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Fitness of a Translocation Homozygote in Cage Experiments with the Onion Fly, *Hylemya antiqua* (Meigen)

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Summary. In *Hylemya antiqua*, a stock homozygous for an autosomal reciprocal translocation was isolated using egg-hatch reduction and karyotype analysis. Sibling translocation homozygous (TT) and heterozygous (T+) females were compared in respect to egg production and longevity. In one full-sib (5 TT and 8 T+ females) significantly higher values for both parameters for T+ than for TT females were scored, in four others (a total of 35 TT and 28 T+ females) no significant differences were found. Cage experiments were started with populations composed of equal numbers of wild type flies (++) and translocation homozygotes. The frequencies of the different karyotypes in three successive, non-overlapping generations, did not suggest substantial differences in fitness between ++ and TT flies. Possible causes of a surplus of T+ individuals found in these experiments are discussed together with the usefulness of the translocation for genetic control of *H. antiqua*.

Key words: *Hylemya antiqua* – Translocation homozygotes – Genetic control – Cage experiments – Fitness

Introduction

Various types of genetic control for insect pests have been proposed (reviews by Smith and von Borstel 1972; Davidson 1974; Whitten and Foster 1975). One of these is to utilize chromosomal translocations (Robinson 1976). To develop a genetic control method for the onion fly, *Hylemya antiqua*, in the Netherlands two different approaches were chosen: the sterile male technique (Loosjes 1976) and methods involving chromosomal rearrangements (van Heemert 1975, 1977; van Heemert and Wijnands-Stäb 1975; Robinson and van Heemert 1975; Wijnands-Stäb and van Heemert 1974).

The genetic load induced in a population by introducing translocations depends on the production of unbalanced (deficiences and duplications) gametes by the translocation heterozygotes (T+). Translocation homozygotes (TT) are expected to be fully fertile when crossed with each other or when crossed with individuals of the normal karyotype (++). A consequence of the partial sterility of the translocation heterozygotes is that, in general, no stable equilibrium for the different karyotypes in a population can be achieved. However in certain cases, when the partial sterility of the heterozygotes is at least 80% and there is sufficient complementation of unbalanced gametes in T+ × T+ crosses, such a stable equilibrium is possible (Stam 1979). The level of partial sterility necessary to reduce a population below the economic injury level has to be established experimentally because density-dependent and other factors may have an adverse effect. Another application of translocations in insect control is the manipulation of gene frequencies in a population by using the translocation as a transport mechanism (cf. Curtis 1968; Whitten 1971). In laboratory-experiments Feldmann (1979) has tested three different strains of *Tetranychus urticae*, homozygous for a structural chromosome mutation (T), for their ability to replace a standard strain. A population replacement could be realized for two strains when the initial frequency of the 'T-karyotype' was at least 0.65.

For both methods an essential requirement is that the translocation-homozygotes have a good fitness. However, in many insects it has been demonstrated that radiation induced translocations are often either lethal or show severe fitness reductions when made homozygous (review by Robinson 1976; Reid and Wehrhahn 1976; Baker et al. 1977; van Heemert 1977; McDonald et al. 1978). In the onion fly three out of eight different translocations appeared to be viable as homozygotes in the adult stage. Recently a few more translocations with viable homozygotes have been isolated, but so far it has not been possible to establish stable pure breeding homozygous stocks, probably due to reduced fitness of the homozygotes (van

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Heemert and Robinson, personal communication), with the exception of the one presented here. There are many reports about cage experiments with translocation heterozygotes, but only a few dealing with homozygotes (Robinson and Curtis 1973; Reid and Wehrhahn 1976; Feldmann 1979).

The object of this study was to assess the fitness of flies homozygous for an autosomal reciprocal translocation under competitive conditions. In separate experiments longevity and egg production of homozygous females were compared with heterozygous females.

Material and Methods

Isolation of Translocation Homozygotes

Seven days old wild type (++) males were irradiated by a dose of 200 rad X-rays and mated with ++ females. Translocation T14 was isolated from a F_1 female which showed a reduced egg-hatch. To remove radiation damage and to obtain genetically diverse material, translocation heterozygous (T+) females were backcrossed with ++ males in mass cages with excess ++ males for at least five generations. Males were not used as backcross parents (T+), as they are achiasmate (no recombination for loci on the translocated chromosomes). After mating, females were separated and each progeny was reared separately. The adults from these progenies were mated in separate cages in order to obtain several 'lines' with a low kinship between lines. Egg-hatch reduction was always used as selection criterium to identify the T+ X ++ crosses. Classification of eggs is simple, the unbalanced karyotypes from T14 die as embryos and can be recognized by a brown colour of the eggs; unfertilized eggs remain white. After intercrossing different 'lines' at the 5th backcross generation (G_6), T+ X T+ progenies were selected on the basis of egg-hatch reduction and karyotype analysis. The crosses made in G_6 and the following generations correspond in main lines with the scheme given in Figure 1. In G_7, males (from T+ X T+ crosses) were testcrossed with ++ females and the TT males could be identified by karyotyping one larva from those crosses with a percentage of brown eggs of 0-4% (++ X ++ and ++ X TT). Six TT males were selected in this way and they were subsequently mass-mated with females (++, T+ and TT) in two cages (3 males/cage). From each mass cage at least one TT X TT progeny was selected, together with some TT X T+ progenies (not shown in Fig. 1). In G_8 some TT X T+ progenies were obtained by direct crossing of T+ X T+ progenies, i.e. without first testcrossing the males. Adult flies of G_8, from either TT X TT or TT X T+ crosses, were outcrossed with T+ to reduce inbreeding effects in the next generations. These T+ parents descended from different backcross 'lines' (T+ X ++). In G_9 TT X T+ progenies were selected (on the basis of egg-hatch and partially by karyotype analysis) and finally by crossing these, in G_{10}, several genetically different TT X TT progenies were isolated; this was confirmed by cytology. In order to rear flies on a large scale (as larvae) for the cage experiments, the adults of G_{10} were mated in groups according to the degree of kinship. For each combination the inbreeding coefficient I (I meaning the chance that the two alleles for each locus of an individual are both a copy of the same ancestral allele) was calculated. In this way four groups of TT individuals (a-d) with an average inbreeding coefficient of 0.04 (range 0.03-0.05) were obtained in G_{11}; these were used for the cage experiments. In G_{11} all larvae were reared on an artificial medium (Loosjes 1976), because this made it easier to rear high numbers under standardized conditions. In preceeding generations the larvae were reared on onion (Vosselman 1978).

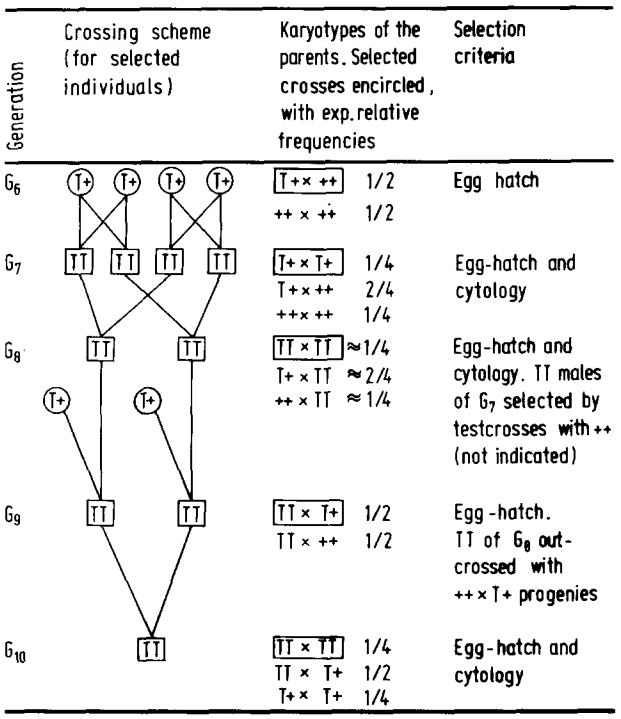

Fig. 1. Basic scheme used for the isolation of homozygotes (TT) for translocation T14 of *H. antiqua*, after five generations of backcrossing of translocation heterozygotes (T+) with wild types (++)

Female Longevity and Egg Production

To compare TT and T+ females with respect to longevity and total egg production, progenies of five different TT X T+ crosses were used. These females were reared as larvae on onion for the first 3-4 days, in the dark at a temperature of 25°C, and subsequently at 20°C and 16 h daylight. The adult flies were kept at 23°C, approximately 70%r.h. and 16 h daylight. Eggs were collected during the first weeks once every three days and later once every four days. Females were only stimulated to lay eggs 48 hours previous to the time of collection (Vosselman 1978), by providing them with a slice of raw onion.

Experimental Design of Cage Experiments

The initial population comprised 3,000 flies, divided over six cages: in each cage were 125 ++♀♀, 125 TT♀♀, 125 ++♂♂ and 125 TT♂♂. The origin of the ++ population used in this experiment was different from the ++ flies used for the backcrosses of T+ in so far that the pupae were collected from different places in the southwest of the Netherlands. The four groups of TT individuals of G_{11} (see above) were sexed and divided between the cages in such a way that in half of the cages only a X b crosses were possible, and in the other half only c X d crosses. The flies were of the same age and placed together one or two days after eclosion of the pupae. For three weeks, when the flies were 14-35 days old, eggs were collected a total of four times. The number of eggs used for

rearing the larvae amounted to 40,000-50,000. The number of pupae obtained was 25,000-35,000. As much as possible equal numbers of eggs per cage were taken. The larvae of the cages with a X b crosses were reared separately from those of the cages with c X d crosses.

A number of 3500-4000 adult flies of G_1, divided over 8 cages were used for rearing the second generation. The inbreeding coefficients of the TT individuals were again on an average 0.04 (0.03-0.05). The flies were not sexed (pupae were placed in the cages) and each cage consisted half of flies of the a X b group and half of the c X d group. Egg collection and larval rearing was equal to the previous generation. The third generation of flies was obtained in the same way as the second one, except for the division into the different groups. During all these experiments adult flies were reared in cages of size 25 X 25 X 25 cm, at 20°C, 70% r.h. and 16 h daylight. For rearing conditions of the larvae and the composition of the larval rearing medium see Loosjes (1976). As it is more difficult to karyotype females, almost exclusively males were scored, either in the pupal stage or one day after eclosion of the pupae. The cytological techniques have been reported earlier (Vosselman 1978).

Results

Cytology and Fertility of the Translocation

The breakpoints of translocation T14 are located in the long arms of the autosomes 2 and 6, near the centromeres (Fig. 2). The translocated chromosome 2^6 can be recognized because it is slightly longer than chromosomes 3 and 4, while chromosome 2 is the smallest autosome. Chromosome 6^2 is shorter than 6 and almost metacentric. The difference in length of the exchanged chromosome segments is sufficient to distinguish TT from ++ individuals, at least in testis preparations. In preparations of embryos, larval brains or ovaria with, in general, a lower number of scorable cells and less contracted chromosomes, the disparity was not always clear. Therefore, predominately males were classified. The T+ individuals are recognizable in all stages due to the presence of a quadrivalent configuration either in somatic or meiotic pairing (Fig. 2).

During backcrossing of T+ females a considerable variation between crosses in the number of dead embryos (brown eggs) was observed. It could not be determined if this was caused by genetic differences. The average percentage of brown eggs in T+ (♀) × ++ (♂) crosses amounted to 34.4 (13175 eggs). In ++ (♀) × T+ (♂) an average percentage of 30.1 (6242 eggs) was found. This difference could be expected, because the frequencies of the disjunction types of the translocation multivalent were not equal for both sexes (Vosselman, in prep.).

Female Longevity and Egg Production

Preceding the cage experiments, TT and T+ females were compared with respect to longevity and total egg production (Table 1). Progenies of five different TT × T+ crosses were used. The results of four of these crosses (35 TT and 28 T+ females) have been combined since the average values for longevity and egg production of the TT females were not different from T+. In one progeny (cross 5) the T+ females had significantly higher values for longevity ($F^1_{11} = 6.9$; $0.01 < p < 0.05$) and egg production ($F^1_{11} = 14.8$; $p < 0.01$).

The variation in number of eggs and longevity of the TT females of cross 5 was remarkably low.

Cage Experiments

The frequencies of karyotypes observed in three successive generations are given in Table 2 starting from a parental population consisting of half TT and half ++ individuals. Assuming that TT and ++ individuals had an equal fitness, one would expect in generation G_1 a ratio of 1:2:1 for ++, T+ and TT respectively. In the following generations complementation of unbalanced gametes in T+ × T+ crosses could occur, but its frequency will have been low because of differences in disjunction of the translocation multivalent between the sexes. In males only adjacent I and alternate orientations occur, while in female adjacent II and alternate orientations predominate

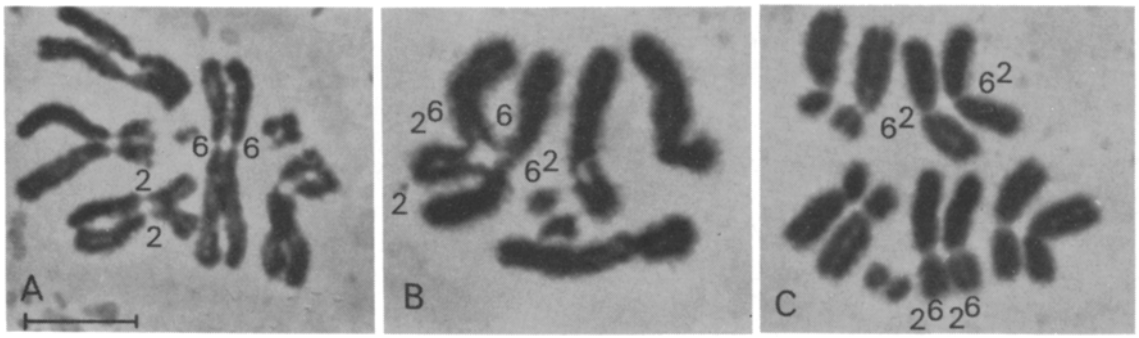

Fig. 2A-C. Karyotypes of *H. antiqua*. A spermatogonial metaphase of ++ male (2266); B prometaphase I of T+ male (2^6 2 6^2 6); C spermatogonial metaphase of TT male (2^6 2^6 6^2 6^2)

Table 1. Egg production and longevity of sibling females homozygous (TT) and heterozygous (T+) for translocation T14 in *H. antiqua*. These females descended from five different TT x T+ crosses, the results of one of which, with significant differences between TT and T+, have been presented separately

Crosses	Female karyotype	Number of females	Number of eggs / ♀		Longevity (days)	
			mean ± S.E.	range	mean ± S.E.	range
1, 2, 3, 4	TT	35	456,4 ± 144.7	213-859	52.4 ± 14.4	27-84
1, 2, 3, 4	T+	28	483.6 ± 169.1	168-893	56.3 ± 19.7	23-96
5	TT	5	469.8 ± 43.3[a]	441-545	43.8 ± 6.7[b]	32-48
5	T+	8	817.5 ± 195.9[a]	438-1067	67.6 ± 19.3[b]	30-82

[a] $F_{11}^{1} = 14.8$, $p < 0.01$ (analysis of variance)

[b] $F_{11}^{1} = 6.9$, $0.01 < p < 0.05$

(Vosselman, in prep.). The estimated increase in the number of T+ individuals in generations G_2 and G_3 due to complementation, therefore, amounts to only 0.5-1.0%.

For reasons mentioned above males were predominately used to establish the karyotype frequencies but in generation G_3 41 females were also karyotyped. As there were no significant differences between females and males the results for both sexes have not been presented separately in Table 2.

Table 2. Karyotype frequencies in adults of *H. antiqua* observed in three successive generations starting from an initial mixed population of wild type flies (++) and translocation homozygotes (TT) in a ratio of 1 : 1

Karyotypes	Numbers (%) of karyotypes in generation:		
	G_1	G_2	G_3
++	36 (23.1)	34 (19.8)	32 (23.0)
T+	81 (51.9)	96 (55.8)	83 (59.7)
TT	39 (25.0)	42 (24.4)	24 (17.3)
Total	156	172	139
Not scorable	4	5	4

The percentage of brown eggs (dead embryos) in generation G_1 was 1.2 (805 eggs), in G_2 32.1 (2179 eggs) and in G_3 36.2 (2317 eggs).

To establish the karyotype frequencies, pupae and newly emerged males were used. For the emerged males it could be determined if differences in time of eclosion between karyotypes were present. The period between the first and last emerging males in all generations varied from 2 to 4 days, but the majority of the males emerged within two days in about equal numbers per day. The males were split in two groups (Table 3), group 1 representing the first emerging 'half' and group 2 the last emerging 'half'. Because the eclosion of pupae occurs in a short period during the night or in the morning, it was not possible to divide the males in two groups with exactly the same numbers. A general tendency was observed to be a surplus of T+ and a shortage of TT in the first emerging group of males. Apparently the pre-adult development time of the TT males was on the average somewhat longer than

Table 3. Time of eclosion of male pupae of *H. antiqua* of Table 2. The males have been split in two groups in sequence of emergence. Group 1 represents the first emerging 'half' and group 2 the last emerging 'half' (see text)

Karyotypes	Percentages of karyotypes in each group/generation								
	G_1			G_2			G_3		
	Group 1	Group 2	Ratio[a]	Group 1	Group 2	Ratio[a]	Group 1	Group 2	Ratio[a]
++	22.9	28.6	0.8	17.5	20.3	0.9	24.5	20.0	1.2
T+	65.7	38.8	1.7	71.4	46.4	1.5	64.2	53.3	1.2
TT	11.4	32.7	0.3	11.1	33.3	0.3	11.3	26.7	0.4
Number	35	49		63	69		53	45	

[a] $\frac{\text{group 1}}{\text{group 2}}$

of T+. The data for the ++ males are more difficult to interpret, but it is suggested that the ++ males had a pre-adult development time in between T+ and TT, at least in generations G_1 and G_2.

Discussion

Female Longevity and Egg Production

The average values for longevity and egg production for ++ females from both a recently colonized and from a laboratory strain of *H. antiqua* obtained by Robinson and Zurlini (1979) with about the same rearing conditions, were somewhat lower than the present values, indicating that the chromosomal rearrangement T14 does not negatively affect these two characters.

However, in one full-sib a significantly higher egg production and adult longevity for T+ compared to TT females were observed (Table 1). This is presumably due to genotypic differences and not due to the chromosomal rearrangement per se, as in four other full-sibs no significant differences were found. Such genotypic differences between the TT and T+ females could be expected since the male parent of these females was T+ and males are achiasmate. Because of the absence of crossing-over genotypic differences were possible for all loci on the chromosomes involved in the translocation which were heterozygous in the male parent. As egg production is related to female longevity it is not necessary to assume that the differences measured for these characters are due to genotypic variation for different loci.

Another conclusion from the present data might be that for determining the effect of chromosomal rearrangements on fitness, it is important to use genetically diverse material to avoid a disturbing effect of linked factors.

Cage Experiments

The data obtained from the cage experiments indicated no substantial differences in fitness between the TT and the ++ flies. In generation G_3 somewhat more ++ than TT individuals were found, but in G_1 and G_2 the opposite was observed.

In all three generations the observed numbers of T+ individuals were slightly higher than expected, but only in generation G_3 was the ratio of T+: ++ and TT significantly different from 1 : 1 ($\chi_1^2 = 5.2$, $0.02 < p < 0.05$). In fact, as a consequence of complementation of unbalanced gametes in T+ × T+ crosses in G_2 and G_3, the expected percentages of T+ should have been 0.5-1.0% higher, but even taking this into account an excess of T+ individuals is apparent.

The T+ individuals probably had a selective advantage in some way, perhaps manifested by the on average earlier eclosion of the male T+ pupae (Table 3). In the plants *Campanula persicifolia* (Darlington and La Cour 1950) and *Clarkia speciosa* (Bloom 1977) translocation heterozygotes can be at a selective advantage under conditions of inbreeding. Also, John and Lewis (1958, 1959) have attributed the presence of unexpected high frequencies of translocation heterozygotes in some populations of the cockroach *Periplaneta americana* and *Blaberus discoidalis* to inbreeding.

Preservation of genic heterozygosity has been generally suggested to be the cause of excess translocation heterozygotes. As the inbreeding coefficients in the present experiments were low, it is questionable if inbreeding was the reason of the excess of T+.

Because all T+ individuals in generation G_1 were hybrids between ++ and TT, a higher level of genic heterozygosity of the T+ (resulting in a selective advantage) might be a consequence of differences in gene frequencies between the parental ++ and TT population. In that case, however, recombination in T+ individuals (males achiasmate) would lead to smaller differences in genic heterozygosity and therefore also a smaller excess of T+ was expected in generations G_2 and G_3. The data did not suggest a decrease but an increase in the relative frequency of T+ from G_1 to G_3. Apparently other unknown factors have attributed to the excess of T+ individuals.

Hitherto only a few reports about cage experiments incorporating translocation homozygotes have been published, although such experiments are indespensable to ascertain the overall fitness of the homozygotes. Robinson and Curtis (1973) established for a translocation in *Drosophila melanogaster* that the homozygotes had practically normal fertility and viability in non-competitive conditions. On the contrary in cage experiments the translocation homozygotes were rapidly eliminated even when the initial mixed population consisted of 9 times as many TT as ++. Four different homozygous-viable translocations in *Drosophila melanogaster* were tested by Reid and Wehrhahn (1976). In small scale experiments they found that starting from initial ratios of 9 : 1 for TT and ++, for two translocations there was no increase in the relative frequency of non-translocated chromosomes after one month. However, a period of one month is too short to draw conclusions about the competitiveness of the TT individuals. In addition it should be noted that only 21 of 57 translocations were viable as homozygotes and the four used in the cage experiments were selected among the best half with respect to 'homozygote viability'. Attempts to replace indigenous populations of *Aedes aegypti* in Kenya by a translocation homozygous strain were not successful (Lorimer et al. 1976). The homozygotes appeared to be deficient in several fitness factors.

Isolation and Viability of Homozygotes

When markers are available, 'pseudo-linkage' methods can be used to isolate translocation homozygotes (Robinson 1976; McDonald et al. 1978). With such methods an efficien selection of desired karyotypes is possible. In *H. antiqua* suitable markers are lacking and therefore a method relying on egg-hatch reduction combined with karyotype-analysis has to be used. Recently Reid and McEwen (1977) proposed a method for *H. antiqua*, based solely on reduction in egg-hatchability. Such procedure is, however, much more cumbersome because to establish the viability of the homozygotes and to select the desired crossing combinations, several testcrosses are necessary. Further, egg-hatch reduction is not a very reliable parameter because a considerable variation can occur due to environmental or genetic factors (Dennhöfer 1975; Hossain et al. 1974; Hossain and Curtis 1975). Reid and McEwen (1977) also suggested using the level of egg-hatch reduction of T+ × T+ crosses as an indication for the viability of the translocation homozygotes. However, when no information about the degree of complementation of unbalanced gametes is availabe, this can lead to wrong conclusions.

It is known from experiments of Robinson (1977) and of own unpublished data, that inbreeding in *H. antiqua* can result in increased mortality, particular in the larval stage. Therefore, in order to obtain sufficient genetic variation, particularly for the chromosomes under selection (the translocated chromosomes), and to remove radiation damage the translocation heterozygotes were backcrossed at least five times with wild type flies (++). Because males are achiasmate females were always used as the backcross parent. This is in contrast to other results where in order to maintain a linkage between translocation breakpoints and markers many workers have used achiasmatic males as backcross parent (e.g. Wagoner et al. 1969; McDonald and Overland 1973a, b; Foster and Whitten 1974; Reid and Wehrhahn 1976). It is obvious, that in these cases the translocation-homozygotes will have an increased chance of being inviable or less fit, due to the presence of higher frequencies of homozygous loci, at least for those loci located on the translocated chromosomes.

Ytterborn (1970) has shown in *Drosophila melanogaster* that the percentage of translocations viable as homozygotes was inversely related to the radiation dose applied for the induction of the translocations. With a dose of 500 rad the percentage of translocations viable as homozygotes was about four times as high as with a dose of 3500 rad. In the present case only 200 rad of X-rays were used.

Significance for Application

In a preliminary field cage experiment it has been established that not only the T14 translocation homozygotes but also a ++ stock maintained for six generations in the laboratory, show higher diapauze sensitivity in comparison with natural populations of *H. antiqua* (Robinson et al. 1979). This illustrates the caution that must be applied when extrapolating from laboratory experiments to the field situation.

The significance of translocation T14 for genetic control purposes seems to be limited, because the genetic load which can be induced amounts only to 30-35%. For other reasons too, this translocation does not meet the requirements for a stable equilibrium (Stam 1979). Further, considering the high variation in egg-hatch between the translocation heterozygotes, it cannot be excluded that under selection the egg-hatch will increase. Such an increase in fertility has been demonstrated e.g. in *Drosophila melanogaster* (Hossain et al. 1974), *Musca domestica* (Hossain and Curtis 1975) and in same plants (Sybenga 1975). Dennhöfer (1975) also found evidence for genetically determined differences in segregation for a translocation in *Culex pipiens*.

However, translocation T14 could be very useful for population replacement or when it is used in combination with other chromosomal translocations. In order to obtain translocations with a higher genetic load, double-translocations have been induced by irradiating some T14 homozygotes. In particular, three-chromosome double-translocations have been studied, because these can have some advantages above four-chromosome double-translocations, or three-chromosome double-translocations obtained by combination of single ones (Vosselman, in prep.). To be able to isolate such double-translocation homozygotes with a good fitness, it is obvious that a re-irradiation makes sense only for translocation homozygotes with a fitness comparable with wild type flies.

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Literature

Baker, R.H.; Sakai, R.K.; Saifuddin, U.T.; Ainsly, R.W. (1977): Translocations in the mosquito, *Culex tritaeniorhynchus*. J. Hered. **68**, 157-166

Bloom, W.L. (1977): Translocation heterozygosity, genetic heterozygosity, and inbreeding in *Clarkia speciosa*. Evolution **31**, 256-264

Curtis, C.F. (1968): Possible use of translocations to fix desirable genes in insect pest population. Nature **218**, 368-369

Darlington, C.D.; La Cour, L.F. (1950): Hybridity selection in Campanula. Heredity **4**, 217-248

Davidson, G. (1974): Genetic control of insect pests. London, New York: Acad. Press

Dennhöfer, L. (1975): Inherited preferential segregation in translocation heterozygotes of the mosquito, *Culex pipiens L.* Theor. Appl. Genet. **45** 250-253

Feldmann, A.M. (1979): Fundamental aspects of genetic control of the two-spotted spider mite *Tetranychus urticae* (Acari: Tetranychidae). Ph. D. Thesis, *L.H.* Wageningen

Foster, G.G.; Whitten, M.J. (1974): The development of genetic methods of controlling the Australian sheep blowfly, *Lucilia cuprina*. In: The use of genetics in insect control (eds.: Pal, R.; Whitten, M.J.), pp. 19-44. Amsterdam: Elsevier

Heemert, C. van (1975): Chromosomal rearrangements in the onion fly, *Hylemya antiqua* (Meigen), induced and isolated for genetic insect control purposes. Studies on cytogenetics and fertility, with emphasis on an X-linked translocation. Ph. D. Thesis, L.H. Wageningen

Heemert, C. van (1977): Isolation of a homozygous X-linked translocation stock with two additional sex-chromosomes in the onion fly *Hylemya antiqua* Meigen. Theor. Appl. Genet. **49**, 123-132

Heemert, C. van; Wijnands-Stäb, K.J.A. (1975): Radiation induced semi-sterility for genetic control purposes in the onion fly, *Hylemya antiqua* (Meigen). 2. Induction, isolation and cytogenetic analysis of new chromosomal rearrangements. Theor. Appl. Genet. **45**, 349-354

Hossain, M.A.; Curtis, C.F.; Jaffe, W.P. (1974): Selection on the fertility of translocation heterozygotes in *Drosophila melanogaster*. 1. The extent of the changes produced by selection. J. Genet. **61**, 205-217

Hossain, M.A.; Curtis, C.F. (1975): The effect of selection on the fertility of translocation heterozygotes in the house fly. J. Med. Entomol. **12**, 59-64

John, B.; Lewis, K.R. (1958): Studies on *Periplaneta americana* 3. Selection for heterozygosity. Heredity **12**, 185-197

John, B.; Lewis, K.R. (1959): Selection for interchange heterozygosity in an inbred culture of *Blaberus discoidalis*. Genetics **44**, 251-267

Loosjes, M. (1976): Ecology and genetic control of the onion fly, *Delia antiqua* (Meigen). Agric. Res. Rep. 857. Wageningen: Pudoc

Lorimer, N.; Lounibos, L.P.; Petersen, J.L. (1976): Field trials with a translocation homozygote in *Aedes aegypti* for population replacement. J. Econ. Entomol. **69**, 405-409

McDonald, P.T.; Asman, S.M.; Terwedow, H.A., Jr. (1978): An alternative method for isolating homozygotes of autosomal translocations in the mosquito *Culex tarsalis*. Can. J. Genet. Cytol. **20**, 581-588

McDonald, I.C.; Overland, D.E. (1973a): House fly genetics. 1. Use of an inversion to facilitate the recovery of translocation homozygotes and to reduce genetic recombination on translocated third chromosomes. J. Hered. **64**, 247-252

McDonald, I.C.; Overland, D.E. (1973b): House fly genetics. 2. Isolation of a heat-sensitive translocation homozygote. J. Hered. **64**, 253-256

Reid, J.A.K.; Wehrhahn, C.F. (1976): Genetic control of insect populations: isolation and fitness of autosomal translocations. Can. Entomol. **108**, 1409-1415

Reid, J.A.K.; McEwen, F.L. (1977): Genetic insect control: chromosome rearrangements isolated using a simple system in the onion maggot, *Hylemya antiqua* (Diptera: Anthomyiidae). Can. Entomol. **109**, 1287-1291

Robinson, A.S. (1976): Progress in the use of chromosomal translocations for the control of insect pests. Biol. Rev. **51**, 1-24

Robinson, A.S.; Heemert, C. van (1975): Preliminary radiobiological studies on *Hylemya antiqua* (Meigen) and data on three radiation induced (0.5 krad) chromosomal rearrangements. IAEA/FAO Symposium on Sterility Principle for Insect Control, Innsbruck 1974, 375-385

Robinson, A.S.; Curtis, C.F. (1973): Controlled crosses and cage experiments with a translocation in *Drosophila*. Genetica **44**, 591-601

Robinson, A.S.; Zurlini, G. (1979: The response of two strains of *Hylemya antiqua* to a constant and an alternating temperature regime. Can. Entomol. **111**, 1207-1218

Robinson, A.S. (1977): Genetic control of *Hylemya antiqua* 2. Can inbreeding depression be a serious obstacle to the development of homozygous rearrangement lines. Entomol. Exp. Appl. **21**, 207-216

Robinson, A.S.; Vosselman, L.; Herfst, M. (1980): Genetic control of *Hylemya antiqua* IV. Sensitivity to diapauze interfering with a field cage experiment using a homozygous autosomal translocation. Bull. Entomol. Res. **70**, 103-111

Smith, R.H.; Borstel, R.C. (1972): Genetic control of insect populations. Science **178**, 1164-1174

Stam, P. (1979): The existence of stable translocation polymorphisms. Genetica **50**, 149-158

Sybenga, J. (1975): Meiotic configurations. Monographs on theoretical and applied genetics 1. Berlin, Heidelberg, New York: Springer

Vosselman, L. (1978): Sex determination of the onion fly, *Hylemya antiqua* (Meigen). I. Sex chromosome polymorphism, gynandromorphism and X-polysomy. Chromosoma **67**, 201-218

Wagoner, D.E.; Johnson, O.A.; Nickel, C.A. (1969): Fertility reduced in a caged native house fly strain by the introduction of strains bearing heterozygous chromosomal translocations. Nature **234**, 473-475

Whitten, M.J.; Foster, G.G. (1975): Genetical methods of pest control. Ann. Rev. Entomol. **20**, 461-476

Whitten, M.J. (1971): Insect control by genetic manipulation of natural populations. Science **171**, 682-684

Wijnands-Stäb, K.J.A.; Heemert, C. van (1974): Radiation induced semi-sterility for genetic control purposes in the onion fly, *Hylemya antiqua* (Meigen) I. Isolation of semi-sterile stocks and their cytogenetical properties. Theor. Appl. Genet. **44**, 111-119 (1974)

Ytterborn, K.H. (1970): Homozygous lethal effects of II-III translocations in *Drosophila melanogaster*. Drosophila Inf. Serv. **45**, 148-149

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