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POTENTIAL ROLE OF STERILIZATION FOR SUPPRESSING RAT POPULATIONS

A Theoretical Appraisal

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POTENTIAL ROLE OF STERILIZATION FOR SUPPRESSING RAT POPULATIONS

A Theoretical Appraisal

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The theoretical advantages of sterilizing both sexes of an organism in a natural population instead of killing them were postulated and proposed as a means of suppressing both vertebrate and invertebrate pest animals (Knipling *1959*).[1] The purpose of this bulletin is to offer a more detailed analysis of the potential advantages of this method of pest suppression specifically as it relates to rats. These animals are among the most obnoxious and destructive pests in the world, and more effective methods of control would be desirable.

The sterilization of wild pests as a method of suppressing reproduction should not be confused with the mass rearing, sterilization, and programed releases of organisms to compete for mates with members of the natural population. Investigators studying chemical sterilization of pests in a natural population often refer erroneously to the success of the screwworm (*Cochliomyia hominivorax* (Coquerel)) eradication and suppression programs in support of the principle of pest control by the sterilization of natural populations. However, it should be emphasized that the technique of reducing reproductive success by sterilizing members of a natural pest population whether vertebrates or invertebrates and the technique of suppressing reproduction by rearing and releasing sterile organisms to compete with the wild members of a population entail different principles, and the basic requirements and effects of the two suppression methods are entirely different. The fundamental differences in the two suppression methods have been previously outlined in detail (Knipling *1968*).

This bulletin will deal primarily with the concept of sterilizing members of a pest population in its natural habitat. It will point

[1] References to Literature Cited (p. 26) are herein indicated by the name of the author followed by the year of publication in italic.

out why efficient sterilization is inherently more effective than conventional methods for suppressing rat populations. The authors do not advocate the use of any chemical sterilants that may now be available. If effective and safe chemical sterilants are developed in the future, authorities on rodent control must determine if and how they might be employed to advantage over conventional suppression procedures. The authors are not authorities on the biology, behavior, and control of vertebrate pests. However, the senior author has devoted many years to studying the principles of pest population suppression by applying sterility techniques, particularly as they may be used for insect control. The results of the studies reported here are intended to show the theoretical advantages of the sterility procedure for controlling rats and other vertebrate pests and thereby stimulate greater research efforts to achieve the potential that this suppression procedure holds for the future.

The basic principles in suppressing reproduction by appropriate sterilization procedures should be essentially the same whether the organisms are vertebrate or invertebrates. That greater suppression of reproduction can be achieved in insects by using chemosterilants in lieu of conventional insecticides, as originally postulated, has been well confirmed through experimentation (LaBrecque and Smith *1968*). The potential advantages of an effective and irreversible sterilization procedure over an equally effective killing procedure in suppressing reproduction should be substantially greater when applied to vertebrate pests than when applied to insects. The reasons for this are the longer life of most vertebrates and the continuing effect sterile members in the population can have on subsequent generations. Insects rarely survive long enough in nature to overlap subsequent generations in sufficient numbers to markedly affect population growth. Thus insects sterilized in one generation generally have little impact on reproduction in the next generation.

The advantage of sterilization over conventional methods for suppressing rat populations was calculated. The results are reported here with the hope that they will stimulate a more intensive research effort by scientists to develop the type of chemicals or other sterilization procedures that will eventually take advantage of this potentially powerful suppression system. For sterilization to achieve its full potential advantage, the sterilized animals must retain normal vigor and behavior and males at least must be competitive in obtaining mates.

Materials are known that can sterilize both sexes of insects without serious adverse effects on their competitiveness and length of life (Borkovec *1966*, LaBrecque and Smith *1968*). However, proved safe methods for using these materials for insect control have not yet been developed. Scientists have also considered the development of chemicals for sterilizing vertebrate pests (Wetherbee *1966*, Howard *1967*, Howard and Marsh *1969*, Marsh and Howard *1969*). Scientists with the Fish and Wildlife Service, U.S. Department of the Interior, are also conducting investigations on sterilization as a means of vertebrate pest suppression (personal communication). Considerable success in sterilizing pigeons has been reported by Joan Sturtevant (*1970*). Ericsson (*1970*) reported the discovery of a chemical designated as U–5897, which produces irreversible sterility in male rats without apparent adverse effects on their mating behavior or length of life.

However, to gain the inherent advantage of sterilization over killing of animals, it is necessary that both sexes be sterilized by a single compound or by a combination of materials. It is also necessary that the sterilized males produce competitive sperms or otherwise produce an effect comparable to normal males in the physiological responses of females to mating.

Procedure in Making the Appraisal

To compare the relative degree of suppression of reproduction resulting from suitable sterilization versus the killing or removal procedures, it is expedient to establish hypothetical rat population models and assign appropriate relevant parameters that depict the dynamics of rat populations. It is then possible to calculate the theoretical suppression of reproduction achieved by different procedures. This is the same method used previously by the authors with considerable success in appraising the relative merits of various insect population suppression techniques.

The establishment of a representative reference population (table 1 and fig. 1) and how it normally grows without control is a basic requirement for calculating the theoretical effects of different kinds and levels of suppression. The establishment of such a model for rats, as employed in this study, was based on information about the biology, behavior, and dynamics of wild Norway rat populations (Calhoun *1963*, Brown *1969*) and on data from a special report (Meyers *1968*) supplied by W. S. Burlew, Director of the Connecticut Research Commission, Hartford. Additional information was supplied by W. W. Dykstra, Department of the Interior (personal communications). However, the authors

TABLE 1.—*Growth of an uncontrolled rat population from one pair of rats*

Generation	Total rats	Progeny
0	2	3
1	4	5
2	7	9
3	14	18
4	28	35
5	53	67
6	102	128
7	196	242
8	373	454
9	701	827
10	1,287	1,439
11	2,269	2,318
12	3,739	3,335
13	5,579	4,197
14	7,370	4,699
15	8,678	4,903
16	9,412	4,969
17	9,756	4,989
18	9,901	4,996
19	9,961	4,998
20	9,985	4,999
21	9,994	4,999
22	9,998	5,000
23	10,000	...

did not review and study all information on the biology and dynamics of rat populations.

If all relevant parameters established for this study, such as the development period to reproductive age, number of generations per year, and natural death and survival rates at different density levels, are reasonably representative and if such parameters are applied equally to populations subjected to sterilization and to killing agents, the relative effect of the two suppression procedures will be readily apparent.

The parameters used in developing the hypothetical rat population models and the effect of the control procedures on population growth will be considered in detail in discussing the theoretical effects of each control procedure. The primary purpose of this study is to show the potential advantage of appropriate steriliza-

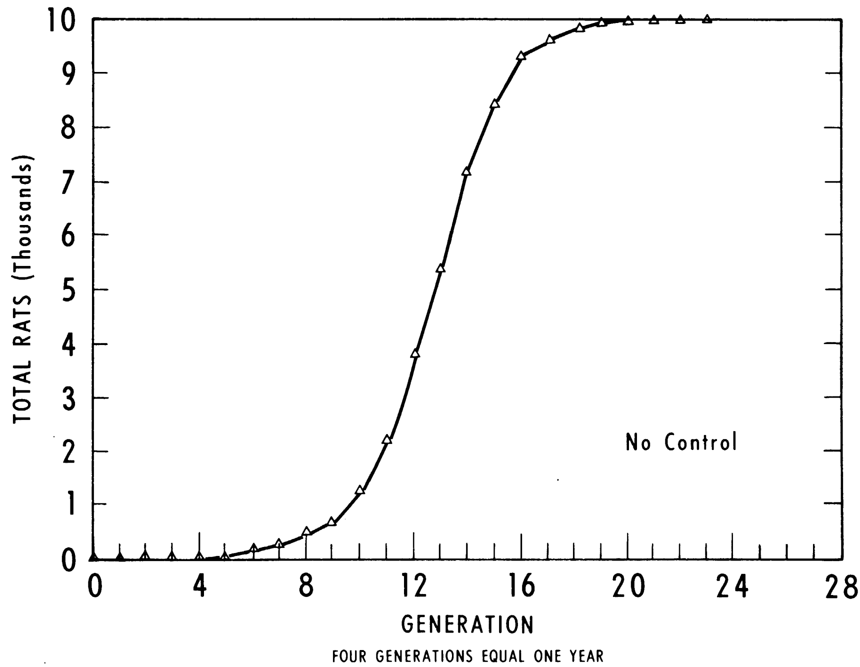

FIGURE 1.—Growth of an uncontrolled rat population from one pair of rats to a maximum of 10,000 (see text for parameters).

tion over conventional killing procedures in suppressing rat populations. It is not the intent of the authors to outline rat suppression procedures in practical control.

Comparison of Suppression Mechanisms in Two Control Procedures

The conventional method of destroying an organism achieves suppression of reproduction by one mechanism only. The percentage of individuals destroyed governs the degree of suppression that results. There can be no other suppression effect. The surviving organisms in the population are all capable of reproducing normally and the population will increase to the extent that conditions in the environment will permit. In a typical environment the reduced population is likely to increase at a greater than normal rate for a time because of less competition between remaining animals in the population. Such an accelerated increase if it occurs because of a reduction in density-dependent regulating factors will last only until the numbers return to levels that result in a slower rate of growth due to a more normal effect of density-dependent population regulating factors.

In contrast with the impact of conventional killing or removal methods, suitable sterilization procedures for both sexes cause suppression effects in several ways.

(1) Sterilizing the same percentage of the population that is destroyed by conventional methods will, by virtue of the direct sterilization effect, exert the same setback in the reproductive potential as is produced by the killing or removal procedure.

(2) The sterilized individuals then become biological control agents, which can compete for mates with the fertile members of the population.

If the sterilized animals are fully competitive and equally distributed, they are theoretically capable of suppressing reproduction in the unsterilized members of the population to a degree equal to the percentage of the population sterilized.

(3) If the procedure is irreversible and the length of life and mating behavior of the sterilized individuals are not adversely affected, the surviving sterilized individuals will continue to compete for mates in subsequent generations during their lifetime and consequently will continue to suppress reproduction in the population.

For species in which some members of the population normally survive for periods spanning several generations, this continued suppression effect is of very great importance in managing pest populations. As previously noted, in most insect species relatively few survivors overlap subsequent generations. However, in vertebrate pests a substantial number may survive for several generations. Thus the sterilization procedure has a much greater potential advantage over killing among vertebrate pests than among invertebrate pests. Obviously if the competitiveness of sterilized individuals is partially impaired, the full bonus effect of sterilization will not be realized. However, even if sterilized individuals are reasonably competitive, this becomes a highly significant added suppression effect.

(4) Sterile organisms in an environment can disperse and exert a population suppression effect throughout the normal range of movement of the treated population. Thus sterilized individuals may be capable of getting into habitats not readily accessible for treatment. Such an effect is not possible when a population is subjected to control by conventional means.

In addition to these potential advantages, the sterilization procedure permits the sterilized individuals in the population to continue to compete for food, nesting sites, and living habitats that may temporarily reduce chances of survival among the animals that do reproduce. This effect is often cited by animal ecologists as one of the chief advantages of the sterilization procedure. Although this can be a temporary advantage over the killing or removal method of suppression, the authors regard this advantage of no real practical significance over the killing procedure in practical pest population suppression. High natural attrition and a low reproductive rate will lead to rapidly declining numbers among the population subjected to sterilization and in turn favor the survival rate.

In contrast, the survivors of a population subjected to the sudden destruction of a substantial percentage of individuals can be expected to have a greater than average reproductive and survival rate immediately after the numbers are reduced. However, this diminishes as the overall population increases in numbers. Therefore, as to the final net result, one method has no advantage over the other that can be attributed to the density-dependent survival factors.

Thus from a technical viewpoint, increased effectiveness of the sterilization technique over killing is due to three major factors. First, the immediate bonus effect of mating competition by sterilized individuals; second, the continuing, though declining, suppression of reproduction caused by sterile individuals that continue to live and compete with normal individuals for mates in subsequent generations, and third, the mobility of sterilized individuals, which may be an advantage in certain circumstances.

Another advantage of sterilization over the killing procedure has no relation to relative efficiency but may be of great value from an esthetic standpoint. The public is much more likely to accept the sterilization procedure as a means of animal population management because it would have no visible harmful effects on the animals. Although this may be a factor of minor importance in the control of rats, it could be of major importance in the control of many other vertebrate pests.

A major disadvantage of sterilization over the killing system is the delay in suppressing a pest population subjected to sterilization. A population that has reached the damaging level will continue to cause damage until the effects of sterilization plus natural attrition cause a decline in the number of animals to acceptable damage levels. Therefore, if a pest population has already reached a highly damaging level, it may be desirable or necessary to first reduce the numbers by conventional means before utilizing the sterilization technique for maintenance of noneconomic populations.

Suppression Procedures To Be Analyzed

In order to calculate the potential effect of any pest suppression procedure, it is important first to establish the trend that would be representative of a normal uncontrolled population starting from a low density level. The authors have not attempted to make a detailed study of literature on the dynamics of rat populations. The primary concern has been to depict the dynamics of an uncontrolled population that can be regarded as reasonably representative of a typical population in a favorable environment. Such a hypothetical population can then be used as a basis for calculating the effects of different suppression procedures.

The suppression procedures to be analyzed are as follows:

(1) Destroying 90 percent of a stable population of 10,000 reproducing rats for one generation with conventional rodenticides.

(2) Destroying 70 percent of an initial population of 10,000 rats each generation for two and for three successive generations with conventional rodenticides.

(3) Sterilizing 90 percent of both sexes of a population of 10,000 reproducing rats in the first generation only.

(4) Sterilizing 70 percent of both sexes of an initial population of 10,000 reproducing rats each generation for two and for three successive generations.

(5) Sterilizing 90 percent of females only in a population of 10,000 rats in the first generation.

Parameters and Development of Models for Populations Subjected to Conventional Control Procedures

The various parameters established as a basis for calculating the theoretical effect of conventional control procedures are outlined as follows:

(1) The hypothetical rat population is well isolated from other rat-infested areas and is therefore not subject to emigration of rats from or immigration into the control area.

(2) The population consists of 10,000 adult rats capable of reproducing. It is assumed to represent the maximum density for the environment. Accordingly, survival of rats to reproductive age and death of rats of reproductive age have reached equilibrium.

(3) One rat generation is assumed to require an average period of 3 months. The females average one rat litter each 3-month period. The average number of six pups per litter is not a relevant parameter in the calculations, but the number might be expected to range from 6 to 10. (King *1924,* Eaton *1928*)

(4) The survival and death rates of the rats will vary depending on the density of the population. The net increase per generation ranges from *2.84* X when the population consists of two rats to *1* X when the population reaches the maximum density of 10,000 rats. The death rate of reproducing-age rats each generation ranges from *33* to *93* percent.

Like any pest population, a rat population is a fairly complex entity in which many interacting factors can be expected to affect its relationship with the environment in which it exists. Fortunately all populations have gross characteristics that allow the construction of a descriptive model, which averages the many details into a relatively few essential factors. Although several features about the biology and behavior of rats, known or unknown, probably have not been adequately considered in developing the population models, we believe that the most essential parameters are reasonable and are accounted for.

The basic model for a rat population, in terms of generations, may be written:

$$R_i = R_{i-1}\, e^s + \frac{1}{2} R_{i-1}\, e^I \tag{1}$$

where

R_i = size of the population in generation i
R_{i-1} = number of adult rats in the previous generation
e^s = survival rate from generation i–1 to i
$\frac{1}{2} R_{i-1}$ = number of parturient females in the previous generation
e^I = finite rate of increase

The exponential e^s, the proportion of survival, applies only to the adult rats in the population. The exponent s was chosen to be a linear function of the number of rats in the total population

$$s_i = a + bR_i$$

The constants a and b were determined so that $e^s = 0.65$ when $R_i = 1{,}000$ and $e^s = 0.5$ when $R_i = 10{,}000$. The proportion of deaths is therefore defined as $(1-e^s)$.

The exponential e^I controls the finite rate of increase in the population. The exponent I was also chosen to be linear, but it describes both the birth and death rates of the population of juveniles

$$I_i = c + dR_i$$

The constants c and d were determined so that $e^I = 2$ when $R_i =$ 2,500 and $e^I = 1$ when $R_i = 10{,}000$. Thus we see that when $R_i =$ 10,000, only 5,000 survive from one generation to the next, but the original 5,000 females will produce exactly 5,000 new adults to take the place of the loss and the population is stationary. The survival rate for juveniles varies from $\frac{2.8}{3} = 0.93$ to $\frac{1}{3} = 0.33$ as the population varies from 2 to 10,000. Normal population trends are shown in table 1 and figure 1.

Effect on Populations Subjected to Conventional Control

(1) A kill of 90 percent of 10,000 rats for one generation with rodenticides:

On the basis of the parameters established for the growth of rat populations at various density levels, we can calculate the theoretical effect of an intensive control program that destroys 90 percent of the rats in a population of 10,000 for one generation. If the level of suppression achieved is reasonably uniform throughout the environment where the rats exist, we can apply the basic parameters including the survival and deaths at different density levels and expect a resurgence of rats as shown in table 2 and figure 2.

It is not likely that rat control programs will be conducted in this manner. However, by depicting the resurgence of rats following a high degree of suppression in a short time, we will be in a position later to compare the results with a similar program involving the sterilization of the same percentage of rats.

(2) A kill of 70 percent of 10,000 rats for two successive generations with rodenticides:

In practical rat control programs it may be difficult to achieve a high level of kill or removal of rats in the short span of 3 months (one generation). It is likely that the destruction of 70 percent each generation over a period of several generations will be more feasible and practical than an all-out effort to drastically reduce rat populations in a single generation. Therefore, calculations were made to show the effects of a moderate level of suppression each

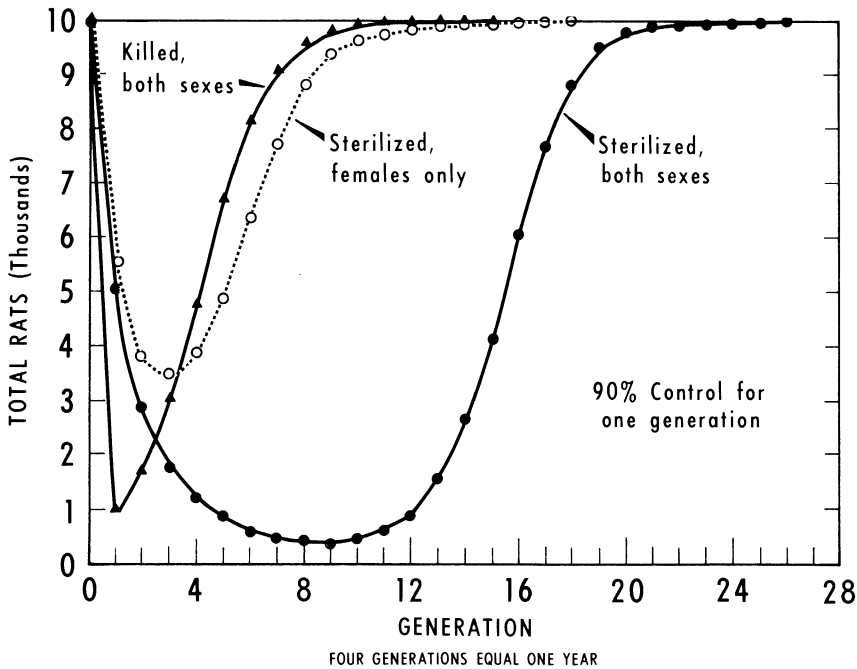

FIGURE 2.—Trends of rat populations subjected for one generation to 90-percent kill of both sexes, 90-percent sterilization of both sexes, or 90-percent kill of females only (see text for parameters).

generation for two generations (6 months). On the basis of the parameters previously discussed, the calculated results are shown in table 3.

(3) A kill of 70 percent of an initial population of 10,000 rats for three successive generations with rodenticides:

The theoretical results of 70-percent kill of rats for three successive generations are shown in table 4. It is apparent that such a program would be substantially more effective than a similar program continued for two generations only. The primary purpose of the model showing the results of control for three generations is to depict the difference in results as compared with sterilization at a 70-percent level, which will be discussed later.

On the basis of the parameters established, tables 2–4 depict what can be expected from different degrees of rat control employing conventional suppression methods. Substantial relief from rat damage results from such control. However, if control measures

TABLE 2.—*Controlling a population of 10,000 rats by killing 90 percent of both sexes for 1 generation*

Generation	Total rats	Progeny
0	10,000	5,000
1	1,000	500
2	1,799	1,149
3	3,061	1,919
4	4,780	2,907
5	6,656	3,872
6	8,201	4,533
7	9,164	4,842
8	9,645	4,950
9	9,856	4,983
10	9,943	4,994
11	9,977	4,998
12	9,991	4,999
13	9,997	5,000
14	9,999	5,000
15	10,000	5,000

TABLE 3.—*Controlling a population of 10,000 rats by killing 70 percent of both sexes for 2 generations*

Generation	Total rats	Progeny
0	10,000	5,000
1	3,000	1,500
2	1,411	859
3	2,467	1,561
4	4,011	2,475
5	5,876	3,488
6	7,615	4,301
7	8,828	4,746
8	9,486	4,919
9	9,788	4,974
10	9,915	4,991
11	9,967	4,997
12	9,987	4,999
13	9,995	4,999
14	9,998	5,000
15	10,000	5,000

TABLE 4.—*Controlling a population of 10,000 rats by killing 70 percent of both sexes for 3 generations*

Generation	Total rats	Progeny
0	10,000	5,000
1	3,000	1,500
2	1,411	859
3	740	468
4	1,356	871
5	2,379	1,507
6	3,891	2,406
7	5,746	3,422
8	7,509	4,257
9	8,764	4,726
10	9,455	4,912
11	9,775	4,972
12	9,910	4,990
13	9,964	4,996
14	9,986	4,999
15	9,994	4,999
16	9,998	5,000
17	10,000	5,000

are discontinued after the treatment programs, the rat populations tend to again revert to high levels in a short time.

When 90 percent of the rats are destroyed during one generation (table 2), the population would reach a level of about 48 percent of the original level by the end of the first year. By the end of the second year the population would reach a level approximately 96 percent of the original level. When a population is subjected to 70-percent control for each of two successive generations (table 3), the results would not differ much from the results obtained by destroying 90 percent of the rats in one generation. The minimum population would be about 1,400 at the end of the second generation and return to a level of about 4,000 by the end of the first year. By the end of the second year the population would reach 95 percent of the original level. The control of rats at the 70-percent level for three generations (table 4) results in about a two-generation delay in buildup.

Parameters and Development of Models for Populations Subjected to Sterilization

The effect of sterilization by appropriate means will be calculated with the same basic parameters applicable to the population of reproducing rats controlled by conventional means. However, additional parameters must be established, which are as follows:

(1) The sterilized rats of both sexes are assumed to be normal in mating competitiveness, behavior, and length of life.

(2) Complete and irreversible sterility is achieved in rats exposed to the sterilization treatment. The sterilization effect is produced in mature rats or in juveniles.

(3) The physiological effects on fertile females mating with sterile males is assumed to be the same as for those mating with fertile males. The sterilized males are assumed to produce sperms fully competitive with normal sperms in fertilizing ova. Thus impregnation will result and young may be produced but progeny will not survive. If sperms are not produced in the sterile rats, false pregnancy effects will delay subsequent mating as for normal fertile matings.

(4) Since the entire population is subjected to the sterilization treatment, the rats successfully sterilized and those escaping sterilization are equally accessible to each other for mates. Rats in different social strata are equally accessible to the sterilization treatment. The same proportion of so-called dominant male rats will be sterilized as for the population as a whole.

(5) It is assumed that there is equal acceptance of baits containing the sterilization chemicals and conventional rodenticides and that the percentage of kill and percentage of sterilization are equal.

The hypothetical sterilization programs to be evaluated have already been listed (see p. 8). Calculations of the effects of such programs will be based on the parameters as stated. It is apparent that the characteristics of the hypothetical sterilizing chemical are rigid. It may be difficult for scientists to develop chemical sterilants that will produce the effects specified, but the purpose of this study is to show the maximum potential of sterilization. It should be pointed out, however, that sterilization procedures that fall far short of the optimum effect could still produce powerful advantages over the conventional system of rodent control.

The equation developed and used to calculate the impact of sterilization is described as follows:

In order to sterilize part of the population, equation (1) must be modified by separating males from females and fertile from sterile rats, resulting in a new equation with four subpopulations as follows:

$$R_i = [M_{i-1}{}^{[n]}e^s + 0.5P_i] + [F_{i-1}{}^{[n]}e^s + 0.5P_i] + M_{i-1}{}^{[s]}e^s + F_{i-1}{}^{[s]}e^s \qquad (2)$$

where

$M^{[n]}$ = normal males
$M^{[s]}$ = sterile males
F = females
P_i = progeny produced = $[F_{i-1}{}^{[n]}M_{i-1}{}^{[n]}/(M_{i-1}{}^{[n]} + M_{i-1}{}^{[s]})] \times e^I$

The population in each generation was computed at the beginning of the generation and consists of the progeny of the previous generation plus survivors of the parents. When sterilizing was done during the generation, the fertile progeny of the previous generation were added to the survivors of fertile parents after the mortality was taken into account at different density levels. The rate of survival of sterilized rats was considered at the end of each generation and also varied with the total rat density in accordance with the basic parameter. All calculations were performed on a Wang 700A with typewriter output. The results of calculations of different models involving sterilized rats appear in tables 5–7.

Effect on Populations Subjected to Sterilization

(1) Sterilization of 90 percent of 10,000 rats (both sexes) for one generation:

The results to be expected when 90 percent of 10,000 rats are sterilized for one generation are shown in table 5. The sterilization of 9,000 of the original population of 10,000 rats will have the same immediate suppression of reproduction as the destruction of 9,000 by conventional means since only 1,000 fertile rats will remain in each case. However, the sterile rats, based on the parameters, are capable of competing with fertile rats in seeking mates. Therefore, 90 percent of the fertile females would theoretically mate with sterile males and thus produce no progeny. The maximum potential effect during the first generation after sterilization would, therefore, be 99-percent suppression of reproduction by the sterilization procedure as compared with a maximum of 90 percent for the killing procedure. This extra suppression effect alone is of great importance in population suppression, but some of the sterile rats would continue to survive and continue to compete for mates in subsequent generations.

According to the parameters, the number of sterile rats will decline in generation 2 to a level of 2,600 (1,300 males and 1,300 females). However, this theoretically would still provide a ratio of about seven sterile to one fertile rat of reproductive age. Therefore, suppression of reproduction in generation 2 would still be substantial. This contrasts with no suppression of reproduction during generation 2 for the rat population subjected to conventional control procedures.

Theoretically surviving sterilized rats will continue to suppress reproduction in subsequent generations, but the degree of suppression will gradually diminish because of declining numbers of sterile rats and a gradual increase in the number of fertile rats

TABLE 5.—*Controlling a population of 10,000 rats by sterilizing 90 percent of both sexes for 1 generation*

Generation	Total rats	Normal rats	Sterile rats	Progeny
0	10,000	10,000	0	5,000
1	5,050	550	4,500	50
2	2,964	365	2,599	47
3	1,863	267	1,596	43
4	1,221	210	1,011	41
5	829	176	653	41
6	585	159	426	44
7	437	156	281	51
8	356	170	186	67
9	335	212	123	99
10	386	305	81	164
11	548	494	54	293
12	895	859	36	534
13	1,541	1,518	23	957
14	2,619	2,604	15	1,633
15	4,185	4,176	9	2,561
16	6,045	6,040	5	3,566
17	7,740	7,737	3	4,348
18	8,899	8,897	2	4,765
19	9,519	9,518	1	4,924
20	9,802	9,801	1	4,975
21	9,920	9,920	0	4,991
22	9,968	9,968	0	4,997
23	9,987	9,987	0	4,999
24	9,995	9,995	0	4,999
25	9,998	9,998	0	5,000
26	10,000	10,000	0	5,000

reaching reproductive age. However, the continuing and accumulative suppression of reproduction in the population subjected to sterilization as compared with no continuing suppression effect in the population subjected to 90-percent kill will theoretically result in a profound difference in the growth rate of the two populations.

The population subjected to sterilization will reach a low of about 335 rats (both sterile and fertile) of reproducing age. This will occur in the ninth generation when the sterile rats will number 123 and the fertile rats 212. At that time the number of fertile rats in relation to the sterile rats will result in enough progeny to exceed natural attrition and a net increase in the population will begin. Since the overall population is at a very low level, the

TABLE 6.—*Controlling a population of 10,000 rats by sterilizing 70 percent of both sexes for 2 generations*

Generation	Total rats	Normal rats	Sterile rats	Progeny
0	10,000	10,000	0	5,000
1	5,450	1,950	3,500	450
2	3,159	382	2,777	48
3	1,972	276	1,696	43
4	1,287	215	1,072	41
5	870	179	691	40
6	610	160	450	43
7	451	155	296	50
8	362	167	195	64
9	333	204	129	93
10	373	287	86	152
11	516	459	57	269
12	831	793	38	491
13	1,426	1,402	24	884
14	2,437	2,422	15	1,522
15	3,939	3,929	10	2,420
16	5,782	5,776	6	3,431
17	7,530	7,526	4	4,260
18	8,772	8,770	2	4,726
19	9,457	9,456	1	4,911
20	9,775	9,774	1	4,971
21	9,909	9,909	0	4,990
22	9,964	9,964	0	4,996
23	9,986	9,986	0	4,998
24	9,994	9,994	0	4,999
25	9,998	9,998	0	4,999
26	10,000	10,000	0	5,000

TABLE 7.—*Controlling a population of 10,000 rats by sterilizing 70 percent of both sexes for 3 generations*

Generation	Total rats	Normal rats	Sterile rats	Progeny
0	10,000	10,000	0	5,000
1	5,450	1,950	3,500	450
2	3,159	382	2,777	48
3	1,932	74	1,858	4
4	1,225	50	1,175	3
5	793	34	759	2
6	521	24	497	2
7	344	17	327	1
8	229	13	216	1
9	153	9	144	1
10	103	7	96	1
11	69	5	64	1
12	47	4	43	0
13	32	3	29	0
14	21	2	19	0
15	15	2	13	0
16	10	2	8	0
17	7	1	6	0
18	5	1	4	0
19	4	1	3	0

high degree of survival of young rats that are produced will result in a rapid growth of the population. However, the overall impact of the control procedure by sterilization is highly dramatic as compared to the impact of the conventional control procedure. This is shown clearly in figure 2. The population subjected to a kill of 90 percent will theoretically return to about 82 percent of the original level by the sixth generation. Theoretically this level will not be reached until sometime between the 17th and 18th generation in the population subjected to sterilization.

Results of calculations are not shown, but sterilization of 95 percent of the rats in one generation would lead to theoretical elimination of the population. In contrast, it would require the destruction of 99.99 percent of a population of 10,000 rats to achieve theoretical elimination of the population.

(2) Sterilization of 70 percent of 10,000 rats (both sexes) for two successive generations:

As previously stated, it may not be feasible in many rat-infested areas to use baits in a manner that will destroy or sterilize 90 percent of the rat population as projected in the hypothetical program already discussed. The treatment of a lower percentage of a rat population by baiting seems more feasible and practical. Therefore, a hypothetical program based on assumed sterilization of 70 percent of a rat population for two successive generations is analyzed for the purpose of comparing results of a similar program involving 70-percent kill for two successive generations as have already been projected (table 3).

It is assumed that 70 percent of the initial population will be sterilized in the first generation. In the next generation 70 percent of the remaining population will also be sterilized. The theoretical impact of such a program is shown in table 6 and in figure 3. The theoretical results obtained are essentially the same as for the population subjected to 90-percent sterilization during one generation. The advantage over destroying 70 percent of the rats each generation for two successive generations may be noted by comparing the results in table 3 and figure 3. The relative advantage

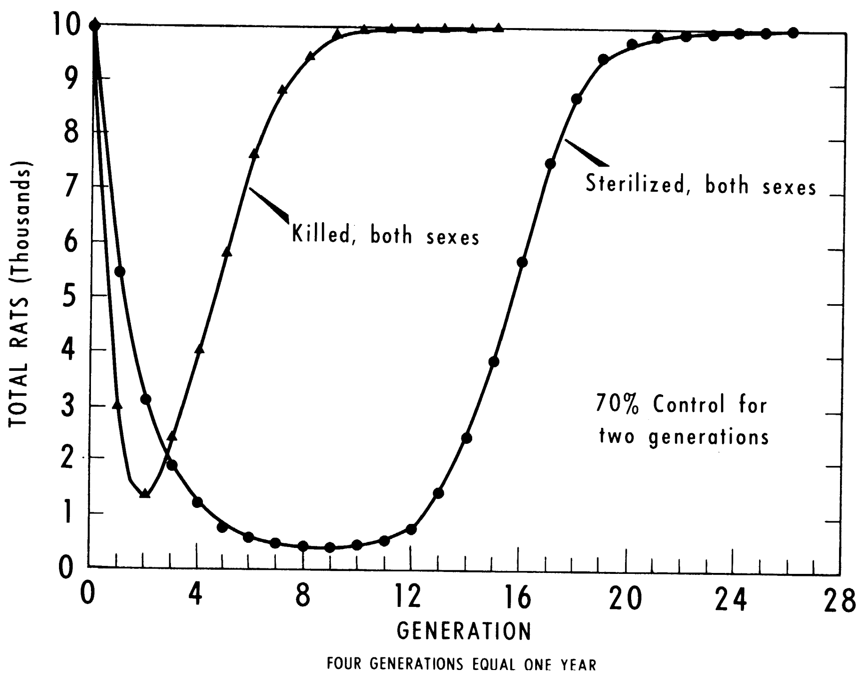

FIGURE 3.—Trends of rat populations subjected to 70-percent kill or 70-percent sterilization of both sexes for two successive generations (see text for parameters).

of sterilization over killing is essentially the same as indicated for the 90-percent sterilization over the 90-percent kill levels.

(3) Sterilization of 70 percent of 10,000 rats (both sexes) for three successive generations:

If a program is instituted with chemosterilant baits that achieves 70-percent sterilization for three successive generations, theoretical elimination of the population will result. This is shown in table 7 and figure 4. By the end of the third generation of continuous baiting, the ratio of sterile to fertile rats would be approximately 25 to 1. This is high enough to lead to elimination in spite of the increased survival rate of progeny at the lower population densities.

The authors fully appreciate the difficulty of achieving the complete elimination of any animal population and they acknowledge that theoretical projections cannot necessarily be realized in practice. Nevertheless, the potential superiority of the sterilization over the conventional killing approach to rat suppression is clearly indicated by noting the difference in the trend of a rat population

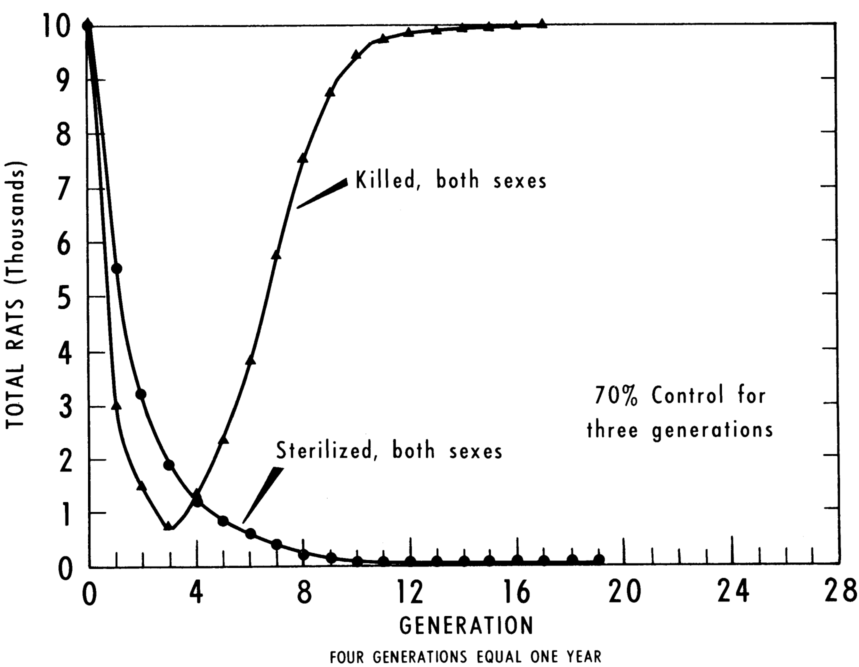

FIGURE 4.—Trends of rat populations subjected to 70-percent kill or 70-percent sterilization of both sexes for three successive generations (see text for parameters).

subjected to 70-percent destruction for three successive generations (table 4) as opposed to the trend of a population subjected to the same level of sterilization for three successive generations (table 7).

If the complete elimination of rats from specified isolated areas should ever be attempted, the chances of success using an effective sterilant should be vastly greater than using conventional killing procedures.

Calculated Impact of Sterilizing Males or Females Only

Some research has been undertaken to evaluate the use of materials that sterilize only one sex of a pest species. Vertebrate pest control based on the sterilization of one sex may have a definite place in the management of vertebrate animal populations because of esthetic reasons. However, we wish to point out that it has no technical advantage over killing in the suppression of animal populations.

The purpose of this study is not only to emphasize the theoretical advantage of appropriate sterilization of both sexes of an organism over killing both sexes as a means of suppression but also to show that the sterilization of one sex only has no technical advantage over the destruction of both sexes. This is clearly shown by the results presented in table 8 and figure 2. All parameters previously established are applicable to the hypothetical sterilization program involving the sterilization of females only.

Results are presented for the hypothetical program involving the sterilization of 90 percent of the females for the first generation. All males are assumed to remain fertile. The trend of the population as compared with that subjected to 90-percent kill of both sexes (table 2) is somewhat different because of the time required for the rat population to decline due to natural attrition. It will not reach the low level achieved when 90 percent of the rats are destroyed. The lowest level will be about 3,500 rats as compared with 1,000 for the population subjected to conventional control of both sexes. However, due to the density-dependent suppression effects as specified in the parameters, the growth of the rat population subjected to sterilization will be delayed to some degree. However, the average number of rats present in the populations during the first 2 years after initiation of the two types of programs will be essentially the same. The theoretical suppression due to the sterilization of males only will be the same as that produced by sterilization of females only if the sterile males produce

TABLE 8.—*Controlling a population of 10,000 rats by sterilizing 90 percent of all females for 1 generation*

Generation	Total rats	Normal rats	Sterile females	Progeny
0	10,000	10,000	0	5,000
1	5,500	3,250	2,250	500
2	3,893	2,611	1,282	758
3	3,494	2,727	767	1,167
4	3,900	3,437	463	1,789
5	4,943	4,666	277	2,613
6	6,366	6,206	160	3,502
7	7,768	7,679	89	4,229
8	8,809	8,762	47	4,664
9	9,424	9,400	24	4,864
10	9,736	9,723	13	4,944
11	9,881	9,875	6	4,975
12	9,946	9,943	3	4,989
13	9,976	9,974	2	4,995
14	9,989	9,988	1	4,997
15	9,995	9,994	1	4,999
16	9,998	9,998	0	4,999
17	9,999	9,999	0	5,000
18	10,000	10,000	0	5,000

false pregnancy or if mated females produce progeny that cannot survive.

The effects of sterilization of one sex only at lower levels over a longer period of time show the same general relationship; consequently, the results of calculations at 70-percent sterility levels for two and three generations will not be presented.

In stressing the limitations of suppression procedures based on sterilization of one sex only, the authors do not wish to discourage research on the development of materials that are active against only one sex. Possible esthetic advantages of the management of certain animal pests if only one sex can be sterilized have been noted. Equally important, it would seem entirely feasible to combine a selective male and a selective female chemosterilant in baits and achieve the same results that would be obtained by using a chemical that sterilizes both sexes provided the combined materials used do not adversely affect the sexual vigor and competitiveness of the males.

Discussion and Conclusions

There are obvious limitations to the degree of confidence that can be placed in the results of theoretical appraisals of the nature reported in this bulletin. Factors such as territorial behavior, competitiveness of rats of different ages, and mating behavior of the rats can affect the results. The chance of scientists discovering a suitable chemical or chemicals that will produce the sterilization effects specified is probably the most formidable obstacle to eventually realizing the maximum advantages of sterilization over the conventional method of suppressing rodents. On the other hand, the development of suitable sterilizing chemicals for rats and other vertebrate pests may be well within the realm of possibility judging from progress already reported. In the case of insects, chemosterilants have been discovered that cause permanent sterility in both sexes of several species without serious adverse effects on the behavior and competitiveness of the males.

Questions might be raised regarding the practical problems of actually treating sufficient numbers of rats in a population to achieve the required level of sterility to accomplish results projected in this theoretical study. Those having practical experience in rodent control will be in the best position to answer such questions. Rex E. Marsh has recently prepared a document issued by the World Health Organization entitled "Theory and Potential Value of Rodent Chemosterilants," WHO/VBC/70.176. He considers some of the practical problems of developing and using chemosterilants for rodent control. Recognizing the potential advantages, however, he urges an intensification of research to develop suitable materials that will accomplish sterility.

Although several practical problems are likely to be encountered and changes in the technique for the most efficient use of chemosterilants will probably have to be developed, the basic techniques should be similar for employing chemosterilants or conventional rodenticides. Using the same baits that are equally active biologically and equally acceptable to rats, it should be possible to sterilize the same percentage of a population as can be killed with a conventional rodenticide. It is even possible that a higher percentage of a rat population will consume baits containing sterilants than will ordinarily consume the same type of bait containing conventional rodenticides because rats may not readily associate sterilizing effects with bait consumption. If this should be the case, the problem of bait shyness encountered in the use of rodenticides may be lessened or avoided and would be an additional advantage in using the sterilization technique.

Questions may also be raised regarding the accuracy of the life history, behavior, and dynamics of the hypothetical rat populations established for this study and the effect this will have on the validity of the conclusions. The authors believe that the parameters concerned with the dynamics of rat population growth are realistic and may be conservative. If the parameters are reasonably sound, the models should serve to indicate the relative magnitude of the effects to be expected from the two suppression procedures. The major objective of this study was to compare the potential merits of sterilization versus killing as a means of suppressing reproduction in rats. Substantial changes in details of the parameters, such as the natural attrition rate, the natural growth rate, and the length of a generation, will not appreciably change the relative effects projected so long as relevant parameters apply to each population. Sterilization of both sexes will have a much greater suppression impact than the killing of equal numbers of both sexes regardless of the biology of the species.

If the most effective sterilizing chemicals available are substantially less effective than projected, especially in regard to the degree of competitiveness of the sterilized males, the potential benefits of sterilization should not be disregarded even with such less effective materials. For example, if sterilized male rats are only half competitive, it would be necessary to sterilize 95 percent of the population to produce the effects projected for 90-percent sterility. On the same basis, the sterilization of 85 percent of the rat populations should achieve the results projected for 70-percent sterility in the models. Also, the maintenance of sterility at levels lower than 70 percent should not be ruled out in practical rat suppression. Continuous exposure of chemosterilant baits that would produce only 50-percent sterilization of rats each generation could lead to virtual elimination of successful reproduction within a relatively few generations.

If promising chemical sterilants for rats are found, experiments to evaluate the effectiveness of such materials should be carefully planned and executed. The treated population should be reasonably well isolated. If not, the advantages of the technique can be readily obscured by emigration of rats from and immigration into the test area. This has been the experience in research on insects. If tests are undertaken on small segments of a large contiguous population, a true measure of the relative effects of the two suppressive procedures is not likely to be possible. Therefore, the authors urge comparative tests on total populations well isolated from other uncontrolled populations in order to fully appraise the potential of this suppression technique.

The population models used to calculate the relative effectiveness of chemosterilants versus conventional rodenticides were established to represent Norway rats in urban areas. The same basic advantage over conventional rodenticides should also apply in principle for field rats that may attack agricultural crops. Research on the possible use of chemosterilants as a means of rat control in agricultural areas has been conducted for some years by A. S. Srivastava, Institute of Agricultural Sciences, Uttar Pradesh, Kanpur, India. In personal communications with Dr. Srivastava, he reports encouraging results with chemical sterilants, and large-scale tests on 90,000 acres are underway.

This study has been limited to an appraisal of the potential role of suitable chemical sterilants used against the natural population for rat suppression. The possible role of the release of reared sterile male rats is a subject that has not been considered. The use of released sterile rats alone in all probability would have limited practical value. However, if highly competitive sterile male rats could be produced, they could have an important role in maintaining the suppression of natural populations after they have been greatly reduced by other means. An example might be cited.

If a population has reached a level of only a few hundred rats, as depicted in models subjected to chemosterilant treatments, it might be much more practical to further reduce such low populations or maintain such low populations by the release of sterile males. The liberation of as few as 100 to 200 sterile males per generation when the population reaches a level of 300 to 400 rats should further suppress and maintain suppression. The cost of maintaining suppression in isolated areas or areas subjected to only occasional immigration of rats may be much less than by any other means of suppression. The low number that would have to be released on a continuing basis should be of little significance from the standpoint of economic losses.

Rats probably cause losses in food production and destruction of stored foods as well as other materials that aggregate billions of dollars each year. They are also reservoirs of important diseases. As shown by theoretical calculations, the potential advantage of appropriate sterilization procedures for the suppression of these pests would seem to justify a major effort in research to discover and develop materials and methods of use that will come as close as possible to achieving the potential suppression effects projected in this theoretical study. Basic sanitation procedures should remain the foundation of good rodent control practices. At the same time effective and safe chemicals to supplement other suppression methods will probably be needed for rat control in many situations for years in the future. The eventual development of effective and safe chemical sterilants of the right type could add a new dimension to rat suppression procedures.

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