect, and that this heterotic effect and a favourable selection of the *asc* chromosome "suggested" the establishment of a polymorphism with the *FM6* chromosome at a low frequency for the *FM6* background. In the case of the combined *FM6* + *Ore-R* background there

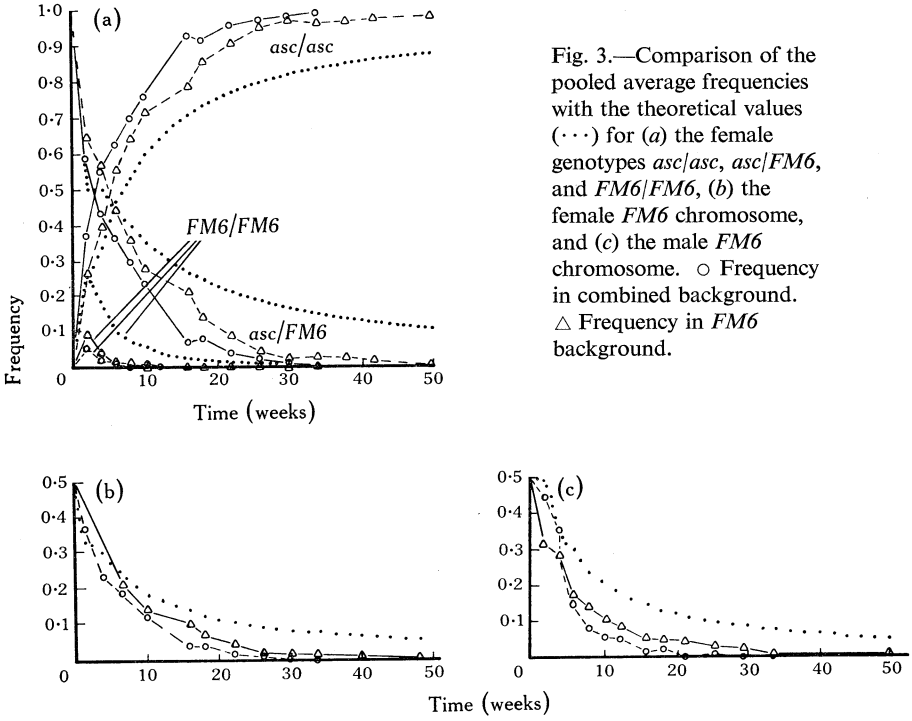

Fig. 3.—Comparison of the pooled average frequencies with the theoretical values (· · ·) for (*a*) the female genotypes *asc*/*asc*, *asc*/*FM6*, and *FM6*/*FM6*, (*b*) the female *FM6* chromosome, and (*c*) the male *FM6* chromosome. ○ Frequency in combined background. △ Frequency in *FM6* background.

seemed to be a greater heterosis in the beginning, but the frequency of the *FM6* chromosome later decreased at a more rapid rate because of selection against it than was the case in the *FM6* background. A polymorphism was not established for the *FM6* chromosome in the combined background; instead, it was eliminated by selection favouring the *asc* chromosome.

Figure 4(*a*) shows that the pooled average population size for the combined background was larger than that for the *FM6* background. Again, the reason for this difference in population sizes could ostensibly be due to the greater heterosis occurring in the combined background.

The unexpected high occurrence of crossovers between *asc* and *FM6* chromosomes in the combined compared with the *FM6* background (crossovers in combined : *FM6* background exceeding 74 : 1; see Fig. 4*b*) could be compared to an immigration effect where new members are being added to the population, with a concurrent introduction of new chromosomes to that population.

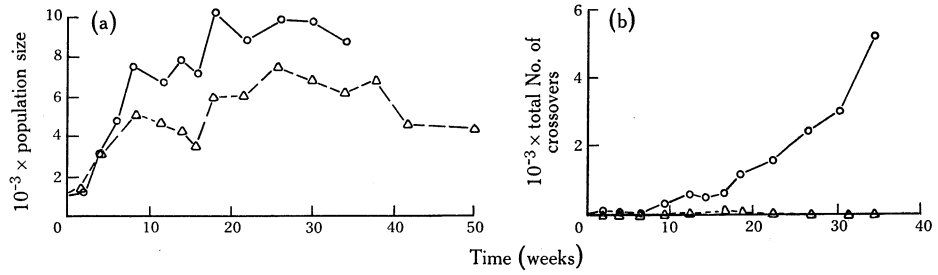

Fig. 4.—(*a*) Comparison of the pooled average population size per cage for the *FM6* (△) and the combined backgrounds (○). (*b*) Pooled average total numbers of possible recombinants in the *FM6* (△) and combined backgrounds (○).

To ensure that the crossovers were a product of combining the backgrounds the autosomes were cytologically examined for inversions. Since autosomal inversions were found (McKay 1971) the existence of *X* chromosome crossovers could influence both the degree of heterosis and the elimination rates. The mechanism for this increase in numbers of crossovers caused by the autosomal inversions is at present unknown.

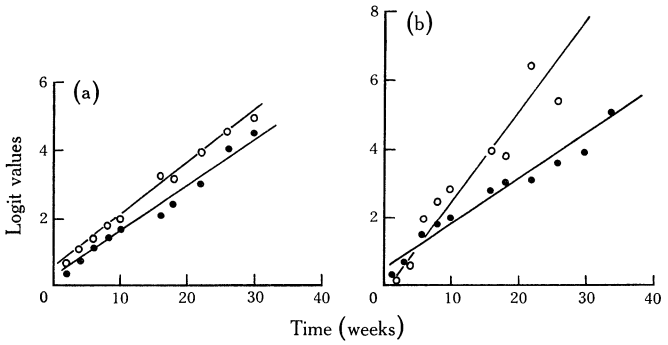

Fig. 5.—Logit comparison of (*a*) the female *asc* chromosome and (*b*) the male *asc* chromosome in the *FM6* (●) and the combined backgrounds (○).

A statistical analysis was done to compare the curved lines obtained for the chromosome frequencies of the *asc* chromosome for both sexes. (Only the *asc* chromosomes were analysed rather than both because the sum of the *asc* and *FM6* chromosomes for each sex equals one.) The curved lines were transformed to linear lines so that a linear regression and a test for parallelism could be performed. The transformation used was the logit (Crow and Kimura 1970) (see Fig. 5). The results showed that the two backgrounds, *FM6* and combined *Ore-R*+*FM6*, were significantly different in their effect on selection of the *asc* versus the *FM6* chromosome (Tables 1 and 2).

IV. Discussion

The reasons for selecting the *asc–FM6* system over other sex-linked variants were:

1. Its uniqueness in that it permitted simplifications both of a theoretical and a practical nature. These kinds of simplifications depended in particular on the availability of a chromosome such as *FM6*.

TABLE 1

ANALYSIS OF DIFFERENCE BETWEEN TWO REGRESSIONS USING LOGIT ON THE FREQUENCY OF THE FEMALE *asc* CHROMOSOME

Source of variation	D.F.	Σx^2	Σxy	Σy^2	$\frac{(\Sigma xy)^2}{x^2}$	D.F.	S.S.†	D.F.
Within *FM6* background	32	64·3	462·7	3600	59·5	1	4·9	31
Within combined background	32	194·3	771·0	3600	165·1	1	29·2	31
Two regressions					224·6	2	34·0	62
Within *FM6*+combined backgrounds (one regression)	64	258·6	1234	7200	211·4	1		63
Regression coefficient (two *v.* one)					13·2	1		

$F = 13{\cdot}20552/(34{\cdot}04513 \div 62) = 24{\cdot}048733$***

*** $P < 0{\cdot}001$. † Residual.

TABLE 2

ANALYSIS OF DIFFERENCE BETWEEN TWO REGRESSIONS USING LOGIT ON THE FREQUENCY OF THE MALE *asc* CHROMOSOME

Source of variation	D.F.	Σx^2	Σxy	Σy^2	$\frac{(\Sigma xy)^2}{x^2}$	D.F.	S.S.†	D.F.
Within *FM6* background	38	53·9	414·5	3652	47·1	1	6·8	37
Within combined background	38	315·6	988·1	3652	267·4	1	48·3	37
Two regressions					314·4	2	55·1	74
Within *FM6*+combined backgrounds (one regression)	76	369·5	1403	7303	269·4	1	100	75
Regression coefficient (two *v.* one)					45·0	1		

$F = 45{\cdot}038/(55{\cdot}0537 \div 74) = 60{\cdot}5375$***

*** $P < 0{\cdot}001$. † Residual.

2. Each possible genotype (*asc*/*asc*, *asc*/*FM6*, and *FM6*/*FM6* females and *asc*/*Y* and *FM6*/*Y* males) in the population exhibited a different phenotype and direct chromosome measurements could be made whether the population was in equilibrium or not.
3. Because of the inversion balancers in the homologues in this system one obtained suppression of crossing-over, which meant that the sex chromosomes maintained their integrity throughout the experiment. (Some crossing-over occurred, but all crossovers were detectable, thus making their removal quite easy.)

One of the reasons for the possible polymorphism of *asc* and *FM6* chromosomes in the *FM6* background could be the seeming "lingering" effect of the heterosis for these chromosomes.

Because the *FM6* chromosome contains the mutant gene *y* (yellow body colour) *FM6* males are poor maters (Grell and Lewis 1956), which may possibly allow selective mating to occur. That selective mating could be one of the reasons for the reduction in the frequency of the *FM6* chromosomes for both backgrounds, and for the elimination of the homozygous *FM6* females in the combined background, was clearly shown by Barker (1962) in his studies of selective mating using sex-linked variants of *D. melanogaster*.

Reed and Reed (1948), working with the *M-5* (*Basc*) chromosome (an *X* chromosome which contains the *Bar* eye mutation in addition to the same inversions and mutations as the *asc* chromosome), found that it could confer semi-sterility and poor viability upon both males and females that are hemizygous or homozygous for it. Its presence in the heterozygous female, on the other hand, resulted in a combination that was sufficiently advantageous to hinder its extinction by selection.

Levitan (1954) has contended that individuals heterozygous for different chromosome arrangements (inversion heterozygotes) have higher adaptive values while homozygotes are inferior to them in survival and reproduction, and that maintenance of a polymorphism depends on the "adaptive superiority of the heterozygotes", a condition also abundantly demonstrated in *D. pseudoobscura* by Dobzhansky and his many co-workers (Dobzhansky 1965). However, Bennett (1958) and Li (1967) point out that with respect to sex-linked variants heterosis in the females by itself is neither a necessary nor sufficient condition for establishing or maintaining a stable equilibrium.

In 1932, Schultz and Redfield (Morgan *et al.* 1932) confirmed Sturtevant's observation (1919) that inversions in the first and second chromosomes increased crossing-over in the third chromosome. It was not until later that Steinberg (1936) found that autosomal inversions increased crossing-over in the *X* chromosome. Since in the present study cytological examinations revealed the presence of autosomal inversions in the combined background, it appears that this occurrence of relatively large numbers of *X* chromosome crossovers (recombinants) with the combined background is due to (1) the "Sturtevant effect", and/or (2) possibly the background itself. One circumstance in which the background could cause an increase in recombinants might have arisen if the autosomes, +/+, of the *FM6* stock (*FM6*/*Ext*; +/+; +/+) contained a few inversions as a result of the original construction of that stock. Then when the crosses were conducted to establish the initial population of 500 virgin heterozygous *asc*/*FM6* females and 250 *asc* and 250 *FM6* males of the combined background (see Fig. 2), some of the heterozygous *R*/+ autosomes could have possessed inversions which may subsequently have increased crossing-over in the *X* chromosome.

Rasmuson (1954), in conducting some experiments involving selection between different chromosomes, noted that as the selection progressed the numbers of crossovers greatly increased. Since a result similar to Rasmuson's was obtained with the combined background it seems unlikely that selection would directly increase crossing-over in a case such as the present one. It would appear more logical to say that as the numbers of recombinants increased they aided in increasing selection against one type of chromosome within the population, so furthering its possible elimination from that population, as with the *FM6* chromosome in the combined background.

Frydenberg (1963, 1964) reported that the *Sb*^{w} (Stubble bristles) mutant showed over-dominance and persisted in cage populations only when *Sb*^{w} was associated with an inversion. When *Sb*^{w}, which is a homozygote lethal, was freed from the inversion it was rapidly eliminated, almost independently of background genotype (Chung 1967). In the present study a corresponding type of heterosis accounts at least in part for the apparent establishment of a balanced polymorphism in populations with the *FM6* background. Unequal fitnesses of the *asc* and *FM6* males probably also account for part of the balanced polymorphism.

Whether selection for rarity (mating of rare males more frequently than common males) could partially aid in accounting for the seeming or apparent establishment of a polymorphism in the *FM6* background is hard to ascertain, in that not enough time had elapsed before cage termination for a stable balanced polymorphism to come into existence at a low frequency for the *FM6* chromosome. Because of this one cannot truly favour or disfavour selection of rarity as a possible factor concerning the seeming or apparent establishment of a polymorphism for the *FM6* background. However, it was noted that at near the time of cage termination the frequency of the *FM6* chromosome was fluctuating about a low value, although still on a slight decline. This may possibly suggest that given more cage running time the *FM6* chromosome might eventually have been eliminated in the *FM6* background.

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