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Genetic Instability in Mass-rearing Colonies of a Sex-linked Translocation Strain of *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae) During a Field Trial of Genetic Control

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Summary. Genetic breakdown occurred in a strain of *Lucilia cuprina* constructed for the purpose of genetic control of this pest. The strain incorporated autosomal recessive eye colour mutations linked in repulsion with a translocation involving the Y chromosome (male-determining) and two autosomes. In the original strain females had white eyes and males were wild type. The spontaneous breakdown involved a failure of the sex-limited inheritance of the eye colour mutations. Characteristically the frequency of white-eyed males increased rapidly in the strain, whereas the frequencies of the three other phenotypically recognizable breakdown products did not. This suggested that the white-eyed males had a selective advantage over both the wild type males and the other breakdown products.

Genetic analysis revealed that recombination, which is normally rare in *L. cuprina* males, is considerably more frequent in the presence of a Y-autosome translocation, but that recombination alone was insufficient to account for the rate of increase of the white-eyed males in the colony. Genetic and cytological analysis of the breakdown products revealed that reversion of the multi-break translocation also occurred, and that many of the white-eyed males had either only a Y-single-autosome translocation or no translocation at all; thus these males were more fertile than the wild type multi-translocation males. In addition, under colony cage conditions the white-eyed males may have had a behavioural advantage in competition with the wild type males.

Key-words: Genetic control – Y chromosome – Male recombination – *Lucilia cuprina* – Population genetics – Mass rearing

Introduction

The use of Y-autosome translocations linked in repulsion with eye colour mutations for genetic control of insect pests which lack meiotic recombination in males, has recently been proposed (Whitten et al. 1977). Semi-sterility of the translocation plus the lethal effect in the field of homozygosis for the eye colour mutations can in theory lead to rates of genetic death greater than 90% per generation (Whitten et al. 1977; Whitten 1979).

During two field seasons from the spring of 1976 to the autumn of 1978 a field trial of the translocation/eye-colour-mutation technique was conducted against a population of *Lucilia cuprina* (Wiedemann) near Canberra (Foster et al. in prep.). The strain used for the bulk of this trial incorporated an eye colour mutation on each of chromosomes 3 and 5 and a translocation involving the Y chromosome and chromosome 3 and 5. Initially, females of this strain had white eyes and males wild-type eyes, but it soon became apparent that the strain was unstable, as evidenced by the appearance of large numbers of white-eyed males in the mass-rearing colonies. Since white-eyed flies are unable to survive in the field (Whitten et al. 1977) this led to considerable wastage of effort during the trial, and necessitated several selections of the colonies for wild-type males. This paper describes this type of strain breakdown and presents a preliminary account of the mechanism of breakdown.

Materials and Methods

Mutations and Strains

The symbols of mutations mentioned in this paper are as follows: *ar* (featherless aristae), *ru* (rusty body) and *w* (white eyes) on chromosome 3; and *bz* (bronze body), *Rdl* (Dieldrin resistance), *mv* (= m_1) (missing M1 veins), *to* and to^2 (topaz eyes) on chromosome 5. The eye colour mutations *to* and to^2 are allelic, and the phenotype of to^2/to (orange eyes) is distinguishable from both to^2/to^2 (scarlet) and *to/to* (yellow). For descriptions of these mutations see Whitten et al. (1975).

The sex-linked translocation T(Y;5;3)23-1 was derived by irradiating adult males carrying the sex-linked translocation, T(Y;5)23 (Foster et al. 1978), and selecting offspring for pseudolinkage of chromosome 3 markers with chromosome 5 markers and sex. Both rearrangements carry *Rdl* on the left arm of chromosome 5.

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Strain T23-1 was constructed by crossing homozygous *w;to* females to males carrying T(Y;5;3)23-1 and then crossing F_1 male offspring to homozygous *w;to* females. The *w;to* stock used for this had been derived from an outcross of a laboratory *w;to* strain to a culture established from flies collected from the field in the autumn of 1976. The chromosomal and genotypic structure of males of strain T23-1 is diagrammed in Figure 1.

Generally three lines of strain T23-1 were maintained in the rearing colony at any one time, separated by one week from each other on a three-week generation cycle. In 1976-7 each colony contained 12 cages, each with approximately 10,000 flies. The number of cages was increased to 64 during the 1977-8 season.

On three occasions during the two seasons the colonies were selected by taking approx. 5,000 white-eyed females and 1,000 wild-type males from a colony and founding a new line from these individuals. Further details are given in Results.

Rearing Procedures

Adult flies in the cages were provided with excess sugar and water, and sufficient protein in the form of a paste of homogenized sheep liver to permit ovarian development.

Eggs were collected on dishes containing liver strips or a small amount of liver paste, and were incubated overnight to allow them to hatch.

Larvae were reared on trays containing a medium consisting of minced ovine or bovine liver, cotton linters, and water in the approximate proportions of 10:1:3 by weight.

When fully fed, the larvae left the medium over a period of 2-3 days and were collected in vermiculite or sawdust. A portion of the larvae were retained for colony maintenance and the remainder packaged for aerial release (Foster et al. 1978).

Sampling for Eye Colour and Sex Ratio

Each generation, samples of approximately 1,000 individuals from each colony were scored for eye colour and sex. Two methods of sampling were used: (1) mature larvae were taken from the mass-rearing trays on the first of the two main days of larval drop-off, were allowed to develop to maturity, and scored; (2) first-instar larvae were collected from the egging dishes of each of 12 colony cages, pooled and reared on liver to the pupal stage, and then the sample of 1,000 individuals was obtained.

The collection-tray sampling procedure yielded significantly[1] fewer females than the egging-dish method ($p < 0.0001$), because females develop more slowly than males and leave the medium later. Within each sex, however, the two sampling methods yielded no significant differences with regard to eye mutant phenotypes (for males $0.5 < p < 0.6$, and for females $0.10 < p < 0.12$). Thus eye colour proportions obtained by either procedure were used interchangeably, and where both procedures were used for a given rearing the results were pooled.

Results

Frequency of Eye Colour Mutants in the Mass-rearing Colonies

The proportions of mutant males in the mass-rearing colonies for 1976-7 are shown in Figure 2. Lines A and C were constructed separately by mating *w;to*♀♀ to T(Y;5;3) 23-1♂♂ in the genetics laboratory before their introduction to mass rearing. Line B was established from offspring of the week 7 culture of line A. However, on two occasions flies from lines A and B were mixed with line C (Fig. 2). Approximately 52% of the flies in the week 6 culture were

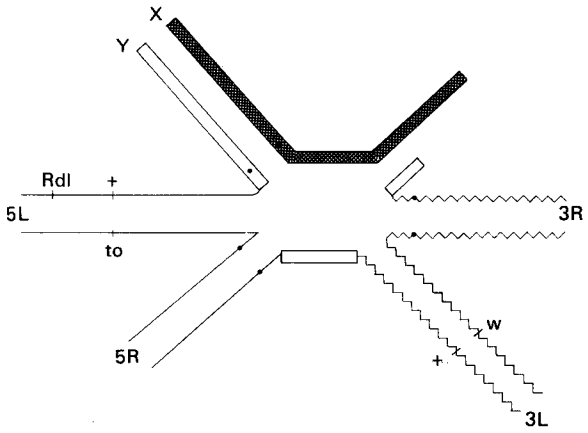


Fig. 1. Diagrammatic representation of chromosomes 3, 5 and the sex chromosomes in males of strain 'T23-1'. The structure of T(Y;5;3)23-1 is after Bedo (1980)

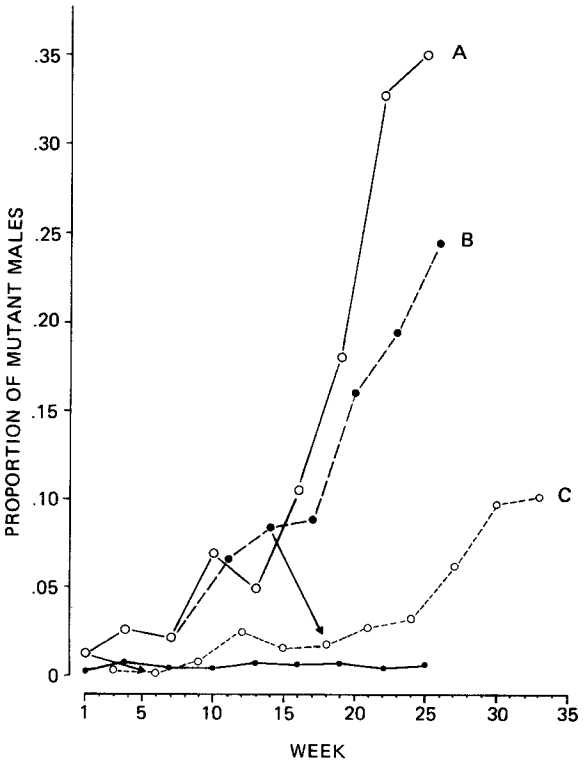


Fig. 2. Proportions of mutant males in mass rearing colonies during 1976-7. o—o line A, white eyed males: •—• line A, yellow-eyed males; •– –• line B, white-eyed males; o– –o line C, white eyed males; ⟶ addition of flies from lines A or B to line C

1 Using a χ^2 test for homogeneity on the pooled results for 20 mass rearings in 1976-7 in which both sampling methods were used.

offspring of line A, and 12% of the flies in the week 18 culture came from line B.

The proportion of white-eyed males in lines A and B increased rapidly to 35.0% and 24.5%, respectively, in 9 generations, after which these lines were terminated (Fig. 2).

Line C differed from line A initially, both in having a lower proportion of mutant males and in showing a lower rate of increase in this proportion. The proportion of white-eyed males increased more rapidly following the addition of flies from line B in generation 6 (week 18), exceeding 10% at the end of the season.

The frequency of yellow-eyed individuals of either sex remained low in all lines, as shown in Figure 2 for line A males. For all 1976-7 samples the mean frequency of yellow-eyed flies was 0.46% (range 0-0.9%) in males and 0.47% (range 0-1.2%) in females.

New lines of strain T23-1 for the 1977-8 season were established by selecting wild type males and white-eyed females from line C at the beginning of the season, and twice later in the season. White-eyed males accumulated in these lines (Fig. 3) at rates similar to those experienced in lines A, B and C (Fig. 2). The proportion of white-eyed males reached high levels in lines J,K and L, which were maintained without artificial selection over a longer period of time (Fig. 3).

None of the 29,471 females examined during 1976-7 had wild-type eyes. In the 1977-8 season no wild type females (N = 29,628 for weeks 1-35) were detected until week 36. From then onward wild type females were recovered in line J at a constant rate (mean = 0.73%, N = 4250) each generation except the last one, when none were recovered (N = 496). After week 36 only 1 wild-type female was detected in line L, and none in line K (combined N = 7916). Two wild type females from line J were progeny-tested by mating them to *w/w;to/to* males, and both proved to be *w/+;to/+*.

Genetic Recombination in Males

The appearance of white and yellow-eyed males, and yellow-eyed and wild type females in T23-1 suggests that genetic recombination was occurring in the males of this strain. Until recently genetic recombination has not been observed in males of *L. cuprina* (Foster and Whitten 1974; Whitten et al. 1975); however Konovalov (1977) reported that recombinant offspring are occasionally produced by males heterozygous for Y-autosome translocations. In strain T23-1 crossing over between the *w* locus and the Y;3 translocation break point (Fig. 1) would yield white-eyed male and yellow-eyed female offspring, and crossing over between the *to* locus and the Y;5 translocation break point would yield yellow-eyed males.

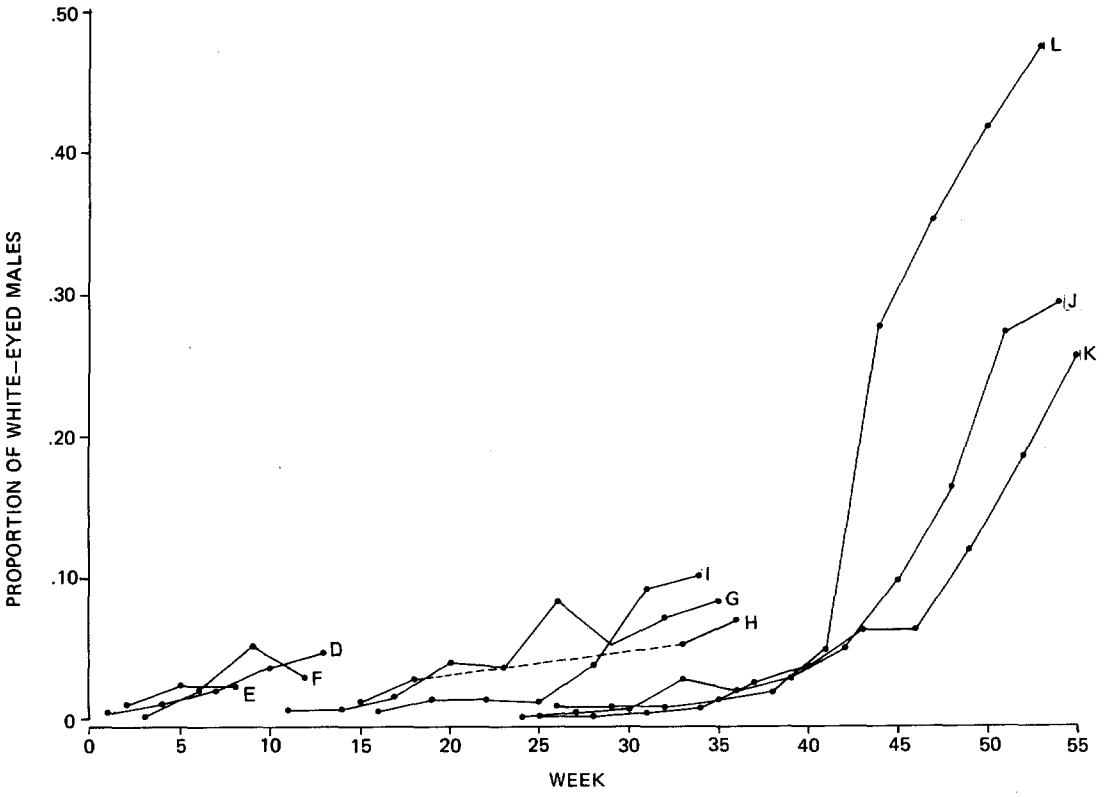


Fig. 3. Proportions of white-eyed males in mass rearing colonies during 1977-8

Table 1. Crossing over on chromosome *3L* in males and females

Chromosome *3L* Markers	Number of progeny				
	Cross A[a]		Cross B	Cross C	Cross D
	♂♂	♀♀			
w ru ar	2	724	3549	2971	245
+ + +	1334	6	3582	3047	305
w + +	9	0	5	0	76
+ ru ar	0	4	2	1	54
w ru +	4	1[b]	5	0	129
+ + ar	0	9	2	2	122
w + ar	0	0	0	0	19[b]
+ ru +	1[b]	0	0	0	14[b]
Totals	1350	744	7145	6021	964
	2094				
frequency of *w – ar* crossing over[c]	2094	1.38%	0.20%	0.05%	46.4%

[a] Crosses: A *w ru ar* ♀♀ × T(Y;5;3)23-1, *Rdl/w ru ar* ♂♂
B *w ru ar* ♀♀ × w ru ar/+ + +;T(Y;5)23, *Rdl* ♂♂
C *w ru ar* ♀♀ × w ru ar/+ + + ♂♂
D *w ru ar*/+ + + ♀♀ × *w ru ar* ♂♂
Crosses B, C and D were performed simultaneously; cross A was performed at a different time

[b] Double crossovers

[c] Chi-square values were calculated from 2x2 contingency tables using *w-ar* crossover data from crosses A, B and C. The frequency of crossing over differed significantly in all pairwise comparisons: A:B and A:C with $p < 10^{-4}$, and B:C with $0.01 < p < 0.05$

To examine whether crossing over in T(Y;5;3)23-1 heterozygotes can account for the frequency of mutant males observed in the mass-rearing colonies, the progeny of T(Y;5;3)23-1,*Rdl/w ru ar* males from a laboratory culture were scored for recombination between the mutant markers and sex. The results are presented in Table 1 along with sample data for comparison from other experiments with *w ru ar*/+ + + females or males. The data clearly show that crossing over does occur in males, and moreover that while the frequency is much lower than in females, crossing over is significantly (see footnote, Table 1) more frequent in translocation-bearing males than in chromosomally normal males. Moreover, this enhancement of crossing over is not restricted to chromosomes involved in the translocation, as shown by the results of cross B (Table 1).

The apparent difference in crossover frequency between T(Y;5;3)23-1/*w ru ar* and *w ru ar*/+ + +;T(Y;5)23 males (Table I) may be due to causes other than their different chromosomal constitutions, since crosses A and B (Table 1) were performed at different times using different stocks. When recombination between *w* and sex was examined in T(Y;5;3)23-1/w;to males taken from the mass rearing colonies, the 0.28% frequency (Table 2) was much closer to the 0.20% between *w* and *ar* observed for *w ru ar*/+ + +; T(Y;5)23 males (Table 1).

If white-eyed males in the mass rearing colonies are as fit as T(Y;5;3)23-1/*w;to* males, and yellow-eyed females are unfit (as suggested by their consistently low frequency), the observed crossover frequencies (Table 2) should result in the accumulation of white-eyed males at a rate of approximately 0.3% per generation. At the time these males were taken from the mass rearing colony (week 45, line J) the frequency of white-eyed males in the colony was 10% and was virtually being doubled each generation (Fig. 3). Thus crossing over of this type clearly cannot account for such a rapid increase. It should be noted that crossing over between *to* and sex was of the same order as that between *w* and sex (Table 2) yet the proportion of yellow-eyed males remained constant at less than 1% in the colonies.

Reversion of T(Y;5;3)23-1

In order to examine the mechanism of strain breakdown, white-eyed males from the mass-rearing colony were examined cytologically and genetically. Preliminary results indicated that three types of males were present: (1) males with the T(Y;5;3)23-1 karyotype, (2) males carrying a T(Y;5) whose chromosome 5 breakpoint was identical to that of the original T(Y;5)23, and (3) males with no detectable chromosome rearrangements. In a later study, of 27

Table 2. Genetic recombination in *T(Y;5;3)23-1, Rdl/w;* to males from the mass rearing colony[a]

Generation	Sex and eye colour phenotypes						Percent recombination	
	♀♀			♂♂				
	White	Yellow	Wild	White	Yellow	Wild	w – sex[b]	to – sex[c]
1	1593	5	1	5	4	1771	0.30	0.23
2	1695	5	1	5	7	2550	0.24	0.27
3	1868	5	0	9	6	2605	0.31	0.23
Totals	5156	15	2	19	17	6926	0.280	0.244

[a] 69 virgin white-eyed females from the week 45 culture of line J (Fig. 3) were each pair-mated with a wild type male from the same culture, and generation 1 progeny were scored for sex and eye colour phenotype. For the second generation 20 white-eyed females and 20 wild type males from each pair were mass-mated (in a separate line for each original pair) and a sample of their offspring reared and scored for sex and eye colour phenotype. For the third generation 20 flies of each sex from the second-generation cultures were mated in a repeat of the above procedure

[b] Using data from both sexes

[c] Using data from ♂♂ only

white-eyed males from the week 25 culture of line I (Fig. 3), 15 were *w/w*;T(Y;5)/*to*, 12 were *w/w; to/to* and none carried T(Y;5;3)23-1.

Unlike the white-eyed males, most yellow-eyed males and all wild type males sampled from the rearing colonies still carried T(Y;5;3)23-1. Of 18 yellow-eyed males from weeks 25-30 of lines G, H and I (Fig. 3), 16 were T(Y;5;3) 23-1,*to/w;to* and 2 were *w/+;to/to*. The latter presumably arose originally from a *w/+;to/to*♀ *x w/w;to/to*♂ mating, and the former from genetic recombination in T(Y;5;3) 23-1/*w;to* males.

In all of the 69 wild type males tested (Table 2) the chromosome 3 marker was linked to sex. To check for the presence of the chromosome 5 marker, *to*, and its linkage to sex, 20 wild type G_2 males from each line were mass-mated to 20 virgin *to*^{2}*bz mv* females, and their progeny scored for sex and eye colour phenotype. All lines exhibited sex-linkage of *to*; i.e. each of the 69 males sampled from the colony carried T(Y;5;3)23-1. The results indicated that 68 of the original pairs had the genetic consitution *w/w; to/to*♀ x T(Y;5;3)23-1/*w;to*♂ and one was either *w/w;to/+*♀ x T(Y;5;3)23-1/*w;to*♂ or *w/w;to/to*♀ x T(Y;5;3)23-1/*w;+*♂.

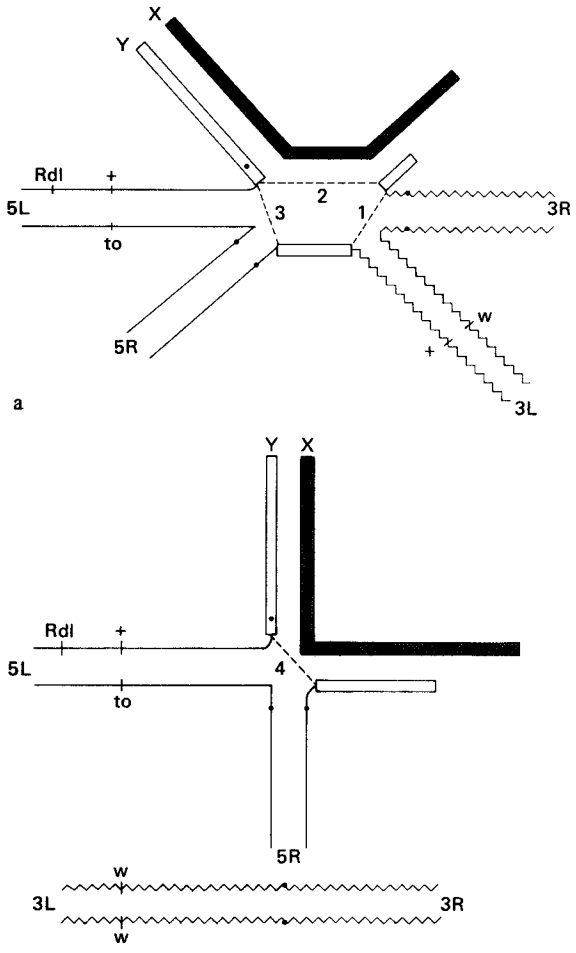
Discussion

The results of the cytogenetic examination of white eyed males from strain T23-1 suggest that T(Y;5;3)23-1 is capable of reverting to chromosome arrangements closely similar, if not identical, to the original T(Y;5)23 conformation and a structurally normal conformation. Since these karyotypes can be expected to be more fertile than T(Y;5;3)23-1 males, the frequency of white-eyed males should accumulate in the colonies, provided that their mating competitiveness with wild type-eyed males is not seriously impaired.

Although the reversion process has not been studied directly, it can be postulated that the mechanism involves unequal exchange events, probably between the regions of Y chromosome on the various elements of the translocation. Three different single-interchange events are possible (Fig. 4a, c), each leading to phenotypically recognizable offspring.

Assuming that reciprocal exchange products segregate from one another, a type 1 event (Fig. 4a) would lead to a white-eyed T(Y;5) male carrying the structurally normal paternal chromosome 3, and a yellow-eyed female carrying the normal paternal chromosome 5 plus a reconstituted chromosome 3 carrying a w^+ allele.

A type 2 event (Fig. 4a, c) would produce a white-eyed fly (presumably male) carrying the normal paternal chromosomes 3 and 5 plus a Y chromosome which must lack the segment of Y chromosome material contained in the 5;3 element of T(Y;5;3)23-1. The fertility of this male would depend on whether any essential fertility loci are contained in this Y segment. The reciprocal product would be a wild type fly which, if physiologically fertile, would contain a T(5;3) and thus should be semisterile. It is uncertain what effect the Y segment in the 5;3 element would have on the phenotypic sex of this fly, or whether fertility would be affected. The cytogenetics of sex and fertility are not fully understood, but it is known that not all of the Y chromosome need be present for a fly to be phenotypically male and fertile (Konovalov 1977). If the white-eyed non-translocation-bearing males arising from type 2 events (Fig. 4a, c) were sterile owing to the missing Y segment, the fertile males of this type must have arisen either from a type 4 event in a T(Y;5) male (Fig. 4b, c) or a double (type 1+3) event.



EXCHANGE TYPE	Y – BEARING SPERM	X – BEARING SPERM
1	Rdl + 5L — Y; 5R; w 3L — 3R (white-eyed ♂)	X; to 5L — 5R; + 3L — 3R (yellow-eyed ♀)
2	Y; to 5L — 5R; w 3L — 3R (white-eyed ♂)	X; + 3L — 5R; Rdl + 5L — 3R (wild-type ♂/♀ ?)
3	+ 3L — Y; to 5L — 5R; 3R (yellow-eyed ♂)	X; Rdl + 5L — 5R; w 3L — 3R (white-eyed *Rdl* ♀)
4	Y; to 5L — 5R; w 3L — 3R (white-eyed ♂)	X; Rdl + 5L — 5R; w 3L — 3R (white-eyed *Rdl* ♀)

c

Fig. 4a-c. Breakdown of T(Y;5;3)23-1. **a** Unequal exchange in T(Y;5;3)23-1/*w;to* males, **b** unequal exchange in *w/w*;T(Y;5)23/*to* males, **c** expected karyotypes of sperm formed by unequal exchange. The phenotypes of flies resulting from union of these gametes with eggs from *w/w;to/to* females are given in parentheses

A type 3 event (Fig. 4a, c) would produce a yellow-eyed T(Y;3) male or a white-eyed dieldrin-resistant female. Out of the 18 yellow eyed males from the rearing colony tested none were T(Y;3), so if this type of exchange does occur it is much rarer than crossing over between *to* and the Y;5 translocation break point and its products are probably selectively eliminated.

In conclusion, to account for the genotypes found, type 1 exchanges must occur as well as either or both of exchange types 2 and 4. There is no evidence, however, for the occurrence of type 3 exchanges.

White-eyed males are much less viable than wild type males in the field (Whitten et al. 1977), and it might therefore appear counterintuitive to assume that they are competitive under cage conditions. Observations on their behaviour suggest, however, that they may actually enjoy an advantage in mating competitiveness in the mass rearing cages. Laboratory experiments (P.H. Smith and C.A. Konovalov, unpublished data) have revealed that while wild type flies exhibit a strong positive phototaxis, white-eyed flies show neither a positive nor a negative phototaxis. In the mass rearing colony, wild type males tend to be distributed towards the tops of the cages (presumably attracted by the ceiling lights in the insectary), whereas white-eyed females and males tend to remain on or near the floor of the cages, near the water, food and oviposition sites (E. Reed and K.G. Fenley, unpublished observations). Thus the white-eyed males could have encountered females more frequently than the wild type males, and could therefore have had a mating advantage which offset any disadvantages accruing from their mutant phenotype.

Unlike the white-eyed males, the yellow-eyed males appeared to be at a competitive disadvantage compared with wild type. If they had been equally competitive, their frequency would have been expected to rise gradually in the colonies simply by the addition each generation of new recombinants to the yellow-eyed males descended from previous recombinant individuals. This did not happen, the proportion of yellow-eyed males remaining low (Fig. 2), indicating that they were being eliminated from the cage populations at a rate which compensated for their formation by crossing over. Similarly, the yellow-eyed female

products of crossing over between *w* and the Y;3 translocation break point appeared to be at a disadvantage in relation to the white-eyed females.

Although crossing over in males is unusual in the higher Diptera, its existence has been documented in *Musca domestica* (Milani 1967; Kerr 1970), *Drosophila melanogaster* (Hiraizumi 1971) and *D. ananassae* (Moriwaki and Tobari 1975). Unlike *L. cuprina*, enhanced crossing over in males of some *Drosophila* strains does not appear to be associated with the presence of a Y-autosome translocation. In *M. domestica* males recombination has been observed in both standard (*XY*) and autosomal holandric strains (Milani 1967; Kerr 1970). In *D. melanogaster*, it appears that both meiotic (Henderson et al. 1978) and premeiotic (Hiraizumi 1979) systems of recombination can occur in males. Mutator activity, distorted transmission frequencies and chromosome breakage also occur in strains exhibiting male recombination (Kidwell 1973; Hirazami et al. 1973; Sved 1974; Voelker 1974; Hiraizumi 1977; Henderson er al. 1978). There is not yet sufficient data in *L. cuprina* to indicate whether recombination in males is meiotic or premeiotic, and there is no evidence concerning mutator activity or transmission distortion. However, chromosome breakage events must be involved in the reversion of T(Y;5;3)23-1.

The occurrence of crossing over and structural reversion of rearrangements in *L. cuprina* males carrying Y-autosome translocations constitutes an unanticipated hurdle in their use in genetic control. Two possible approaches to the resolution of this problem are being investigated: (1) the construction of strains less prone to break down, and (2) the construction of strains in which breakdown does occur but in which products of breakdown are automatically eliminated. A study of the cytogenetics of sex determination, fertility, and recombination in males has been initiated, in order to discover whether the Y chromosome contains any loci which affect these characteristics. In addition, the use of certain marker combinations to eliminate genetic breakdown products is currently being tested in population cages.

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