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Genetic Analysis of Field Trials of Sex-linked Translocation Strains for Genetic Control of the Australian Sheep Blowfly *Lucilia cuprina* (Wiedemann)

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Abstract

The results of progeny tests of males and females captured during two field trials of sex-linked translocation strains for genetic control of *L. cuprina* are presented. Males released as mature larvae survived to adulthood and mated with field females. However, the levels of genetic death introduced into the population were insufficient to suppress the native population. This was due partly to seasonal ineffectiveness of the release method, and partly to poor performance of the released males. On average, the mating competitiveness of the released males was only one-third that of field males, whereas their field-reared, translocation-bearing sons were fully competitive with native males.

Introduction

The use of males carrying sex-linked translocations to transport lethal mutations into pest populations was proposed for genetic control of *Lucilia cuprina* (Wiedemann) by Whitten *et al.* (1977). This method combines the immediate genetic death caused by semisterility of the rearrangement with a delayed genetic death caused by homozygosis of the lethal mutations in later generations. Released males carrying recessive conditional lethal mutations linked in repulsion to a Y-autosome translocation transmit the translocation to their sons and the mutations to their daughters, all of which are thus heterozygous (Fig. 1*a*). When such a heterozygous female is mated by another released male, a portion of her female offspring (depending on the number and linkage relationships of the lethal mutations) will be homozygous for one or more of the lethal mutations (Fig. 1*b*) (Whitten *et al.* 1977; Whitten 1979).

It has been established (Whitten *et al.* 1977) that *L. cuprina* homozygous for eye colour mutations such as *w* and *to*, are inviable under field conditions although they are viable in laboratory culture. The present paper describes the results of progeny tests of flies trapped during two trials in which males heterozygous for these mutations and a multiple Y-autosome translocation were released into natural populations near Canberra. Ecological data pertinent to these trials are presented in Vogt *et al.* (1985).

Materials and Methods

L. cuprina *Mutations and Strains*

The symbols and names of mutations mentioned in this paper are as follows: *to* (topaz eyes) and *Rdl* (dieldrin resistance) on chromosome *5*, *w* (white eyes) and *yw* (yellowish eyes) on chromosome *3*. The genetic and cytogenetic mapping of these mutations have been reported elsewhere (Foster *et al.* 1980*b*, 1981).

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T(Y;5;3)23-1 and *T(Y;5;3)23-3* are sex (male)-linked translocations involving the *Y* chromosome and chromosomes *3* and *5*. Both translocations were isolated as described for *T(Y;5;3)23-1* by Foster *et al.* (1980*a*). Their cytogenetic structures have been described by Bedo (1980). Matings involving males carrying either of these rearrangements are partially sterile, because of the inviability of certain aneuploid segregation products. The effective fertility of translocation-bearing males relative to chromosomally normal wild-type males is 40·3% for *T(Y;5;3)23-1* heterozygotes and 44·2% for *T(Y;5;3)23-3* heterozygotes. These estimates are based on the number of females reared from eggs laid by wild-type females mated to either wild-type males (22 662 eggs), *T(Y;5;3)23-1* males (18 589) or *T(Y;5;3)23-3* males (18 287).

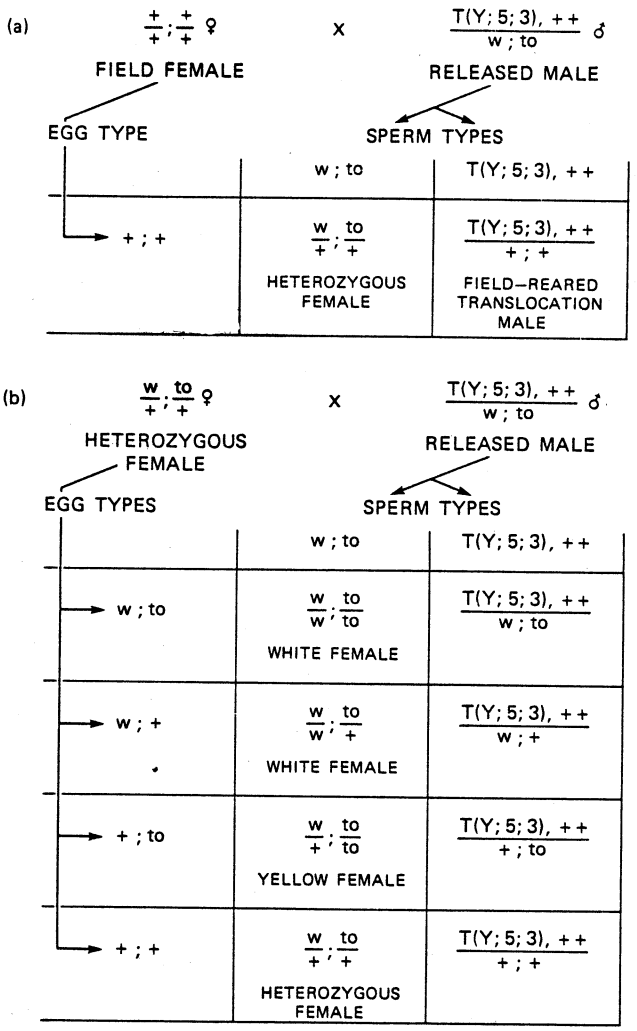

Fig. 1. (*a*) Transmission of the eye colour mutations *w* and *to* to the daughters of field females mated by released males. (*b*) Production of homozygous daughters in matings of *w*/+;*to*/+ heterozygotes by released males.

Strain T23-1 was constructed as described by Foster *et al.* (1980*a*). Originally this strain had the genotypic constitution *w*/*w*;*to*/*to* ♀ × *T(Y;5;3)23-1,Rdl*/*w*;*to* ♂. Females were susceptible to dieldrin and had white eyes, whereas males were resistant to dieldrin and had normally coloured eyes. In addition, several other phenotypic classes (white or yellow-eyed males, and yellow-eyed females), derived by genetic recombination or chromosomal interchange in *T(Y;5;3)23-1,Rdl*/*w*;*to* males, were present in this strain (Foster *et al.* 1980*a*). The male : female ratio in this strain was approximately 1 : 1.

Strain T23-1A was similar to strain T23-1, except that its genotypic constitution was *w yw/w yw;to/to* ♀ × *T(Y;5;3)23-1/w yw;to* ♂.

Strain T23-3 was constructed in an identical manner to strain T23-1, and had the same phenotypic properties as the original T23-1 strain, except that genetic recombination or chromosomal interchange was not observed in strain T23-3 during the period of large-scale rearing. The male : female ratio in this strain was approximately 2 : 1. However, cytogenetic studies revealed that approximately half of these males were aneuploids carrying a sex-linked duplication (cf. Foster *et al.* 1980*b*) of the distal half of chromosome *3L*. These males were able to inseminate females in the laboratory, but were probably not competitive in the field (Konovalov *et al.* 1983; R. J. Mahon, unpublished data), and as such represented wasted rearing and release effort.

In the first trial, at Wee Jasper, N.S.W., strain T23-3 was released from the beginning of September 1976 to November 1976. It was then replaced with strain T23-1 for most of the remainder of the trial. Strain T23-1A was released during the last month of the trial (March 9 and 16 and April 11 1978). In the second trial, near Boorowa, N.S.W., strain T23-1A was released from July 1978 to February 1979.

Rearing and release procedures, and descriptions of the experimental areas, are contained in Vogt *et al.* (1985).

Sampling of Flies for Progeny Testing

For the entire 1976–77 season and the first 2 months of the 1977–78 season, *L. cuprina* from traps 1–10 (Vogt *et al.* 1985) were pooled and then a sample obtained for progeny-testing. From November 18 1977 onwards, flies from trap 1 were progeny-tested separately from those from traps 2–10. When trapping at sites 21–24 commenced, two new groupings of flies (one from traps 21 and 22, and one from traps 23 and 24) were also progeny-tested separately. Flies from traps 11–20 were not progeny-tested.

During the second trial, flies from different traps were not pooled before progeny-testing. Males and females from traps in the inner release area (Vogt *et al.* 1985) were individually progeny-tested weekly, but flies from the buffer and non-release areas were tested only occasionally prior to January 1979.

Table 1. Possible outcomes of progeny tests of trapped males

Eye-colour phenotypes of progeny		Results of dieldrin resistance tests of progeny		Inferred genotype of trapped male
Females	Males	Females	Males	
Red[A]	Red	Die[B]	Die[B]	$w^+/w^+;to^+/to^+$
White	Red	Die	Survive	*T(Y;5;3)Rdl/w;to*[C] or *T(Y;5;3)Rdl/w;+*[C]
Red	Red	Die	Survive	*T(Y;5;3)Rdl/+;+*
Yellow	Red	Die	Survive	*T(Y;5;3)Rdl/+;to*
2 white: 1 yellow: 1 red	2 white: 1 yellow: 1 red	Die[B]	Die[B]	*w/+;to/+*
1 white: 1 red	1 white: 1 red	Die[B]	Die[B]	*w/+;+/+*
1 yellow: 1 red	1 yellow: 1 red	Die[B]	Die[B]	*+/+;to/+*

[A] i.e. wild-type eyes.

[B] Note that resistance tests on females were only performed if males survived the dieldrin treatment; tests in which approximately half of both sexes survive indicate the presence of a resistance allele of field origin.

[C] Because the allele present at the *to* locus cannot be scored in these tests, such males are designated *T(Y;5;3)/w;–* in the text.

Progeny Tests of Trapped Males

Males were mated individually to virgin *w/w;to/to* females and their progeny scored for sex and eye colour phenotype. If no eye colour mutants appeared in the progeny, 10 F_1 male offspring aged 3–5 days were tested for dieldrin resistance by topical application of 0·5 μl of 0·01% (w/v) dieldrin in octane or deodorized

kerosene (Foster *et al.* 1978), followed by incubation for 24 h at 25°C. If any males survived this treatment 10 of their sisters were treated with 0·5 μl of 0·03% (w/v) dieldrin (Foster *et al.* 1978) and incubated as above. From the results of these tests it was possible to assign males to one of seven classes (Table 1).

Table 2. Possible types of mating in the field
Letters in parentheses indicate mating category—see Table 3

Male parent	Female parent			
	+/+;+/+	*w*/+;*to*/+	*w*/+;+/+	+/+;*to*/+
+/+;+/+	1 (A)	2 (B)	3 (C)	4 (D)
w/+;*to*/+	5 (B)	6 (E)	7 (F)	8 (G)
w/+;+/+	9 (C)	10 (F)	11 (F)	12 (B)
+/+;*to*/+	13 (D)	14 (G)	15 (B)	16 (G)
T(Y;5;3)/w;to	17 (H)	18 (J)	19 (L)	20 (M)
T(Y;5;3)/+;+	21 (I)	22 (K)	23 (R)	24 (S)
T(Y;5;3)/w;+	25 (P)	26 (L)	27 (L)	28 (O)
T(Y;5;3)/+;*to*	29 (Q)	30 (M)	31 (N)	32 (M)

Table 3. Possible outcomes of progeny tests of trapped (field-inseminated) females

Mating category	Observed G_1 eye colour phenotype[A]		Observed results of dieldrin tests[B]		Observed test-cross eye colour phenotypes[A,B] (G_1 females × *w;to* males)	Inferred mating types (see Table 2)
	Females	Males	G_1 males	Test-cross females		
A	+	+	Die	—	+	1
B	+	+	Die	—	4W:3Y:9+	2, 5, 12, 15
C	+	+	Die	—	1W:3+	3, 9
D	+	+	Die	—	1Y:3+	4, 13
E	4W:3Y:9+	4W:3Y:9+	—	—	—	6
F	1W:3+	1W:3+	—	—	—	7, 10, 11
G	1Y:3+	1Y:3+	—	—	—	8, 14, 16
H	+	+	Survive	—	2W:1Y:1+	17
I	+	+	Survive	Die	+	21
J	2W:1Y:1+	+	—	—	—	18
K	+	+	Survive	—	4W:3Y:9+	22
L	1W:1+	+	—	—	—	19, 26, 27
M	1Y:1+	+	—	—	—	20, 30, 32
N	+	+	Survive	—	2W:3Y:3+	31
O	+	+	Survive	—	4W:1Y:3+	28
P	+	+	Survive	—	1W:1+	25
Q	+	+	Survive	—	1Y:1+	29
R	+	+	Survive	—	1W:3+	23
S	+	+	Survive	—	1Y:3+	24

[A] + = wild-type, W = white eyes, Y = yellow eyes. [B] — = not tested (see text).

Note that although the data of Shanahan (1961) indicate '100% kill' of susceptible females at 0·02% (w/v) dieldrin, experience in this laboratory revealed that 0·03% (w/v) was necessary to kill all susceptible females (M. J. Whitten, personal communication). Since Shanahan's (1961) data show only 1% kill of heterozygotes by 0·05% (w/v) dieldrin, the 0·03% (w/v) dose adopted in the present study is unlikely to kill a significant proportion of heterozygotes and result in misclassification of progeny tests.

Progeny Tests of Trapped Females

General procedure

Progenies were obtained from individual field-inseminated females and scored for sex and eye colour phenotype. If no eye colour mutants occurred among the first-generation (G_1) progeny, up to 12 (generally 10) G_1 males from each brood were tested for dieldrin resistance, and up to 15 virgin G_1 females from each brood were mass-mated to *w/w;to/to* males. Progenies of these test-crosses were scored for eye colour phenotype. If any of the G_1 males in a brood showed resistance to dieldrin *and* no eye colour mutants appeared among the test-cross offspring, 20 female offspring of the test-cross were tested for dieldrin resistance. With respect to the eye colour mutations and the translocations there are 32 possible mating genotypes (Table 2). However, because (*a*) tests of females mated by non-translocation males do not indicate the direction of mating (i.e. there is no sex-linkage of the mutations), and (*b*) certain other mating types could not be distinguished by the procedure adopted, only 19 categories of matings were identifiable in these tests (Table 3).

Table 4. Possible misclassification of translocation-male mating types due to test-cross sampling error in female progeny tests

Actual male genotype	Mating type	Possibility of misclassification	Possible erroneous conclusions[C]
T(Y;5;3)/w;to	17	No	—
	18	No	—
	19	No	—
	20	No	—
T(Y;5;3)/w;+	25	No	—
	26	*[A]	—
	27	*[A]	—
	28	Yes	17, 25
T(Y;5;3)/+;to	29	No	—
	30	†[B]	—
	31	Yes	17, 29
	32	†[B]	—
T(Y;5;3)/+;+	21	No	—
	22	Yes	17, 25, 28, 29, 21, 23, 24
	23	Yes	21, 29
	24	Yes	21, 25

[A] Not distinguishable from type 19. [B] Not distinguishable from type 20.
[C] — = not applicable.

Statistical considerations

With the translocation matings it was usually possible to infer the genotype of the male parent with respect to the eye colour mutations. However, the use of mass-matings in the test-cross of G_1 females to *w/w;to/to* males permitted misclassification of certain types of matings (Table 4), since not all the offspring of females, themselves heterozygous for one or both of the eye colour mutations, have the same genotype. For example, in the case of *w/+;to/+* ♀ × *T(Y;5;3)/+;+* ♂ matings (type 22), the female offspring would be expected to consist of equal numbers of *w/+;to/+*, *w/+;+/+*, *+/+;to/+* and *+/+;+/+*. If only one or a few of these females oviposited in the test-cross, a range of phenotypic ratios other than the expected average 4 white : 3 yellow : 9 wild-type would be generated, leading to the types of misclassification shown in Table 4. The consequences of this sort of misclassification can be predicted and appear to be minimal with respect to interpretation of the field data. Nearly half of the misclassifications do not alter the inferred genotype of the male (Table 5), and those that do so are unidirectional. Matings involving *T(Y;5;3)/w;to* males would not have been misclassified, although certain matings involving *T(Y;5;3)/w;+* or *T(Y;5;3)/w;to* males either could not be distinguished from, or could have been misinterpreted as *T(Y;5;3)/w;to* matings.

Similarly, *T(Y;5;3)/w;+* or *T(Y;5;3)/+;to* matings could not have been misclassified as *T(Y;5;3)/+;+* matings, although certain of the latter could have been misclassified as involving a male of one of the other three genotypes. The data from both the male and the female progeny tests suggest that: (1) the incidence of misclassifiable matings was relatively low, and (2) the incidence of actual misclassification of such matings was also low.

A different sort of error was also possible because in practice it was usually not possible to distinguish statistically between a 2 : 1 : 1 ratio (mating type H) and 4 : 1 : 3 or 2 : 3 : 3 ratios (types N, O). However, the male progeny-test data indicated that the expected frequencies of types N and O should be negligible. In any case, comparison of the frequencies of yellow-eyed males and females in the rearing colony (see below) with the progeny-test data (Tables 5 and 6) suggests that most, if not all *T(Y;5;3)/w;+* and *T(Y;5;3)/+;to* males were probably released males.

The net effect of the two types of errors described above would be to overestimate the mating performance of the released males, and underestimate that of their field-reared descendants.

Identification procedure adopted

The following procedure was adopted in categorizing the female progeny tests:

(1) Tests in which eye colour mutations appeared in the G_1 progeny were classified as types E, F, G, J, L or M on the basis of which eye colour phenotypes were present, and whether or not they were sex-linked.

(2) Tests in which all G_1 males were killed by the dieldrin treatment were classified as non-translocation matings. These were further classified as A, B, C or D if the test-cross was completed.

(3) Tests with one or more G_1 male survivors of the dieldrin treatment in which the ratio of mutant : non-mutant offspring in the test-cross indicated sex-linkage in the original male parent, were classified as translocation-male matings. In the case of test-crosses producing both white- and yellow-eyed flies the mating was classified as type H if the ratio of white : non-white was not significantly ($P < 0{\cdot}05$) less than 1 : 1. In crosses producing only white or yellow (in addition to wild-type), the matings were classed as P or Q if the mutant : wild-type ratios were not significantly less than 1 : 1.

(4) Tests in which the test-cross offspring were all wild-type, or in which the mutant wild-type ratios were significantly less than 1 : 1, were classified as *T(Y;5;3)/+;+* matings (categories I, K, R or S) if *either* the proportion of G_1 males surviving the dieldrin test was significantly greater than the expected 0·5 frequency (binomial probabilities), *or* all test-cross progeny females (if tested) were killed by the dieldrin treatment.

(5) Tests were classified as non-translocation matings involving a *Rdl* allele of field origin if one or more females (test-cross offspring) survived the dieldrin treatment (provided that the survival of G_1 males treated with dieldrin was not significantly greater than 0·5).

(6) Tests were classified as uncertain (either field *Rdl* or *T(Y;5;3)/+;+*) if survival of G_1 males was not significantly greater than 0·5 and females were not tested for *Rdl* (provided that the test-cross did not indicate sex linkage of eye colour mutations), or if no test-cross was completed. Treatment of the 'uncertain' tests will be described further in Results.

Results

Genotypes of Released Males

Because of recombination in *T(Y;5;3)23-1/w;to* males (Foster *et al.* 1980*a*) some of the released males were probably *T(Y;5;3)23-1/w;+* or *T(Y;5;3)23-1/+;to*. Although the incidence of such males in the rearing colony was not monitored directly during the trial, several lines of evidence indicate that it was low. Firstly, in a post-trial sample of the rearing colony, to^+ was present on only one structurally normal fifth-chromosome in 69 mated pairs (i.e. on only one of 207 chromosomes sampled), and all 69 of the males tested carried *w* on the normal third-chromosome (Foster *et al.* 1980*a*). Secondly, the incidence of yellow-eyed females (*w/+;to/to*) remained low throughout both trials (first trial 0·61%; second trial 2·42%). These females either arise by *de novo* recombination between the *w* and sex-determining loci in *T(Y;5;3)23-1/w;to* males, or they are descended from *w/+;to/to* females or *T(Y;5;3)23-1/+;to* males. Thus their frequency sets an upper limit to the estimate of

the frequency of *T(Y;5;3)23-1/+;to* males in the colony. Thirdly, the incidence of yellow-eyed males (*T(Y;5;3)23-1,to/w;to*) among the non-white-eyed males was also low (0·46% during 1976–78, 1·42% during 1978–79). Such males are the reciprocal product of *w/w;to/+* females (indistinguishable from *w/w;to/to*), which arise from recombination between *to* and sex. Thus the frequency of *T(Y;5;3)23-1/w;+* males, which would normally be the sons of *w/w;to/+* females, is likely to have an upper limit similar to the frequency of yellow-eyed males in the colony. One male trapped during the first trial, which had the genotype *T(Y;5)/to;w/+*, was presumably a descendant of a revertant of *T(Y;5;3)23-1* in the rearing colony (Foster *et al.* 1980*a*).

The absence of wild-type females in samples (first trial, $n = 40\,542$; second trial, $n = 5824$) of the released strains, and the low frequency of yellow-eyed females, further imply a low frequency of *T(Y;5;3)23-1/w;+* males. Foster *et al.* (1980*a*) detected wild-type females regularly in line J of strain T23-1A but larvae from this line were never released; one wild-type female ($n = 7916$) was discovered in lines K and L but this was three generations after cessation of releases at the end of the Wee Jasper trial. The incidence of *T(Y;5;3)23-1/+;+* among the released males was therefore regarded as negligible.

Recovery of Released Males

The trap data and their interpretation are given by Vogt *et al.* (1985). The results of progeny-tests of males trapped during both trials are presented in Tables 5 and 6 respectively. In the first trial high proportions of released males did not occur until the third week. In the second trial released males were recovered in high proportions in the first week. The *T(Y;5;3)/+;to* males recovered were almost certainly products of genetic recombination in the rearing colony. Only 12 such males were recovered in both trials, compared to 1673 *T(Y;5;3)/w;−* (see footnote to Table 1) males. This frequency (0·7%) is similar to that in the rearing colony (see above). It was therefore assumed that *T(Y;5;3)/+;to* males detected in progeny tests were released males which arose by recombination, rather than from a mating of a heterozygous field female with a translocation-bearing male (Fig. 1*b*). From this inference (i.e. that the frequency of field-reared *T(Y;5;3)/+;to* males was negligible), it was assumed that the frequency of field-reared *T(Y;5;3)/w;+* males (which should equal that of the former), was also negligible. Thus, although progeny tests of translocation males heterozygous for *w* did not distinguish between *T(Y;5;3)/w;to* and *T(Y;5;3)/w;+* (Table 1), it can be assumed that all of the *T(Y;5;3)/w;−* males recovered were released males.

The results for the second year of the first trial are presented separately for different groups of traps (Table 5). These were tested separately after 28 November 1978 because statistical analysis revealed significant differences in proportions of released and wild males recovered. In the second trial, the proportions of released and field-reared males did not differ significantly between the release and buffer areas (Table 6).

The progeny test results showed large seasonal fluctuations in released : wild male ratios. In the first trial this ratio reached a peak of 4 : 1 in the third week of November 1976, then declined rapidly and remained low from late November 1976 to February 1977. From March 1977 until the end of May, released males again outnumbered wild males. In the first 6 weeks of the following year the weekly released : wild ratio averaged 15 : 1, but dropped abruptly in mid-November. Field males outnumbered released males from mid-December 1977 to the end of January 1978, and during this period, differences between the edge and main traps were not significant (Table 5). From February on,

Table 5. Results of progeny tests of males trapped during the first genetic control trial at Wee Jasper, N.S.W.
***$P < 0{\cdot}001$ (3 × 2 contingency tables—non-translocation versus released males versus field-reared translocation males)

Year and month	Trap area[A]	Genotypes and numbers of tested males: +/+;+/+[B]	*T(Y;5;3)/w*;−[C]	*T(Y;5;3)*/+;+	*w*/+;*to*/+	*w*/+;+/+	+/+;*to*/+	Homogeneity $\chi^2_{(2)}$	Proportion among field-reared males: Translocation-bearing	Eye mutant heterozygotes[D]
1976–77										
Oct.		18	11	0	0	0	0	—	0	0
Nov.		75	82†††	2	0	0	0	—	0·03	0
Dec.		113##	52	8	0	0	0	—	0·066	0
Jan.		149##	23	6	4	0	2	—	0·037	0·037
Feb.		91	20	2	1	0	3	—	0·02	0·04
Mar.		67#	127	3	1	4	4	—	0·04	0·11
Apr.		27	65	4	0	0	0	—	0·13	0
May		10	26	0	0	0	0	—	0	0
Totals[E]		550		25 (0·042)	6 (0·010)	4 (0·007)	9 (0·015)			
1977–78										
Oct.		10	101	0	0	0	0	—	0	0
Nov.		27	128†	8	0	1	0	—	0·22	0·03
Dec.	Main	34	34	8	1	1	1	2·53	0·18	0·07
	Edge	46	27†	8	1	1	2		0·14	0·07
Jan.	Main	22	8	2	0	0	1	5·25	0·08	0·04
	Edge	17	16††	7	0	0	1		0·28	0·04
Feb.	Main	28	53	4	1	0	0	1·17	0·12	0·03
	Edge	36	53	3	1	0	2		0·07	0·07
Mar.	Main	46#	119	10	4	3	2	24·15***	0·15	0·14
	Edge	46#	29	9	0	2	2		0·15	0·07
Apr.	Main	42	50[F]	7[G]	0	2	1	36·95***	0·13	0·06
	Edge	61#	5†	6	0	1	2		0·09	0·04
May	Main	25	79	14	0	2	0	36·88***	0·34	0·05
	Edge	63#	35	12[G]	0	3	5		0·14	0·10
Totals[E]		503		98 (0·152)	8 (0·012)	16 (0·025)	19 (0·030)			

[A] Main area includes traps 2–10, 23 and 24; edge area includes traps 1, 21 and 22 (Vogt *et al.* 1985). December totals in 1977–78 year include flies trapped on 28 November 1977. [B] Values indicated by # (##) include 1 (2) *Rdl*/+ male(s). [C] Values indicated by † (††, †††) include 1 (2, 3) *T(Y;5;3)*/+;*to* male(s). [D] Proportions among non-translocation males only. [E] Totals for field-reared males (frequencies in parentheses). [F] This value includes one male of genotype *T(Y;5)/to;w*/+ (see text). [G] This value includes one male homozygous for *Rdl*/*Rdl* (see text).

Table 6. Results of progeny tests of males trapped during the second genetic control trial at Boorowa, N.S.W.

Year and month	Area[A]	Genotypes and numbers of tested males						Homogeneity $\chi^2_{(4)}$ [D]	Proportion among field-reared males	
		+/+;+/+ [B]	*T(Y;5;3)/w*; – [C]	*T(Y;5;3)*/+;+	*w*/+;*to*/+	*w*/+;+/+	+/+;*to*/+		Translocation-bearing	Eye mutant heterozygotes[E]
1977–78										
Oct.	B	0	3	0	0	0	0		—	—
	C	2	17	0	0	0	0	—	0	0
	D	1	0	0	0	0	0			
Nov.	B	2	3	0	0	0	0			
	C	45	177†	4	0	2	1	—	0·07	0·06
	D	0	12	0	0	0	0			
Dec.	B	—	—	—	—	—	—		—	—
	C	57#	109	27	1	0	2	—	0·31	0·03
	D	—	—	—	—	—	—		—	—
Jan.	A	49##	2[F]	1[F]	0	2	0		0·02	0·04
	B	49##	22	6	3	4	3		0·09	0·15
	C	98	61††	12	4	10	7	1·31	0·092	0·160
	D	39	23	5	3	3	0		0·10	0·12
	E	27	1[F]	1	1	2	1		0·03	0·13
Feb.–Mar.	A	55	0	0	1	5	0		0	0·10
	B	54###	19	3	1	8	3		0·04	0·17
	C	102##	59†	10	2	7	3	5·89	0·081	0·097
	D	59#	31	2	0	4	3		0·03	0·10
	E	59#	4[G]	4[H]	0	1	2		0·06	0·05
Totals[I]		503		75 (0·112)	16 (0·024)	48 (0·072)	25 (0·037)			

[A] A, northern non-release area; B, northern buffer area; C, release area; D, southern buffer area; E, southern non-release area (Vogt *et al.* 1985). [B] Values indicated by # (##, ###) includes 1 (2, 3) *Rdl*/+ male(s). [C] Values indicated by † (††) include 1 (2) *T(Y;5;3)*/+;*to* male(s). [D] 3 × 3 contingency tables—non-translocation versus released versus field-reared translocation males; areas B, C, D only. [E] Proportions among non-translocation males only. [F] Males trapped within 2 km of buffer zone. [G] Three out of these four males trapped within 2 km of buffer zone. [H] One out of these four males trapped within 2 km of buffer zone. [I] Totals for field-reared males, all areas (frequencies in parenthesis).

released males predominated in the main-area traps, but usually not in the samples from the edge traps. Results were similar in the second trial, with released males predominating during October–December, but then declining during the summer months (Table 6).

Recovery of Field-reared Male Descendants of Released Males

In both trials, the first *T(Y;5;3)*/+;+ males were recovered 3 or 4 weeks after detection of the first released male. As noted earlier, their frequency among the released males was low, probably in the order of 1×10^{-5}. Their much higher recovery in the progeny tests (among total translocation males) (Tables 5 and 6) suggests a different origin. Thus it is assumed that all *T(Y;5;3)*/+;+ males detected were descendants of released males.

Non-translocation males heterozygous for the eye colour mutations were first detected at least one generation later than the first *T(Y;5;3)*/+;+ males, in both trials. Although nearly all field-derived males are expected to be $w^+/w^+;to^+/to^+$, a proportion, possibly as high as 1%, may be heterozygous for *w* or *to* mutant alleles of field origin. Flies heterozygous for *w* are frequently detected in field collections (Mackerras 1933, and unpublished data). For example, the frequency of such heterozygotes was 0·6% (n = 800) in a sample collected near Braidwood, N.S.W. (Whitten *et al.* 1973). The mutation *to* was not recovered in the Braidwood study, but was originally discovered as six *to*/*to* homozygotes (out of approximately 100 flies in the sample) reared from one of 30 samples of larvae from infested sheep near Murrumbateman, N.S.W. (R. A. Helman, personal communication). The frequency of naturally occurring *w*/+;*to*/+ double heterozygotes is thus likely to be low (probably less than 1×10^{-4}). Their observed frequency of 0·010 or more among non-translocation males (Tables 5 and 6), strongly suggests that they were descended from released males (i.e. through F_1 *w*/+;*to*/+ females, Fig. 1*a*).

In the first year of the first trial, the total frequency of males heterozygous for one or both eye colour mutations among non-translocation males was 3·2% (Table 5). The frequencies of the single-mutation heterozygotes were similar to the anticipated background (i.e. of field origin) frequencies. However, the similarity of these frequencies to that of the double heterozygote, which must have arisen from *w*/+;*to*/+ females, suggests that the single heterozygote males also arose mainly from such females. In the second year, the total frequency of eye mutant heterozygotes was 6·7%, double that of the first year. Although the frequencies of the single-mutant heterozygotes were twice or more that of the double heterozygotes, their incidence was not significantly different from a 1 : 1 : 1 expected ratio ($\chi^2_{(2)} = 4{\cdot}51$, $P > 0{\cdot}05$).

In the second trial the frequency of mutant heterozygotes among non-translocation males rose more rapidly than in the first trial, totalling 13·3% for the season. The apparent inequality of the three classes ($\chi^2_{(2)} = 18{\cdot}36$, $P < 0{\cdot}01$) was due, at least in part, to a defective strain used for progeny-testing. Analysis of the results of the progeny tests and a later check of the strain, revealed that a large proportion of flies in the putative *w*/*w*;*to*/*to* stock were *w*/*w*;*to*/+ or *w*/*w*;+/+. This would have had the effect of underestimating the frequency of *w*/+;*to*/+ and +/+;*to*/+ males, and overestimating that of *w*/+;+/+ males. However, the effect of this on estimation of the numbers of released or field-reared translocation males was negligible. In the first trial, *T(Y;5;3)*/+;+ males, like the eye-colour mutant heterozygotes were more frequent during the second year than in the first year. The monthly proportions of both fluctuated considerably,

but remained generally steady during the second year rather than increasing with time. The pattern during the second trial was similar; after an initial rapid increase in the frequency of *T(Y;5;3)*/+;+ and mutant heterozygotes, their proportions tended to decline, particularly in the case of the translocation males (Table 6).

Incidence of Dieldrin Resistance among Non-translocation Males

Results of resistance tests on males which did not carry eye colour mutations revealed a total of 21 non-translocation males heterozygous for *Rdl*, and two males homozygous for *Rdl* (Tables 5 and 6). The latter were probably *T(Y;5;3)Rdl/w*$^+$;*to*$^+$*Rdl* males descended from matings of *Rdl*/+ females by released males. Although the *Rdl*/+ flies could have descended from released *w*/+;*to*+/+*Rdl* females or arisen by recombination in released males, it seems more likely that they carried resistance alleles of field origin. Their frequency at Wee Jasper (excluding the homozygotes) was 0·0085 (n = 1053) and at Boorowa 0·017 (n = 698), somewhat less than the 2–3% cited by Whitten *et al.* (1980) for field populations of *L. cuprina* in Victoria. It is possible that this discrepancy reflects the lower discriminating dose (0·02% w/v dieldrin) adopted by these authors than that used in the present study.

Progeny Tests of Females: Matings by Released Males and Field-reared Descendants

As noted earlier, a small portion of the progeny tests of females did not indicate whether a female had been mated by a field-reared, translocation-bearing male or a non-translocation male carrying a field *Rdl* allele. However, the independent data on field *Rdl* frequency from the progeny tests of males (Tables 5 and 6) allows these tests to be partitioned into matings involving translocation and non-translocation males. Because *Rdl* is not normally sex-linked, the frequency of matings by field males in which at least one of the parents was *Rdl*/+, should be approximately double that of *Rdl*/+ males. Thus the observed frequencies of *Rdl*/+ among field males suggest that during the first trial 1·7%, and during the second trial 3·4%, of non-translocation matings should have involved a resistance allele of field origin. Thus in the first year, 14 of 829 non-translocation matings (from completed progeny tests) were expected to involve *Rdl*. Subtracting the 10 observed such matings (Table 7) from this figure suggests that four of the 22 'uncertain' matings should be classified as field *Rdl*, and 18 as field-reared translocations. Similarly, 25 out of 26 'uncertain' tests in the second year were classified as field-reared translocations, and 0 out of 16 during the second trial. Tests which indicated that the mating had been by a translocation male, but for which there were no test-cross data, were assumed to be released-male matings, as were all 'uncertain' tests for which there were no test-cross data (totals for both types of tests were 18, 20 and 9 in the three respective years). Note that this procedure tends to overestimate matings by released males, and underestimate those by field-reared translocation males.

The results of the progeny tests of females are summarized in Tables 7–10. Seasonal patterns of matings of field females by released males were similar in all three years. Generally, the highest proportion of matings by released males was achieved during the spring months, followed by a decline in summer, rising again in the autumn. The proportion of females mated by field-reared, translocation-bearing males also fluctuated considerably, but showed no consistent seasonal pattern.

In the first trial, when groups of traps were tested separately (1977–78) the results indicated substantial differences in mating by released males, between trap groupings (Table 7). In the sample from traps 2–10 half or more of the females were mated by

Table 7. Results of progeny tests of females trapped during the first field trial 1976–78: observed and expected numbers of matings by different types of males
*$P < 0{\cdot}05$, ***$P < 0{\cdot}001$ (3×2 contingency table)

Year and month	Area	No. of matings by released males Obs.	Exp.[A]	Number of matings by field-translocation males Obs.	Exp.[A]	No. of matings by non-translocation males Obs.[B]	Exp.[A]	Homogeneity $\chi^2_{(2)}$
1976–77								
Oct.		2	15·6	0	0	39#	25·4	—
Nov.		30	75·8	2	1·8	115	69·3	—
Dec.		27	57·4	11	8·8	153	124·8	—
Jan.		8	22·8	5	5·9	169###	153·3	—
Feb.		9	24·1	5	2·4	127###	114·5	—
Mar.		34	106·7	6	2·5	133#	63·8	—
Apr.		33	88·0	13	5·4	84##	36·6	—
May		4	14·4	3	0	13	5·6	—
Totals		147	404·8	45	26·8	833	593·3	
1977–78								
Oct.		23	37·3	2	0	16	3·7	—
Nov.		58	100·7	6	6·3	65	22·0	—
Dec.	Main	31	30·1	9	7·1	30#	32·8	16·15***
	Edge	9	21·0	9	6·2	48	38·8	
Jan.	Main	18	25·9	8	6·5	81#	74·6	1·21
	Edge	5	15·2	5	6·7	29	17·1	
Feb.	Main	28	42·5	7	3·2	34#	23·3	17·22***
	Edge	10	40·7	3	2·3	60	30·0	
Mar.	Main	55	135·2	29	11·4	125	62·5	6·55*
	Edge	12	30·3	16	9·4	64####	52·3	
Apr.	Main	33	46·6	8	6·5	54#	41·9	16·98***
	Edge	11	6·6	6	7·9	82###	84·5	
May	Main	10	66·5	11	11·8	80#	22·7	7·60*
	Edge	5	36·7	5	12·6	114##	74·6	
Totals		308	635·3	124	97·9	882	580·8	

[A] Expected matings based on male progeny-test data. [B] Values with # (##, ...) indicate 1 (2, ...) matings involving field *Rdl* allele.

Table 8. Results of progeny tests of females trapped during the first field trials 1976–78: frequency of mutations in the population and estimates of genetic death

Year and month	Area	Proportion of heterozygotes among non-translocation flies[A]	Translocation matings (*a*)	Proportion of matings causing genetic death: Mating types producing mutant G_1 offspring J (*b*)	L, M (*c*)	E (*d*)	F, G (*e*)	Estimated genetic death: From semisterility (D_s)[B]	From mutations (D_m)[C]	Total
1976–77										
Oct.		0	0·05	0	0	0	0	0·03	0	0·03
Nov.		0·038	0·218	0·020	0	0	0	0·12	0·007	0·13
Dec.		0·038	0·199	0·010	0	0	0	0·12	0·003	0·12
Jan.		0·055	0·071	0	0	0	0	0·04	0	0·04
Feb.		0·047	0·099	0	0	0·007	0	0·06	0·003	0·06
Mar.		0·056	0·231	0	0	0	0·006	0·14	0·002	0·14
Apr.		0·127	0·354	0·008	0·015	0·008	0	0·21	0·009	0·22
May		0·15	0·35	0·05	0·05	0	0	0·21	0·025	0·23
1977–78										
Oct.		0·22	0·61	0·10	0·07	0	0	0·36	0·04	0·41
Nov.		0·232	0·496	0·140	0·016	0	0·008	0·30	0·05	0·34
Dec.	Main	0·18	0·57	0·09	0·03	0	0	0·34	0·03	0·37
	Edge	0·15	0·27	0·05	0	0	0·02	0·16	0·02	0·18
Jan.	Main	0·090	0·24	0·02	0·02	0	0	0·14	0·01	0·15
	Edge	0·11	0·26	0	0	0	0	0·16	0	0·16
Feb.	Main	0·13	0·51	0·03	0	0	0	0·30	0·01	0·31
	Edge	0·094	0·18	0	0·03	0	0·01	0·11	0·01	0·12
Mar.	Main	0·088	0·402	0·043	0·024	0	0·005	0·24	0·02	0·26
	Edge	0·123	0·30	0	0	0	0·02	0·18	0·005	0·18
Apr.	Main	0·163	0·43	0·02	0·03	0	0·01	0·26	0·02	0·27
	Edge	0·140	0·17	0	0·01	0·01	0·02	0·10	0·01	0·11
May	Main	0·116	0·21	0	0	0	0	0·13	0	0·13
	Edge	0·150	0·081	0	0	0	0·024	0·05	0·006	0·05

[A] Calculated from the progeny tests of females which were completed, i.e. those which yielded mutant G_1 offspring plus those in which the test-cross of G_1 females was completed as follows (T = translocation):

$$\text{Proportion of heterozygotes} = \frac{[B + C + D + 2(E+F+G) + J + K + M + N + O + R + S]}{2\,(\text{No. of non-}T\text{ matings}) + \text{No. of }T\text{-matings}}.$$

[B] $D_s = a(1-f)$, where f is the fertility of the translocation, using fertility of *T(Y;5;3)23.3* for October and November 1976, and that of *T(Y;5;3)23.1* thereafter.

[C] $D_m = 0{\cdot}75f.b + 0{\cdot}50f.c + 0{\cdot}4375d + 0{\cdot}25e$ (see Table 3 for expected mutant phenotypic ratios for these mating categories).

released males in three of the first four trappings after week 8, whereas in the samples from trap 1 the proportions were much lower, ranging from 0·1 to 0·3. During January 1978 differences were not significant, but from February until the end of the season the proportion of females mated by released males was significantly higher in the main area traps than in the edge traps. On the other hand, during the second trial, there were no significant differences in the proportions of matings by the three types of males, between the buffer and release areas.

Table 9. Results of progeny tests of females trapped during the second field trial: observed and expected numbers of matings by different types of males

Month	Area[A]	Number of matings by Released males		Field-translocation males		Non-translocation males	
		Obs.	Exp.[B]	Obs.	Exp.[B]	Obs.[C]	Exp.[B]
Oct.	A	1	0·2	0	0	13	13·8
	B	5	9·0	0	0	6	2·0
	C	17	27·6	0	0	14##	3·4
	D	0	0·9	0	0	1	0·1
	E	0	0·5	0	0	10	9·5
Nov.	A	1	0·2	0	0	9	9·8
	B	7	17·1	2	0·5	14	5·5
	C	46	64·2	2	1·4	35#	17·4
	D	18	23·2	2	0·4	8	4·5
	E	2	0·4	0	0	6	7·6
Dec.	A	0	0·1	1	0·1	6	6·8
	B	2	12·4	2	4·2	22	9·4
	C	46	82·3	14	20·4	88#	45·3
	D	6	14·8	4	4·6	16	6·6
	E	0	0·2	0	0·2	4	3·6
Jan.	A	1	3·9	3	2·0	101#	99·1
	B	10	26·3	9	7·2	85	70·5
	C	28	58·5	20	11·6	136#	114·1
	D	17	28·4	8	6·1	65	55·4
	E	0	2·9	3	2·9	95##	92·1
Feb.[D]	A	0	0	2	0	117##	119
	B	5	24·4	3	3·8	105#	84·8
	C	17	53·1	6	9·1	142##	102·8
	D	4	25·4	3	1·6	74	54·0
	E	6	5·6	4	5·6	89##	87·7
Totals		239	481·6	88	81·7	1261	1024·8

[A] As defined in Table 6.
[B] Expected matings based on male progeny-test data where available for a given month and area; expected released-male matings for buffer areas (Oct.–Dec.) based on data from inner area and sex ratios in traps; expected field-translocation matings for buffer areas (Oct.–Dec.) based on inner area field-translocation: non-translocation ratios; expected field-translocation assumed 0 in control areas in October–November and December estimates based on January–February average.
[C] Values with # (##) indicate 1 (2) matings involving field *Rdl* allele.
[D] Includes March 6 trapping.

Competitiveness of Released and Field-reared Males

The data (Tables 7 and 9) reveal that the frequency of matings by released males was much less than that expected from the observed frequencies of the different types

of males (Tables 5 and 6), while that of their field-reared offspring was greater than expected. The differences between expected and observed were highly significant ($P < 0{\cdot}001$) in all three years. Note that even if all 'uncertain' matings (see above) had been classified as non-translocation males, the difference between released and field-reared translocation males is still statistically significant.

Mating competitiveness of the two types of translocation-bearing males relative to that of the wild (i.e. non-translocation) males can be estimated using the formulae

$$C_R = (O_R/E_R) \times (E_w/O_w)$$

and

$$C_F = (O_F/E_F) \times (E_w/O_w)$$

where, respectively, C_R and C_F are the competitiveness of released and field-reared translocation males, O_R, O_F and O_w are the observed matings by released, field-reared translocation, and non-translocation males, and E_R, E_F and E_w are the expected numbers of matings. The competitiveness values thus obtained were 0·26, 0·32 and 0·40 for released males, and 1·20, 0·83 and 0·88 for field-reared translocation males, in 1976–77, 1977–78 and 1978–79 respectively. Thus, on average, the competitiveness of released males was 0·33, compared to 0·97 for their field-reared offspring.

Frequency of Eye Colour Mutations in the Population

Estimates of the proportion of mutant heterozygotes among non-translocation flies, derived from the progeny tests of females, are included in Tables 8 and 10. During the first year of the first trial, the proportion of heterozygotes grew in two stages, reflecting the spring and autumn incidence of matings by released males. During the second year, the proportion of heterozygotes was highest during October (22%) and November (23%), then fluctuated between 9 and 18% for the remainder of the trial. There were no consistent differences between the main and edge-trap groupings. During the second trial, the proportion of heterozygotes in the release area built up rapidly to 15% in December, then levelled off for the rest of the trial. There were no consistent differences between the buffer and release areas. The proportion of heterozygotes was lower in the non-release areas, but reached a constant level of 4–6% during the last 2 months of this trial.

Estimates of Genetic Death

Estimates of the incidence of matings resulting in genetic death, and of the levels of genetic death thus generated, are included in Tables 8 and 10. The levels of genetic death attributable to homozygosis of eye colour mutations were low in both trials, never exceeding 5%. Thus variations in the levels of genetic death were due mainly to variations in incidence of matings by translocation-bearing males. The highest levels of sustained genetic death (34–41%) were achieved in the first trial, during the first 3 months of the second season.

Discussion

The overall objectives of these trials are summarized in Vogt *et al.* (1985). The specific objectives of the genetic studies reported in the present paper were: (i) to assess the ability of translocation-bearing males to mate with field females, (ii) to monitor the introduction of deleterious mutations and rearrangements into the population, and (iii) to estimate levels of genetic death from homozygosis of the mutations and from

Table 10. Results of progeny tests of females trapped during the second field trial: frequency of mutations in the population and estimates of genetic death
For explanation of terms see Table 8

Month	Area[A]	Proportion of heterozygotes among non-translocation flies	Translocation matings (*a*)	Proportion of matings causing genetic death: Mating types producing mutant G_1 offspring J (*b*)	L, M (*c*)	E (*d*)	F, G (*e*)	Estimated genetic death: From semisterility (D_s)	From mutations (D_m)	Total
Oct.	A	0	0·07	0	0	0	0	0·04	0	0·04
	B	0	0·45	0	0	0	0	0·27	0	0·27
	C	0	0·55	0	0	0	0	0·33	0	0·33
	D	0	—	—	—	—	—	—	—	—
	E	0	0	0	0	0	0	0	0	0
Nov.	A	0	0·10	0	0	0	0	0·06	0	0·06
	B	0·16	0·39	0	0	0·04	0	0·23	0·02	0·25
	C	0·104	0·58	0·05	0	0	0	0·35	0·01	0·36
	D	0·11	0·71	0·04	0	0	0	0·42	0·01	0·44
	E	0	0·25	0	0	0	0	0·15	0	0·15
Dec.	A	0·09	0·14	0	0	0	0	0·08	0	0·08
	B	0·10	0·15	0	0	0	0	0·09	0	0·09
	C	0·148	0·405	0·061	0·007	0	0	0·23	0·02	0·26
	D	0·05	0·38	0	0	0	0	0·23	0	0·23
	E	0·17	0	0	0	0	0	0	0	0
Jan.	A	0·058	0·04	0	0	0	0	0·02	0	0·02
	B	0·127	0·18	0	0	0	0·01	0·11	0·003	0·11
	C	0·131	0·261	0·005	0·022	0·005	0·011	0·16	0·01	0·17
	D	0·136	0·28	0·03	0	0·02	0·02	0·17	0·02	0·19
	E	0·059	0·03	0	0	0	0·01	0·02	—	0·02
Feb.[B]	A	0·058	0·017	0	0	0	0	0·01	0	0·01
	B	0·120	0·07	0	0	0	0·01	0·04	0·003	0·04
	C	0·138	0·139	0·006	0	0·006	0·006	0·08	0·006	0·09
	D	0·130	0·09	0	0	0	0	0·05	0	0·05
	E	0·044	0·10	0	0	0	0	0·06	0	0·06

[A] See Table 6. [B] Includes March 6 trapping.

semisterility of the rearrangements. The results indicate that the released translocation males were on average one-third as competitive as field males for mating with field females, whereas their field-reared translocation-bearing sons were fully competitive. Deleterious mutations and translocations were successfully established in the breeding population, but at levels too low to cause sufficient genetic deaths to have a measurable effect on population size.

The heterogeneity observed in proportions of released males in different groups of traps in the second year of the first trial (Table 5), probably reflects the uniform rate of distribution of released larvae over an area that was heterogeneous with respect to native fly density. Traps 1, 21 and 22, which tended to yield low proportions of released males, caught more flies on average than traps 2–10, 23 and 24, which tended to yield high proportions of released males.

The uniformity of the progeny-test results (Tables 6, 9 and 10) in the release and buffer areas of the second trial, and the low numbers of released males in the non-release areas, suggest that, despite the apparent lack of natural barriers, there was little movement of flies between the adjacent areas. Six of the seven released males from the non-release areas were trapped less than 2 km outside the buffer area, as were nine of the 11 females mated by released males. This apparent drift could have been due either to fly movement or navigational errors during releases. However, field-reared translocation males recovered in the non-release areas tended to be more than 2 km outside the buffer area (four of six *T(Y;5;3)*/+;+ males, and 11 of 13 females mated by such males), suggesting that some fly movement was occurring. Perusal of the data for all areas reveals that 13% of females mated by *T(Y;5;3)*/+;+ males (season totals), and 7% of the *T(Y;5;3)*/+;+ males themselves, were trapped more than 2 km outside the buffer area.

The summer decline in released : wild male ratios had several causes, which included variations in the numbers of males released, fluctuations in the emergence rates of field males, and differential mortality of released and field-reared males. These are discussed fully by Vogt *et al.* (1985). In particular, the high loss of males released as larvae during midsummer indicates a need for re-evaluation of release tactics. One option is the release of later developmental stages (either adult flies or ready-to-emerge pupae). Alternatively, it may be necessary to devise genetic-control schemes for which it is sufficient to restrict releases to the cooler months.

The data indicate a limited success of the released strains in introducing deleterious rearrangements and mutations into the population. However, with the possible exception of the brief period in the spring of 1977, the frequency of these deleterious genetic factors was insufficient to effect a substantial genetic load on the population. As indicated elsewhere (Vogt *et al.* 1985), a major part of this failure can be attributed to seasonal reductions in the effective release rates (i.e. through temperature-caused death of released immature stages). Another major contributing factor, however, was the poor mating performance of the released males.

The high competitiveness of the field-reared (translocation-bearing) offspring of the released males indicates that the rearrangement itself was not responsible for the low competitiveness of the released males. This observation leaves open the important question of whether other genetic factors, rearing/release conditions, or environmental factors were primarily responsible for the differences between released and field males.

Several genetic arguments could be postulated to explain the difference between released and field-reared translocation males. For example, the field-reared descendants

may have been more competitive because they are the offspring of the *successful* released males, i.e. selection of the fittest released males had occurred at the stage of mating with field females. Another possibility is that hybrid vigour was responsible, since the field-reared offspring were mainly F_1 hybrids of field females and released males. Yet another possibility is that one or both of the mutations *w* and *to*, carried by the released males but not their field-reared offspring, could have had a dominant adverse effect on the competitiveness of the released males.

Among the possible non-genetic reasons for poor performance of the released males, perhaps the most likely relate to rearing and handling procedures. Larval rearing and holding temperatures, ventilation during the rearing and pre-release period, and the aerial release method itself are all possibly deleterious (E. M. Reed, unpublished data). Recently, R. J. Mahon (unpublished data), has found a high positive correlation between size and mating competitiveness of released *L. cuprina* males, suggesting that larval nutrition and crowding during rearing may have contributed to the poor mating performance of the released males. Soil conditions experienced by the released larvae and pupae are likely to differ from those experienced by field-reared immature stages of *L. cuprina* (Smith *et al.* 1981*a*; Wardhaugh *et al.* 1983; Vogt *et al.* 1985). In particular, released larvae and pupae are likely to encounter higher levels of sublethal temperature stress which may adversely affect mating competitiveness. The effects of stress, due to exposure of larvae to sublethal doses of insecticides, on field recovery of adults, have been reported elsewhere (Smith *et al.* 1981*b*).

The results of these trials have prompted several studies, two aimed at the development of improved rearing and release methods, one at determining whether or not the poor performance of released males has mainly a genetic basis, and one involving computer simulation and evaluation of genetic control using sex-linked translocations and deleterious mutations. The results of these studies will be reported separately.

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References

Bedo, D. G. (1980). C, Q and H-banding in the analysis of Y chromosome rearrangements in *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae). *Chromosoma* **77**, 299–308.

Foster, G. G., Whitten, M. J., Vogt, W. G., Woodburn, T. L., and Arnold, J. A. (1978). Larval release method for genetic control of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae). *Bull. Entomol. Res.* **68**, 75–83.

Foster, G. G., Maddern, R. H., and Mills, A. T. (1980*a*). 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. *Theor. Appl. Genet.* **58**, 169–75.

Foster, G. G., Whitten, M. J., Konovalov, C., Bedo, D. G., Maddern, R. H., and Boon, D. J. (1980*b*). Cytogenetic studies of *Lucilia cuprina dorsalis* (Wiedemann) (Diptera : Calliphoridae). Polytene chromosome maps of the autosomes and cytogenetic localization of visible genetic markers. *Chromosoma* **81**, 151–68.

Foster, G. G., Whitten, M. J., Konovalov, C., Arnold, J. T. A., and Maffi, G. (1981). Autosomal genetic maps of the Australian sheep blowfly, *Lucilia cuprina dorsalis* R.-D. (Diptera : Calliphoridae), and possible correlations with the linkage maps of *Musca domestica* L. and *Drosophila melanogaster* (Mg.). *Genet. Res.* **37**, 55–69.

Konovalov, C. A., Foster, G. G., and Whitten, M. J. (1983). Viability and fertility of sex-linked autosomal duplications in *Lucilia cuprina* (Wiedemann). *Theor. Appl. Genet.* **65**, 9–16.

Mackerras, M. J. (1933). Note on the occurrence of a white-eyed mutant race of *Lucilia cuprina* Wied. *Aust. J. Exp. Biol. Med. Sci.* **11**, 45–7.

Shanahan, G. J. (1961). Genetics of dieldrin resistance in *Lucilia cuprina* (Wied.) 'Atti VII Congresso annuale Soc. Italiana Genetica Agraria, 1960'. In 'Genetica Agraria'. Vol. XIV. Fasc. 3–4. pp. 307–321.

Smith, P. H., Dallwitz, R., Wardhaugh, K. G., Vogt, W. G., and Woodburn, T. L. (1981*a*). Timing of larval exodus from sheep and carrion in the sheep blowfly, *Lucilia cuprina*. *Entomologia Exp. Appl.* **30**, 157–62.

Smith, P. H., Konovalov, C. A., Foster, G. G., and Kerr, R. W. (1981*b*). Assessment of the quality of mass-reared *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae) males treated with dieldrin as larvae in a female killing procedure. *Bull. Entomol. Res.* **71**, 1–10.

Vogt, W. G., Woodburn, T. L., and Foster, G. G. (1985). Ecological analysis of field trials conducted to assess the potential of a sex-linked translocation strain for genetic control of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann). *Aust. J. Biol. Sci.*, **38**, 259–73.

Wardhaugh, K. G., Smith, P. H., and Crompton, G. W. (1983). A comparison of ground and aerial release methods for the genetic control of *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae). *Gen. Appl. Entomol.* **15**, 37–46.

Whitten, M. J. (1979). The use of genetically-selected strains for pest replacement of suppression. In 'Genetics in Relation to Insect Management'. (Eds M. A. Hoy and J. J. McKelvey.) pp. 31–40. (The Rockefeller Foundation: New York.)

Whitten, M. J., Dearn, J. M., and McKenzie, J. A. (1980). Field studies on insecticide resistance in the Australian sheep blowfly, *Lucilia cuprina*. *Aust. J. Biol. Sci.* **33**, 725–35.

Whitten, M. J., Foster, G. G., and Kitching, R. L. (1973). The incorporation of laboratory-reared genetic material into a field population of the Australian sheep blowfly, *Lucilia cuprina* (Diptera : Calliphoridae). *Can. Entomol.* **105**, 893–901.

Whitten, M. J., Foster, G. G., Vogt, W. G., Kitching, R. L., Woodburn, T. L., and Konovalov, C. (1977). Current status of genetic control of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae). Proc. XV Int. Congr. Entomol., Washington, D.C. 1976. pp. 129–39.

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