Simulation of Release of Sex-Linked Translocation Homozygotes for Population Replacement[1]

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ABSTRACT

A deterministic computer model was built to evaluate various release strategies of sex-linked translocation homozygotes for the purpose of replacement of a local population of *Aedes aegypti* (L.) in a Kenyan village. The model incorporated overlapping generations, density-dependent larval survivorship, mating competiveness of males for females, immigration of wild types, and the release of adults or pupae.

The results of exercising the model indicate that the immigration of wild types can prevent the achievement of total replacement of the local population and that an equilibrium translocation frequency will be reached. The particular value of the translocation frequency depends on immigration and release rates, as well as the sex of the immigrants. In the absence of immigration, and with the exception of translocation homozygous females that have not been mated to like males, selection is frequency dependent. If immigration is allowed when the release is stopped, the translocation frequency declines. The rate at which it declines depends on the immigration rate. Most of the kinds of adult releases are more efficient than release of pupae. Reduced mating competitiveness of wild males for released homozygous females has little influence on the success of releases, if females have mated to homozygous males before release. It is surmised that the high intensity of larval competition decreases the influence of mating competitiveness in both adult and pupal releases. A decrease in adult survivorship has little effect in continous releases, if translocation females have been mated to like males before release. It does increase the time in which fixation of the translocation is achieved, if adult releases are stopped or if pupae are released.

Deleterious effects of pesticide accumulation in the environment and development of insecticide resistance (Pal and LaChance 1974) have required the investigation of alternative methods of insect pest control. Genetic control is one of the alternatives that has been suggested (Davidson 1974). A number of techniques is included under the rubric of genetic control. One of these is to utilize chromosomal translocations (Robinson 1976). Curtis (1968) suggested use of translocation homozygotes that bear a gene for refractoriness to transmit a disease or a parasite. The mating of the local population with the translocated individuals would yield partially sterile translocation heterozygotes. Theoretically, if sufficient numbers of translocation homozygotes were released, they would eventually replace the local vector population with a refractory population.

Such a release program was conducted in Mombasa, Kenya. The goal was to replace a local population of *Aedes aegypti* (L.) with a released sex-linked translocation homozygous population (Lorimer et al. 1976). As part of this project, a computer model was constructed to evaluate different release strategies that might be employed in a control program. Reported here is a description of the model and a comparison of results of several different release strategies of sex-linked translocation homozygotes simulated on the computer.

MODEL.—In any mathematical model, there is the problem of satisfying 3 suggested attributes of a model, i.e., realism, precision, and generality (Levins 1966). In computer simulations, usually some degree of generality is sacrificed for more realism and precision. This model is an extension of one developed for evaluating genetic control methods of mosquito populations by Dietz (outlined in Pal and LaChance 1974). It can be considered intermediate in its level of realism and precision. The main characteristics of the model are that it considers overlapping generations, density-dependent larval survivorship, all stages of the life cycle, migration of wild adults into an area, and the probability that mating is dependent on mating competitiveness and abundance of different classes of males. The model is deterministic.

For application of the model to the field study in Kenya, it was decided that it would be best to model the mosquito (*A. aegypti*) population of the whole village, rather than consider the dynamics of the populations in the individual huts. Adult mosquitoes breed and immatures develop in clay water pots in the huts (Lorimer et al. 1976). The number of pots in a village was a variable in the model. The model was designed to accomodate sex-linked translocation homozygotes and translocation heterozygotes. Sex is determined in *A. aegypti* by one locus. A female is homozygous recessive at the locus (m/m). The male is heterozygous (M/m). Because translocation heterozygous males could be either M-linked or m-linked, there were 7 kinds (karyotypes) of individuals (4 male and 3 female karyotypes). Each of the 7 kinds of individuals was followed in the model. For the sake of clarity and in the tradition of Wright (1941), the translocation is considered as a simple autosomal gene. Because the translocation used in Kenya involved the sex-determining locus, they were considered together as 2 linked loci. It was assumed that there was no crossing-over between the translocation breakpoint and the sex locus. There was no crossing-

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Table 1.—Offspring frequencies for possible matings.

Parents		Offspring						
Male	Female	TM/Tm	TM/+m	+M/Tm	+M/+m	Tm/Tm	Tm/+m	+m/+m
TM/Tm ×	Tm/Tm	1/2				1/2		
TM/Tm ×	Tm/+m	1/2	1/2			1/2	1/2	
TM/Tm ×	+m/+m		1/2				1/2	
TM/+m ×	Tm/Tm	1/2					1/2	
TM/+m ×	Tm/+m	1/3	2/3				2/3	1/3
TM/+m ×	+m/+m		1/2					1/2
Tm/+M ×	Tm/Tm			1/2		1/2		
Tm/+M ×	Tm/+m			2/3	1/3	1/3	2/3	
Tm/+M ×	+m/+m				1/2		1/2	
+M/+m ×	Tm/Tm			1/2			1/2	
+M/+m ×	Tm/+m			1/2	1/2		1/2	1/2
+M/+m ×	+m/+m				1/2			1/2

over between the marker, black tarsi, and sex in the T3 stock used for the Kenya release. Because the breakpoint was near black tarsi, there was presumably no crossing-over between the breakpoint and sex. I chose to represent them as TM/Tm for a translocation homozygous male, Tm/Tm for a translocation homozygous female, TM/+m for a M-linked translocation heterozygous male, etc. The females were classified according to their karyotype and the karyotype of the male to which they were mated. Males and females did not mate until one day after their emergence. Although this assumption was a bit unrealistic (they usually mate 48–72 h after emergence), this was done to keep the model simpler. It was assumed that females mated only once. Fecundity was assumed to be constant and the same for all of the different classes of females. Fertility depended on the karyotype of the female and the male to which it was mated. Table 1 shows offspring frequencies produced by the appropriate matings. The equations for adult survivorship, larval survivorship, and mating competitiveness are as described by Dietz (in Pal and LaChance 1974). A constant proportion of the adults was assumed to die each day. This was the same for all of the different kinds of adults. Larval development time was assumed to take 15 days. The effect of density on larval survivorship varied for the 1- to 3-, 4- to 7-, and 8- to 14-day-old larvae. It was assumed that the wild, village mosquito population had an equilibrium population size. In this model, release of translocated males and females can be either as adults or pupae, or both. Also, the translocation homozygous females can be released as having been mated to the same kind of males, or as virgins.

The steps involved in implementing the model on the computer will be described. The changes occurring in the numbers of individuals in the different classes are arranged so that some of the natural time lags are present in the simulation.

The program starts at the beginning of a day with the change in the number of mated females in the population due to death, immigration, and the release of translocated individuals. The adult females then lay eggs according to their karyotype and the kind of males with which they have mated (Table 1). For each mating, the probabilities are multiplied by the number of appropriate females. Then the columns are summed to give the number of eggs of a particular kind. It is assumed that all the eggs from homozygote × homozygote (wild or translocation) crosses are viable; 0.500 of the eggs of a heterozygote × homozygote cross are viable; 0.375 of the eggs from a heterozygote × heterozygote cross survive (Davidson 1974).

After the change in the number of adult females is calculated, the same is done for the adult males. This includes the adding of immigrated and released individuals. Following the adult males, if any adult, unmated translocation homozygous females are released, then these are added to the group of unmated translocation homozygous females that are the result of offspring that have developed from eggs laid by previous females. Thus, males and females that will participate in mating have been determined. Mating of virgin females occurs according to the values of the mating competitiveness coefficients of each of the different kinds of males for each of the different kinds of females along with the abundance of the different classes of males. At this point, the newly mated females are added to the old mated females, and adult males that emerged on the previous day are added to the old adult males.

Following the change in the number of old adults, pupae emerge as new adults. Any released female or male pupae are added to the pupae at this time. Advancement of larvae one day in age and the loss of some larvae is the next step, along with moving eggs into 1st instars. Finally, the translocation frequency is calculated for males, females, and for their sums both combined. At this point, one day has been concluded. All these procedures are repeated for each day for the number of days desired. At the end of each day, the numbers in each class

of adults are output, along with the translocation frequencies for males, females, and for males and females combined. In the following discussion, TRF = translocation frequency of adult females, TRM = translocation frequency of adult males, and TRT = translocation frequency of adult males and females combined.

DESCRIPTION OF SIMULATION.—To investigate some of the features of different release strategies, as well as the effect of relaxing certain assumptions, simulations were run on the computer. These are outlined in the following discussion. For this set of simulations, it was assumed that there were 45 pots in the village. The survival coefficients for the adults were set equal to 0.750. This meant that 75% of the adults survived from one day to the next. The survival coefficient for larvae (k) varied depending on the age of the larvae. (k = 0.001 for 1- to 3-day-old larvae; k = 0.0004 for 4- to 7-day-old larvae; k = 0.0003 for 8- to 14-day-old larvae.) k is equivalent to the k in Dietz's equation (Pal and LaChance 1974). Survivorship increased with age of the larvae. Under equilibrium conditions, these values for larvae and adult coefficients gave an avg larval density of 208/pot. Survivorship from 1st instar to pupa was 24.6%. Ninety % of the pupae emerged as viable adults. The adult population size was 610 adults of each sex that had participated in mating and 152 of each sex that were newly recruited adults. Oviposition rates were 3 eggs/female/day. Values for the constants were either based on estimates for the Mombasa villages or were selected so as to produce an equilibrium population size similar to what had been found in the villages (Lorimer et al. 1976).

Releases Continuous, with no Immigration. — The following 5 different kinds of releases for translocation homozygous adults were simulated: males and mated females; mated females alone; males alone; unmated females alone; and males and unmated females. These releases were made on intervals varying from every day to every 4th day. The avg number of individuals released per day was either 610 or 1220. The term "mated females" means translocation homozygous females that have been mated to like males before release. In all these simulations, mating competitiveness was assumed to be 1.000. Also, there was assumed to be no immigration of wild adults into the village. Finally, an analysis was made of the release of male and female pupae to compare the rate at which the translocations were incorporated into the population when pupae were released with that of males and mated females (adults) and with males and unmated females (adults). For the pupal releases, 305 of each sex were released every day.

Releases Stopped, with no Immigration.—Because releases would be stopped at some point in the field situation, computer runs were made for the 5 described classes, but releases were stopped at different times after the beginning of the releases. The dynamics of the population were then followed to monitor any change in translocation frequency. These releases presumed a total of 610 individuals released each day.

Releases Continuous, with Immigration. — It also was of interest to relax the assumption of no immigration of wild adults into the village while releases were taking place. This was done for 3 of the classes of releases (males alone, mated females alone, males and mated females). The immigration rates were 10 or 20 males, females, or equal numbers of both per day. It was assumed that the female immigrants had mated with wild males. Either a total of 610 or 1220 individuals was released per day.

Releases Stopped, with Immigration.—The obvious next step after the previous 2 was to have immigration and to consider the effect of immigration when releases were stopped. This was done for the release of mated females alone, and for males and mated females. Either 610 or 1220 individuals were released/day. The frequency of releases also was altered, but the overall release rate was kept the same (e.g., 305 of each sex every day, 610 every 2 days, 915 every 3 days, 1220 every 4 days). Immigration rates were 3, 5, or 10 of each sex/day. Again, female immigrants were assumed to have mated with wild males.

Mating Competitiveness.—Because mating competitiveness of released males for wild females and vice versa is usually considered important in the success of any release program, the effect of varying mating competitiveness was investigated. The coefficients of mating competitiveness were varied from 1.000 to 0.005 for the competitiveness of (1) translocation homozygous males for wild females, (2) wild males for homozygous females, and (3) wild males for heterozygous females. The coefficients were varied individually and simultaneously for (1) and (2), and for all three simultaneously. Releases were 305 each of male and mated female adults, and 305 each of male and female pupae.

Adult Survivorship.—To investigate the effect of decreased survivorship of translocated adults on the success of releases, values of coefficients that determine adult survivorship rates were varied from 0.600 to 0.500 and 0.400. (Recall that in all other simulations survivorship was fixed at 0.750.) The releases were 305 each of male and mated female adults and the same number for male and female pupae. Adult releases were run with and without stopping the releases. Releases of pupae were not stopped.

RESULTS.—*Releases Continuous, with no Immigration.*—Of the 5 kinds of releases, that of mated females is the most effective means of introducing the translocations into a wild population (Table 2). This is not too surprising because all of the 1st generation offspring of released females would be translocation homozygotes. The release of males and mated females is the 2nd fastest, whereas release of males only is the slowest. Interestingly, release of unmated females alone does not result in a 1.000 translocation frequency (TRT). The 1.000 translocation frequency is not reached because the translocation frequency of males becomes fixed at 0.500,

Table 2.—Week in which TRT=1.000 for different release strategies.

Combinations of adults released	Release every day (total no.)		Release every 2nd day (total no.)	
	610	1220	610	1220
Males and mated females	13	9	19	13
Mated females	11	7	16	11
Males	37	31	—[b]	38
Unmated females[a]	0.912	0.958	0.858–0.879	0.907–0.925
Males and unmated females	17	11	26	17

[a] Data for unmated females alone are equilibrium values for TRT.
[b] No data.

even though the females are 1.000. The reason is that the crossing of unmated females with wild males produces male and female translocation heterozygotes as offspring. With the decrease of the wild males, the large majority of matings in the population would be between the heterozygous males in the villages and the released unmated females (homozygous). Eventually, because the only males in the village population would be heterozygotes, the male translocation frequency would be 0.500.

The same order of effectiveness of the different release strategies holds for releasing different numbers of individuals and for releasing at different intervals of time. By comparing releases of different numbers of individuals for the same release schedule, we see that releasing twice as many individuals does not mean that the goal will be achieved in one-half the time (Table 2). This decrease in efficiency when there is an increase in the numbers released is an intrinsic property of the replacement phenomenon. It is due to the nonlinearity of the elimination of normal chromosomes from the population. Another interesting aspect of these results is that releasing the same total number of individuals, but on different schedules, produces the same level of replacement. For males and mated females it took 13 wk with 610 released every day, 1220 every 2nd day, 1830 every 3rd day, or 2440 every 4th day. Data for the 3 and 4 day releases are omitted from the Table. This means that if a village were relatively inaccessible and difficult to reach, releases could be made less frequently with the same end result expected. (Recall, however, that these data assume no immigration of wild adults.)

As would be predicted from the aforementioned data, release of pupae is the slowest procedure when both males and females are released, but it is not much slower than releasing males and unmated females. TRT reached 1.000 in week 18 for the pupae. There obviously is a lag because of emergence. Also, the effect of abundance on the probability of matings must be taken into account. These factors would have to be considered when deciding on the appropriate manner in which to release in a village.

Releases Stopped, with no Immigration.—For simulations in which release of translocated individuals was halted, but the population dynamics were still recorded, there is a pivotal day for each of the different kinds of releases (with the exception of unmated females alone). If the releases are stopped before the critical day, the population reverts to all wild types. If, however, releases are stopped after the critical day, then the translocation goes to fixation. The pattern of the values of the critical day parallels that of the effectiveness of the various release combinations. For mated females the critical time period is 7 days, whereas it is 8 days for males and mated females. It is 11 days for males and unmated females. The longest period is 20 days for males alone. The farther away from the critical day that a release is stopped (either less or greater than), the more rapid the approach to the fixation of the translocation or the wild type. There is not an obvious pattern to the values of the translocation frequencies on these critical days.

Releases Continuous, with Immigration.—The adding of immigrants to the village population is important in making the releases more realistic. Table 3 shows results of the effect of immigration on the translocation frequencies at equilibrium for the different kinds of releases. Only the results for a total release of 610 adults are presented because the patterns are the same for the releases of 1220 adults. Obviously, immigration inhibits the attainment of 1.000 translocation frequency, even when releases are continued for a long period of time. TRT, however, does approach very close to 1.000, when there are large releases and a low immigration rate.

Definite patterns appear in the effect of immigration on the different kinds of releases. If the immigrants are of the same sex as the released material, then there is no differential effect on either TRM or TRF. When the sex of the immigrants is opposite that of released individuals, then the trans-

Table 3.—Equilibrium translocation frequencies for different combinations of releases and kinds of immigrants.

No. of males released	No. of mated females released	No. of immigrant wild males	No. of immigrant wild females	Stabilized translocation frequencies		
				TRM	TRF	TRT
610	0	20	0	0.969	0.970	0.969
610	0	0	20	0.942	0.626	0.883
610	0	10	10	0.951	0.766	0.919
0	610	20	0	0.825	0.998	0.973
0	610	0	20	0.968	0.968	0.968
0	610	10	10	0.889	0.983	0.970
350	350	20	0	0.954	0.998	0.976
350	350	0	20	0.983	0.940	0.961
350	350	10	10	0.968	0.968	0.968

location frequency of the sex of the immigrants decreases the most. If there are both male and female immigrants, the translocation frequency of the sex of the released material decreases the least. For releases of both sexes, the pattern is reversed. With male immigrants, TRM decreases more than TRF, whereas if the immigrants are females, then TRF decreases more. When only males are released, immigration of females causes a greater reduction in TRT than immigration of both sexes, which in turn is larger than the decrease due to male immigrants. Similar patterns of differences in TRT occur for the other 2 kinds of releases, but the decreases in TRT are smaller. The same trends hold for the lower immigration rate of 10 immigrants/day, but the results are not shown here.

Releases Stopped, with Immigration. — When releases are stopped in the presence of immigration, the translocation frequency begins to decrease. This is true whether releases are stopped before or after the equilibrium translocation frequency has been reached (Tables 4), although it decreases at a slightly faster rate if the release is stopped before the equilibrium is reached. The rate at which the translocation frequency declines depends primarily on the immigration rate. This can be seen by comparing TRT on day 651, for an immigration rate of 3 of each sex/day, with TRT for an immigration rate of 5 of each sex/day. Interestingly, the latter rate produces a much greater decrease than the former. Apparently, there is some critical point between 6 and 10 immigrants/day which markedly alters the effect of immigrants. When the immigration rates are compared to the population size of the translocation homozygous adults (that have participated in mating) 1 wk after the releases are stopped (Table 4), this gives immigration rates of 0.2–1.8% of the adult homozygous population. Although not shown here, the results for releases other than every day are similar, except that there is oscillation around an eqilibrium rather than there being a stable equilibrium point. The number of values through which the translocation frequencies cycle is the same as the frequency of the release, e.g., 3 values when releases are every 3 days.

Mating Competitiveness. — For constant releases, variation in the mating competitiveness coefficients for the range of values of 0.005 to 1.000 did little to alter the rate at which 1.000 TRT was reached. This included releases of male and mated female adults, and male and female pupae. In the case in which the release was stopped after 5 wk, the change in TRT was slowed, but the slow change occurred between the values of 0.923 and 1.000 for TRT. The most likely explanation for this pattern of behavior, in terms of the releases, is that the decline of wild types must be the result mainly of larval competition. The release of large numbers of pupae, or adults, causes the production of large numbers of larvae, which in turn leads to a high larval mortality rate. Because in the model the larvae are assumed to be equally competitive, the wild larvae are unable to replenish their losses as quickly as the released individuals and therefore eventually lose. This equal competitiveness of larvae may be considered an unrealistic aspect of the model which should perhaps be changed in the future (Lorimer et al. 1976).

Adult Survivorship.—Altering survivorship of translocated adults has little effect on the efficiencies of the release strategies in the adult releases, if the releases are not stopped. For survival probabilities of 0.750 and 0.600, it takes 13 wk for TRT to reach 1.000. It takes 14 wk for probabilities of 0.500 and 0.400. There is, however, a noticeable increase in the time to reach 1.000 translocation frequency in the release of pupae. It takes ca. 10 wk longer when the survivorship probabilities are changed from 0.750 to 0.400. This difference between adults and pupae is because the adult females already have been mated by like males when released. They produce trans-

Table 4.—Translocation frequency (TRT) on day 651, for different immigration rates, when releases are stopped before and after TRT reaches equilibrium.[a]

No. released	No. of immigrants		Day reach equilibrium	Equilibrium TRT	Day stopped	TRT on day 651	No. adult homozygotes[b]
	Males	Females					
610 mated females	3	3	76	0.991	68	0.423	1115
	3	3			83	0.440	1117
	5	5	75	0.985	68	0.053	1108
	5	5			83	0.063	1110
	10	10	68	0.970	60	0.002	1088
	10	10			75	0.002	1101
305 males and 305 mated females	3	3	80	0.990	71	0.425	1368
	3	3			86	0.442	1373
	5	5	87	0.984	78	0.059	1360
	5	5			93	0.070	1363
	10	10	79	0.968	71	0.002	1332
	10	10			86	0.002	1336

[a] Release and immigration rates are per day.
[b] Population size, 1 wk after release stopped, of adult translocation homozygotes that have mated.

location homozygous offspring immediately. Therefore, survivorship would be involved only in the subsequent generations. With the pupae, adult survivorship is obviously important in determining the success of the introduced translocated stock because mating has yet to occur.

Lowered adult survivorship does have an effect on the success of the release of adults, if the releases are stopped. I showed previously that 8 days is the critical time period for the release of 305 males and 305 mated females. If a release is halted after that day, then the translocation will go to fixation. When adult survivorship decreases, the critical day increases. For an adult survival probability of 0.600, the critical day is 32; for a probability of 0.500, it is 45, and 58 for a probability of 0.400. The apparent explanation is that in continuous releases, the major source of mortality is larval competition. Because there are always newly released adults being added to the population, adult survivorship is less important. When releases are stopped, larval competition becomes relatively less important, and adult survivorship has a greater influence. There is no longer the constant influx of adults to replace those lost. Therefore, lowered adult surviviorship would be expected to have a negative effect in adult releases if the release were stopped, or if the releases were infrequent.

DISCUSSION.—In vector control the concept of population replacement has become a possible means of population control of insect vectors. The goal in a replacement program is to displace a local vector population with a strain that is less susceptible to the transmission of a disease. An advantage of this technique is that a void is not created by the loss of a local population and therefore the maintenance of natural interactions in the system is promoted. Also, for situations in which a population is not well isolated and eradication would be impossible, this approach is more realistic.

In considering the results of the aforementioned simulations, I would expect that the release of mated females would be the fastest way to introduce translocations. It appears that the poorer performance of the males alone is the result of the time lag of larval development. It takes time to get translocated females into the mating population when only males are released because larval development takes 15 days. There also is a time lag in the release of male and female pupae, but the release of translocated female pupae compensates for most of this developmental lag. Thus, the release of pupae is just slightly slower than the release of adult males and unmated females. Of course, with the exception of the release of unmated translocation homozygous females, the end results are the same. Curtis and Hill (1968) found for a simple model with autosomal translocations that, in terms of population elimination, the release of males and females together was nearly as good as the release of equal numbers of males alone.

In the absence of immigration, and with the exception of unmated females alone, there is a critical time period for each kind of release after which the releases can be stopped and fixation of the translocation will be achieved. Thus, selection in the release of sex-linked translocation homozygotes is frequency dependent, as are autosomal translocations (Curtis and Hill 1971). In contrast, Curtis and Hill (1971) found that M-linked translocations when released as heterozygotes were not frequency dependent. The model of sex-linked translocation homozygotes presented here exhibits more complex behavior than the autosomal case. In this initial series of simulations, I was interested only in the frequencies of the translocations according to sex. I did not monitor M-linked or m-linked translocation frequencies separately. As a result the translocation frequency values did not exhibit obvious trends in terms of the critical values for the unstable equilibria. To understand the dynamics of this system thoroughly with regard to selection and critical values, it will be necessary to consider the releases in terms of chromosome frequencies. Because I assumed the sex locus and the translocation to be tightly linked, we can view this as a system with a single locus and 4 alleles: TM, Tm, +M, and +m. Such a system can have multiple stable and unstable equilibria. The relationship between the chromosome frequencies and the critical values will be described in a subsequent paper.

The immigration of wild types dilutes the effect of translocation releases. Although there are differential effects depending on the sex of the released material and of the immigrants, the important general result is that if immigration is sufficiently high, then replacement is impossible. A constant translocation frequency (frequencies) is reached, the value of which depends on the kinds of releases, and the relative rates of release and immigration. Depending on the immigration rate, in a control program it may be possible to maintain a sufficiently high translocation frequency by periodic releases. The frequency and size of the releases would depend in part on the immigration rate. Curtis and Hill (1968) found the same result. The effect of the releases also depends on the nonlinearity of the replacement process. The gain in effectiveness of releases is not linearly related to the numbers released. After a certain point, the gain in releasing more translocated individuals is not worth the cost in terms of effort.

The results from mating competitiveness and adult survivorship emphasize that the effect of some of the parameters can be swamped by releasing large numbers of translocated individuals. Also, they show that larval competition may be an important factor in large releases. Both variables would be expected to become more important if releases are stopped, or if lower numbers are released.

The major aspects or variables of the translocation release considered in this study have been the kinds and frequency of releases, immigration, mating competitiveness, and adult survivorship. Lorimer et al. (1976) found that the sex-linked translocation homozygotes released in Kenya were inferior in fertility,

larval development time, larval and adult survivorship, and mating competitiveness. The translocation homozygotes also showed oviposition preference for nonnative containers. The combination of these deficiencies probably contributed significantly to the failure of the released population to become established. This points to 2 basic problems in any genetic control program. First, it is difficult to produce an organism that is well adapted to the field and that mates well with the wild population. Therefore, released animals usually are deficient in some aspects. Second, it often is difficult to assess the relative importance of these deficiencies to the success or failure of a release program because of the complexity of the dynamics of the system. In such situations the modeling of the populations may provide assistance. If the model includes major aspects of the species' biology, then by manipulating the variables, one can develop an estimate of the relative importance of these variables to the overall dynamics of the system. For example, is adult survivorship or larval survivorship more important, or are they equally important? Sensitivity analysis is a technique that allows one to do this (Miller 1974). Using this approach, Miller et al. (1973) found larval and adult survivorship to be very important to the dynamics of a mosquito population. Thus, if it were possible to manipulate genetically, in the strain to be released, characteristics such as mating competitiveness, survivorship, etc., then it would be advantageous to produce a strain superior in those characteristics judged to be critical to the success of a release program. Obviously, one can not produce a strain superior in all respects, but by coordination of modeling of the system and construction of strains to be released, it may be possible to produce strains with an enhanced probability of displacing a local population because of superiority in particular aspects of their biology. Lorimer et al. (1976) discussed some of the difficulties involved in producing competitive strains. The succcess of such an approach depends a great deal on a good knowledge of the ecology and genetics of the target species and of the introduced strain, and requires a detailed analysis of the model. The modeling and experimental aspects also serve to complement one another. For example, the results of Lorimer et al. (1976) suggest that differences in larval development time and larval survivorship may be important variables in a sex-linked translocation release. The results from the simulation in this study also suggest that larval competition is important in large releases. Unfortunately, these factors were not varied in the initial simulations because it would have required major modifications of the computer program. However, based on this combined evidence, it is clear that these factors should be investigated in future simulations to determine their relative importance.

This computer model has provided some insight into the dynamics of a release program of sex-linked translocation homozygotes. Those factors varied in the simulations were varied singly or in pairs. In a typical field release program, one would expect differences in larval and adult survivorship, and mating competitiveness, and for there to be immigration of wild adults. Therefore, future simulations should deal with altering these factors simultaneously to determine whether there are particular values of the variables that provide for interesting or unexpected interactions. Also, sensitivity analysis, or another similar technique, should be applied to the model to provide a systematic rating of the relative importance of the different parameters. Finally, this model is deterministic, even though the population size is rather small. It would be more realistic to add a stochastic component to the dynamics of the populations in future modeling.

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