STERILE-MALE TECHNIQUE FOR ERADICATION OR CONTROL OF HARMFUL INSECTS

PROCEEDINGS OF A PANEL
ON APPLICATION OF THE STERILE-MALE TECHNIQUE FOR THE
ERADICATION OR CONTROL OF HARMFUL SPECIES OF INSECTS,
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CONTENTS

ON THE POSSIBILITY OF A NEW METHOD
FOR THE CONTROL OF INSECT PESTS *

A.S. SEREBROVSKY
Genetics Laboratory, Institute of Zoology,
Moscow State University,
Moscow, USSR

Abstract [†]

ON THE POSSIBILITY OF A NEW METHOD FOR THE CONTROL OF INSECT PESTS. The new principle of insect control consists in disturbing the propagation of the pest population by means of translocations. It is well known that individuals heterozygous for some translocations usually form a portion of aneuploid gametes and give a more or less inviable aneuploid progeny. On releasing, therefore, a sufficient number of individuals with a chromosome set altered by translocations into a wild population (with allogamous propagation), there will arise heterozygotes for translocations yielding a certain percentage of inviable offspring. Crosses inside this population will be similar to those between species with resulting sterility of hybrids. The theoretical analysis reveals that if a wild population is mixed in proportion 1:1 with some race containing only one translocation viable in homozygous condition and giving in heterozygotes 50% of aneuploid gametes, the reproduction of the population will be reduced by 43%. If several races with different allelic translocations are released the reduction of reproduction in the population can reach 75%, and if races with 4-5 independent translocations are used the reduction can attain 95%-99% and even more. A population consisting of races with different translocations cannot remain in balance. Those types of chromosomes which happened to be in minority are subjected to elimination. Yet this process of elimination will go on during many generations and thus the disturbance of reproduction will be protracted. By an additional releasing of eliminating race, this disturbance can be maintained permanently. Diverse variants of this method are possible, depending upon the biology and economic importance of injurious insects, the cost of breeding translocated races in laboratories, the difficulties of obtaining viable translocations, etc. It is possible, for instance, to release only males, a method in which there is evidently no danger at all. The present investigation is a purely theoretical one. For the purpose of verifying experimentally this idea work has been started with Musca domestica and Calandra granaria — two insects widely differing in their cytogenetics, ecology and the kind of damage caused.

1. In the last two years, while studying the question of the significance of translocations for natural selection and evolution, we arrived at a somewhat unexpected and very interesting conclusion about a completely new application of genetics — the control of insect pests. At the present time there has been quite a wide acceptance by geneticists of the "general theory", put forward by us in 1929, about the origin of various types of mutations, particularly chromosome translocations and inversions. From experiments on Drosophila it is known that because of the similarity, or even identity, of their mechanism of origin, translocations and inversions arise with comparable frequency, though translocations have in fact a better chance of being formed than inversions. It is already known with complete certainty from comparative genetics and population studies in Drosophila that, in the evolution of the karyotype, inversions are encountered incomparably more

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frequently than are translocations. The causes of this are quite clear.
While an inversion, provided that it is not accompanied by additional gene
mutations or definite position effects, is a virtually insignificant change,
leaving the viability and fertility of the organism unaffected, translocations
in the overwhelming majority of cases, from the first generation onwards,
begin to be eliminated by natural selection. This is because an organism
which is heterozygous even in respect of a fully viable translocation begins
to produce a greater or smaller percentage of unbalanced aneuploid gametes.
The proportion of these varies but it may be as much as 50% even when
there is only one translocation. Thus the reproduction of individuals
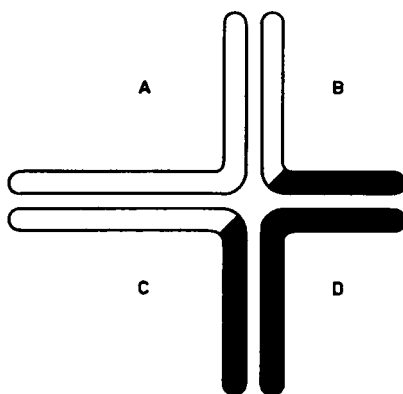
FIG.1. Diagram of the conjugation of four chromosomes in an individual heterozygous for one translocation.

inheriting a translocation is more or less markedly reduced, and the trans-
location is quite quickly eliminated by natural selection. An extremely
fortunate, and almost incredible, coincidence is required for a translocation
to be able to establish itself in a population with the status of a species
characteristic.

     While considering this question we came to the conclusion that since
translocations are so deleterious to the reproduction of the organism, the
possibility arises of the practical application of translocations to influence
the reproduction of a harmful species. Our detailed examination of this
question showed there are prospects here which are thoroughly practical
and highly attractive.

2.   The occurrence of various types of gamete in the presence of a hetero-
zygous translocation is quite a complicated process, which has not yet been
expressed in precise quantitative terms. As is well known, at conjugation
two translocated and two normal chromosomes of a heterozygote usually
form a ring or a cross (Fig.1), and the percentage of each type of gamete
depends on how the chromosomes are distributed to each pole of this ring.

     In a number of plants the chromosomes, as a rule, segregate regularly
with A and D going to one pole and B and C to the other. In these cases
there are obviously no aneuploid gametes formed. Gametogenesis of this
kind was found in several cases in Datura (Blakeslee, 1927, 1929). In

Oenothera one ring gave not more than 6.4% aneuploids, but, on the other hand, in Tradescantia reflexia (Sax and Anderson, 1933) one four-chromosome ring gave 80.3% aneuploid gametes.

However, the more usual pattern of segregation of the chromosomes is that in which about 50% of aneuploids, or a little less, are produced (Drosophila, maize, Pisum, Tradescantia edwardsia, many cases in Datura, etc.). Aneuploids can be formed if the chromosomes segregate as follows: A and B to one pole, C and D to the other, or A and C to one pole and B and D to the other. The final result is governed by the ratio between the
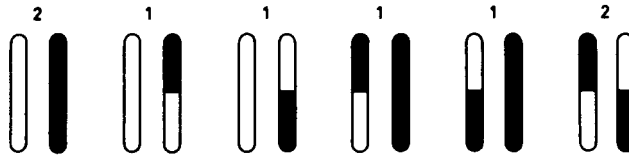
FIG.2. Diagram of the six types of gamete from an individual heterozygous for one translocation. The types at each end are orthoploid and the four in the middle are aneuploid. At the top are shown the relative frequencies, which give a total of 50% of aneuploid gametes.

frequencies of these two aneuploid types and the orthoploid (A, D ↔ B, C). At the same time, however, there are often cases of non-segregation, in which three chromosomes go to one pole and one goes to the other, which further complicates exact calculations. The percentages of the various types of segregation apparently depend on the characteristics of the trans- locations, i.e. on the lengths of the sections of chromosome that have been exchanged.

For our purposes, however, it is important to consider that in many cases, especially in Drosophila (as a typical insect), the presence of a translocation gives 45-50% aneuploids, and this can easily be represented diagrammatically as shown in Fig.2.

In the following account we shall proceed from the principle that, al- though in different examples of translocations the proportion of aneuploids is variable, nevertheless translocations do occur in which this is close to 50% and in these cases the formation of the various types of gamete can be basically represented by the simple scheme shown in Fig.2.

3. The occurrence of the inversion and translocation types of chromosome aberration is accompanied, in most cases, not only by a change in the position and redistribution of the chromosomes, but also by a change in the genotype itself. The nature of these concomitant changes may vary. In some cases, at the sites of the chromosome breaks, destruction of small sections of chromosome occur and deletions result. In other cases, at the sites of breaks or adjacent to them, gene mutations occur. In the third type, which is difficult to distinguish from the second, the changes are regarded as position effects caused by the loss of contact between certain sections of chromosome and the establishment of contact between others.

As with all mutations, the majority of such genetic changes are lethal in the homozygous state, or at least reduce homozygote viability.

However, translocations were long ago obtained in which there was a redistribution of sections of chromosome not accompanied by any deleterious consequences for the organism, and the homozygotes were found to be viable. This category of viable translocations and inversions clearly includes all those which are preserved in the evolution of species. Recently four very interesting viable translocations were obtained in <u>Crepis</u> by Gerasimov (1939).

Since later on we shall be interested in translocations which are viable in the homozygous state, the above-quoted facts permit us to state a second guiding principle to the effect that, although in most cases, as with any mutations, translocations in the homozygous state are accompanied by lethal effects, nevertheless it is possible to obtain translocations whose homozygotes are fully viable, and these will be briefly referred to as "viable translocations".

4. The general idea of our proposed new method for controlling insect pests is as follows. If in a particular species of pest the chromosome apparatus can be modified by one or more translocations, and the translocated line bred and released among the wild population so that individuals of the translocated strain mate with normal ones, then heterozygous offspring will be produced which will show reduced reproduction. Thus the overall reproduction of the pest population will be reduced to a greater or lesser degree and this should have a positive economic effect. In order to estimate the magnitude of this effect it is necessary to investigate under what circumstances and to what extent the reproduction of the pest can be reduced.

5. We shall investigate the simplest case. Let us assume that we have bred a strain bearing one viable translocation among two non-homologous autosomes. By establishing a mixed population of normal wild individuals, A, and translocated individuals, T, we shall have four possible matings (fertilizations) by individuals of type A and type T, namely: $A♀ \times A♂$, $A♀ \times T♂$, $T♀ \times A♂$ and $T♀ \times T♂$. At relative frequencies (probabilities) of p for A and q for T, (p + q = 1), we obtain the following distribution of matings:

$$p^2 (A \times A) + 2 p q (A \times T) + q^2 (T \times T)$$

The $A♀ \times A♂$ matings give entirely fertile progeny AA. The $T♀ \times T♂$ matings give entirely fertile progeny TT. The $A♀ \times T♂$ and $T♀ \times A♂$ matings give heterozygous progeny AT with 50% of aneuploid gametes, i.e. their reproductive capacity is defective.

It is easy to see that the quantity 2 pq reaches a maximum when $p = q = \frac{1}{2}$. 2 pq then equals $\frac{1}{2}$ or 50%.

We thus obtain the optimum effect when we mix with the wild population an equal number of individuals of the T strain.

In the next generation we obtain the following distribution and frequencies for the matings of the various types of individual (substituting whole numbers

for the fractional coefficients):

♀♀ \ ♂♂	AA	2AT	TT
AA	1	2	1
2AT	2	4	2
TT	1	2	1

The composition of the progeny from these matings are as follows (in order to obtain whole number coefficients we assume four offspring from each pair):

1	AA × AA	4AA			
1	TT × TT		4TT		
2	AA × TT			8AT	
4	AA × AT	4AA		4AT	8 die
4	TT × AT		4TT	4AT	8 die
4	AT × AT	1AA	1TT	3AT	11 die
		9AA	9TT	19AT	27 die

Total = 64

In summary we obtain:

(1) 27/64 (42.2%) embryos die;

(2) The following generation has a composition of 9AA + 19AT + 9TT.

This composition (9:19:9) is obviously very close to that of the preceding generation (1:2:1); the difference lies in the direction favourable to us, thanks to the small excess of heterozygotes.

At the same time, the equality of numbers between AA and TT individuals was maintained, and in this respect the population was stable. In the next generation, the calculations for which we will not present here, the percentage of embryo mortality increases somewhat, and finally reaches a value of 43.

Thus we obtain an extremely encouraging result: by the release among the wild population of a single strain with a single translocation, in numbers equal to that of the wild population, we achieve a.more or less stable mixed population, the reproduction of which has undergone an overall reduction of 43%.

6. If we rear a strain carrying two translocations among four pairs of chromosomes, then each translocation will exercise independent action as shown in the above scheme. Their overall effect can be expressed as follows:

Translocation I kills 42% of embryos, 58% survive.
Translocation II kills 42% of the 58%, i.e. 24.5%.

TABLE I. POSSIBILITY OF EMBRYONIC MORTALITY AS RELATED TO
THE NUMBER OF CHROMOSOMES IN AN INSECT SPECIES WHEN
APPLYING THE PRINCIPLE OF TRANSLOCATION AS A MEANS OF
INSECT CONTROL

Group of insects	Number of pairs of autosomes	Number of possible independent translocations	Possible percentage of embryo mortality[a]
Mosquitoes	2 - 5	1 - 2	43 - 58
Flies	2 - 8	1 - 4	43 - 88
House fly	5	2	58
Locusts	6 - 11	3 - 5	67 - 93
Beetles	9 - 19	4 - 9	88 - 99
Bugs	6 - 19	3 - 9	67 - 99
Butterflies	12 - 30	6 - 15	99

[a] Translator's footnote:
The figures given in this column by the author do not seem to be consistent with the figures
given in the text for percentage lethality with different numbers of translocations. The
column apparently should read:

<div align="center">

42 - 67

42 - 88

67

80 - 93

88 - 99

80 - 99

99

</div>

The total mortality is then 24.5% + 42% = 66.5%. With three translocations
among six pairs of autosomes, 80% of the embryos in the population are
killed, with four translocations the mortality is about 88%, and with five
translocations it is about 93%.

The possibility of obtaining a strain with many independent translocations,
in which each pair of chromosomes is limited by only one translocation
(I with II, III with IV, V with VI, etc.) depends on the number of chromo-
somes in the species of insect concerned. Table I illustrates the possi-
bilities in this connection.

With regard to species with many chromosomes, however, it is possible
that aneuploidy in respect of several sections of chromosome may not always

be lethal for the embryo. This question requires special experimental investigation.

7. In species with few chromosomes, as, for example, mosquitoes and most flies, where only one or two independent translocations can be obtained, there arises the question whether the method can be further developed. Analysis of this point has led us to the discovery of a further important principle. This is that the lethal effect could be considerably increased if we could produce and release not one, but two or more translocated strains.

Let us refer back to Section 5 above and see what will be the reproduction of a population consisting in equal parts of the normal type and two different translocated types T and U, where the translocated strains each have one translocation among the same chromosome pairs, and where the translocations are markedly different from each other.

The composition of the first generation will then be:

$$AA + TT + UU + 2AT + 2AU + 2TU$$

Whereas in the case of the population of A and T we had 50% heterozygotes in the first generation, here there are 67% heterozygotes.

In the next generation we shall have the following distribution of matings of the various types:

♀♀＼♂♂	AA	TT	UU	2AT	2AU	2TU
AA	1	1	1	2	2	2
TT	1	1	1	2	2	2
UU	1	1	1	2	2	2
2AT	2	2	2	4	4	4
2AU	2	2	2	4	4	4
2TU	2	2	2	4	4	4

In the boxes containing 1's there will be no embryo mortality and in those containing 2's there will be 50% embryo mortality. In the boxes containing 4's the proportion of lethals is either 11/16 (for the three boxes on the diagonal AT x AT, AU x AU and TU x TU) or 75% in the remaining six boxes.

In total:

0	lethals in	9 cases	0	x	9	=	0
50%	" "	36 "	50	x	36	=	1800
68.7%	" "	12 "	68.7	x	12	=	824
75%	" "	24 "	75	x	24	=	1800
		81					4424

4424 : 81 = 54.6%

Whereas by releasing a single translocated strain carrying one trans-
location we achieved in the second generation 42.2% embryo mortality in
the population, by releasing two strains we achieve 54.6%. This difference
is due to the fact that the frequency of those matings which give 100% viable
embryos falls (9/81 against 4/16 or 11% against 25%), and correspondingly
the frequency of matings giving a proportion of lethals increases and a new
class of matings appears which gives 75% embryo mortality. This class
of matings includes those of the AT x AU, AT x TU and AU x TU types, in
which different types of translocation are involved.

It is easy to see that if the number of successfully selected strains is
increased, the frequency of matings of the later type would increase, and
it can therefore be concluded that the mortality of embryos after the release
of many such strains will approach 75%. In the case of the release of many
strains with two translocations each, the corresponding limit will be:

$$75\% + (75\% \times 25\%) = 93.75\%$$

For three translocations:

$$93.75\% + (6.25\% \times 75\%) = 98.4\%$$

and so on.

8. How can we evaluate the results given in the previous sections? The
population dynamics of a species, particularly a pest, present a highly
complicated phenomenon, depending on many factors — climate, food, the
activities of parasites, predators, disease, etc. Reproduction[1] must also
be included in this list of factors but, although important, it is only one
factor among several others. The question may be asked what effect on the
numbers of the species will be caused by, for example, a 40% lowering in
reproduction, to take the minimum of the figures discussed above.

It is, of course, impossible to answer this question in its general form.
For example, when the reproduction of a pest begins to be reduced by
shortage of food, such a reduction may have no influence. Under other
conditions, on the other hand, even a reduction by 40% could have a decisive
influence. We can imagine, for example, a population which, after reaching
a minimum, is beginning a new phase of increase, with conditions favour-
able for reproduction and parasites having almost disappeared. In these
circumstances the rate of production of offspring is very important, since
with a high reproductive rate the host can escape from the regulating
influence of parasites by outstripping the parasite's own reproduction.
A 40% reduction, in these circumstances, in the host's reproduction is
equivalent to a 40% increase in the reproduction of the parasite, and would
allow the parasites to begin to suppress the host's reproduction relatively
early and hence prevent it from attaining the maximum that it could have
reached with unrestricted reproduction. The more the host's reproduction
is reduced, the greater will be the reduction in the population maximum,
and the more pronounced will be the state of suppression in which it exists.

Naturally the extreme lowering of the reproduction rate referred to in
the preceding sections would have even more influence. Let us assume that

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[1] Author's footnote: We always use the word "reproduction" and not "fertility", because the special
feature of translocation heterozygotes is not that their fertility is changed but that their embryos die at some
stage of development.

we are dealing with a species in which one male and one female produce, on average, 100 eggs. A lowering in the reproductive rate by 98% would leave only two viable embryos per pair, i.e. only a replacement for the parents. In these conditions, even with 100% survival from the embryo to adult stages and to the time of egg-laying, the species will not increase in numbers. But because of well-known and inescapable factors, mortality of individuals in the larval, pupal and imaginal stages, and up to egg-laying is very significant and this mortality would lead to a decrease in numbers and eventual extinction. In other words, in order to deprive such a species of the ability to increase in numbers, it would be necessary to lower reproduction by translocations not to the extent of 98%, but to a much smaller extent — according to circumstances perhaps 70%, 60% or even only 40% — particularly in view of the fact that reproduction is reduced not for one generation but for a whole series of generations.

From these considerations we conclude that the utilization of trans-location strains can produce veritably catastrophic results for the species subjected to the treatment.

9. We must now consider one weak aspect of the method. From population genetic theory and a number of actual observations it is known that in the case of a sufficiently large population with the structure

$$p^2 AA + 2pqAa + q^2 aa$$

where A and a are two alleles of any gene and are more or less equivalent in their significance for the viability and fertility in the organism, such a population may retain its structure (i.e. the quantities p and q) for a practically unlimited time for any values of p and q not too close to 1 or 0. In these circumstances the only factor which can change p and q will be stochastic processes (genetic drift) acting in large populations extremely slowly when there is complete panmixy and acting scarcely at all if the population is divided into more or less inbred groups.

Under other conditions a population may be found with structure $p^2 AA + 2pqAT + q^2 TT$ where A and T are two types of chromosome structure distinguished by the presence of one translocation. Such a population can be stable, preserving p and q from generation to generation, only on condition that $p = q$. The equilibrium is unstable and if it should happen that $p > q$ a process will begin of progressive increase in the inequality until $p = 1$ and $q = 0$. In other words, type T will be gradually eliminated. On the other hand if it should happen that $p < q$, a process of elimination of type A will begin.

This elimination occurs because, when the embryos are destroyed as a result of aneuploidy, equal numbers of chromosomes of type A and type T are also destroyed. If type A is commoner in the population than type T (i.e. $p > q$), these equal numbers of destroyed chromosomes will represent a greater percentage of the total number of T and a smaller percentage of that of A. Therefore in the following generation the inequality $p > q$ will increase still further and so on.

Figure 3 shows the approximate course, calculated by us, for the process of elimination for populations of A + T (top curve) and A + T + U (bottom curve). At first, near the equilibrium point, the process goes very slowly, then it accelerates sharply, reaching a value of 5-6% per generation, and then it decelerates again as it approaches the complete

displacement of one type. As shown in Fig. 3, in a population of A + T the change from 52.5% to 90% occupies roughly 12 generations and in a population of A + T + U one of the types displaces the others, in the range 36% - 90%, in approximately 15 generations.

Thus, if a panmictic population is constituted (i.e. a population in which mating between males and females of all types is absolutely random and depends only on the frequencies of the types), then over the course of a few generations one of the types practically displaces all the rest. The measure thus turns out to be a temporary one.
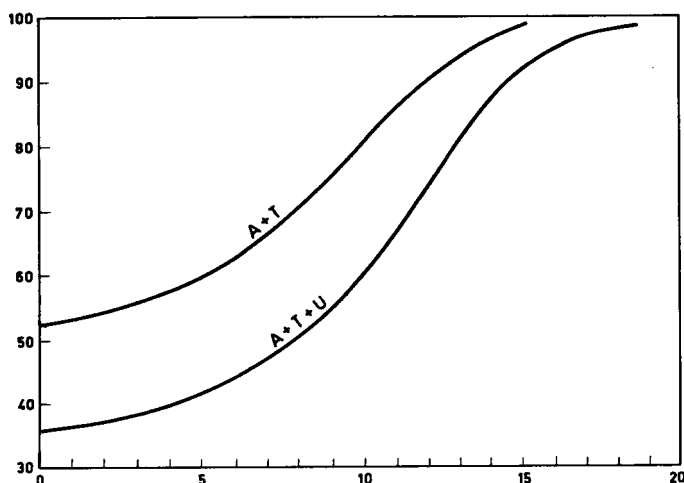

FIG. 3. Course of displacement by one type of the other types in populations of A + T and A + T + U; abscissa: generations; ordinate: frequency of eliminating type.

Before examining the possibility of preventing this "temporaryness", we shall consider what effect the temporary measure can have. For this purpose it is necessary to ascertain how the lethal effect of the translocations on the population varies with different ratios of types A and T. The curve corresponding to this relationship is given in Fig. 4.

As shown in the figure, the decrease in the percentage of embryo mortality proceeds much more slowly than the decrease in the percentage of T (or of A, if this is the type which is eliminated). With the ratio 1: 1 the mortality is 42%, at 2:1 it is 37%, at 3:1 it is 32% and even at 9:1 it is still 17%. If there were two translocations in the strain which was released these figures would be even more striking; for the ratios in question they would be 64%, 60.3%, 53.8% and 31.1% respectively. In this situation, even if the release of translocation strains is a temporary measure and its effect continues for only 10-15 generations, nevertheless its effect will be very considerable and the numbers of the pest population will be dealt a severe blow.

Figure 4 shows us several other important possibilities as well. It can be seen that the release of translocated strains in the proportion 2A: 1T and even 3A: 1T has a very marked effect, particularly with two or three

translocations in the strain which is released. Therefore in a situation where it is difficult to make a release in the proportion 1A:1T it would be possible to release the translocated strain in an amount two or three times less and then, having thereby reduced the numbers of the pest, to effect a second release of strain T and thus raise the ratio to the most advantageous level (1A:1T); this is a considerably easier procedure. Using strains with two, three or four translocations it is possible to obtain a still greater reduction in the numbers to be released at this preliminary treatment of the population.
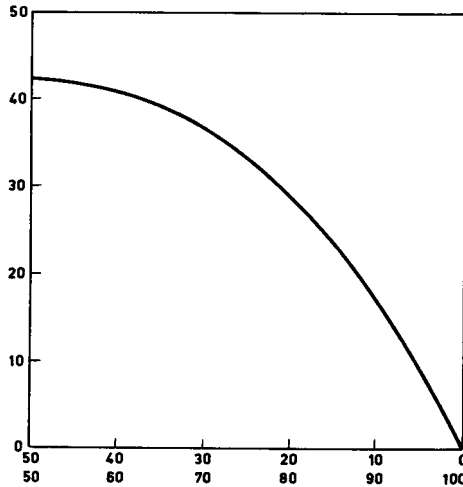
FIG.4. Percentage mortality of embryos in a population of A + T with various ratios of A:T; the abscissa shows the percentage of A and T gametes in the population, the ordinate shows the percentage of embryo mortality.

10. Is there any method for controlling the process of elimination? Is it possible somehow to slow down the process or even to stop it when the population has been brought to equilibrium? Study of the process of elimination itself reveals that it could possibly be controlled and that the question can be answered affirmatively.

In general, the control of undesirable elimination should be based on the fact that the elimination process itself can proceed in either direction, i.e. either towards elimination of the translocated type or towards elimination of the normal type.

We can proceed, for example, as follows. We divide the territory which is to be treated into squares, like a chessboard, and in the white squares we release the translocated strain in excess (producing, for example, a population with 40A + 60T) and in the black squares we release them in a minority (producing, for example, a population with 60A + 40T).

There will then begin in the white squares the elimination of type A and in the black squares the elimination of type T. Thanks to the chessboard arrangement, each white square will be continually invaded by the opposite type from the neighbouring black squares and vice versa. This migration

will, in the first place, markedly slow down or even stop the actual elimi-
nation process. But even if elimination occurs in the centres of the squares,
there will nevertheless result a chessboard network of mutually lethal forms,
which will continuously invade one another and produce heterozygotes with
consequent embryo mortality. Although in this situation the equilibrium
will be of an unstable type, the process of removing one of the forms from
the whole population will continue for a very long period and it requires
comparatively slight periodic attention to the "chessboard" population in
order to maintain it in the most advantageous state.

It is, of course, not our intention here to enter into a discussion of
technical details. Our intention is only to show that the process of elimi-
nation, with which the method here proposed conflicts from the very outset,
is not fatal to the method as a whole. Analysis shows, on the contrary,
that this process has properties which can be exploited in the further de-
velopment of the method, in respect both of different variants of the latter
and of the peculiarities of different species of insect. In addition we should
like to indicate the interesting problems which arise in connection with the
further theoretical development of the proposed method.

11. However, what in the first place are the practical possibilities of the
method? Here three main questions arise: (1) the feasibility of rearing
and releasing sufficient numbers of individuals of the translocated strains;
(2) the advisability of releasing these additional numbers of the pest; and
(3) the possibility of obtaining the translocated strains themselves.

The problem of releasing sufficiently large numbers of individuals, for
example in the ratio 1:1 to the wild population, may at first sight appear
absolutely insoluble. This is only true if one has in mind, say, massed
numbers of sugar-beet pests or swarms of beet webworm. But, as is well
known, the beet webworm, like various other pest species, produces massive
outbreaks only periodically, and in the intervals the species may decline to
a minimum with far smaller numbers. There are also distinct oscillations
as regards location, and in certain regions the pest may disappear almost
completely in some years.

The disappearance is temporary and a new wave of activity with an in-
crease in numbers then begins again. The opportune moment for release
of translocated strains is precisely when the population is at its minimum.
The release of sufficient numbers may then be much easier and, in addition,
would protect the region concerned from the ensuing outbreak on its usual
scale.

In other cases, use could be made of the seasonal minimum. In July
and August millions of flies emerge in many areas and invade living quarters
in vast clouds. In spring, however, in April and May, such clouds do not
occur and, on the contrary, the number of flies after the winter is often
insignificant. Clearly in autumn the release of a number of flies equal to
the natural population would hardly be possible, but in spring this task
would be thousands of times simpler.

Depending on the characteristics of the insect concerned, the appli-
cation of the proposed method may vary considerably and to enter into
details here would be premature. It may just be mentioned that the release
need not be made in one operation but can be effected in several separate
operations, and here there is scope for the theoretical investigations to

discover the most economic procedures for application of the method, to which we referred in Section 9.

If, for example, five translocated strains are obtained and it is desired to produce a population in the ratio 1:1:1:1:1:1, it would be necessary to release a number exceeding that of the natural population, by a factor of five. However, the operation can be performed quite differently. One can first release one strain in the ratio 1:1 with the wild population, and then pause until this release has had some effect. Then a third type is released in the ratio 1:2, i.e. the number released is half that of the diminished mixed population, and there is then another pause for a further reduction to occur. Then the fourth strain is released in the ratio 1:3, i.e. a number equal to one third of the new mixed population, and so on. The result is that the total of insects released is not in the ratio 5:1, but considerably less. In the end, however, the practicability of such an arrangement will be determined by economic considerations, taking into account the harm done by the pest and the cost of rearing the translocated strains, which vary greatly from species to species.

12. As regards the advisability or even safety of releasing additional numbers of pests (even though these are of the translocated strains), this question must be answered specifically for each species. In a number of cases these releases could be made without any misgivings. For example, in spring the small numbers of house flies can safely be increased by as many again or even by two or three times as many in the certainty that after $1-1\frac{1}{2}$ months there will be a marked decrease in fertility and that in July and August there will be a big drop in the mass reproduction of flies in the field. In other cases, however, it may be necessary to be more cautious. In these cases there is at our disposal, however, a method of effecting the introduction of translocations into the population without any risk, even temporary, of increasing the reproduction of the pest. This can be done by releasing only males of the translocated stocks and retaining the females. The released males begin to compete with the wild males for the females, but since the eggs will only be laid by wild females, the number of their progeny resulting from the release of the translocated males will not rise at all. It is only necessary to prolong releases for several generations, although this will render the operation somewhat more expensive.

13. The greatest difficulty in the use of this proposed method will be the production of the translocated strains. The stages in this process will be approximately as follows: (1) the mastering of a technique for laboratory rearing the insects continuously over a number of generations; (2) the production of a small number of suitable mutations to serve as "markers", which are needed for the continued securing of translocations and the combinations of these marker mutations at least in pairs; (3) the production of the translocation; (4) the conversion of translocations into the homozygote state and the selection of viable translocations; (5) the combination of translocations two, three or more together in individual strains, if this is considered necessary; and (6) the mass rearing of the selected strains. All these stages will occupy a fair number of generations.

The rearing of some insects, for example, cereal-feeding ones such as the grain weevil, is very simple, but the rearing of others, such as

moths which feed on green plants, is much more difficult, while the breed-
ing of yet others, such as mosquitoes or horseflies, is extremely difficult,
and even for the time being impracticable. Another point is that the raising
of ten generations of the horsefly or grain weevil can be completed in the
course of one or two years; in insects producing one generation per year
it would take ten years, while such species as cockchafers and wireworms,
with two- or three-year life cycles, are hardly worth considering, unless
a better method of working with them can be found.

However, there are enough species of insect pests with a short life
cycle and which are more or less suitable for laboratory rearing, and so
there is a wide field of work available without us having to consider the
cockchafer or wireworm. As it proceeds this work will undoubtedly lead
to the discovery of methods for shortening several stages of the process;
thus, for example, marker mutations may be found in natural populations
and translocations might be sought without markers by cytological methods
or by observing embryo mortality in eggs, and so on.

14. Up to the present time the only practical applications of genetics have
been the selection of domestic or semi-domestic animals and cultivated
plants. Altogether, particularly in animal genetics, the number of suitable
and practically significant subjects for treatment has been extremely
limited.

It is, therefore, with a great sense of satisfaction that we note the
emerging prospects for the practical application of genetics to a new,
extraordinarily wide, and economically important field, the subjects of
activity in which are numbered literally in hundreds.

Nature is certainly more complex than our theoretical models, and
the new method proposed by us here for the control of pests (in addition to,
and in no way in conflict with other methods—agronomic, chemical,
mechanical and biological) requires practical verification before one can
say that the method is fully worked out. It is possible that in some cases
unexpected difficulties will arise in the production of translocations, in the
maintenance of the viability of the translocated strains, in the lethal effects
of aneuploidy on the embryo, and so on. However, genetic calculations
are always found to be so accurate that there are no particular grounds for
fearing that, in this case, they will not turn out to be correct, especially
as the phenomena on which the present method is based occur in Drosophila,
i.e. a species which is quite closely related to many insect pests.

On the other hand studies on translocations and the methods of obtaining
them are a comparatively young branch of our science, being mainly con-
fined to the last decade. There is therefore no doubt that as soon as the
work we have in mind is under way, involving the pursuit of a variety of
new objectives, many new advances in the study of translocations will be
made and even more effective opportunities for their practical application
will certainly be found. We are confident that in its efforts to serve
practical purposes Soviet genetics will produce new theoretical achieve-
ments to the benefit and honour of our great socialist homeland.

CONCLUSIONS

1. The fact that individuals which are heterozygous for translocations
form aneuploid gametes and produce aneuploid, inviable progeny opens up

the possibility of developing a new method for the control of (allogamous) insect pests.

2.   Theoretical calculations show that the release into an insect pest population of strains of the same species possessing a chromosome apparatus modified by the presence of translocations should cause considerable damage to the reproduction of the pest.

3.   The more translocations there are in each strain released, the larger the number of different strains released, and the nearer the approach to equality between the numbers of the pest and the numbers of each strain released, then the greater will be this damage to reproduction.

4.   The utilization of translocations viable in the homozygous state has important advantages.

5.   The mixed population thus produced cannot come to a stable equilibrium and will tend towards uniformity of type by elimination of all the chromosome types except one.   However, this process should last many generations, and for this reason the disruption of the reproductive process of the pest population should last a long time.

6.   Periodic supplementary releases of the chromosome type which is being eliminated should maintain the disruption of the reproductive process continuously at a high level.

7.   It is possible to devise variants of the method in accordance with the biology of the pest, the cost of rearing it in the laboratory, the difficulty of producing translocated strains, the harmfulness of the pest, etc.   One of these variants, which may hold out the best prospects thanks to its inherent safety, involves the release of males only.

8.   The proposed method can be applied in combination with any other current method and without interfering with or suffering from it.

9.   The present paper presents a purely theoretical investigation of the subject.   Experimental development work on it has been started using the housefly Musca domestica and the grain weevil Calandra granaria, two insect which differ widely in their biology and the damage which they cause.