insect ecology and the sterile-male technique

Proceedings of a Panel,
Vienna,
7-11 August 1967

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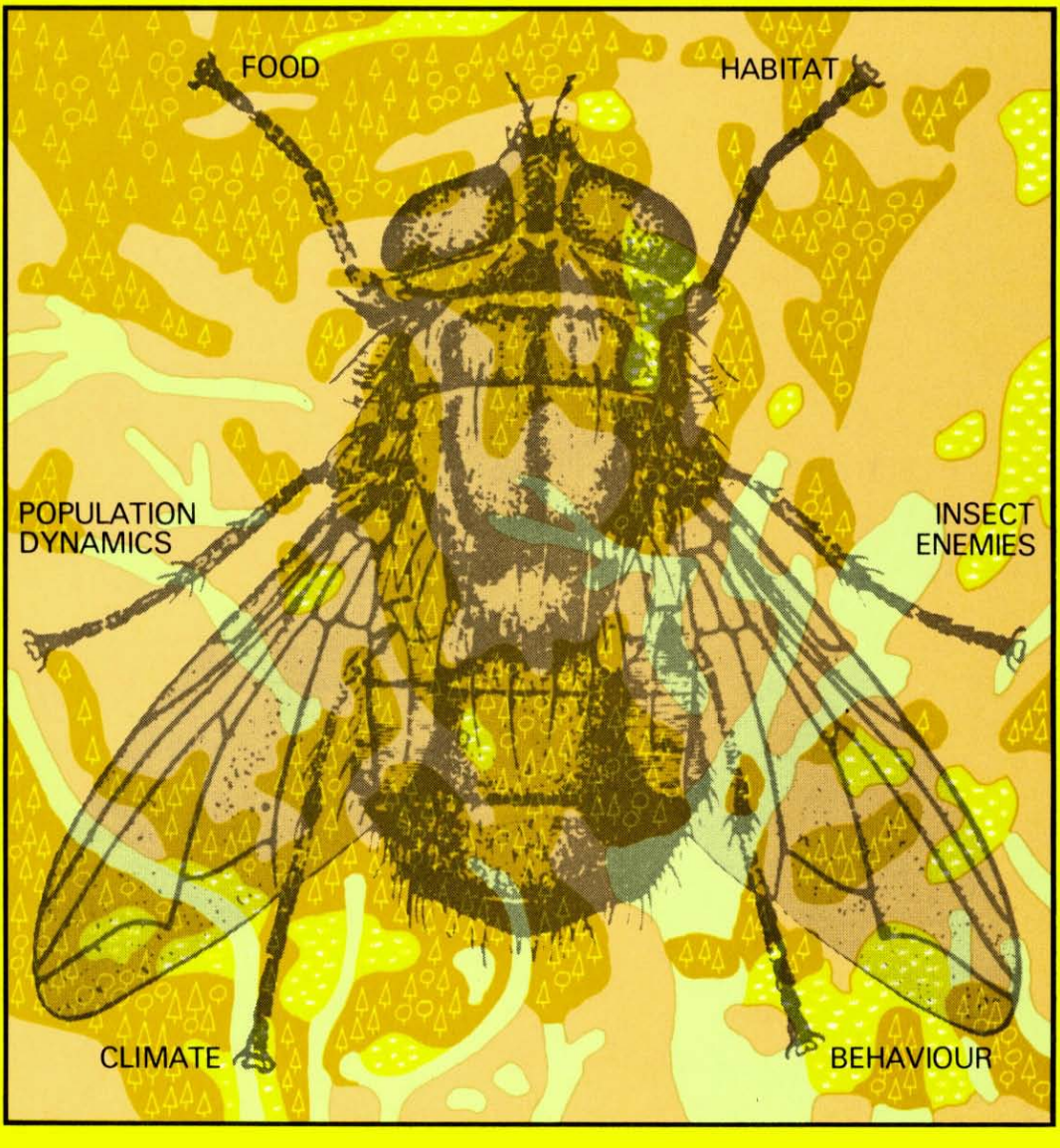

INTERNATIONAL ATOMIC ENERGY AGENCY, VIENNA, 1969

INSECT ECOLOGY AND THE STERILE-MALE TECHNIQUE

PANEL PROCEEDINGS SERIES

INSECT ECOLOGY AND THE STERILE-MALE TECHNIQUE

PROCEEDINGS OF A PANEL
ON INSECT ECOLOGY AS RELATED TO CONTROL OF NOXIOUS INSECTS
BY THE STERILE-MALE TECHNIQUE
ORGANIZED BY THE JOINT FAO/IAEA DIVISION
OF ATOMIC ENERGY IN FOOD AND AGRICULTURE AND
HELD IN VIENNA, 7-11 AUGUST 1967

INTERNATIONAL ATOMIC ENERGY AGENCY
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FOREWORD

Before the sterile-male technique is applied for the eradication or control of a noxious insect, the practical ecology of the species must be well understood. Examples of essential data include: the distance the insects will fly, the rate of population increase during various times of the year and under various climatic conditions, realistic estimates of total populations in a given area, and a thorough knowledge of wild and cultivated hosts.

The panel on Insect Ecology as Related to Control of Noxious Insects by the Sterile-Male Technique, held on 7-11 August 1967, was the first insect ecology meeting arranged by the Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture. The present publication contains the papers and recommendations of the panel. It is hoped that these will be of value to scientists working on the practical application of the sterile-male technique.

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POPULATION STUDIES OF THE CHERRY FRUIT FLY, Rhagoletis cerasi L.

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Abstract

POPULATION STUDIES OF THE CHERRY FRUIT FLY, Rhagoletis cerasi L. A summary of recent investigations into the ecology of the cherry fruit fly, Rhagoletis cerasi L., is given. These studies indicate that, from an ecological viewpoint, the cherry fruit fly may be a good candidate for control or eradication by the sterile-male technique.

The sterile-male technique, like any other method of pest control, must be considered within the framework of the complex program of plant protection. It would be of little value, for example, to develop the sterile-male technique to control any one species when in orchards there are other species requiring chemical control at the same time and for which the same pesticides would be required as for the species being controlled by the sterile-male technique. In such cases use of the sterile-male technique against the one species would not reduce the number of insecticide sprays still required. Moreover, the sprays would kill the sterile males. For this reason the best use of the sterile-male technique in orchards would be to control insects directly injurious to the fruit, such as the codling moth, Carpocapsa pomonella (L.), and the cherry fruit fly, Rhagoletis cerasi L. These species cause considerable losses in orchards and require extra spraying shortly before harvest time. The replacement of insecticides by the sterile-male technique would decrease the hazard to man and beneficial fauna. Some difficulties would occur in apple orchards where fruit are injured not only by the codling moth but also by tortricid larvae (leaf rollers). However, in those cases the control of many species of leaf roller may be carried out earlier in spring or even in winter.

Ecological information of possible interest in respect to the use of the sterile-male technique in orchards will be presented with the cherry fruit fly as an example. This insect has been studied in detail for several years in Poland.

Table I presents some data on the population dynamics of the cherry fruit fly as measured by the degree of infestation by this insect. The earliest record of an outbreak was in 1923 - 1924, and a second outbreak occurred in 1931 - 1933. Appreciable losses did not occur in the period 1925 - 1930. The longest and most severe outbreak started in 1954 and continued until 1962. During that period, as is shown in the table, the species was found throughout Poland with the exception of the two most northern districts and of the most industrialized districts. The extremely heavy population in the central district gave rise to more than 90 cherry fruit fly larvae per 100 fruit. The peak of this outbreak occurred in 1957 - 1958; from 1959 on there was a steady decrease of the cherry fruit fly population,

TABLE I. INCIDENCE OF THE CHERRY FRUIT FLY, Rhagoletis cerasi L., IN VARIOUS PROVINCES OF POLAND, 1954 - 1962.

Year	Białostok	Bydgość	Gdańsk	Katowice	Kielce	Koszalin	Kraków	Lublin	Łódź	Opole	Olsztyn	Poznań	Rzeszów	Szczecin	Warsaw	Wrocław	Zielna Góra
1954			0													0	
1955			0				0	++	0			++			0	0	++
1956			0				0	++	0			++		0	0	0	+
1957			0		++		0	++	0			++	0	++	+	+	0
1958			0	x	+		++	++	0			+	+	++	++	+	++
1959		++	0	x	0	0	+	++	+	0		0	+	+	+	++	+
1960		0	0	x	0+	0	0	0+	0++	0		0	0	0	0+	0	0
1961		0	0	x	0	0	0	+	0			0	0++	0	++	0	
1962		0	0	x	0	0	0	0	0	0	0	0	0	0	+	0	0

Infestation by the cherry fruit fly: 0 - slight < 10% of affected fruit, + - moderate 10 - 30% of affected fruit, ++ - strong > 30% of affected fruit, x - in the province of Katowice the occurrence of the fly was confirmed only in the Kobuck district.

Note: The figures quoted are for the maximum infestation by the cherry fruit fly during the year in question in the individual provinces. The occurrence of two different signs side by side refers to a difference in the degree of infestation by the fruit fly in orchards which have been sprayed under the eradication campaign (first sign) and those which have not been sprayed (second sign).

followed by a sharp decline in 1961 and 1962. At present severe infestation by this pest is observed only in a few small regions.

The fruit of all cherry varieties examined were found to contain larvae of the fruit fly with the exception of the earliest, Fruherte der Mark. The fruit of this variety are picked at the time the cherry fruit flies are ovipositing. Late-ripening varieties are attacked more heavily than the early-maturing ones. However, in 1951 and 1952 only the late-maturing varieties were infested.

There is no evidence that any other characteristic of a given variety besides the maturing time of the fruit influenced the degree of fruit infestation. Data on fruit ripening and cherry fruit fly infestation are shown in Fig. 1.

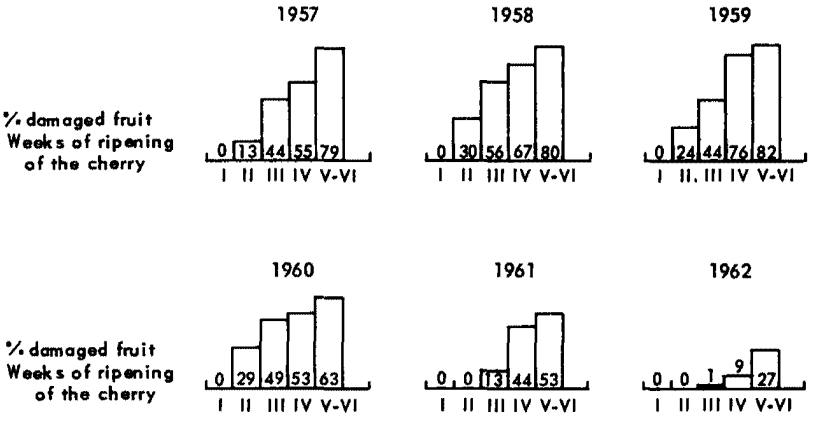

FIG. 1. Damage to cherry varieties by the fruit fly as a function of the degree of ripeness.

The only attempt to study the causes of increases and decreases of the fruit fly population was carried out by Wiesmann in 1934. He observed that outbreaks occurred after severe winters and concluded that low temperatures killed cherry fruit fly parasites.

According to the results of our studies, Wiesmann's explanations are not correct. The lowest temperature observed in Poland in the soil at a depth of 5 cm (the depth at which most of the cherry fruit fly pupae overwinter) was -12°C and lasted for periods of one week or less (Table II). This temperature had no influence on the survival rate of parasitic larvae in tests with the pupa of R. cerasi.

The exact analysis of climatic data showed that at least the last outbreak was related to the rainfall distribution. This outbreak was preceded by very scarce rainfall in June (26 mm) and heavy rainfall in July (169 mm) in 1964. Due to this distribution of rainfall, females found very good conditions for oviposition in June, and the heavy rainfall in July caused cracking of the fruit, which prevented the farmers from picking. This enabled most of the larvae to complete their development and resulted in a good start for the outbreak. According to our observations, a similar rainfall pattern often occurred after a severe winter.

Once the outbreak started, the population density was dependent on ecological factors. The cherry fruit fly was more numerous in orchards

TABLE II. EFFECT OF LOW TEMPERATURES AT DIFFERENT PERIODS OF THE DIAPAUSE ON MORTALITY OF CHERRY FRUIT FLY PARASITES, SKIERNIEWICE FRUIT RESEARCH STATION, 1962

Temperature	Duration		Dead parasite larvae (%)
-12	1.I - 8.I	- 1 week	28
-12	1.II - 8.II	- 1 week	15
-10	1.XII - 15.XII	- 2 weeks	19
-10	1.I - 15.I	- 2 weeks	37
-10	1.II - 15.II	- 2 weeks	33
-10	1.III - 15.III	- 2 weeks	47
- 5	1.XII - 15.XII	- 2 weeks	25
- 5	1.I - 15.I	- 2 weeks	22
- 5	1.II - 15.II	- 2 weeks	42
0	1.XII - 1.II	- 2 months	36
0	1.XII - 1.III	- 3 months	33
0	1.XII - 1.IV	- 4 months	43

with light sandy soil, in orchards with slopes facing south where earlier emergence took place and in orchards with many varieties of fruit. The dynamics of the population also depended on the temperature during July and on oviposition rates.

A very important factor seems to be the indirect effect of climatic conditions on the plant host. The absence of cherry fruit fly in northern Poland is not caused by the effect of low temperatures on the fruit fly itself but rather frost injury to cherry trees or blossoms. When part of the cherry blossom 'crop' is destroyed by spring frosts, the remaining fruit are picked so thoroughly that almost none are left in which the cherry fruit fly can complete its development.

There are several factors which may cause a decline of the population of the cherry fruit fly. Fruit growing practices, spraying and early and thorough fruit picking may reduce the cherry fruit fly population considerably. There is also a natural factor which can cause a population decline.

As may be seen in Table III, the cherry fruit fly population in an experimental unsprayed block was very severe until 1961 when it started to decline. This decline was even sharper in 1962.

The parasite limited the cherry fruit fly population to a great extent, but, as there was no increase in the degree of parasitization during a three-year period (Table IV), it is evident that parasites cannot be the primary cause of the suppression of outbreaks.

The main cause of suppression was the delayed emergence of the flies in relation to the ripening of the cherry fruit in 1961 and 1962. In these years the cherry fruit fly infested only the latest variety of cherries

TABLE III. INCIDENCE OF CHERRY FRUIT FLY, Rhagoletis cerasi L., AT THE SKIERNIEWICE FRUIT RESEARCH STATION, 1956 - 1962

Year of observation	Average per cent of damaged fruit of all varieties
1955	33
1956	39
1957	48
1958	58
1959	57
1960	49
1961	28
1962	9

TABLE IV. PARASITIZATION OF CHERRY FRUIT FLY LARVAE AT SKIERNIEWICE FRUIT RESEARCH STATION, 1959-1962

Year	Parasitized fruit fly larvae (%)	Per cent of total parasite population		
		O. rhagoletícolus	Ph. wiesmanni	Others
1959	28	-	-	-
1960	27	-	-	-
1961	32	88.3	8.4	3.3
1962	22	74.7	24.1	1.2

Breakdown of parasite varieties determined by Bakowski and Wiackowski.

(Table III). For this reason the females were unable to lay the full complement of eggs (reduced fecundity).

For the purposes of the sterile-male technique it is important to know not only the trends of population dynamics, but also to estimate the actual number of a given species per unit area. With R. cerasi these data are difficult to obtain. The population at the beginning of emergence is obviously much lower than at the peak of emergence, and measuring the population density at the peak of emergence would be too late, since the release of sterile males should occur much earlier. One way of obtaining population data would be to collect cherry fruit fly pupae from a given area under

infested trees. The correction for mortality factors in overwintering pupae should be taken into account. Our data show that 40 flies emerge from 100 pupae collected.

Biological studies of the cherry fruit fly were carried out in detail. The most important facts from the point of view of the sterile-male technique are listed below.

(a) The time of emergence may not only be observed but also predicted by using the sums of effective temperature. Emergence started when the sum of effective temperature above 7°C achieved an average of 320°C.
(b) Copulation takes place on the third or fourth day after emergence and each female copulates several times.
(c) Oviposition starts on the sixth or seventh day after emergence and one female lays an average of 30 eggs during a three-week period; a maximum of 111 eggs are laid.
(d) The incubation period of the eggs lasts about ten days and the period for development of the larvae is 20 days.
(e) Diapause is obligatory and the shortest period of low temperatures needed for further development is two months, the optimum period being four months. About 10% of the pupae remain in diapause for a second year and some probably for a third year.

For studies of the dispersal rate, the cherry fruit flies were fed on a sugar solution labelled with ^{32}P. Unfortunately, the eggs deposited by the labelled flies were also radioactive, and, since they are inserted into the fruit, this method could not be applied to field studies. A method of hastened emergence was therefore developed. The flies emerged earlier than the native ones, due to the pupae being kept at higher temperatures, and were released in an orchard of mixed cherry varieties. An observation of the dispersion and oviposition of the released flies, made before the natural population appeared, and of the deposited eggs enabled the dispersion rate to be estimated. Very few adults dispersed from the cherry tree in which the release was made and then only for a very small distance during the first few weeks. Later on the flies were more active, but the dispersion only attained 350 meters. The poor mobility of cherry fruit flies could also be observed in natural populations. The degree of infestation of trees of the same variety sometimes differed widely, depending on the severity of infestation of neighbouring, earlier ripening varieties. It showed that the fly most often moves only to neighbouring trees with fruit that ripens later.

The following conclusions may be drawn in respect to the sterile-male technique:

(a) The cherry fruit fly may be a good object for control by the sterile-male techniques at times when no other pests in need of control are present.
(b) Since the flight range of this insect is rather short, it would be possible to use the sterile-male technique in isolated orchards or regions.
(c) There are sequences of years with a high population density of the cherry fruit fly and with a low population density, and it would be advisable to take advantage of the low density periods.

(d) The obligatory diapause makes mass rearing difficult, but pupae may be obtained from infested fruit.
(e) Since the flies do not move willingly from tree to tree, it might be necessary to release males at several points in the orchard or even on individual trees. The males would be released on the tree of the given variety as the fruit starts to ripen, thus influencing migration.
(f) The actual density of the population may be most reliably estimated by collecting pupae from the soil and correcting the obtained figures for mortality.
(g) Since some pupae remain in diapause for two or three years, it would be necessary to continue releasing sterile males one or two years after no flies had been observed in treated orchards.

INVESTIGATION OF POPULATION DYNAMICS OF THE GYPSY MOTH BY MEANS OF TRAPS*

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Abstract

INVESTIGATION OF POPULATION DYNAMICS OF THE GYPSY MOTH BY MEANS OF TRAPS. The use in Yugoslavia from 1957 to 1964 of traps containing the sexual odour of the gypsy moth made it possible to study the population dynamics of the insect. The method was used in the wooded areas of three republics, Serbia, Bosnia and Herzegovina, and Croatia. The efficiency of the traps was also investigated. Thus, the critical number of males caught in a trap was determined and compared with the critical number of egg clusters per unit area.

During the observation period, a percentage of traps with the critical number of males was found in Serbia. The smallest number of such focal points (4.2%) was recorded in the lowest population period. This increased to 51.1% in the pre-peak year (1964) of the cycle. The existence of the focal points and the variations in numbers during the lowest population period show that this period does not appear everywhere at the same time. The traps showed various changes in the numbers of the insect in different ecological conditions, as a result of various factors which restrict or accelerate propagation. It was learned by using the traps that the smallest population density is not found in areas larger than a single wood, and even within a single wood the density varies. By establishing the ecologically unsuitable places for gypsy moths, the traps made it possible to investigate the factors which make the existence of the insect possible.

The traps recorded the population movement as a whole. The lowest population period occurred in 1959 and 1960. The new cycle began in 1961 and increased in the following years, with 1964 the pre-peak year.

In Bosnia and Herzegovina the traps gave similar results to those found in Serbia, and also showed the differences resulting from ecological factors. The trends in population density differed from that in Serbia for one year. In Croatia, however, the trend is very similar to that in Serbia.

With the trap method, it was possible to follow the progress of a cycle through the changes in the average numbers of males caught in traps in a republic, a region, a district, a wood, or within the effective range of a single trap. Thus, the traps in Yugoslavia showed that during the lowest population period the gypsy moth has an extensive habitat in deciduous forests, since it was found in the lowlands, in the hills and, to some extent, in mountain forests.

The use of the trap method gave a clear insight into the need for control during the lowest population period. This was hitherto not recognized and control measures were not taken. It has now been realized that the gypsy moth should be destroyed in the initial focal points.

1. INTRODUCTION

The use over a period of eight years of traps containing the sexual odour of female gypsy moths has made it possible to study the dynamics of gypsy moth populations. An extract of the natural scent-producing material was first produced in 1955 and 1956 [1], and was employed until 1963. More was then produced and has been used since 1964.

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* The research was carried out at the Forestry and Timber Institute in Belgrade. The author wishes to thank the forestry industries and their specialist personnel in Serbia, Bosnia and Herzegovina, and Croatia for their assistance in providing data, collecting the results and making them available for analysis. Thanks are also due to Mr. Danica Krstić of the Forestry and Timber Institute in Belgrade, who classified the data received.

TABLE I. NUMBER AND PERCENTAGE OF MALES CAUGHT IN TRAPS, SERBIA 1957 - 1964

Year	Number of forestry zones		Males caught in traps						
	Attacked by moths	Not attacked by moths	Less than 25		25 - 100		over 100		Total number of traps
			No.	%	No.	%	No.	%	
1957		17	258	57.9	121	27.2	66	14.9	445
1958		13	329	82.4	67	16.8	3	0.8	399
1959	1	18	456	95.8	19	4.0	1	0.2	476
1960	1	17	439	93.2	29	6.2	3	0.6	471
1961	2	23	426	90.6	35	7.4	9	2.0	470
1962	1	17	334	67.3	133	26.8	29	5.9	496
1963		14	239	56.1	124	29.1	63	14.8	426
1964		13	158	48.9	76	23.5	89	27.6	323

Traps were used in several wooded areas of Yugoslavia from 1957 to 1964. This timespan covered periods of population decline, lowest population and population increase. The effectiveness of the traps was also investigated during this period, and this led to general utilization of the method. Inter alia, the critical number of males caught in a single trap was determined and compared with the critical number of egg clusters over a given area [2]. Regularity and correlativity of these relationships were established.

The data on the use of the trap method made it possible to carry out a detailed population analysis, which is given here.

2. VARIATIONS IN THE NUMBERS OF GYPSY MOTHS IN SERBIA IN THE YEARS 1957-1964

Traps were set in a number of forestry posts in Serbia in 1957, during the period of gypsy moth population decline. The method was selected because it afforded a relatively simple way of determining the size of the gypsy moth population. Each year about 400 traps were set in the woods. The method was applied in 14-24 forestry zones, covering in practice the greater part of Serbia.

Analysis of the data (Table I) shows that in a certain number of traps less than 25 males were caught annually at the time of the moths' flying period. According to earlier studies [2], 10 egg clusters per hectare is average for these areas. Control measures are not recommended at the population level. We can see from the table that at the end of the cycle in 1957 this was the case in 57.9% of the traps. Somewhat later, in the lowest population period which began in 1959, there was evidence of this situation in 95.7% of the traps. At the beginning of a new cycle, this percentage again decreases, so that in the pre-peak year 1964 it amounted to only 48.9%. Similar changes are also seen in the traps in which 26-100 males were caught. In the pre-peak year 1964 such traps were in the majority, totalling 51.1%. Of the traps which caught over 100 males, 0.2% were recorded at the lowest population level in 1959, and 27.6% in 1964.

During the observation periods it was possible to determine a percentage of the traps in which the critical number of males was caught, and also the critical number of egg clusters per hectare. These were the first focal points for propagation. They were smallest in number in 1959 (4.2%), but even then over 100 males were caught in one trap. This shows that propagation had already begun and that the critical number was already exceeded. In 1960 the percentage of traps with the critical number of males rose to 6.2%, and that with the supercritical number to 0.6%. This means that the traps succeeded even in one year, during the lowest population period of the cycle, in recording the propagation situation and also the fluctuations in different populations.

The existence of the focal points and the differences in numbers in the lowest population period show that this period does not appear everywhere at the same time. There are places where it is already over and the gypsy moth population has already entered upon the increase cycle. The traps showed the different modes of variation in numbers of gypsy moths in different ecological conditions, as a result of various factors which either restricted or accelerated propagation. Thus the lowest population period

in areas bigger than a single wood is a relative concept which gives information only about predominant or average population densities. The smallest population density does not exist over areas larger than a single wooded area. Continuing the analysis, we can show that the use of a number of traps in a single wood indicates that the density varies in different parts. However, in one and the same area these differences are clearly distinguished only at the lower densities.

The first focal points of gypsy moth propagation in Serbia in the last cycle were in the regions of Niš and Kraljevo. Table II shows that as early as 1959 four traps in these districts caught over 100 males and that the population density was already in excess of the critical level. At the same

TABLE II. MALES CAUGHT IN TRAPS IN SERBIA DURING THE LOWEST POPULATION PERIOD, 1959 - 1960

Forestry zone	Year	Total number of traps	Number of traps which caught males				Percentage of traps which caught over 25 males
			0	1 - 25	26 - 100	over 100	
Valjevo	1960	30	18	10	2		6.6
Loznica	1959	50	40	9	1		0.5
	1960	53	35	18			
Vršac	1959	19	1	17	1		5.2
Smederevo	1960	9	1	5	3		33.3
Negotin	1959	8	4	3	1		12.5
	1960	20	15	3	2		10.0
Sombor	1959	15	1	11	3		20.0
	1960	14	5	6	3		21.4
Kraljevo	1960	44	15	21	5	3	18.1
Kragujevac	1959	6	3	2	1		16.6
Svetozarevo	1959	54	24	26	4		7.4
Niš	1959	46	6	37	2	1	6.6
	1960	44	28	12	4		9.0
Prokuplje	1959	12		10	2		16.6
	1960	36	17	16	3		8.3
Leskovac	1959	57	22	35			
	1960	52	7	40	5		9.6
Novi Pazar	1959	20	12	7	1		5.0
	1960	6	3	1	2		33.3
Peć	1959	20	9	8	3		15.0
Total	1959	307	122	165	19	1	6.5
	1960	308	144	132	29	3	10.3

time localities with critical counts were recorded in the districts of Sombor, Smederevo, Peć, Kragujevac and Prokuplje. This shows that the last decline in 1958 was an average one, but not in these districts, where it began earlier. In fact the gypsy moth was propagating at certain focal points over the whole area of Serbia even at the time of the general average decline. In the further course of propagation, the traps at these initial focal points were the first to register the peak of the cycle and damage by defoliation. The cycle was completed first in these regions.

The sensitivity of the trap method in recording gypsy moth population densities is shown by the fact that in the localities in which the critical number of males was found in 1959, this number was already higher in 1960 around Niš, Prokuplje and Novi Pazar. This shows that the method gives a very precise definition of the beginning of the cycle and of the initial focal points, and that the dynamics of population density can be followed from year to year.

The traps also showed areas where no gypsy moths were found during the lowest population period. Table II shows that in 1959 no males were caught in 39,8% of the traps. These were probably in ecologically unsuitable places which did not fulfil the requirements for life and propagation or in which the population had been exterminated by control measures during the last cycle. By determining these places, the traps made it possible to investigate the factors conducive to the life and survival of gypsy moths. Synecological studies in these ecosystems will afford more possibilities for combating the propagation of the insect.

The beginning of the cycle in Serbia was determined on the basis of data from the traps in 1961 (Maksimović, M. and Marović, R., 1961). The destruction of the first focal points was recommended. Since this was not done, the population density increased rapidly, and the cycle developed into one of the largest. In the peak year 1965, 1.2 million hectares of woods and orchards were attacked in Serbia. Control measures began on a small scale in 1962 and were expanded to some extent in 1963, but it was not until 1964, when the gypsy moth began to affect vast areas, that a comprehensive campaign was initiated, and even then it covered only a part of the areas attacked. In 1965 a very large control campaign was organized. Even though 360 000 hectares were sprayed by planes alone, 50% of the areas affected had to be surrendered to the moth. To reduce the extent of the damage, control measures were implemented in the most valuable woods, orchards, wooded strips around orchards, and green belts around towns, health resorts, etc.

We selected five forestry zones in various areas (Kraljevo, Novi Pazar, Pančevo, Belgrade and Sremska Kamenica) for analysing the population density of the gypsy moth in Serbia. The curve in Fig. 1 shows the average number of males caught in the traps, and a comparative movement of population density [2]. The curve shows that the lowest population period appears in the years 1959-60. Propagation begins in 1961 and increases in 1962, after which there is a substantial annual increase resulting in high population density in 1964. At this point the gypsy moth had entered the pre-peak phase of the cycle. This is a factual picture of the situation in the woods of Serbia, and shows that the traps can be used to study propagation over large areas like Serbia. On the other hand, by separating the data for the smaller parts of a region, a district or a wood, all the variations in the density of individual populations can also be determined. Such a

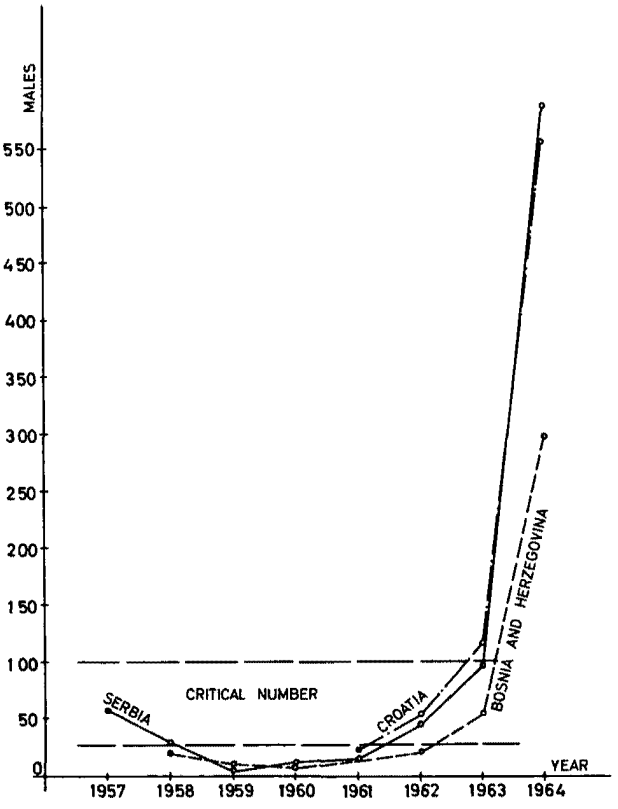

FIG. 1. Average number of males caught in Serbia, Bosnia and Herzegovina, and Croatia

detailed analysis makes it possible to find the focal point in each forestry zone and to destroy it to prevent further propagation.

3. POPULATION DENSITY OF THE GYPSY MOTH IN BOSNIA AND HERZEGOVINA, 1958-1964.

In Bosnia and Herzegovina, as in Serbia, the traps recorded the increase in population density of the gypsy moth. Table III shows that in 1963 the critical number of males was caught only in six traps, while none at all were found in 46% of the traps. This is a somewhat higher percentage than in Serbia (39.8%), which can be attributed to the fact that Bosnia and Herzegovina are much more mountainous, and at higher levels the gypsy moth is not everywhere an autochthonous member of the biogeographic zoonose.

If the changes in the number of males caught in the traps from year to year are presented graphically in the form of a curve which is equivalent to the cycle curve, and compared with the shape of the population density curve in Serbia (Fig. 1), it can be seen that the progress of the cycle is somewhat different. In Bosnia and Herzegovina it began somewhat later, and

TABLE III. NUMBER AND PERCENTAGE OF MALES CAUGHT IN TRAPS, BOSNIA AND HERZEGOVINA, 1958 - 1964

Year	Total number of traps	Total number of males caught	Males caught in traps									
			0		1 - 25		26 - 100		101 - 200		Over 200	
			No.	%	No.	%	No.	%	No.	%	No.	%
1958	45	987	9	20.0	22	48.8	12	26.7	2	4.5		
1959	92	944	28	30.4	56	60.9	6	6.5	2	2.2		
1960	100	531	46	46.0	48	48.0	6	6.0				
1961			No Data									
1962	91	2149	26	28.5	45	49.5	16	17.8	1	1.0	3	3.2
1963	199	10459	7	3.5	58	29.2	87	43.7	20	10.1	7	3.5
1964	59	17472	8	13.5	27	45.8	11	18.6	5	8.5	8	13.6

TABLE IV. NUMBER AND PERCENTAGE OF MALES CAUGHT IN TRAPS, CROATIA, 1961 - 1964

Year	Total number of traps	Total number of males caught	Males caught in traps									
			0		1 - 25		26 - 100		101 - 200		Over 200	
			No.	%	No.	%	No.	%	No.	%	No.	%
1961	276	6389	66	23.9	108	39.2	89	32.2	13	4.7		
1962	206	10847	14	6.8	71	34.4	97	47.1	18	8.7	6	3.0
1963	190	21704	4	2.1	19	10.0	99	52.1	40	21.1	28	14.7
1964	111	61326	14	12.6	32	28.8	45	40.6	13	11.7	7	6.3

also ended a year later. The lowest population period lasts from 1959 to 1961 (we have no data for the year 1961), and then the population density begins to increase, reaching the critical number throughout Bosnia and Herzegovina in 1962-1963 and thereafter increasing rapidly. This rapid increase was, however, less marked than in Serbia. Bearing in mind that mechanical control was practised in Bosnia and Herzegovina in 1963, which was not the case in Serbia, we can assume that this had an influence on the total increase in population density. We can also conclude that the traps can be used to demonstrate the overall success and value of the control measures. Finally, it appears from Fig. 1 that the shape of the curve, i.e. the increase in population density during the cycle, is very similar in Bosnia and Herzegovina to that in Serbia, apart from the differences already pointed out,

4. POPULATION DENSITY OF THE GYPSY MOTH IN CROATIA, 1961-1964

The use of traps in Croatia was restricted to the woods in Slavonia. Table IV shows that in Slavonia the increase in propagation had begun by 1961. In 13 traps over 100 males were caught, and the critical number was found in 89 traps. In the following year there was a rapid increase in population density, as can be seen from Fig. 1. The increase curve almost coincides with that in Serbia, and the progress of the cycle and the extent of the increase in population density are also almost the same. As in Serbia, no steps were taken in Croatia to combat the insects. To be more precise, control in Croatia was limited to restricted areas and was performed only with aircraft; this could have no effect on the traps, since after these measures had been taken no trapping was carried out in the areas treated.

The use of traps in Croatia showed that the gypsy moth has here a cycle of the same duration as in Serbia. Nevertheless, certain variations can be seen from Fig. 1. In Croatia, the increase in population density in 1963 spread more rapidly out of the critical zone than was the case in Serbia. The number of focal points in 1961 was also greater in the former than in the latter. In the pre-peak year (1964) the population density was the same as that in Serbia.

5. DISCUSSION

The use of the trap method in the period between two gypsy moth cycles over the whole area of Yugoslavia made it possible to carry out a detailed study of population dynamics. We were able to differentiate and compare small changes in the density during the lowest population period in various districts and republics, and to determine the beginning of the cycle. The traps showed that even during the lowest population period focal points of propagation and differences in population density exist. This is confirmed by the data from all three republics, and it is precisely this fact which gives a clear insight into the need for control measures during the lowest population period; this was hitherto not proven, and no control measures were taken. It was made evident that the gypsy moth must be destroyed

in the initial focal points. This becomes feasible because the focal points can be discovered by the traps. The destruction of focal points makes it possible to arrest propagation in individual woods and to maintain a lower population level. It is easy to destroy the points during the lowest population period,, since they are few in number and cover small areas. This is therefore an economical way to combat the gypsy moth.

The use of traps has also indicated that during the lowest population period the gypsy moth is found over a much larger deciduous forest area than had hitherto been thought to be the case [3]. This was found not only in Bosnia and Herzegovina but also in Croatia and Serbia. During the lowest population period the gypsy moth is not confined to the oak forests of the lowlands (in river valleys), but is also a permanent member of the geophysical zoonose in the hills and, up to a certain altitude, in mountainous regions where there are deciduous forests.

It is likewise important to know that during the lowest population period there are no gypsy moths in certain places. The determination of these sites makes it possible to study them in detail and to discover the factors affecting the presence or disappearance of the pest.

The data from the traps throughout the country represent average values for all the gypsy moth populations. The traps also record the individual data for each population in a wood or within the effective range of a trap, an area of 200 hectares. Kovačević [4] noted that in Slavonia in 1964 there were slightly and moderately attacked areas of woodland, and also parts in which the peak population density was to be found. With the traps it was possible to make an exact delineation of such populations.

Table IV shows that there was a sharp increase in the total number of males captured in 1964 as compared with 1963. However, these relationships are not complementary if we take into account the percentage of traps in which 26-100, 101-200 or over 200 males were captured. These discrepancies can be explained by the fact that in 1963 far fewer males, on average, were captured in these traps.

6. CONCLUSIONS

The use in Yugoslavia from 1957 to 1964 of traps containing the sexual odour of the female gypsy moth afforded more detailed knowledge of changes in gypsy moth population density. It was also possible to discover the duration of the lowest population period and the beginning, increase and decline of the cycle.

The progress of a gypsy moth cycle can be expressed by means of the change in the average number of males caught in traps in a republic, a region, a district, a wood, or within the effective range of a single trap. This made it possible to establish a correlation between the number of egg clusters in a area and the number of males caught in the traps.

During the lowest population period the traps recorded the beginning of the population increase and signalled the start of the cycle. It was found that during the lowest population period there are places where the population density is higher, and these constitute the first focal points of propagation. In this way the use of traps makes it possible to begin control measures at the right time. Hitherto, no such measures had been taken against gypsy moths in the lowest population period.

It was established that the use of traps can distinguish various gypsy moth populations within a region or a district, etc., on the basis of the degree of propagation, even over a period of two years. The cycles of the individual populations therefore end at different times and may even end after the other populations are already in the lowest population period.

The gypsy moth in Yugoslavia has a wide range of habitat in deciduous forests during the lowest population period, since it was found in the lowlands, in the hills, and to some extent in mountain forests. The traps also showed the ecologically unsuitable places for the gypsy moth, which made it possible to undertake a closer study of the factors governing the essential conditions of life of the insect.

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RADIATION-INDUCED STERILITY IN THE CONTROL OF THE OLIVE FRUIT FLY Dacus oleae (GMEL)

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Abstract

RADIATION-INDUCED STERILITY IN THE CONTROL OF THE OLIVE FRUIT FLY Dacus oleae (GMEL). In the application of the sterile-male method of control, some prior information on the required ratios of sterile flies/normal flies is of primary importance. Initial experiments in large cages built over mature olive-bearing trees in the orchard at the College of Agriculture, Athens, have been completed, and the results have shown that the number of damaged fruit is drastically reduced with ratios of 4:1, 6:1 and 8:1 irradiated /normal laboratory flies. At the last ratio only 4% of the fruit showed any damage other than oviposition scars, and we have concluded that this ratio might give good control in field application, especially when populations are low during the early spring.

A major requirement for field tests of the sterile-male technique is some estimate of the ratio of sterile to normal flies required to affect a population under natural conditions. Current research on the olive fly, Dacus oleae, at the College of Agriculture, Athens, is concerned with this question and experiments are being conducted on mature trees enclosed in large screened cages. For the present tests, four large trees (5 metres in height) bearing copious crops of green olives were selected near our laboratory. Over each tree, a framework of steel Dexion (slotted angle irons) was covered with aluminium fly screening. The ground in each enclosure was covered with white canvas to aid in the recovery of larvae and pupae from infested fruits and of dead flies. Before the cages were closed, the trees were sprayed with Rogor to remove all wild adults on the foliage. During the ensuing two weeks, several McPhail traps with ammonium sulphate as a lure were operated in each cage to detect and capture emerging adults. As a further precaution, the olives on each tree were carefully inspected for oviposition scars before the release of experimental insects. Any infested olives were removed from the trees. To avoid predation by ants, wide strips of tar were poured on the ground around the walls of the cages.

Insects for release on the caged trees were reared from infested olives collected in Crete in early autumn. These olives were incubated at 25° C (65% r.h.) in rearing rooms and the flies were collected as pupae from rearing trays. For the tests, 7- to 8-day-old pupae were irradiated with 8000 rad

and reared with separate groups of untreated pupae to the adult stage. The irradiation was carried out at the Nuclear Research Centre "Democritus" in a Gammacell 300 (Atomic Energy of Canada Ltd.) at a dose rate of 5640 rad per minute. As shown by Tzanakakis [1] and by unpublished tests at this laboratory, exposure of 7- or 8-day-old pupae to 8000 rad will sterilize both males and females. Further, our work has shown that, although mating activity is somewhat depressed in irradiated males, sterile individuals are very active and will mate several times. To mark the adults, irradiated pupae were placed in mixtures of red "Daylight" fluorescent pigment (Switzer Bros., Cleveland, USA) and fine sawdust, mixed at 1 part to 10. On emergence, the dye adhered to the thoracic regions of the adults, making those flies easily distinguishable by eye from normal insects. Thus, mortality among both irradiated and normal flies could be determined, and dead flies were replaced weekly to maintain proper ratios in all cages throughout the experiment.

In the first cage (Table I), unmated insects were released in pairs on the basis of a 4:1 ratio; that is, 400 sterile to 100 normal pairs. In the second cage, the totals amounted to 600 to 100 couples (6:1), and in the last cage, 800 and 100 normal pairs (8:1). The control cage received 100 normal pairs of adults. Sterile females were included in the experiment not only because it would be impossible to separate the sexes as pupae in a field experiment, but because sterile females may play a prominent role in control by mating with normal males. The flies in all cages were fed daily on special liquid food prepared after the formula by Hagen [2]. Drops of this diet were placed on waxed paper strips on the screening and on the foliage. Water was supplied each day in cotton suspended from the branches. The flies were released in the cages on 13 October (control and 4:1 groups), 20 October (6:1), and 4 November (8:1), and all fruit remaining on the trees were collected early in January for inspection in the laboratory. Larvae and pupae and dead flies were collected from the cages each day during the experiment.

The results, based on the number of fruit spoiled by the feeding of Dacus larvae and on the numbers of larvae and pupae recovered (Table I), show that the presence of substantial numbers of sterile individuals in the cages

TABLE I. RESULTS FROM TESTS OF DIFFERENT RATIOS OF STERILE TO NORMAL FLIES

Ratios of sterile to normal pairs	Total number fruit	Fruit with damage	Total[a] larvae and pupae	Spoiled fruit (%)
Control	877	683	631	78
4:1	1680	491	481	29.3
6:1	3301	652	751	19.7
8:1	652	26	33	4.0

[a] Includes pupae and larvae collected from cages and larvae dissected from fruit at end of experiment.

resulted in a drastic reduction in damage and in the numbers of Dacus. In the cages, all fruit bore several oviposition scars, many of which had not produced larvae owing to sterility of males and/or females in the cages. In our opinion, the data relating to spoiled fruit represent a better criterion of effect than numbers of pupae, since several pupae may be produced by one olive. Bachetti [3] has reported that a 3:1 ratio of sterile males resulted in a reduction of pupae to 20%, but he gave no details pertaining to numbers of flies, numbers of fruit, or the size of the trees in his tests. It is interesting, however, that his estimates at the 3:1 ratio are in good agreement with the present results. At the 8:1 ratio of irradiated to normal pairs only 33 pupae were recovered. This figure and the low incidence of damaged fruit indicate that this ratio approximates the relative numbers required to give control in a field experiment.

Several factors may have influenced the results of these studies. For instance, it was necessary in our orchard to use three different varieties of olive in selecting fruit-bearing trees. The control and 4:1 ratio tests were done on Megareteke olives, while in the 6:1 and 8:1 experiments Coroneibi and Crondal, respectively, were employed. However, subsequent observations on unsprayed trees showed that all three varieties were heavily attacked by Dacus in the same orchard. The possibility also existed that differential survival between irradiated and untreated flies may have reduced the effect of the sterile individuals. Our records of deaths, from tagging irradiated flies with luminescing dyes, proved that survival was slightly higher among sterilized individuals and the precaution of replacing dead flies each week with live ones reduced the risk of this effect. Conditions of temperature and humidity during the test period (e. g. from 14 October to 14 December) were favourable for mating and oviposition in 1966, as proved by unpublished data from our laboratory on the required climatic conditions for mating and oviposition. We have thus concluded that our results are valid and that future attempts to test the sterile-male method with Dacus must be conducted with these proportions in mind.

The work reported here formed part of the control program against Dacus being developed by the Phylopathology Division of the Greek Ministry of Agriculture. The second author, W. F. Baldwin, was in Greece as a UN expert, employed by the International Atomic Energy Agency, Vienna.

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POPULATION DYNAMICS OF THE SCREW-WORM FLY, Cochliomyia Hominivorax (COQUEREL), WITH RESPECT TO CONTROL BY THE STERILE-MALE TECHNIQUE

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Abstract

POPULATION DYNAMICS OF THE SCREW-WORM FLY, Cochliomyia hominivorax (COQUEREL), WITH RESPECT TO CONTROL BY THE STERILE-MALE TECHNIQUE. The current program to control screw-worms with the sterile-male technique involves an area in northern Mexico 1500 miles long and 300 miles wide together with parts of the States of Texas, Arizona, New Mexico, and California. Since it is beyond the capability of the program to release sterile flies simultaneously in the entire control zone, priorities for treatment are based on estimates of regional and seasonal variations in screw-worm populations. The research support for this program includes efforts to determine the time-space relationship of these changes in populations. Ancillary studies include the behavioural characteristics of both native and released flies, especially in regard to mating habits and dispersal.

Trapping records made after mass releases of laboratory-reared, marked flies are used to obtain information on the local distribution and movements of sterile flies. Released flies tend to congregate along water-courses in hot, dry weather, but these concentrations are transitory. Some of the released flies disperse rapidly for distances up to 180 miles, but the inefficiency of present trapping methods requires artificially large concentrations of released flies and poses concomitant difficulties in interpreting data on recoveries. Bait animals are used to collect egg masses as a means of determining ratios of sterile to fertile egg masses after releases of sterile flies. These data are used in evaluating various fly release techniques.

Methods of integrating research findings with information on the incidence of screw-worm cases are also discussed.

1. INTRODUCTION

The current program to control screw-worms with the sterile-male technique covers an area in northern Mexico 1500 miles long and 300 miles wide and parts of the States of Texas, Arizona, New Mexico and California. The screw-worm eradication program is a co-operative venture of the United States Department of Agriculture and the Mexican Ministry, and the livestock authorities of the south-western States. Livestock growers in the United States and Mexico have petitioned their respective Governments for an international program to eradicate screw-worms from the Republic of Mexico. If this is undertaken, the scope of operations will be extended over an additional 300 000 square miles of territory. Since the present control zone in Mexico would also be included, the total area would involve 750 000 square miles.

Since it is beyond the capabilities of the program to release sterile flies simultaneously over the present control zone, priorities for the release of sterile flies are based on estimates of regional and seasonal variations

in screw-worm populations. The formulation of these estimates requires a knowledge of the effects of weather, ranching practices and other factors on local populations of wild flies. Other factors which must be considered in these estimates include the local distribution, dispersal patterns, longevity and behaviour of both wild and released flies. This paper deals with the methods used in obtaining this information and the integration of these research findings into program operations.

2. BIOLOGY

Female screw-worm flies lay eggs on wounds in warm-blooded animals. In domestic livestock, the navels of newborn animals are frequently attacked. Other oviposition sites include wounds from branding, dehorning, or castrating cattle and shearing cuts on sheep and goats. Since these husbandry practices frequently involve hundreds of animals on a single ranch, screw-worm populations can increase rapidly as a result of these operations. Larvae hatch from the eggs in about 16 hours and larval growth is completed in 6 to 9 days. The pupal stage is passed in the soil and is completed in about 8 days in warm weather. Adults are ready to copulate 2 to 3 days after eclosion, and the females can begin ovipositing 5 to 6 days after eclosion. After the initial egg mass, female flies are capable of producing an egg mass every 4 to 5 days until death. The eggs are laid in cemented masses of about 350 eggs each. Females rarely mate more than once, as a single mating is sufficient to fertilize the normal life-time production of eggs. In the laboratory, the mean life span for female flies is about 28 days, and the production of as many as 10 egg masses per female has been noted. However, both these estimates are probably too high for females in nature.

3. LOCAL DISTRIBUTION OF FLIES

Most of the recent information on the local distribution and dispersal of local populations of flies has been derived from the release and recapture of laboratory-reared, irradiated flies. The trapping studies were conducted in co-operation with the Methods Development Section of the Animal Health Division, Agricultural Research Service, Mission, Texas. The effects of this prior conditioning and the creation of large, artificial population concentrations on the subsequent behaviour of the released flies is largely unknown. The validity of applying findings thus obtained to native populations is still open to question.

4. TECHNIQUES

Cone-type, plastic screen traps baited with 1 kg of liver are used to capture the flies. Marking techniques include coating the puparia with acetone-soluble dyes so that the eclosing flies pick up enough dye for subsequent detection, feeding the flies a sugar solution containing radio-active phosphorus, or dusting the adults with fluorescent powder. Since it is frequently necessary to conduct trapping studies in areas within the

flight range of flies released for the suppression of cases, the problem of the origin of artificially reared, unmarked flies in the traps has been alleviated by the use of a genetically marked strain. This strain with visible dark spots along the wing veins is also used to evaluate marking techniques. The percentages of doubly marked flies recovered indicate the effectiveness of the technique.

Most of the habitat formations, as far as screw-worm fly populations in the south-western part of the United States and in northern Mexico are concerned, can be categorized as follows:

(1) Riverine: Dominant vegetation trees over 3 metres in height or scrub from 2 to 3 metres in height in flood plains of permanent streams or rivers.

(2) Scrub-Water: Dominant vegetation trees and scrub 2 to 3 metres in height surrounding earthen-dam ponds.

(3) Scrub-Dry: Dominant vegetation scrub 2 to 3 metres in height; no surface water within 1 km.

(4) Field-Water: Dominant vegetation grasses; within 100 metres of concrete or metal livestock watering troughs.

(5) Field-Dry: Dominant vegetation grasses; no surface water within 1 km.

The results of these trapping studies indicate that released flies tend to congregate along streams in semi-arid areas and during periods of drought. Peak catches are usually noted about 3 days after the release of newly-eclosed flies. Catches decline rapidly after the third day, indicating that these concentrations are transitory. Similar transitory concentrations are noted in scrub-water formations. Differences in catches among traps in scrub-water and scrub-dry formations are more marked during dry seasons than during wet seasons. Flies are rarely trapped in field formations even during favourable seasons. However, cases do occur in livestock confined to these areas. Since less than 0.1% (0.01-0.09%) of a released population of sterile flies is recovered from liver-baited traps, it is probable that the relatively small numbers of flies in field formations are not detected by this method of trapping. Trap catches as related to formation types are similar regardless of whether the flies are released from aircraft or from a point on the ground.

Additional data on the local distribution of released flies have been obtained by treating flies with fluorescent powder and making night searches with an ultra-violet light. About 90% of the recovered flies were found resting on leafless twigs 4 to 5 feet above the ground. Flies of both sexes were found near animal pens and along a stream. However, flies were rarely found on the second night after a release. Here again, less than 0.01% of the released flies was recovered.

Evidence from the investigation of cases of screw-worms reported by livestock growers indicates that the first cases in an area and the heaviest concentrations of cases tend to occur along streams and rivers. However, the concentration of livestock populations in lowland pastures near streams in semi-arid areas is also a factor in these observations.

5. DISPERSAL

Both wild and laboratory-reared irradiated female screw-worm flies are apparently capable of dispersing considerable distances within a few days. Since males are rarely captured in traps or observed in the field, little is known about their dispersal habits. In three separate trapping experiments conducted along rivers in south-western Texas, sterile female flies were recovered from traps up to 290 km from the release area. In an effort to determine if flies were being transported by motor vehicles or railroad cars, releases in the last experiment were made from aircraft over a remote area in Mexico with no highways or rail lines leading toward the traps. In this test one fly was trapped on a river 100 km from the release area. In the two earlier tests, flies were caught in the more distant traps only during the spring and autumn months when weather was favourable to screw-worm activity.

Additional evidence that the released sterile flies tend to disperse along streams has recently been obtained in a trapping experiment conducted in north-western Sonora, Mexico. In this test, aerial releases were made over a deep, narrow river canyon. No releases were made over the canyon within 20 km of the traps nor within 20 km on either side of the canyon in the area where the traps were located. Over a period of 48 days, 7 traps placed along the river averaged 1177 flies per trap as compared with 66 flies per trap in 5 traps placed along a dry canyon leading off the river canyon.

In all the tests with sterile flies, the effects of releasing thousands of flies in a relatively small area on the subsequent dispersal of these flies have not been ascertained. The effects, if any, of these releases on the subsequent dispersal of wild flies from the release areas have not been determined.

There is some evidence from the northward spread of screw-worm cases in Texas during the period 1963-1967 that wild female flies tend to disperse for long distances. During 1962, releases of sterile flies were confined to Texas. These releases were continued throughout the winter in the known screw-worm overwintering areas in South Texas. By 15 April, 1963 (about the time when weather is warm enough for screw-worm fly activity in Central Texas) the northernmost case was 490 miles north of untreated overwintering areas in Mexico. During the winter of 1963, releases of sterile flies were extended up to 100 miles into Mexico and the northernmost infestation recorded by 15 April 1964 was 230 miles north of known infested areas in Mexico. During the past three winters, releases have been extended up to 200 miles into Mexico. The northernmost extension of infestations by 15 April in 1965, 1966, and 1967 was 122, 136 and 26 miles, respectively. Before the initiation of the present program, it was estimated that screw-worm flies dispersed northward from over-wintering areas in southern Texas at the rate of about 35 miles per week. If this estimate is assumed to be correct, the distribution of cases after releases were started indicated that the flies were dispersing at a more rapid rate. There is the interesting possibility that the dispersal behaviour of the wild flies changed as a result of 'overloading' suitable habitats with sterile flies. Increased harassment of mated females by sterile males may be a factor. Since gravid females are quite persistent in attempting

to oviposit, it is unlikely that harassment by sterile females at oviposition sites would prevent oviposition. It is also unlikely that increased competition for food from flowering plants would be a factor except possibly during dry or cold seasons.

6. ESTIMATES OF POPULATIONS OF WILD AND STERILE FLIES

At present, there are no ecologically valid means of estimating the absolute numbers of screw-worm flies per unit area. Estimates of populations of wild or released flies expressed in terms of flies per square mile imply a more or less uniform distribution over a given area rather than the actual patchy distribution. Estimates of the relative abundance and activities of wild populations of flies are obtained by trapping and case incidence studies. Ratios of sterile-to-wild females trapped in an area are used to determine if adequate numbers of sterile flies are reaching population centres of wild flies. Ratios of sterile-to-fertile egg masses collected from wounded bait animals are used to determine the effectiveness of the releases in terms of the ability of the sterile males to find and mate with wild females.

Trap catches of wild flies in populations 'undisturbed' by releases of sterile flies vary from maxima of 15 to 20 females per trap day in areas with large concentrations of flies to less than 1 fly per trap day in areas with relatively low populations. The use of traps to sample native populations is currently confined to central and southern Mexico. Since a difference of only a few metres in the placement of a trap in relation to shade or terrain features can affect the size of the catches, it is difficult to compare catches from different areas unless all the traps are placed and serviced by the same personnel. With this qualification, catches of less than 1 fly per trap day in a long-term trapping experiment in southern Mexico indicate that screw-worm populations are lower and more stable than those formerly found in Texas.

In a study of the ratios of sterile-to-wild female flies captured in traps, there was no correlation of this ratio with the ratio of sterile-to-fertile egg masses collected from nearby wounded bait animals. This lack of correlation may have been the effect of gravid females migrating into the area from distant untreated areas. Tests of this type should be conducted with isolated populations of wild flies, but such populations probably are found only on islands.

Ratios of sterile-to-fertile egg masses collected from wounded bait animals have been used to evaluate the effectiveness of sterile-fly releases since the beginning of the present release program. Data collected in heavily infested areas in Texas (high populations of sheep and Angora goats) indicated that 1000 sterile flies per square mile per week released on flight lanes two miles apart were required to achieve sterility ratios of more than 50%. In south-western Texas, where livestock populations per unit area are lower and favourable screw-worm habitats are more limited, releases of 400 flies per square mile per week or 4-mile flight lanes were effective in achieving the desired sterility ratios. Several field tests of this type have been conducted along the coast of southern Mexico at least 200 miles (350 km) below the zone of control operations. Flight lanes up

to 12 miles (20 km) apart have been used with release rates varying from 400 to 1000 flies per square mile per week over release areas of 2000 to 5000 square miles. Sterility ratios in these tests varied from 20 to 60%. The former percentages were obtained from areas with persistent screw-worm population centres, and the latter from areas with relatively low, scattered populations. Higher percentages of sterile egg masses were also obtained during seasons unfavourable to screw-worm fly activity. There were indications in these tests that the effectiveness of the released flies decreased as a function of distance within 4-5 km from the line of release. Sterility ratios of less than 70% were not sufficient to control screw-worms during seasons favourable to population increases.

Estimates of the relative abundance and seasonal trends in screw-worm populations are also obtained from samples of larvae submitted by livestock growers and cases reported by teams of Animal Health Division Inspectors. The locations and times of occurrence of thousands of cases of screw-worms have been plotted as a result of these co-operative surveys. Ancillary information on each of the cases included the kind of animal and type of wound in which the maggots were found as well as a report of screw-worm fly activity in the surrounding area.

7. INTEGRATION OF RESEARCH AND SURVEY FINDINGS INTO ESTIMATES OF CHANGES IN SCREW-WORM POPULATIONS OVER EXTENSIVE AREAS

The results of field observations, prior research on the behaviour and reproductive biology of screw-worm flies and all available records of case incidence have been integrated into estimates of where and when screw-worm outbreaks are likely to occur in any part of Mexico. The ability to utilize a knowledge of the seasonal fluctuations in screw-worm populations in different regions has already been demonstrated in northern Mexico. Officials of the Animal Health Division can limit or omit releases of sterile flies over most of the northern part of the Central Plateau of Mexico until the onset of the late summer seasonal increase in screw-worm fly activity.

Low winter temperatures and hot, dry periods are the two most important climatic factors which affect screw-worm populations in Mexico. The former is a critical factor in the northern part of the vast Mexican Central Plateau. This is possibly the only region in Mexico where the term 'overwintering' can be applied in the same sense as it was formerly used in the United States. Cool, dry seasons affect populations of screw-worm flies in the southern part of the central plateau. Populations in these regions are low and scattered except for a single peak of activity in late summer or fall.

The coastal plains of Mexico are infested with screw-worms throughout the year. Two seasonal peaks of screw-worm activity are usually noted in these regions. The first occurs in April and May and the second in September and October. The duration and intensity of these outbreaks vary with onset and frequency of the seasonal rains. During the period from October through March, the eastern coast of Mexico is subject to high velocity, cold north winds. Drastic reductions in the numbers of screw-worm egg masses collected from wounded animals and in the numbers of cases reported by livestock growers have been noted after the passage of

a 'norther'. These winds do not occur along the western coast of Mexico. The north-western coast of Mexico is part of the Sonoran Desert and the incidence of screw-worms is low throughout this region except for brief periods following infrequent rains. During seasons favourable to screw-worm fly activity, the availability of host animals with natural wounds or those induced by ranch husbandry is a factor in determining the extent and abundance of screw-worm infestations in all these regions.

Although screw-worm cases occur at some time during the year throughout most of the three major mountain chains in Mexico at altitudes up to 2400 metres above sea level, little is known of the tempero-spatial fluctuations of these populations.

It is beyond the scope of this report to speculate on the possibility of an extension of releases of sterile flies over areas of Mexico not included at present in release zones.

DEMOGRAPHIC MODELS OF POPULATION RESPONSE TO STERILE-RELEASE PROCEDURES FOR PEST CONTROL

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Abstract

DEMOGRAPHIC MODELS OF POPULATION RESPONSE TO STERILE-RELEASE PROCEDURES FOR PEST CONTROL. Existing models to describe demographic effects of sterilized contingents released in field populations were found to be unrealistic and potentially misleading. In particular, they failed to consider the functioning of density-related processes and stabilizing mechanisms in the life systems of target populations. Attempts were made to account for the operation of such agencies in theoretical instances, which suggested a number of inferences immediately relevant to the feasibility and optimalization of sterile-release procedures. Tentative conclusions are drawn regarding strategy planning in pest control.

1. INTRODUCTION

The improvement of existing procedures and the development of new methods in pest control today require long and involved programs of research. To be accepted and applied, new developments must offer not just one, but a series of proven advantages, and this prerequisite is getting increasingly difficult to fulfil. A worthwhile innovation must be economically sound, i.e. immediately profitable in material returns, under existing conditions in the social, commercial, industrial, administrative and political areas which the change may affect. The innovation must also meet a number of technological requirements of various kinds. Finally, it should comply with biological demands, such as they are, to guard against long-term disadvantages, and thereby ensure the lasting value of the new method.

For those reasons, decisions to pursue any particular approach to the control of a pest, in preference to other possible approaches, are becoming increasingly necessary and increasingly hard to make. Institutions concerned with research and development cannot gamble with their limited resources. They therefore need to do more and more preliminary thinking before they finally commit their facilities and personnel to a definite course of action. Properly defined criteria to guide their choice are obviously required.

Experience suggests that such criteria are best derived from predictive models which can mimic realistically and with appropriate accuracy any phase of the projected operations– which we will call 'strategies'.

A number of considerations must govern the construction of models for strategy evaluation. Two of the most important are discussed below.

Pest control is in essence a form of applied ecology, in which technology must play an ancillary and not a leading role. That is how Egler's reference to pest control as a "2-strand discipline" must be understood [1]. From this premise, it follows that problems in pest control must be stated in ecological terms, i.e. as a functional description of the relationships that link together the pest species, the target-organisms or target-objects of the pests, and man as the subjective party in the triangle.

A first step in strategy evaluation is to survey the pathways whereby control might be achieved. By this is meant discovering how, and to what extent, an existing pest situation would need to be altered, in one or more of its components, in order to reduce sufficiently the immediate injuriousness of the pest. Those desirable alterations should ultimately be translated into measurements of the ecological changes required to be effected in the pest-target-man system. Then, and only then, is it wise to consider the material means by which the desired effects could be accomplished, and to seek appropriate agents, or convenient substitutes, amongst the technological instruments currently available.

Another important consideration relates to the way in which strategy-planning models are best constructed. It is essential that a model should reproduce realistically the working of the life system which it purports to imitate, i.e. that it incorporate the functions served by the processes and mechanisms that ensure the persistence of populations and stabilize their numbers in nature. Having recognized the critical elements of a natural system and determined their interrelationships, the model-maker can piece together a functional mock-up, with which to refine the input values of single variates, using one (or more) accurately-measured parameter as a yardstick for the good fit of the others. Thus, in a well-conceived model, the values initially assumed for most variates need be no more accurate than is necessary to define realistic orders of magnitude. Starting from even rough approximations, the model-maker normally proceeds to test whole series of hypothetical values by computer, and draws his working data from the range of best fit; the values finally adopted being obtained by mutual compatibility in the model as a whole. For that purpose, the components of the natural system to be included in the model should be comprehensive from the start. Although interpretations of functions might become more elaborate as the work progressed, the reliability of the model would increase primarily with the increasing verisimilitude of input values. The final accuracy of a model need not exceed that required from the answers to the questions which the model was built to resolve.

No further discussion is intended here on the problems of strategy selection, important though they are in formulating policies of research and development. The paper will now be limited to illustrating the following points of the Introduction:

the general usefulness of predictive models in strategy evaluation;
the need for comprehensiveness in the initial conception of a model;
the value of even crude single estimates in broadly conceived models.

We will endeavour to do this by re-examining critically certain models of population response to sterile release on which early discussions of the merits of this method of control have often been based, notably in Australia [2].

2. OBJECTIVES

We assume that a strategy is placed under review as a possible instrument with which to perform a given task of control, the particulars of which have been ecologically defined. A predictive model is required, to compare the profitability of the projected method to that of alternative approaches. For that purpose, the model must first describe, qualitatively and quantitatively, the effects which the method considered is likely to exert on target populations, under generalized yet realistic conditions. Secondly, it should show, in more specific instances, at what cost the method might achieve the particular task of control for which it is being vetted.

We shall be concerned here with some theoretical questions pertaining to the first step of the process, i.e. with the crude description of method-impact and population-response, adopting the practical objectives proposed by Knipling [3] and leaving the ultimate evaluation of profitability out of account.

The task of control envisaged in Knipling's discussion [3] is in the form of extermination. It consists of eliminating an unwanted species from an area in which the species is becoming permanently established before the new population has fully colonized the area. Given this objective (for which one presumes there is sound justification), the sterile-release method is seen as a likely instrument, and the validity of this view is argued on the basis of the prediction derived from a theoretical model.

3. ASSUMPTIONS

To develop his model, Knipling makes a series of explicit or implicit assumptions, i.e.:

A certain area forms an ecological entity capable of supporting a discrete demographic unit, or population, of the target species.

That environment is fairly constantly favourable to the target species.

It has a limited carrying capacity for the species, and properties that interact with those of the pest to prevent the numbers of the species from seriously overshooting that limit, in a manner that would cause the population to crash periodically. The species is therefore capable of numerical adjustment at, or very close to, the carrying capacity of the environment.

The species has discrete generation cycles, with short, well-synchronized mating periods.

Reproduction is obligatorily bi-sexual; the sex ratio is 1:1; mating is random and occurs only once in females;

Individuals of the species can be sterilized and released without affecting the sex ratio, and in such a way as not to impair the mating behaviour and performance of either sex.

All those assumptions are consistent, and reflect well enough conditions that have been found to occur in nature.

At the time considered, the hypothetical population is on an increase that would take it, in the natural course of events, from a small colony of 1000 reproducing individuals to an assumed ceiling of 125 000 in three generations. In all circumstances, fertile matings are assumed to result invariably in a mean production of 10 viable offspring per fertilized female. Thus, Knipling's model entails a constant natural rate of increase of 5 per generation-cycle, regardless of population density, for as long as the population has not reached the saturation limit of the environment (125 000), whereafter the rate recedes immediately to 1.

Such events have never been recorded for any arthropod population in nature. On the contrary, the weight of evidence, both clinical and experimental, would point, as a general rule, to the prevalence of density-related change in the rates of population increase. Population studies indicate that there is usually an optimum density range at which the typically high reproductive potentials of arthropod pests are almost fully realized in a favourable environment. Below and above that range, rates of population increase fall steadily, as under-population effects become operative at lower densities, and as denser populations become exposed to mounting stress from depleted resources and from numerically or functionally responsive antagonists. Examples of that trend sequence are commonplace today, and useful discussions of the subject have been published [4, 5].

Following those authors' findings, it seemed of interest to revise Knipling's model on the sole point of rates of generation increase, in order to test the bearing of that assumption on the model's predictions. The rates adopted for this exercise are shown in Fig. 1. They imply that the relation of rates of increase to population densities forms an Allee-type curve [5], reflecting both the occurrence of increasingly intense under-population effects, and of mounting 'environmental resistance', respectively, on either side of a central range of optimum densities. It was assumed

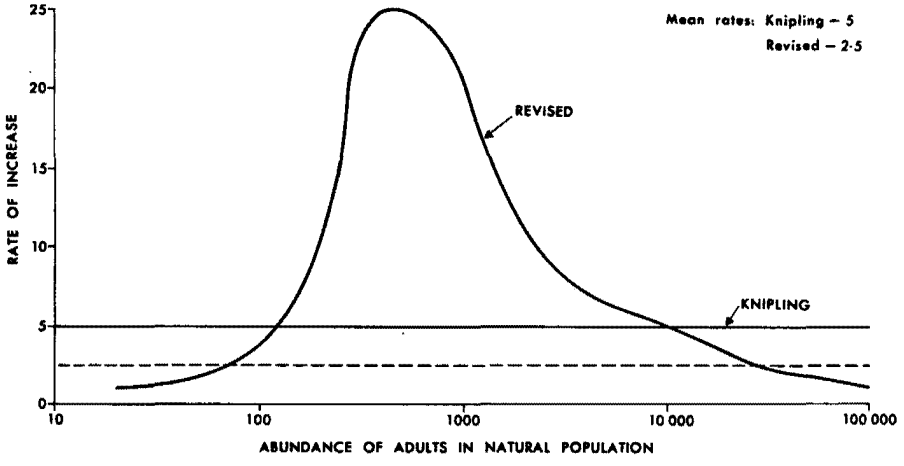

FIG. 1. Assumed rates of increase over density range.

that the rate of generation increase reached an absolute maximum of 25 (50 surviving offspring per fertilized female) at a population density of about 500, from which the rate fall to 1, gradually as population rose towards the saturation density at which it became stabilized (100 000 in this instance, versus Knipling's 125 000: the difference is irrelevant to the discussion), and more abruptly as population fell to the critical density of 20 fecund adults, below which it could no longer replace its numbers and was fated to extinction.

Two major concessions were made to facilitate calculation. Both are unrealistic, and require justification. First, as in Knipling's premise, it was assumed that the target-population was effectively sealed off, and that neither immigration nor emigration occurred. This would imply in effect that (a) stringent quarantine measures were enforced, and (b) the infested area constituted an island-like environment from which no escape was possible. More important, changes in the rate of generation increase were related solely to the changing density of fertile (i.e. non-sterilized) adults in the parent generations, ignoring any modifying effects that would accrue both from the addition of large numbers of sterile adults to the parent generation, and from the resultant changes in the density of the immature stages of the progeny. Although those oversimplifications would grossly reduce the predictive value of the general model in almost any specific instance, they do not affect the gist of the present argument to any extent that would warrant refining the mock-up at this stage.

4. COMPARATIVE PREDICTIONS

The predictions produced by Knipling's model before and after including the assumption of differential rates of increase can now be compared (see Table I).

Starting from an initial population of 1000 fertile adults, Knipling concludes that successive releases of 9000 sterile individuals at each generation would result in a probability of fertile mating of 1/10, 1/19, 1/69 and 1/900 for all females of generations P to F_3 respectively, and, thereby, in the loss of the population after 4 releases.

With the revised model, the actual progeny expected in generation F is estimated by multiplying the probable number of females actually fertilized in generation P by twice the rate of generation increase. In the present assumptions, the probable number of females actually fertilized in P equals the number of females produced in that generation multiplied by the proportion of fertile individuals in the total population of adults after sterile release, i.e.

$$N_1 = rN_0^2 \ / \ (N_0 + S)$$

where N_1 is the number of progeny, S is the number of sterile individuals (males and females) released, N_0 is the number of fertile adults (males and females) in P, and r is the rate of generation increase of a population at density N_0.

In the revised hypothesis, far from leading to extinction, the liberation of 9000 sterile adults per generation would actually allow the initial population of 1000 adults to increase until it reached a ceiling of 83 000 after

TABLE I. WORKING MODELS OF THE STERILE-RELEASE METHOD

CONSTANT RATE OF GENERATION INCREASE (=5, after Knipling, 1965)			DENSITY-RELATED RATE OF GENERATION INCREASE						
	ABUNDANCE OF FERTILE POPULATION(adults)		ABUNDANCE OF FERTILE POPULATION(adults)		OPTIMAL RELEASE PROCEDURE		Fertile population (adults) in the event of constant sterile releases per generation of:		
Generations	Natural increase	In the event of 9000 sterile adults released per generation	Natural increase	In the event of 9000 sterile adults released per generation	Sterile adults released per generation	Fertile population (adults)	20 000	100 000	400 500
Parent	1 000	1 000	1 000	1 000	38 494	1 000	1 000	1 000	1 000
F_1	5 000	500	20 000	2 000	24 339	506	952	198	0
F_2	25 000	132	60 000	4 000	9 342	256	876	0	
F_3	125 000	10	90 000	8 615	906	130	809		
F_4	125 000	0	94 500	22 124	202	69	715		
F_5			96 400	44 034	47	41	588		
F_6			97 800	69 100	11	25	411		
F_7			99 000	80 090		(19)	208		
F_8			100 000	82 079		(18)	28		
F_9			100 000	82 846		(16)	0		
F_{10}				82 948		(13)			
F_{11}				83 000		(8)			
F_{12}						(3)			
F_{13}						(0)			
				TOTAL RELEASED:	73 341		180 000	200 000	400 500

11 generations, at which it would become stabilized for as long as the releases continued unchanged. The repeated releases would act here, as it were, to increase "environmental resistance", i.e. to decrease the reproductive capacity of the population, and thus to make it more vulnerable to those subtractive influences in particular that operate with a time-lag (e.g. certain natural enemies). This suggests that sterile individuals exert primarily a 'conditioning influence' in the life systems of target populations, in the sense defined by Clark et al. [6].

In the assumption of density-related rates of generation increase, extermination would call for the release of much greater numbers of sterile adults than Knipling has envisaged. Even if the revised model were but slightly more representative of natural events than the original, it would suffice to show that assumptions which were almost entirely acceptable, yet ignored one essential demographic fact, could lead to major errors of judgement in the evaluation of control strategies.

5. INFERENCES

The predictions of the revised model suggest two possibilities that might have practical importance if they were confirmed and followed up in future work. Both concern the relative effect which each sterile individual released can exert on the demography of the target population.

First, an individual's effect could vary with the nature of the processes that governed the increase of a target population. It would tend to decrease as the mortality affecting immature progeny became limiting, because sterile mating would prevent more and more frequently the birth of surplus, expendable individuals. Practical efficacy would be greatest for sterile individuals released in sparse target colonies, whose low densities were already close to entailing dangerous under-population effects. This particular characteristic of the sterile-release method has been noted by authors.

More importantly, the demographic efficiency of sterile individuals could vary in direct relation to the actual rate of generation increase in the target population (in the present instance, with target density), in a manner that determined an optimum sterile : fertile ratio for each value of generation increase. Above and below that optimum ratio, the contribution of each released sterile individual towards reducing the expected progeny of the target would be smaller, and the overall effect achieved on the target correspondingly more costly in relative expenditure of sterile individuals. In the assumptions of the revised model, the relation is expressed as:

$$S = N(r - 1 + \sqrt{r(r - 1)})$$

where S is the optimum number of sterile individuals to be released, N is the number of fertile adults in the target population, and r is the corresponding rate of generation increase. The release of any numbers of sterile individuals different from S (yet sufficient to induce a decrease) would cause the following generation to be reduced at a greater cost in relative expenditure of sterile adults.

Consequently, the task of exterminating the original population of 1000 individuals postulated in the model could be accomplished at very

different costs in total numbers of sterile individuals released, according to whether that relation were considered or ignored. Theoretically, the target population could be annihilated with a minimum of 73 341 sterile individuals, if these were released over seven generations, according to the optimal schedule shown in Table I. These releases would depress the population to low densities from which it would not recover, entailing extinction after 6 further generations, during which the remnants of the population would reproduce below replacement rate. It is noteworthy that releasing constant contingents of 20 000 sterile individuals per generation would not accelerate extermination — in fact would be less efficient from the point of view of actual control — while requiring more than twice as many sterile units. Finally, extinction would necessitate far greater numbers still to be sterilized and released, if operations were to be completed in one or two generations only.

These findings are not definitive, and much work remains to be done before they can be generalized with assurance. No serious difficulties are anticipated in the process. In fact, the crude assumption of one obligatory mating per female adopted in the present model has been widened already with relative ease to consider two and more obligatory matings, and finally to include random mating regimes of any mean frequency, with any degree of dominance of fertile over sterile sperm. Similar improvements are readily conceivable to account for migration, various mortality structures, and density-related effects, both automatic and probabilistic. It might even be possible in time to construct a general matrix to describe the basic functions of the sterile-release strategy. This, together with other strategy matrices, could be designed to link up both with specific population models (e.g. describing the life systems of pests) and with ad hoc models to describe the working of current technological procedures relevant to each strategy. By integrating those three elements, complete strategy-evaluation systems would be obtained, which could be kept up to date at little cost, and made readily available for assessing or re-assessing particular situations at any time.

Such developments would help to promote pest control from a medley of empirical techniques to a scientifically conducted operation. They would depend primarily on the advances made in population biology, and on the readiness of specialists directly concerned with pest control to apply them.

Regarding the sterile-release strategy in particular, it is suggested that the feasibility of the method, i. e. its chances of accomplishing a stated objective and the probable cost of operations, cannot be evaluated with any assurance at all unless the ecological and demographic requirements of the enterprise have been appreciated in sufficient detail. No realistic assessment of prospects is possible before the expected rates of increase and the natural mortality structures of target populations have been determined over the range of relevant densities, allowing for seasonal fluctuations and paying particular attention to conditions obtaining at low levels of abundance. The general lack of such basic information might well constitute at present the greatest single obstacle to concerted progress in pest control.

6. CONCLUSIONS

Knipling's attempts at predicting the efficacy of the sterile-release method are criticized on the grounds that they do not invoke a functional model of population response in the target species. The probable consequences of this failure serve to illustrate in theory the critical part that a realistic conception of population dynamics should play in strategy evaluations. Strategies can only be properly assessed by reference to the ecological and demographic conditions by which injuriousness is initially determined, and to the changes required in those conditions for control to be achieved.

Predictive evaluation of control strategies must rest on realistic models of natural events. The reliability of predictive models depends in the first place on their ability to reproduce the critical features of a pest system, i.e. on the comprehensiveness of their structure rather than on the initial precision of input data. It is therefore important that strategy evaluation should be broadly based from the start, and even extend beyond biological considerations to include such wider issues as resources management and economics.

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THE ABILITY OF STERILIZED IRRADIATED MALES OF Dacus cucurbitae COQ. AND Dacus zonatus (SAUNDERS) TO COMPETE WITH NORMAL MALES

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Abstract

THE ABILITY OF STERILIZED IRRADIATED MALES OF Dacus cucurbitae COQ. AND Dacus zonatus (SAUNDERS) TO COMPETE WITH NORMAL MALES. A preliminary study was conducted to evaluate the competitive ability of normal versus gamma-irradiated males of Dacus cucurbitae Coq. and Dacus zonatus (Saunders). Five- to six-day-old pupae of both species were irradiated with 9 kR from a ^{60}Co source of 250 Ci. Both sexes of the emerging flies were completely sterilized and there was no apparent serious effect on either vigour or behaviour. When sterile males, normal males and females were caged in the laboratory at the ratio 5:1:1, no reproduction occurred. Field cage studies with D. cucurbitae indicated, however, that ratios greater than 9:1:1 would be necessary for complete cessation of reproduction.

1. INTRODUCTION

Among the most noxious insect pests are the tropical fruit flies, belonging to the family tephritidae (Diptera). This is a large family comprising some 4000 species distributed throughout the world. The losses caused by tropical fruit fly larvae as they feed and live in the fruit of host plants place these flies in the front rank of the world's foremost plant pests.

In West Pakistan, species belonging to three genera, Dacus, Myiopardalis and Carpomyia, attack almost all types of cultivated fruit and vegetables and are responsible for the greater part of the damage caused in the ripe and semi-ripe stages of their hosts. In the Hyderabad region of West Pakistan, Dacus species cause tremendous damage to fruits and vegetables. The losses caused by these fruit flies have not been estimated, but one can easily realize their extent by considering the following categories of losses:

1. Direct loss of fruits and vegetables.
2. Cost of chemical spray and extra labour involved in destroying the infested fruits and vegetables.
3. Loss of market value of the fruits.

The chemical means of controlling fruit flies have not proved to be very successful, and therefore alternative means of controlling the existing population of fruit flies without disturbing the natural fauna of parasites and predators are essential. The use of the sterile-male technique as a control measure seems to hold great promise.

The purpose of this paper is to determine the most suitable ratio of irradiated sterile males to normal males which could enable the sterile males

to compete successfully in mating with normal females, thus providing effective control of the fruit flies.

2. MATERIALS AND METHODS

The flies used in the experiments were obtained from the stock cultures maintained at the Entomology Laboratories of the Atomic Energy Agricultural Research Centre, Tandojam. The temperature and relative humidity of the rearing laboratory were maintained at 80°F ± 2 and 60% ± 5, respectively. The flies of both the species were made sterile by subjecting 5- to 6-day-old pupae to gamma rays from a 250-Ci cobalt-60 source at a dose of 9 kR. The dose rate at the time of irradiation was 560 R/min. The irradiated pupae were kept in moist sand (2% moisture) contained in petri dishes. After emergence male and female adult flies were confined in separate cages to avoid prior mating.

To study the competitive ability of sterilized males of Dacus cucurbitae Coq. and Dacus zonatus (Saunders) versus normal males under laboratory conditions, the normal males and females were caged (18 in × 18 in × 24 in) with the irradiated sterile males in different ratios. The flies were supplied with liquid as well as dry diet in separate containers. The eggs were collected from each treatment on pieces of gourd in the case of D. cucurbitae, and in lemon-shaped plastic juice dispensers in the case of D. zonatus. The eggs thus collected were checked for viability. These observations were recorded until all the flies died.

To determine the most suitable ratio of sterile to normal males of D. cucurbitae under field conditions, an experiment was also laid out in a cucurbit field. Five wire-gauze cages measuring 4 ft × 4 ft × 6 ft were used for this purpose. There were two to three creepers of long gourd (Langenaria vulgaris) in each cage. Five- to six-day-old pupae were irradiated at the sterilizing dose of 9 kR. After emergence the male flies were separated from the treated lot. Normal flies of the same age were also separated according to sex from the untreated lot. The flies were caged in different ratios, ranging from 0:1:1 to 9:1:1 (sterile males : normal males : normal females). Each cage was supplied daily with liquid as well as dry diet. For collection of eggs, fresh fruits, free from any active infestation, were placed in the cages and removed four days later. These fruit were then kept in wooden boxes containing sand, so that pupae could be recovered.

3. RESULTS

3.1. Laboratory studies on the ability of irradiated sterile males of D. cucurbitae and D. zonatus to compete with normal males

Sterile males, normal males and normal females of each species were caged as follows:

0:1:1 - 0 TR (treated)males: 10 UTR (untreated) males: 10 UTR (untreated) females;
5:1:1 - 50 TR males: 10 UTR males: 10 UTR females;
10:1:1 - 100 TR males: 10 UTR males: 10 UTR females;
15:1:1 - 150 TR males: 10 UTR males: 10 UTR females.

From Table I it can be seen that a ratio of 5:1:1 produced no pupae. However, a total number of 48 punctures were observed in gourd pieces kept to collect eggs. In control treatment the total number of punctures made was 173; 603 pupae were recovered. The percentage of adult emergence from these pupae was 94.5. At higher ratios, i.e. 10:1:1, 15:1:1, the number of punctures made was 54 and 86, respectively, but there no pupae were recovered. At the lower ratio of 1:1:1, 154 punctures were made and 470 pupae were recovered. The adult emergence from this treatment was 93.8%.

With D. zonatus (Table II) the total number of eggs laid in the 5:1:1 ratio was 419, and all were found non-viable. Similarly, at the ratios of 10:1:1 and 15:1:1 no fertile eggs were recovered. In the control cages a total of 1063 eggs was found with 74.4% hatch. At a ratio of 1:1:1 the total number of eggs collected was 601 with 52.6% hatch. The adult emergence in this case was 44.6%.

TABLE I. MATING COMPETITIVENESS IN LABORATORY CAGES OF GAMMA-STERILIZED MALES OF Dacus cucurbitae COQ. VERSUS NORMAL MALES

Ratio[a]	Total number of punctures made	Number of pupae recovered	Adult emergence (%)
0:1:1	173	603	94.5
1:1:1	164	470	93.8
5:1:1	48	0	-
10:1:1	54	0	-
15:1:1	86	0	-

[a] Sterile males : normal males : normal females.

TABLE II. MATING COMPETITIVENESS IN LABORATORY CAGES OF GAMMA-STERILIZED MALES OF Dacus zonatus (SAUNDERS) VERSUS NORMAL MALES

Ratio	Number of eggs laid	Number of eggs hatched	Eggs hatched (%)	Number of pupae recovered	Adult emergence (%)
0:1:1	1063	791	74.4	714	86
1:1:1	601	315	52.6	224	44.6
5:1:1	419	0	0	-	-
10:1:1	817	0	0	-	-
15:1:1	732	0	0	-	-

3.2. Competitive ability of irradiated sterile D. cucurbitae males versus normal males in field cages

The irradiated sterile males were caged with normal males and females in the following ratios:

0:1:1 0 TR (treated) males: 100 UTR (untreated) males: 100 UTR females;

3:1:1 300 TR males: 100 UTR males: 100 UTR females;
5:1:1 500 TR males: 100 UTR males: 100 UTR females;
7:1:1 700 TR males: 100 UTR males: 100 UTR females;
9:1:1 900 TR males: 100 UTR males: 100 UTR females.

From the data in Table III it is clear that as the ratio of sterilized males to normal males increases, the pupal recovery decreases. At the ratio of 9:1:1 only 29 pupae were recovered as compared with control, where 259 pupae were recovered.

TABLE III. MATING COMPETITIVENESS IN FIELD CAGES OF GAMMA-STERILIZED MALES OF Dacus cucurbitae COQ. VERSUS NORMAL MALES

Ratio[a]	Number of pupae recovered	Reduction in pupae produced (%)	Number of adults emerged	Reduction in adult emergence (%)	Adult emergence (%)
0:1:1	259	-	173	-	67
3:1:1	113	56	58	66	51
5:1:1	66	74	45	74	68
7:1:1	43	83	36	79	83
9:1:1	29	89	25	86	86

[a] Sterile males : normal males : normal females.

4. CONCLUSION

From the above results it is concluded that a ratio of 9:1:1 is quite promising for reducing the fruit fly population. The results obtained under laboratory conditions, where no hatching took place at a ratio of 5:1:1, seem to be misleading.

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ECOLOGY OF THE RICE STEM BORER, Tryporyza incertulas WALKER, IN WEST PAKISTAN
Preliminary studies

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Abstract

ECOLOGY OF THE RICE STEM BORER, Tryporyza incertulas WALKER, IN WEST PAKISTAN: PRELIMINARY STUDIES. There are at least three important species of rice borer in West Pakistan of which Tryporyza incertulas Wlk. is the most persistent and seems to occur only in rice. Of the different control measures practised in Pakistan, only repeated ploughing of the fields and pesticidal treatment seem to produce beneficial results.

Observations on the hibernating larvae showed that approximately 1.4 larvae per hill and 0.09 per tiller hibernated in 1965, while in 1967 the respective figures were 0.72 and 0.06. In 1965 the data indicated that the highest mortality of the hibernating borer occurred in hard soils which were left fallow, while maximum survival was observed in medium hard soils. On the analysis of data collected in 1967, it was found that medium hard soils in which additional winter crops were sown after shallow ploughing and which remained moist provided maximum protection to the borers. Hard and dry soils cause highest mortality of the borers especially when left fallow after ploughing. Larval mortality was high also in low-lying fields which remained very moist for extended periods.

In 1967, the emergence of moths from the hibernating larvae took place early in April due to unusual rains. All moths appeared to have emerged by the end of May. The highest catches of moths were obtained in the light traps immediately after the period of large diurnal variations of temperature.

1. INTRODUCTION

About 3.7 million acres of rice are grown in West Pakistan under canal irrigation. The rice is sown from May to June and harvested from August to November, depending on the climate and the rice variety. Several species of pest damage the rice crop. Lepidopterous borers, of which the yellow borer (Tryporyza incertulas Walker) is by far the most important, take the heaviest toll.

The Government of West Pakistan has recently entered into a contract with FAO/IAEA to study the ecology of T. incertulas, with the aim of introducing the sterile-male technique to control the pest. Work was started on this project in March, 1967, in the Lower Indus Basin Region, which is the main rice growing area of West Pakistan. Some studies were also carried out prior to March 1967 on the seasonal history of T. incertulas.

2. STEM BORERS

About five dozen species of insects have been recorded as damaging rice in Pakistan. Of these, about a dozen species are considered serious in West Pakistan and include the following species of lepidopterous borers:

Yellow Borer: Tryporyza incertulas Walker
White Borer: Tryporyza innotata Walker (? T. nivella F. = T. monostigma Zell or Scirpophaga ochroleuca Meyrick.)
Pink Borer: Sesamia inferens (Walker)
Striped Borer: Chilo suppressalis Walker

About 5 different names have been used for the white borer. However, it appears that two (or possibly only one) species are involved. The correct taxonomy has yet to be determined. Similarly, there seem to be more than one species of the striped borer. In addition to the above species, the rare occurrence of about half a dozen other borer species has been recorded.

The striped borer occurs in rice only rarely. The yellow borer is the most persistent, while the pink and white borers may be found in insignificant numbers or their occurrence may assume serious proportion in borer epidemic years. In such years it is not uncommon to find that, in certain fields or even in a certain small ecological zone, the pink or the white borer is causing much greater damage than the yellow borer.

Both the white and pink borers have many host plants, while the yellow borer is considered to be monophagous. The pink borer is active almost throughout the year in the region of the Lower Indus Basin whereas the white and yellow borers undergo varying periods of hibernation. In the case of the yellow stem borer, the hibernation period starts about 1 November and continues into the period of aestivation in summer (the middle of June).

The damage by the borers varies from about 2% to 10% in normal years to as much as 70% or more in different areas of this region in borer epidemic years.

3. YELLOW STEM BORER

The life history and biology of the yellow borer has been fully studied in West Pakistan, especially in the Lower Indus Basin. The life history of the insect is completed in about 30 days during the active season; during the long cycle, including the hibernation and aestivation period, the life history may take 5 to 8 months. The moths generally lay 300 to 400 eggs in about 3 to 4 egg masses. The eggs and larvae are parasitized by several species of hymenoptera.

Current control measures consist of ploughing to destroy the larvae in the stubble, application of light irrigation in the fields at the end of winter, submerging the young infested plants under water for a short duration, collection and destruction of egg masses, collection and destruction of 'dead-hearts', trapping the moths with light, changing the date of sowing, and treatment of both nursery plants and crop with pesticides.

In West Pakistan, repeated ploughing after the harvest of the crop, late sowing, use of light traps and chemical control of the pest have been used for many years. Only ploughing during winter and chemical control have shown any beneficial effect. It was therefore considered necessary to make detailed studies of the insect, especially the ecological aspects, with a view to determining the possibility of using the sterile-male technique to control this pest.

4. STUDIES OF THE ECOLOGY OF THE YELLOW STEM BORER

The working program of the project includes the following studies:

(1) Density of borer population in the stubble and crop, with details such as density of crop, cropping procedure, irrigation, etc.
(2) Time of first emergence of moths from the hibernating larvae.
(3) Seasonal history and population dynamics.
(4) Phenological events in discrete environments such as growth stages of paddy as related to growth stages of selected uncultivated perennial plants.
(5) Search for alternate hosts and their relationship to rice fields.
(6) Parasitization and predation.
(7) Records of maximum and minimum humidity and temperature of the laboratory and field where the studies are conducted and determination of cumulative day-degree temperature index.

Observations to date are discussed below.

4.1. Studies of hibernating larvae in rice stubble

Studies of the population of hibernating borers and their mortality in stubble, in fields representing different ecological conditions, were made in 1965 in seven different areas. The fields were separated from each other by a maximum of about 100 miles. In 1967 similar studies were performed, mainly within a radius of about 20 miles around the Rice Research Station, Dokri, and in two areas situated about 60-70 miles away from Dokri.

In both years, the effects of soil moisture (dry soils versus moist soils), soil texture (hard soils versus medium hard soils), and agricultural practices (ploughed fallow, unploughed fallow, unploughed under 'dubari' and ploughed under 'dubari') were studied. Besides these, other factors such as level of soil and harvesting were also considered, but too few samples were taken for conclusive results to be obtained. Ten to 20 stubbles were examined in each field. The tillers were dissected to observe the numbers of living and dead larvae inside the remains of the stems. Soil humidity and temperatures could not be recorded because of non-availability of proper instruments and hence it is not possible at this stage to correlate the data with the prevailing micro-climatic factors. Efforts are being made to obtain these instruments. It is proposed that these factors be studied in selected fields from the beginning of the hibernating stage. Observations so far made on the effect of different factors on the survival of hibernating larvae during the years 1965 and 1967 are presented in Table I.

In 1965, 1.4 larvae hibernated per stubble and 0.09 larvae per tiller. The table indicates that medium hard soil which remains moist favours the survival of the insect. It is also indicated that the highest mortality of the borer should be expected in fields with hard soil which are left fallow.

In 1967 (Table II) approximately 0.72 larvae hibernated per stubble as against 1.4 in 1965 and 0.06 per tiller as against 0.09 in 1965.

The work in 1967 was started at the end of March following heavy rains in the middle of the month. Moisture was thus plentiful in all the fields.

TABLE I. DATA OBTAINED IN 1965 FROM STUDIES OF THE EFFECT OF SOIL AND MOISTURE FACTORS ON HIBERNATING LARVAE OF T. incertulas

Factors	Number of stubbles examined	Total number of tillers	Larvae recovered		
			Total number	Per cent dead	Total number per tiller
Dry soil	683	11192	993	85.0	0.09
Moist soil	278	3897	447	79.8	0.11
Dubari (2nd crop raised)	363	5310	402	86.6	0.08
Fallow (no 2nd crop)	392	6221	443	93.4	0.07
Hard soil	446	7746	593	92.9	0.08
Medium hard soil	373	5543	605	68.7	0.11

TABLE II. DATA OBTAINED IN 1967 FROM STUDIES OF THE EFFECT OF SOIL AND MOISTURE FACTORS ON HIBERNATING LARVAE OF T. incertulas

Factors	Number of stubbles examined	Total number of tillers	Total number	Percent dead	Total number per tiller
Hard soil	1464	14095	1114	73.0	0.07
Medium hard soil	490	5328	342	55.9	0.05
Dry soil	971	11024	685	93.1	0.06
Moist soil	303	3451	220	73.1	0.06
Dubari unploughed	260	2935	129	44.9	0.05
Dubari ploughed	1101	12342	753	87.4	0.06
Fallow ploughed	320	3920	336	87.7	0.08
Fallow unploughed	324	3981	258	72.2	0.06
Low-lying fields	128	1918	47	78.7	0.03

Nevertheless there was a marked difference in mortality percentage between the larvae in the dry and moist fields.

Maximum survival of hibernating larvae was found in fields in which 'dubari' crop was raised without ploughing. Next came the fields with soils of medium hardness. Minimum survival was found in fields with dry soils, followed by ploughed lands left fallow and those with dubari crop. The mortality was 93.1%, 87.7% and 87.4 %, respectively. In the low-lying fields which remained wet during the winter and contained excessive moisture in April and May, the mortality of the borer was high.

When the samples were taken from the fields, they represented the resultant effect of a combination of different factors. The data of 1967 were therefore analysed to determine the effect of the combination of these factors on the survival of the larvae (Table III).

Since the sample size representing the factor of soil hardness in the unploughed fields with dubari crop was very small, mortality figures have not been shown for combinations 7, 8, 9 and 16 in Table III. From the combinations analysed, the lowest mortality of 41.7% was found in the fields in which a second crop had been raised after ploughing and the soil was moist and of medium hardness. The other combinations which gave 53.8%, 54.2% and 55.5% mortality were, respectively, hard and moist soils which were left fallow after ploughing, medium hard soil with moisture in which dubari crop was sown without ploughing, and hard and moist soils in which dubari crop was sown after ploughing.

TABLE III. EFFECT OF THE COMBINATION OF FACTORS ON THE SURVIVAL OF LARVAE, 1967

Factors	Mortality (%)
1. Ploughed 'dubari', medium hard and moist soil	41.7
2. Ploughed 'dubari', hard and moist soil	55.5
3. Ploughed 'dubari', hard and dry soil	88.2
4. Ploughed 'dubari', medium hard and dry soil	74.8
5. Unploughed 'dubari', medium hard and moist soil	54.2
6. Unploughed 'dubari', hard and moist soil	82.6
7. Unploughed 'dubari', hard and dry soil	--
8. Unploughed 'dubari', medium hard and dry soil	--
9. Fallow unploughed medium hard and moist soil	--
10. Fallow unploughed hard and moist soil	63.7
11. Fallow unploughed medium hard and dry soil	62.3
12. Fallow unploughed hard and dry soil	76.7
13. Fallow ploughed hard and dry soil	95.7
14. Fallow ploughed hard and moist soil	53.8
15. Fallow ploughed medium hard and dry soil	69.9
16. Fallow ploughed medium hard and moist soil	--

TABLE IV. LIGHT TRAP CAPTURE OF T. incertulas, 1967

Date	Number of moths trapped	Temperature (degF)				Relative humidity (%)			Rainfall (in)
		Mean maximum	Mean minimum	Highest maximum	Lowest minimum	Highest	Lowest	Mean	
22.3 to 31.3	0	64	63	68	58	84	74	80	0.74
1.4 to 10.4	27	89	52	99	58	82	54	68	0
11.4 to 20.4	128	100	68	103	60	80	44	61	0
21.4 to 30.4	17	90	66	106	51	90	51	55	0.3
1.5 to 10.5	108	101	69	104	66	51	30	42	0
11.5 to 20.5	97	110	73	113	72	49	35	37	0
21.5 to 31.5	6	108	77	118	70	36	63	47	0

4.2. Emergence pattern of Tryporyza incertulas

To estimate the emergence pattern of T. incertulas adults, an electric light trap was operated at Dokri from March through July in an area surrounded by rice fields. The trap was operated for two hours, starting half an hour after sunset. The first emergence of moths was observed on 2 April 1967. The emergence continued through 31 May (at Dokri), after which no moth was trapped (Table IV).

It appears from the data in Table IV that the emergence of moths was higher when the maximum temperatures climbed rapidly and there is a noticeable difference between the maxima and minima. Factors such as moonlight, presence of electric lights in the neighbourhood, wind velocity and storms were not considered. Efforts are being made to find other suitable locations where bright street lights are not present. All the other factors will then be considered in evaluating light trap catches.

4.3. Seasonal history and population dynamics

Because of the unusual rains at the end of March and during April 1967, and the early increase of humidity, there was abundant emergence of the moths from April to the third week in May (Table IV). In the nursery plots sown at Dokri for the training of extension workers in April, the population of egg clusters averaged 1.9 to 2.2 per tiller.

At Kamber (about 25 miles from Dokri) a crop of Bidri (a short-duration, 70-day variety of rice) was found infested by T. incertulas larvae. This rice had been sown on 1-5-67 and transplanted on 1-6-67. The infestation recorded in certain patches reached 14.0 % of the tillers on 14-7-67. Average population of the borer per square foot was found to be 1.43. The insect completed its first generation on this crop on 20-7-67 when the rice plants had just started flowering. No eggs were laid by these moths by 21-7-67. In an adjacent field, Bidri variety sown on 28-5-67 and transplanted on 4-6-67 was totally free from borer attack on 21-7-67. This rice had not started flowering. Moths emerging from the adjacent crops were found resting on this crop, but had not laid eggs by 21-7-67.

At Mirokhan (15 miles from Kamber), moths were neither collected in light traps nor observed in fields up to 21-7-67.

4.4. Effect of environmental factors on population build-up

General surveys were made of the incidence of borer attack on rice crops in the Jacobabad and Larkana districts in September 1966. The attack in the Jacobabad district generally ranged between 30% and 40% with a number of fields much higher. In the Larkana district it varied from 2% to 8%. To determine the cause of this difference in the intensity of attack of T. incertulas in these two areas, meteorological data for both the areas were collected (Table V and Fig. 1). Humidity records could not be collected.

Ordinarily, winters are very dry in Jacobabad, the relative humidity often falling below 30%. During the winter of 1965-66 the rains at Jacobabad from December to April probably provided sufficient moisture to the hibernating larvae to decrease their mortality. In Larkana, the total precipitation in two days, i.e. 11-2-67 and 2-3-66, was higher than that in

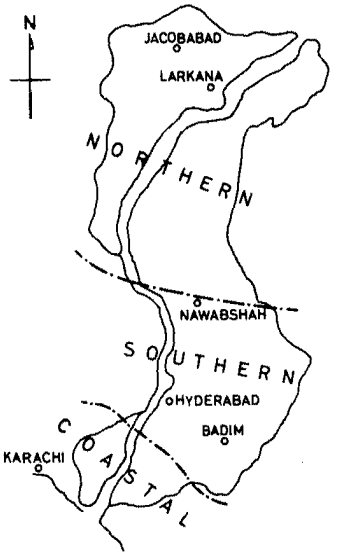
TABLE V. TEMPERATURE AND RAINFALL RECORDS OF JACOBABAD AND LARKANA

Months		Temperature (degF)				Rainfall (in)
		Mean maximum	Mean minimum	Highest maximum	Lowest minimum	
			Jacobabad			
October	1965	100	70	107	77	0.0
November	1965	89	60	100	51	0.0
December	1965	75	45	79	37	0.02
January	1966	78	46	83	42	0.02
February	1966	76	53	90	45	0.04
March	1966	90	61	100	51	0.05
April	1966	100	70	112	60	0.1
			Larkana			
October	1965	88	83	101	58	0.0
November	1965	86	69	93	49	0.0
December	1965	76	43	82	33	0.0
January	1966	77	43	82	40	0.0
February	1966	74	52	87	45	0.22
March	1966	80	49	101	43	0.17
April	1966	96	65	107	51	0.0

Jacobabad spread over five days. Since the temperature had risen by the time the rains came in Larkana, it is possible that moth emergence took place early there when there were no rice plants on which to lay eggs. This fact might have contributed to low borer infestation in the rice crop sown later. In Jacobabad, enough moths probably emerged when rice plants were available for oviposition to result in severe infestation. Other factors worth considering for Jacobabad are that the fields are not ploughed in winter, and the rice seed is directly broadcast in the field. A cleaner picture should be obtained when humidity records of the two places are available.

4.5. Correlation of the growth stages of paddy, uncultivated perennial plants, and borer population

Work on correlation is being carried out at Dokri, Kamber and Mirokhan in the district of Larkana. At Dokri 50 plants of 5 different varieties (Kangni-27, IR-8, Banglao, Sunari Kangni and Dokri Baspati) have been tagged for observation. Furthermore, the weeds present in the



	COASTAL	SOUTHERN	NORTHERN
Rainfall (in inches)	7-8	5-10	3-5
Rainstorms	Large in area.	Large in area	Small in area
Temperature (deg F)			
Mean summer maximum	95	100-105	110
Maximum recorded	115	122	127
Mean winter minimum	50	45-50	40-45
Minimum recorded	35	30	25
Frost	Unlikely	Possible	Likely
Mean relative humidity	%		
Summer	80	70	60
Winter	50	40	30
Wind-summer			
Direction	W to SW	SW to S	S to SE
Force	Fresh	Light to fresh	Light
Cloud cover - tenths			
Summer	3-7	1-6	0-3
Winter	1-3	0-2	0-3
Annual evaporation (in)	60-80	80	70-80

FIG. 1. Climate of the region (summary).

paddy fields have also been tagged for possible correlation of their growth stages to the paddy crop. The weeds tagged at Dokri and other places are Kal (Cyperus iria), Kabah (Cyperus rotendus), Gandheer (Elusine flagellifera), and Sawari (Echinocoloa colonum).

At Kamber and Mirokhan 30 plants each of the Bidri and Kangni-27 varieties have been tagged for similar studies. In all three locations, records are being taken, including the number of irrigations applied both before and after sowing and transplanting, cultural operations, fertilizer doses, etc. The observations are recorded by measuring the height and girth of the plant, number of tillers, length of first internode, and percentage of non-productive tillers in order to determine the duration of the following stages of different varieties exposed to varying environments:

(1) Active vegetative phase (from transplanting to the maximum tiller stage).
(2) Reproductive phase (from the maximum tiller stage to the panicle initiation stage).
(3) Reproductive phase (from the panicle initiation stage to the flowering stage).
(4) Ripening phase (from flowering to full maturity).

Observations on weeds record the height of the plants, number of tillers/branches, date of flowering and date of seeding.

Five promising uncultivated perennial weeds selected in June 1967 achieve good height and grow outside the paddy fields under different moisture conditions. The local cultivators have already made certain observations on the growth stages of these plants, which they correlate

with the changes in atmospheric humidity and temperature. These plants are:

1. Pun (Typha elephantiana)
2. Kanh (Saccharum spp.)
3. Kooro Sar (Saccharum spp.)
4. Sacha Sar (Saccharum spp.)
5. Kangore (Saccharum spp.)

The above five weeds are said to have a definite period for flowering and grow in abundance in the region.

4.6. Alternate hosts and natural enemies

No alternate host of T. incertulas has so far been recorded. Eggs of T. incertulas are normally parasitized in the field by Trichogramma sp. No egg parasites were recorded during the studies in 1966 and 1967. It has been observed at Dokri that dragon flies prey on the moths of T. incertulas and an undetermined species of mite preys on its egg clusters. While the density of the borer population in stubble in April and May 1967 was being studied, 17.2% to 20.0% of the hibernating larvae were found to be parasitized. Further studies on the insect's natural enemies are continuing.

4.7. Laboratory studies

Since the borer was not found in the field, methods of rearing the insect were studied. However, difficulty was experienced in procuring several chemicals for preparing the artificial media for rearing.

METHODS OF ESTIMATING THE SIZE OF POPULATIONS OF CODLING MOTHS, Carpocapsa pomonella (L.), FOR STERILE-MOTH RELEASE PROGRAMS

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Abstract

METHODS OF ESTIMATING THE SIZE OF POPULATIONS OF CODLING MOTHS, Carpocapsa pomonella (L.), FOR STERILE-MOTH RELEASE PROGRAMS. The United States Department of Agriculture at Yakima, Washington, and the Canadian Department of Agriculture at Summerland, British Columbia, are currently releasing gamma-irradiated codling moths, Carpocapsa pomonella (L.), in semi-isolated orchards. The following methods have been used to estimate size of the native populations of codling moths as a basis for determining the release rate of sterile males necessary for effective control:

(1) The rate of emergence of native moths is estimated on the basis of prevailing temperatures, numbers of moths captured in traps, and rate of emergence of diapausing larvae in screen cages.

(2) The total population entering diapause is estimated by examining all cull fruit at harvest for the number of exit holes and of nearly mature live larvae.

(3) The ratio of sterile : native males captured in traps is used to estimate the fluctuating abundance of native moths.

(4) The number of natives captured in relation to the number of moths released gives a useful estimate of the size of the native spring-brood population.

1. INTRODUCTION

Research on codling moth control by release of sterile codling moths has been in progress at Summerland, British Columbia, Canada, for the past 11 years and at Yakima, Washington, United States of America, for the past 6 years. Results of this research have been promising. In 1967 the Canadians controlled codling moths in a 4- to 6-hectare apple orchard and the Americans controlled moths in a 37-hectare apple orchard by releasing sterile moths of both sexes. An accurate estimate of the size of native populations and of population dynamics of the codling moth is necessary to conduct a successful release program.

2. BEHAVIOUR OF THE CODLING MOTH

Under natural conditions, the size of the maximum codling moth population is determined by the availability of food and pupation sites [1]. In commercial orchards, codling moth populations have been reduced to very low levels by pesticides. The distribution throughout the orchard is determined by the flight range of the moths. Marked, sterilized codling moths have been caught in Washington 4.8 km from their point of release in traps baited with live females [2]. In Indiana, 847 flight records were made for marked, normal moths released in orchards baited with fermenting sugar solutions plus oil of sassafras or bromostyrol. For this test, the distance from the point of release to the recovery point, in areas where such a trap was located in nearly every tree, averaged 61 m compared with maximum flights of from 287 to 634 m recorded for a 5-year study [3]. The longest flights in Indiana were made by moths that left the trapped orchards and flew to traps in other orchards. Probably many flights were made to untrapped orchards at greater distances.

Since most moths that do not leave the orchard fly a short distance, infestations occur in pockets. These pockets not only make population estimations difficult, but also complicate release programs. When moths are released at a uniform rate, those released in the non-infested areas of the orchard are wasted, while the number released in the infested pockets may not be sufficient to overflood the native population.

The codling moth becomes sexually mature soon after emergence and in the laboratory is capable of mating within 12 hours. Maximum frequency of mating occurs by the 4th day, and most females have completed oviposition by the 6th day [4]. Thus, little time is available for the dispersion of released moths and more timely releases are required than with other insects.

The short life of the moth (about 14 days or less in the summer) means that rates of release must be carefully controlled and that sound estimates of maximum rates of emergence of mature moths must be made on an almost day-by-day basis.

At Summerland, B. C. [5], the rate of emergence of native moths was estimated by reference to prevailing temperatures in the orchard, the number of moths captured in light traps and in traps baited with females in neighbouring orchards, and the rate of emergence in screen cages where known numbers of diapausing larvae had been placed the previous autumn. Attempts were then made to adjust the rate of release to fit the fluctuating abundance of native moths.

3. METHODS OF ESTIMATING THE SIZE OF POPULATIONS

3.1. Examination of cull fruit

A convenient method of estimating the size of codling moth populations in commercial orchards is to examine cull fruit at the packing sheds. The cull fruit is a small part of the total production but should include all fruit that is or has been attacked by codling moth.

This method has several weaknesses in estimating overwintering populations. It does not account for winter mortality. Overwintering larvae

may be killed by pesticide residues at pupation sites in sprayed orchards or by predators and parasites in unsprayed orchards. Newcomer [6] reported the following mortality for moths exposed to cold in orchards:

Minimum temperature (degC)	Mortality (%)
-26 to -29	78 to 80
-29 to -32	80 to 90
-32 and lower	100

There was little mortality below the snow line. All larvae below the snow survived.

At the time of examination of cull fruit, it is often difficult to determine if damaged apples have been attacked by first- or second-brood larvae. In addition, some first-brood larvae diapause.

3.2. Search for overwintering larvae

Larvae overwinter in a great variety of places where numbers cannot be estimated, i.e. pruning logs, packing sheds, and storage boxes. However, in such situations they can be destroyed. Most larvae that will provide the next year's infestation spend the winter on the trees or in the ground underneath. Generally, the numbers of these larvae are unknown because of the labour required to make a detailed examination of trees and ground and because of the variability among trees. In southern Indiana, during an 8-year period, 83 native apple trees that were considered representative of average conditions in the Middle West were searched for hibernating larvae. Of the surviving larvae, 75% were in twigs, crevices, cavities, and under bark. The range was 35 to 100%. Of the mean 25% on the ground, 67% were within 6 ft of the trunk, generally in bits of wood or weed stems [7]. If examinations are made in late autumn or early winter, larvae that will not survive the winter will be counted. Counts of overwintering larvae on trees chosen at random in an abandoned orchard near Yakima, Washington were:

Month	Number of trees examined	Average number of larvae/tree
December	10	78.2
March	10	24.6
May	5	16.4

Parasitization can often be determined in diapausing larvae.

3.3. Release and capture

Total populations and population changes may be estimated by the ratio of released to native moths caught in blacklight traps or in traps baited with live virgin females or extracts of female codling moth.

The trap used with live females at both Summerland and Yakima is a screened cage containing about 10 virgin females suspended inside a 1.9- to 3.8-litre paper can with an opening at each end; the inside is coated with a sticky substance. Its efficiency is greater when it is baited with live females than when it is baited with extracts from virgin females. Traps baited with

females at Summerland and set 183 m from the orchard caught both sterile and native moths; 6 other traps baited with females caught moths believed to have come from commercial orchards 8.05 m away [5].

The response of both reared and wild male moths to the traps baited with live females was identical [8]. However, recent observations [2] indicate that traps baited with laboratory-reared females caught more males than traps baited with wild females and that the effectiveness of the traps baited with live females is greater than that of traps equipped with black-light lamps during spring-brood emergence but less than that of the light traps in late summer.

At Summerland, traps containing a 15-W blacklight lamp were several times as attractive as traps containing a 5-W lamp [9]. In a large experiment in Indiana [10], 32% of the released moths were recaptured in traps equipped with electrocuting-type grids or baffles that had been placed around lamps emitting light in the near ultra-violet range. The area contained 216 traps, 1 per tree or missing-tree space. Those in trees captured an average of 175 moths during the season compared with 5 captured per trap placed in missing-tree spaces 10.7 m from trees. These latter traps attracted most moths within two days after emergence.

As already mentioned, at Yakima and at Summerland total exits from culls are estimated at the packing house during harvest. By using this method in 1965-66, the probable surviving overwintering population was estimated to be 2.4 moths per tree; the estimate of the spring-brood population obtained from sterile release and capture data indicated the population was 5 moths per tree [2].

3.4. Knockdown of moths

Another method has been used in the Midwest to obtain a census of populations on any day from well-distributed single trees. Nicotine alkaloid is metered into the hot exhaust of an orchard duster and from there into the blower outlet, and these fumes are directed quickly into all parts of a tree. Since nearly all moths in the tree are knocked down within 15 minutes, they could be collected from canvas or plastic sheets placed under the tree before treatment. In this method, the foliage must be dry to keep the moths from sticking to wet areas, and variability in populations of single trees and the number of sample trees needed can also be determined.

The method avoids possible differences in the response of moths from different sources for the traps. Also, since it includes only the moths in the treated tree, absolute estimates of the size of the population are possible. The method could be used to determine the efficiency of traps in exhausting populations in baited trees, and, on the day of treatment, it would reduce the overall population proportional to the percentage of available trees that were sampled (most sampling methods have this effect).

3.5. Infestation of fruit on trees

In Yakima, Washington, and Summerland, B.C., population estimations based on counts of infested fruit on trees were found inaccurate. Even when the workers examine the fruit from ladders and by climbing into the trees, many entries are overlooked. Codling moth larvae often enter the apple where it touches a leaf, branch or other fruit. Even when not obscured, a new entry is difficult to observe.

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METHODS OF ESTIMATING THE SIZE OF POPULATIONS OF STERILE PEST TEPHRITIDAE IN RELEASE PROGRAMS

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Abstract

METHODS OF ESTIMATING THE SIZE OF POPULATIONS OF STERILE PEST TEPHRITIDAE IN RELEASE PROGRAMS. The ecology of such tephritids as the Mediterranean fruit fly, Ceratitis capitata (Wiedemann), the oriental fruit fly, Dacus dorsalis Hendel, and the melon fly, D. cucurbitae Coquillett, prevents accurate estimates of the size of total populations. Among the most important of these biotic factors are the sensitivity of the three species to environmental changes that affect longevity, the ability of the insects to move long distances and to multiply rapidly, and the ease with which they find new host sites as needed.

Expected sizes of populations can be estimated from previous trap records and from release-recovery data if the sterile-insect release program is to involve temporary suppression in semi-isolated localities where small but concentrated areas of high-value crops exist. The same methods may be used when the program is intended to eradicate an incipient outbreak if the infested zone is surrounded by a fly-free area. In addition, in such isolated regions the marked sterile : wild ratio of flies obtained in male lure traps will indicate the rate of release required and the progress in eradication.

However, for large eradication programs involving a long established infestation, a survey of at least a year should be made to estimate requirements. The preferred method for such an estimate is use of male lure traps containing trimedlure, methyl eugenol, or cue-lure. (These synthetic lures are far more uniformly efficient in attracting male flies than the most attractive liquid baits.) The catches per trap per day of non-competitive males in representative sample areas can then be multiplied by a factor that approximates the minimum number of traps required per square mile to attract all male flies before they become sexually mature. (The factor represents a hypothetical situation in which there is no competition between traps and no part of the square mile is unexposed to an effective concentration of lure.) This factor is first multiplied by 2 to correct for females released but not caught in the non-competitive traps; then the sum is multiplied by the catch per trap day and by the square miles of an area surveyed. The resulting figure is the daily natality for the total area.

Another factor, based on release-recovery data, that compensates for the high rate of loss occurring in fruit fly release programs is used to estimate the required release rate. With this method, the data obtained during the year or more of pretreatment surveys can be used to estimate the number of sterile flies needed and the best time for starting releases. Also, the trap catches made during the few weeks immediately before the start of the program permit reasonably accurate estimates of the ratio of sterile to wild flies that can be anticipated from a given release rate. Subsequently, the ratio of marked sterile and wild flies captured can be used to make any adjustments needed.

1. INTRODUCTION

Practical means of estimating the size of native fly populations and the necessary rates of release of sterile-male flies are necessary if the method of sterile-insect release is to be used for suppression of a tephritid species. However, exact figures cannot be provided at any given time and may never be available. Each worker in each area will need to

modify any method to fit his specific needs. The recent book by Southwood [1] will be helpful to most investigators.

This discussion is based on information (much of it unpublished) developed by the author with the help of many associates and reflects the research done and the results obtained during the past 18 years at the Hawaii Fruit Fly Investigations' Laboratory of the US Department of Agriculture. The discussion will thus be concerned mostly with the three tephritid species we have in Hawaii, the Mediterranean fruit fly (Medfly), Ceratitis capitata (Wiedemann), the melon fly, Dacus cucurbitae Coquillett, and the oriental fruit fly, D. dorsalis Hendel. These species were involved in the first three successful applications of the sterile-insect release method to fruit fly control [2-4].

2. TYPES OF RELEASE PROGRAM

Methods of estimating population sizes are needed in the following three types of sterile-fly release program:

A. A program involving temporary suppression in unisolated areas where sufficient pressure by sterile flies can be maintained on both the native and immigrant populations to prevent economic damage.

Many relatively small areas exist where fruit production is concentrated and valuable enough to justify annual suppression or temporary eradication. For example, in Hawaii we were able to suppress 90% of the Medfly damage for 6 months in a 12-square-mile area by releasing 1/2 million flies weekly [4]. At current rates, the cost of 1 million Medflies is less than $20.00 [2] when a production and irradiation facility is available. In such localities, the numbers needed for release could be estimated each season by making use of the ratio of marked and sterile to wild flies caught in male lure traps (to be discussed later).

B. A program involving incipient outbreaks in new areas where the infestation can be delimited and where quick eradication is necessary.

Some sites of incipient outbreaks have zero infestation in the surrounding areas; however, such outbreaks expand rapidly unless they are checked. We use appropriate sprays for a short time, and then populations of sterile flies are built up.

Again, male lure survey traps will give an estimated ratio of the sterile-to-wild flies and will also provide information on the progress of the release program and the end point. No time will be available and no need will exist to estimate the initial abundance of wild flies.

C. A program involving eradication of long-established infestations in isolated areas that can be protected from reinfestation.

In isolated sites with long-established infestations, ample time is available and should be used for estimating populations. Surveys should be made to determine fluctuations at least one year ahead of any program. Male lure traps are probably most useful for this purpose.

3. FRUIT FLY BEHAVIOUR AND ECOLOGY AFFECTING METHODS OF ESTIMATING POPULATIONS

Populations of fruit flies are seldom static, and those species that do not enter diapause for part of the year may produce a generation each month.

On Rota, Marianas Island [5], the abundance of oriental fruit flies during 1960-62 inclusive, measured by the mean daily trap catches, ranged from 14 in April to 427 in October, an average two-fold increase each month for 5 months. Additional sudden increases also often occurred with the advent of the rainy season in June. Because of the rains, increased cloudiness, and rapid growth of foliage previously thinned by drought, the high internal temperatures of the growing host fruit (sometimes 44°C), which had been killing a large proportion of eggs and larvae, returned to near ambient levels. In contrast, in Central America infestations of Medflies and catches in traps in the rainy season decline for unknown reasons.

In either case, if the stresses that cause changes in population apply mostly to the immature stages, the overflooding ratios of sterile flies obtained with a given rate of release should increase rapidly. However, the high biotic potential of most tephritidae when the adult flies can find diets that are high in essential amino acids can also induce rapid changes in population. These sharp increases, unless they are anticipated, can nullify sterile release programs. Moreover, the magnitude of these increases, even if they are anticipated, cannot be estimated accurately.

Probably the ability of tephritid species to disperse, to find and concentrate on hosts, and to move from one crop area to another when they are stimulated by a host type or abundance is the factor of major importance in population fluctuations. In Hawaii, isotope-labelled flies of the three species that were allowed to emerge in favoured feeding areas were found in traps 20-25 miles downwind after over-water flights of at least 12 miles. Marked oriental fruit flies spread over more than 100 square miles of the surrounding terrain after emerging among fruiting guavas (a preferred host). Marked sterile melon flies were captured 45 miles from their release points on Guam and Rota after inter-island flights (probably assisted by wind) over about 40 miles of ocean [4], and sterile and wild melon flies of both sexes congregated in scattered host areas on Rota, many before they were sexually mature [3] and before the crop had produced fruit (which made the species vulnerable to special control measures but increased the variability in population density over the 33-square-mile island). With the oriental fruit fly, because its hosts were widely scattered, wind movement was the dominant dispersing influence. Populations in the leeward parts of the island were four times greater than those to windward during the months when the north-east tradewinds were dominant, but they became evenly distributed soon after the rainy season started when wind direction became more variable. (In each of the three species, the female is attracted to the immediate vicinity of the male, but until sexual maturity this response appears to be dominated by the need to find fruiting hosts. Movement after maturity is less extensive.)

If the ability of the three species to disperse and to find hosts makes accurate estimates of population size difficult, most fruit fly species do have one helpful characteristic – the several days that occur between

emergence and sexual maturity. This period obviates the need to disperse treated flies manually; released flies have time to find the wild populations by locating and moving to the host areas.

Estimates of the longevity of released sterile flies can be made by periodic release-recapture tests. These are necessary to supplement density estimates. Differences in the longevity of wild and released flies affect the necessary rates of release and the efficiency of the released flies. Native flies emerge in scattered locations, and their abundance seldom taxes the local environment for essential nutrients. In contrast, sterile flies released from containers dropped from the air or from emergence cages on the ground compete strongly with each other for available food and may be forced to disperse to find it or to die [2]. Greatly reduced longevity thus occurs when food is short to the extent of reducing the lifespan to little more than the length of the sexually immature period. Overflooding ratios could thus be high and the sterile flies could be relatively ineffective.

Another difficulty in estimating population size arises because the hosts frequently receive more eggs (usually during a period of declining abundance) than they can support as larvae. Thus even when substantial sterility has been induced in the population, fruit infestation is not reduced because the host can support only part of the larvae that hatch and the hatch rate is adequate to fill the fruit. Laboratory personnel have recorded infestations (larvae per pound) of 300 and 1300 Medflies in peach and Jerusalem-cherry (Solanum pseudocapsicum L.), respectively, of 1500 oriental fruit fly larvae in breadfruit, of 1000 mixed species in tropical almond, and of several hundred melon flies in young cantaloupe, watermelon, or squash. With such crowded conditions, the flies are usually small. Given such a situation, a sudden increase in abundance of the host could cause an explosive and unpredictable increase in flies.

Because of the ecological factors discussed, the total (absolute) size of adult fruit fly populations can hardly be estimated with accuracy or sufficient speed to be useful, except with efficient traps.

4. MANIPULATION OF FRUIT FLY POPULATIONS

Sometimes a species, because of the distribution of its host, becomes concentrated in a small proportion of a total area. If population estimation methods can reveal such a situation, then this species is vulnerable to partial control. For example, concentrated protein hydrolysate-malathion bait sprays applied to 25 small farm plots on Rota throughout the time of emergence of one brood [3] reduced the populations of melon flies over the 33 square miles by about 65%. Such sprays have little residual effectiveness, but they attract and kill all existing adults in the area if they are timed to prevent attainment of sexual maturity and if they are continued until the current immature generation emerges. The residual population was thus limited to transient flies and to those able to find the inaccessible hosts. Again the information obtainable from an appropriate trapping program would be most useful.

5. METHODS OF ESTIMATING THE SIZE OF FRUIT FLY POPULATIONS

To determine the rates of release required to overflood an area with sterile males, researchers need estimates of the total population before the releases start and estimates of the ratio of sterile to wild flies present during a period of stable abundance of wild flies after the releases have been under way long enough for the mortality rate of the released sterile flies to equal the rate of addition. These estimates must be in terms of numbers per unit of area and number of areas to be treated. When these data are used (except in very small areas), some allowance must be made for errors and for unexpected changes in rates of increase. Indeed, more extensive sampling to obtain better representation may be a less costly method of improving reliability of the estimate than increasing the precision in limited intensive sampling. This general observation applies particularly to fruit flies because of the mobility of their adult stage, because of the importance of the adults in sterile-fly release programs (they represent the functional survivors of the egg and larval populations in host fruits), and because this stage is the one to be overflooded by sterile flies. Since the movements and changes in abundance of adult flies can best be followed by using traps, a sound trapping program is superior to fruit infestation records, to netting or visual on-site counts of adults, to fumigation, to knockdown sprays applied to sample trees for instant counts, or to capture-mark-release and recapture methods as a method of estimating a population.

In semi-isolated areas where eradication is not possible, estimates based on infestation records may be useful because of the small size of the area and the availability of records of host production and infestation (including the effectiveness of parasites and predators). However, estimates based on translating infestation data into numbers of adults are likely to be less correct than estimates obtained by trapping adults. For example, the ratio of sterile to normal eggs oviposited was helpful in determining when to end a sterile-melon-fly release program on Rota since the old females continued to deposit infertile eggs long after the last trapped native males could be differentiated from sterile males [3]. In this test, cucumbers and newly set pumpkin, squash, and cantaloupe (all attractive hosts of the melon fly) were especially useful because the differential rate of growth at and around the oviposition site soon made the site conspicuous. If fruit samples were held more than 36 hours, the hatch of fertile eggs was assured, after which careful dissection of the puncture revealed the number of fertile and infertile eggs deposited.

The abundance of sterile females provided in a release program and the low efficiency of liquid baits as attractants for females make the use of trapped live females for checks on fertility impractical. Also, rates of survival of eggs and young larvae cannot be forecast with accuracy. In addition, large samples of fruit are necessary if scattered infestations of low density are used as the basis for estimates, and such estimates must be accurate for both host abundance per unit area and for the incidence of immature insects present in the sample.

When the goal is eradication, male lure traps are preferable for estimating the populations of the three species found in Hawaii. The lures presently used are trimedlure, methyl eugenol, or cue-lure. If toxicants

are not used in these traps, the lures can be adapted to the capture-mark-release and recapture method of estimating numbers (traps are observed and the attracted flies are processed and released again). In tests at our laboratory, these lures have been as attractive to wild flies as to our laboratory strains, but they are less attractive to newly emerged males than to those half through their sexually immature period.

Methyl eugenol is powerful enough to exhaust the male population of the oriental fruit fly before the males mature sexually if it is combined with a toxicant and properly distributed [6]. The US Department of Agriculture combined it with naled and distributed it by air to eradicate the oriental fruit fly from Rota, Saipan, and Tinian [2, 5]. Methyl eugenol dropped on part of Rota reduced the male catches about 94% in traps as much as one mile downwind within two days. More recently, when it was applied in Hawaii as a liquid formulation at 3 pounds per square mile to plots of about 7 square miles, it reduced trap catches nearly two miles away by about 98% within a few hours. Trimedlure and cue-lure are also very attractive to Mediterranean fruit fly and melon fly males, respectively, if enough lure is used. However, trimedlure is apparently not powerful enough to outdraw host trees, and to obscure differences in the efficiency of traps in high and low position in the trees, of exposure to sun or shade (depending on temperature), and of certain trap colours (black, red, and other darker colours reduce catches [2]). In addition, relative humidity may affect the response. Nevertheless, methyl eugenol and cue-lure bring flies into a wide variety of traps in many positions, often during rainy weather, though the response is stopped by darkness, high wind velocities, and temperatures that are above maximum and below minimum thresholds. In addition, the size of the catches is affected by wind velocity and direction in relation to available populations and the trap location.

The unusually strong and stable attractiveness of these lures is not generally realized. Liquid baits are affected greatly by competition from other nutrient sources and by outside moisture, the method of use, the position in the tree, and the type of host. However, since they are short-range attractants, they may be more useful for sampling small habitats than the male lures. Further, their variable performance means that the catch is a constantly changing and unpredictable percentage of the total adult population. On the other hand, they are generally more attractive to females and can thus provide female catches useful for determining the ratio of gravid to non-gravid or sterile to wild females. Medflies, however, are often damaged by other insects captured and are left in poor condition for identification.

Recent research has indicated that gamma-irradiated females live considerably longer than wild females. Thus, since the ratio of sterile to wild males is so important to release programs, dependence on the ratio of sterile to wild females caught in liquid baits could give too high an estimate of the effective ratio. No evidence exists that the presence of sterile females adversely affects the method of sterile-fly release.

The relative efficiency of the lures can be estimated from results on Rota [2]. About 30 million oriental fruit flies (15 million males) were released throughout the island in one eight-week period during August and September 1961 when environmental conditions favoured high infestations of fruit and maximum longevity of the flies. Two hundred and twenty-nine thousand of these males were recaptured in the 45 survey traps distributed

at 1.36 per square mile. Thus, the average recovery per single trap/square mile was about 1.12%. A year later, 17.7 million sterile melon flies were released in the same manner, and 68 000 were recovered in three weeks in the same location; this is about 0.56%/trap/square mile [3].

In Hawaii [2], where releases have been made when conditions were favourable to survival of the flies but where some emigration was probable, 0.04% of the released Medflies were recovered per trimedlure trap/square mile, 0.6% of the melon flies were recovered from cue-lure traps, and 1% of the oriental fruit flies were recovered in methyl eugenol traps. In these tests, the standard plastic traps [7] used were usually baited with a $\frac{3}{4}$ by $1\frac{1}{4}$ in. cotton wick containing about 8 ml of lure; they were soaked to saturation every 3-4 weeks. In addition, traps for the oriental and melon flies contained 1% naled, and one eighth of a level teaspoonful of a 1:1 lindane wettable powder-20 and chlordane wettable powder-40 was placed in all traps to help kill flies and exclude ants and spiders. No poison except this wettable powder mixture was used in the medfly traps because most other toxicants tested, including naled, reduced or did not improve the catches.

When traps are used for sampling the ratios of sterile to wild flies, appropriate methods of marking released flies are essential. Sterile flies can sometimes be identified by microscopic examination, but such a practice is impractical when millions of flies are involved. Genetically marked strains that are competitive with native flies are helpful if the identifying character is visible and permanent after death. For example, the strains of oriental fruit flies used on Rota had white instead of yellow thoracic markings. Further, a dark strain of melon flies has been segregated by continuous selection, but the longevity of these flies in the field is somewhat less than that of the normal laboratory strain. This and other genetically marked strains can probably be developed to retain the marker and function competitively in sterile-fly releases.

Marking with dyes is a method receiving widespread attention. We have used the oil-soluble dyes Calco Oil Blue RA and Calco Oil Red N-1700, American Cyanamid Company[1], since 1959. Pupae are marked by gently rolling them in dye (4 grams per litre of pupae) or by forcing the adults to emerge through vermiculite or sand containing 10 grams of dye per litre. At emergence, the ptilinum of these flies contacts and holds the dye, which is later retracted into the head where it withstands fading by sunlight. Meanwhile, sunlight, plus the fly's attempt to clean itself, destroys most of the exterior deposits within 24-48 hours and thus reduces the serious danger of transferring dye to wild flies when trap catches are heavy. Then, when samples of trapped flies are to be examined to determine the ratio of sterile to native flies, the catch is spread out an inch apart on filter paper over a hard, non-porous surface (preferably glass), and the head and thorax are crushed with a flat-tipped bolt or rod carrying a drop of acetone [8]. This action transfers any colour present to the paper. More recently, fluorescent dyes (Da-Glo, Switzer Bros., Inc.) have been applied in the same manner to the pupae; also adults treated with fluorescent colours that cannot be easily identified under a black light can be subjected to the head-crushing procedures to transfer any colour in the head

[1] Mention of a proprietary product does not necessarily imply endorsement of this product by the United States Department of Agriculture.

to the paper. These dyes appear to have no adverse effect on longevity, but they do not always produce 100% marked flies.

6. ESTIMATING NATALITY AND RELEASE RATES BY USING MALE LURES

Estimates of the rate of natality and the necessary rate of release for large programs are needed as much as a year ahead of any releases. Intelligent budgeting and planning for space, for rearing rooms, and for the irradiation facility, for distribution, and for personnel are not possible without an approximate estimate of the numbers of flies needed. In addition, populations generally have regular seasonal patterns, and declining infestations improve the chances of success. Thus releases begun during periods of low infestation are likely to produce more overflooding of the native population than anticipated. Overestimation will shorten the program; underestimation may cause it to fail.

It is the personal opinion of the author that methyl eugenol has a sufficiently high level of attraction to justify consideration of a new method of estimating the natality of oriental fruit flies in large areas. The rate of daily trap catches in representative survey traps could be multiplied by a number representing the estimated efficiency of the minimum number of traps required per square mile to exhaust the sexually immature male population, assuming a situation in which intertrap competition can be avoided. The product would then approximate the daily rate of natality of males that live long enough to respond to the lure that surrounds them. When this rate is multiplied by 2 to correct for females and is adjusted by an empirical formula that provides 20× overflooding and allows for losses of as much as 80%, the approximate required rate of release of sterile flies per square mile would result. Losses of as much as 80% have been experienced in programs already completed.

The suggested formula for determining the rate of natality and release for the oriental fruit fly is given below, with tentative factors included to adjust the formula for the melon fly and the Mediterranean fruit fly.

$$N = 2\,CKtA \qquad (1)$$

where

N = estimate of natality;
K = estimate of trap efficiency (number of non-competitive traps per square mile needed to exhaust the male population; for the oriental fruit fly, the number is 50, for the melon fly, 80, and for the Mediterranean fruit fly, 500);
C = catch of males per trap per day;
t = time (days); and
A = area trapped in square miles.

The 2 is used to correct for both sexes since only males are caught. Then

$$R = 20\,NL \qquad (2)$$

where

R = number of flies required for release to obtain a 20-to-1 ratio of sterile to wild flies;
N = estimate of natality by Eq.(1);
L = loss compensation factor to adjust for the increased loss of released sterile flies by early death (in excess of that of the wild population by a factor of 5 for the oriental fruit flies and Medflies and by a factor of 4 for melon flies).

In preliminary field tests of the male annihilation method in Hawaii [6], 40 uniformly distributed methyl eugenol-poison bait stations per square mile exhausted the population of oriental fruit fly males within the area. These stations were later found to be twice as effective as the standard plastic traps described; hence, 80 competitive traps per square mile should exhaust sexually immature male populations in large areas.

Poor rates of recovery of sterile flies on Rota and Saipan were caused largely by the reduced longevity of the packaged flies resulting from emergence on hot soil, damage from overheating, insufficient food near release sites, predation by birds, poultry toads, lizards, and ants, and off-island drift. None of these factors affected the wild population to the same extent. Obviously, the loss factor is likely to be more variable than the birth rate, but it may be possible to adjust it after other ratios have been ascertained. The L value for Rota was obtained by using the estimated N and the actual ratios of sterile to wild populations that existed during a year when releases totalled 337 million sterile oriental fruit flies, that is, 0.99 million sterile males and 2.573 million wild males were captured for a mean C of 138. Thus the mean weekly rate of release averaged 5.7 million sterile flies, and the trap catches showed a sterile-to wild ratio of only 0.386:1. Then R of $20/0.386 \times 5.7$ million (about 300 million per week) was needed, and C of 138 in the natality formula would produce a weekly value of N of 3.19 million. This number times 20 would be 63.8 million. Since the 300 million required to produce a 20× over-flooding was 4.7 times the 63.8, the L factor was set at 5.

Our research indicated that 6 well distributed oriental fruit fly traps per square mile on Rota were non-competitive. Also, as mentioned, the rate of recovery on Rota was 1.12% per trap per square mile. The factor of 50 suggests that 56% of the flies could be recaptured if all odour could be efficiently used as in non-competitive traps. In Hawaii, recoveries of 30% have been accomplished by trap densities of 12-16 per square mile. Since 80 would be too high a K factor and 6 would be too low, a K value of 50 is probably representative of average conditions.

Flies that die during or soon after emergence are not included in the estimate of natality. Variations in trap efficiency caused by changes in wind direction, velocity, age of the insect, and extremes in weather conditions will provide good average data if records for short periods are avoided. During the first two weeks after setting, the survey traps bring mature males into their vicinity. Thereafter, the number of older males coming within range from some distance away will be largely offset by the number of newly emerged males that escape the influence of the traps and are beyond reach when they become responsive. Depressed temperatures that affect the output of the lure and the activity of the flies also regulate

the rate of fly development and allow the trap more time to make its catch (it would have twice as long at 68°F as at 80°F).

The formula for the melon fly was derived in a similar manner after completion of the melon fly eradication program on Rota [3]. The formula for the Mediterranean fruit fly requires further research but may be useful in current Medfly programs. The number of survey traps need not exceed 2 or 3 per square mile for melon and oriental fruit flies and 10 per square mile for the Medfly in areas of more than 25 square miles and may be progressively fewer as the size of the area increases. However, there must be enough to extract reliable samples of the whole population.

The formulas suggested here are intended to provide estimates that can be used as base points subject to easy verification after marked fly releases have been in progress long enough for the rate of recovery to stabilize. If properly used, they should provide more accurate estimates of the numbers of sterile flies that must be produced and released than those at present obtainable by any other method.

The importance of random but representative placement of survey traps and their maintenance in the best possible condition cannot be overemphasized. Furthermore, the formulas are not applicable without appropriate modification if the trap catches are obtained with lures, toxicants, and trap designs different from those described.

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MEDITERRANEAN FRUIT FLY RESEARCH IN HAWAII FOR THE STERILE FLY RELEASE PROGRAM

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Abstract

MEDITERRANEAN FRUIT FLY RESEARCH IN HAWAII FOR THE STERILE FLY RELEASE PROGRAM. Research on the use of sterile fly releases to control the Mediterranean fruit fly, Ceratitis capitata (Wiedemann), in Hawaii involves (a) the development of a strain with easily recognizable genetic markers; (b) breeding into laboratory strains increased longevity and increased capability of mating, foraging and dispersal; (c) investigation into the effects of various methods of release on fly longevity, vigour, and survival; (d) improvements in larval rearing medium to produce more vigorous flies at a lower cost than the current $20 per million flies; (e) development of more efficient traps; (g) improvement in methods of population detection, surveillance, and size estimation; (h) evaluation of new ultra-low volume bait-spray formulations for possible use in suppressing heavy concentrations of native flies before or during programs; (j) investigation of the potential value of methods of annihilating males and improving them to supplement the sterile release method; and (k) continued detailed research on behaviour and ecology relating to rhythms, confinement during emergence, sexual behaviour, and adult movement.

1. INTRODUCTION

The Hawaii Fruit Fly Investigations Laboratory, a research field station of the Fruit and Vegetable Insects Research Branch, Entomology Research Division, US Department of Agriculture, is one of two field stations of the US Department of Agriculture that are doing full-time research on tephritid fruit flies; the other is in Mexico. The station at Hawaii includes facilities on the island of Oahu and Hawaii and a total staff of 29, 11 members of which are professional entomologists or chemists.

Hawaii is the only place in the United States where the oriental fruit fly, Dacus dorsalis Hendel, the melon fly, D. cucurbitae Coquillett, and the Mediterranean fruit fly, Ceratitis capitata (Wiedemann), are permanently established and the only place in the world where they are sympatric. There is a constant danger that one or more of these species may become established in the continental United States. Infested fruit or vegetables from many parts of the world are intercepted almost daily by quarantine officers at United States ports of entry.

The responsibility of the Hawaii Fruit Fly Investigations Laboratory is therefore to provide new information on the ecology and behaviour of the three species for use in research (this effort also aids the quarantine and regulatory agencies), to find better low-cost methods of disinfesting commodities to permit their safe export from Hawaii to the continental United States or to other fly-free areas, to develop and improve methods

of survey and detection, and finally to improve control and eradication. At the present time, eradication procedures are intended primarily for use in suppressing incipient outbreaks on the mainland, but the steady improvement in the effectiveness of older methods, the development of new procedures, and the decrease in cost of eradication that have resulted to date from research make ultimate eradication of the three species from Hawaii's 6000 square miles highly probable.

The Mediterranean fruit fly (Medfly) is present on all the islands of Hawaii, but below 3000-ft altitude, where competition from the oriental fruit fly is greatest, the density is generally low. Above 3000 ft, and sometimes at lower elevations if coffee plants are available to help build up large populations, infestations of 50-100% of the fruit often occur in favourable host situations. Since more than 15% of all ripe coffee berries are usually infested, the Islands' small coffee belt (about 8000 acres) produces millions of flies annually. The species formerly infested the areas and hosts now dominated by the oriental fruit fly.

At present, no parasite of the Medfly in Hawaii is important as a control. Opius oophilus Fullaway, an introduced parasite, has the highest incidence, but in Medfly larvae it is usually associated with mixed infestations of oriental and Mediterranean fruit flies where some of the Medfly parasitization appears accidental.

Although this discussion relates to the Medfly, the other two species receive more attention because of their importance and greater availability in Hawaii. Thus new discoveries may often be adapted quickly to the Medfly after prior development in research on the melon fly or oriental fruit fly.

2. BIOLOGY AND ECOLOGY OF THE MEDFLY AND ITS NATURAL ENEMIES

2.1. Host evaluation

The relative attraction of the host species and their individual capacities for increasing the reproductive capacity of the Medfly is important to eradication programs. We must know where the fly will persist longest and be present in greatest numbers during the later stages of any such program. In Hawaii, such research means a continuous search for previously unknown hosts; also, by fruit sampling and by holding fruit for fly emergence, we are accumulating important information on host preferences.

2.2. Breeding of laboratory strains to produce genetic markers or other attributes

Artificial methods of marking flies complicate the mechanics of preparing and releasing large numbers of sterile flies and can cause injury to a substantial number. Flies with conspicuous genetic markers but which are otherwise normal would not need artificial marking and could be separated rapidly from native flies after capture. Our work has so far included (a) holding and producing highly inbred strains, (b) accomplishing genetic analysis by pair-mating (with examinations of the

F_2 generation) for new recessive visible mutants, and (c) clarifying the nature of mutants and evaluating them in behavioural and field studies. In addition, laboratory studies are made of rates of emergence and of the fertility, fecundity, male competitiveness, and longevity of promising strains.

The results of Medfly breeding have so far been disappointing; no satisfactory strains with visible markers have the desired fecundity and stamina.

Attempts are now being made to select long-lived flies from which to develop strains that have long-lived males, without lengthening the time required to reach sexual maturity and without destroying other desirable characteristics. Special laboratory strains should also be developed to suit the conditions of use; not enough has been done to increase or condition the tolerance of the flies to extremes of heat, cold, or starvation.

Laboratory strains are usually well adapted to the laboratory. Thus, when they are compared with wild flies in the laboratory, they may show greater fecundity, longevity and mating competitiveness. Sometimes, even when they are diseased, injured, or deformed, they are still able to reproduce normally in cages. However, such flies could not forage for themselves in the field, and laboratory cages and olfactometers are thus not suitable for the final evaluation of a strain.

We have now provided an intermediate step between the laboratory and actual release in the field. Large cubical cages containing small trees are used. In these large cages, we can develop reliable information about traits that adversely affect the fly's flight and foraging ability. When genetically marked strains are available, we can place equal numbers of laboratory males, wild males, and wild females in the cage and determine whether genetically marked strains can compete with the wild males in mating by identifying their progeny. Some indication of foraging ability can also be obtained by forcing both types of males to obtain their food from foliage to which they must fly. Our research indicates that laboratory-reared Medflies often appear sluggish. Sometimes they only require a period of adjustment to field conditions. However, sometimes their behaviour is abnormal. Also, when sluggish flies are released, they are more susceptible to predation and to the effects of hot sun or hot soil than flies that leave the release container rapidly.

2.3. Observation of sex behaviour by means of an olfactometer

Recently we extended our research tools by devising an olfactometer (unpublished data) with which we can study the apparent lack of sex pheromone in the Medfly female, the absence of attraction of mature virgin females to sexually immature males, and the strong attraction that sexually mature males have for mature virgin females. The equipment will be used to compare the effectiveness against such females of the attractant in males of different strains and ages and the effect on female response of different degrees of sperm exhaustion (of the sterile males) in males fed different diets or given different radiation treatments. The comparative ability of sterile and wild males to elicit a response from virgin wild females will also be studied. Strains of laboratory-reared females that have a pre-

ference for the sterile males of their own strain compared with wild males should not be released.

The olfactometer is expected to help us define the conditions at which sex pheromones are emitted most strongly and will therefore improve our chance of capturing and identifying the attractive substances, an effort in which we have failed to date.

2.4. Attraction of females to male lures

Sperm-deficient Medfly females (also oriental fruit fly females) respond to male lures in traps, on foliage, or at bait stations when live mature males are not available. The peak of this response occurs at midday, about two hours later than the usual mating time. We believe the lure may simulate the male sex attractant, which may be more effective than supposed in attracting females to the vicinity of the male at midday when conditions in Hawaii are better for flight than at dawn or dusk.

2.5. Dispersal and movement studies

Information resulting from releases arranged so that radioisotope-labelled Medflies emerged in the field in areas where adequate food was available indicated that the male may move as much as 25 miles and that more movement occurs in the downwind direction than in other directions when wind movement is predominantly from one direction. Perhaps because we have released many more melon and oriental fruit flies than Medflies and because traps have been available at greater distances, we have recovered marked oriental fruit flies 30 miles and melon flies 67 miles (from Rota to the south tip of Guam) from their point of emergence. This latter distance (recorded in July 1967) is the record for the males of the three species in Hawaii. When Mediterranean fruit fly release points were ringed with traps placed in concentric circles, the average distance from the point of release to the point of recovery was about one quarter mile.

In such tests, we are trying to obtain more information on fly movement: (a) to determine when a release area is adequately isolated, (b) to position properly the field emergence cages from which sterile flies are allowed to emerge in the field, (c) to discover the distance apart that flight lines for dropping containers of flies should be spaced, (d) to determine whether flies should be released high in the air or allowed to ride the drop container to the ground, (e) to determine the effect of different types of diet during the first two days after emergence on subsequent movement, (f) to establish the effects of supplemental food placed around ground release sites to increase the longevity of the released flies without retaining them too long at the site, and (g) to determine the effect of various methods of packaging and release on dispersal and longevity. It is also important to determine how far the flies will allow themselves to be carried by strong winds when they are released high in the air. Will they drop through clouds to land or will they react positively to the light above the clouds and thus allow themselves to be transported farther away from the intended drop areas if the dispensing plane is forced to fly over instead of under the clouds?

3. METHODS OF MASS PRODUCTION AND MANIPULATION

Costs of larval diets for fruit flies have been reduced substantially within the last few years, and production of pupae per unit of this medium (15 000-18 000 per litre) is approaching the maximum possible without a reduction in the size of the pupae produced. Within the past 18 months, costs of materials have been reduced from $45 per million flies to $10 per million. Labour requirements have also been reduced somewhat, but they can only become substantially less with large-scale production where labour-saving devices can be used. The combined cost of labour and materials only a few years ago was more than $350 per million flies compared with the present cost of $20.

Nutrients in the larval diet are now provided mostly by torula yeast and sugar, though some additional nutrients are supplied by the wheat shorts and middlings that make up most of the bulk. Fungi and bacteria are controlled by adjusting the pH with HCl to 4.5 and by including sodium benzoate and Nipagen® (methyl-p-hydroxybenzoate)[1]. Enough water is included to make a thick mixture. Excessive moisture is absorbed by a fire-fighting polymer (Gelgard M, Dow Chemical Co.) that is mixed with the medium. In addition, the medium is used for only six days, since the eggs are incubated until they are at the point of hatch. The medium has the added advantage that it can be flushed with water through a strainer that will retain all larvae. Thus the recovery of pupae in terms of eggs available amounts to 65-76%. Since larval production cabinets can be emptied and reset every seven days, all larvae from one batch start pupating at the same time and can be blended volumetrically with the proper amount of the vermiculite pupation medium. Research with this formula is continuing into methods of inducing larvae to leave the medium voluntarily and over a short time, but progress is slow. Such a method will be needed when conditions of sewage disposal will not permit the used medium to be washed into the drains.

Undoubtedly, overall production costs can be halved again with the proper facilities, use of skilled personnel, and a few additional improvements in diet. Since the cost of sterile flies is a major item in sterile fly release programs, methods of mass production will continue to receive much attention, but a stronger effort must be made to maintain or improve the quality of the end product.

While sterile adults are emerging in the containers from which they are to be released or transferred, food is required. Experience in the Western Pacific program indicated that sugar and water or sugar, honey, and water were adequate, but additional experiments are under way to determine whether the inclusion of protein hydrolysate will help the male or encourage the female to compete with wild females for the attention of wild males.

The possibility that strains of the Mediterranean fruit fly from different parts of the world may require different amounts of gamma irradiation to produce irreversible sterility is raised by investigators whenever males retain ability to fertilize females after doses above 9 or 10 krad. A recent restudy of our dose rates confirmed earlier work in which we determined

[1] Mention of a proprietary product does not necessarily imply endorsement of this product by the United States Department of Agriculture.

that 9-10 krad were required. However, the rapid increase in temperature that often occurs when naked medfly pupae are held in bulk and the anoxia that develops substantially reduce the effectiveness of a dose of irradiation applied to pupae held in bulk for 15 minutes or more. In some facilities, therefore, forced ventilation through the pupae may be necessary both before and during irradiation.

The well-ventilated, expendable cartons containing six shallow trays and holding 13.2 litres of pupae that we devised for shipping nearly 1.4 billion pupae of two species 3800 miles by air to the Marianas Islands are being used to ship Medflies from Panama to Costa Rica for the eradication program recently in progress there and are used in Mexico to ship Mexican fruit flies, Anastrepha ludens (Loew), to release areas. When these cartons must be enclosed in screened containers to retain any flies that emerge, overheating is almost certain to occur. Since stock Medflies may be needed to start programs in other areas or to supplement or even conduct new programs well away from the production facility, shipping containers are needed that will provide adequate security against escape of emerging flies, prevent overheating, and be light in weight. Since heat is generated within the pupae, the low temperatures of enclosed ice or other frozen materials cannot penetrate the pupae without forced ventilation. Continued work in this area is important.

4. LABORATORY AND FIELD SCREENING OF ATTRACTANTS

Many thousands of candidate lures prepared by chemists of the US Department of Agriculture or obtained from industry have been tested in a large outdoor 9 ft × 9 ft × 9 ft cage olfactometer. Any material that is significantly more attractive than water alone is further tested on wicks supported on paper panels on a rotating hexagonal device that permits observation of the comparative numbers attracted and the reaction of the flies (do they make contact or hold back at some distance). In addition, by holding these wicks and re-exposing them at intervals, we can evaluate the duration of attractiveness. The tests have not revealed anything superior to trimedlure since that lure was developed for the Medfly in 1959 [1].

Field tests are made in traps (replicated at least 10 times) and are conducted over two or three months to ensure maximum reliability. In addition, any promising lures or trap modifications are now field-tested in areas having high temperatures (by releasing sterile flies if it is necessary to provide test populations) and at the highest cool areas (5-25°C) in which the species is quite numerous.

Expendable low-cost boards and containers coated with a sticky compound and baited with trimedlure have occasionally caught more flies than standard traps, but identification of flies caught in such viscous material is difficult, if not impossible, and labour costs are increased. If the sticky traps are positioned within 150 ft of standard traps, they intercept many flies attracted by standard traps, but where they are more than 150 ft from the standard traps, they generally show little if any superiority in numbers caught. Sticky traps are least useful in hot, dry or windy climates except when they are used to make quick surveys of the population of adults in the vicinity.

5. LABORATORY EVALUATION OF INSECTICIDES AND CHEMOSTERILANTS

Candidate attractants for use as bait spray are generally hydrolyzed proteins and are evaluated by applying controlled amounts, with a toxicant included, to clusters of foliage over trays in well-replicated tests. Dead flies that drop to the trays are counted. This procedure was used to develop the first protein hydrolysate-organic phosphate bait spray nearly 18 years ago, and it has been a standard procedure for preliminary tests ever since. The results provide information on the duration of effectiveness, the effects of rainfall, the relative attractiveness to species and sexes, and the effective ratio of toxicant to attractant.

New candidate insecticides for fruit flies are constantly becoming available, and we systematically test many of them for topical and residual effectiveness. The most promising are then evaluated further in bait-spray formulations by using the tray method or in field tests. Tests of chemosterilants are also made to determine dose rates and to compare their effectiveness with that of gamma irradiation in producing sterile flies of good quality. In addition, methods of using the attractive protein hydrolysate and male lures to expose wild populations to chemosterilants are tested.

6. DISINFESTATION OF FRUITS AND VEGETABLES

A major effort has been made to improve fumigation by using heat, cold, and irradiation to kill all fruit fly stages present in a commodity without leaving objectionable residues or adversely affecting the quality of the product.

The appearance of the Mediterranean fruit fly in a previously uninfested fruit-producing area can cause the imposition of an immediate quarantine to prevent further spread, and the pressure for early eradication then becomes great. Availability of methods of disinfestation would avoid serious losses by permitting the export of disinfested commodities while a sterile fly release program or other method of eradication was being worked out. Disinfestation methods are also important when a program is established to keep an area from becoming reinfested after an eradication program has been started or completed.

A 230 000-Ci cobalt-60 facility for treatment of commodities at rates as high as 4000 lb/h with 75 to 100 krad to delay ripening processes and for disinfestation is now in operation in Hawaii. The facility was built jointly by the US Atomic Energy Commission and the State of Hawaii as a quasi-commercial facility to be used for processing export shipments of papayas and mangoes in lieu of fumigation, subject to the final approval of the processing by the Food and Drug Administration. Our research showed that minimum doses of 25 krad provided adequate security against emergence of fruit flies present as eggs or larvae.

7. DEVELOPMENT AND LARGE-SCALE FIELD TESTING OF NEW PROCEDURES FOR CONTROL AND ERADICATION

7.1. The method of sterile fly release

At present we have no large-scale field tests of the sterile fly release method in progress. However, we have supplied the Trust Territory of the Pacific Islands with sterile melon flies to eradicate five reintroductions of the melon fly to Rota since the 1963 eradication [2]. Because of early detection (about four survey traps per square mile are in constant operation on Rota), these reintroductions were eradicated by releases of 0.5 to 2 million sterile flies per week, usually for 10 to 12 weeks. Guam, 37 miles away, remains infested and is the probable source of the flies. This island may soon become the site of a sterile fly release program financed by its own government. These successes indicate that similar reinfestations of areas from which the Medfly has been eradicated could as easily be eliminated. They also strengthened our belief that the feasibility of using sterile Medfly releases to suppress incipient outbreaks should be investigated at every opportunity.

Far too little research has been done on methods of dispensing or distributing sterile Medflies among the wild population. In our Western Pacific tests, we used a box with corrugated inserts that provided a large surface area of 5800 cm^2 on which about 4000 flies rested. The longevity of both the oriental fruit fly and the melon fly was reduced by about 40% with this procedure. This box has not been used to release Medflies. The paper bag method currently used to release Medflies in Central America may be causing considerable damage to the sterile flies: in preliminary tests, we have found that crowding in the bags increases visible mutilation and results in some adverse effect on longevity, despite the inclusion of food. Studies of emergence suggest strongly that crowding while the flies are expanding their wings may cause damage that is not readily noticeable. This could subsequently be expressed in reduced longevity. Unless this subject is exhaustively studied, we may continue releasing far less effective flies than preliminary laboratory tests indicate.

We have also conducted several large comparative tests of the longevity and recovery of flies released two or more days after they emerge in large cages with ample food and without overcrowding compared with those allowed to emerge in the field and forage for themselves without supplemental food. No significant difference in longevity is apparent, but flies that emerge in the field and forage for themselves seem to become more widely dispersed before sexual maturity and over the whole period of their lives than flies released as adults. These tests have been made in both urban and rural areas; additional tests should be made during the extremely dry weather to which the fly is especially susceptible. Perhaps flies should be well fed and allowed to develop almost to sexual maturity before they are released to disperse among wild flies. Such a program would be particularly useful if the areas of greatest concentration of wild flies were known and the adults could be expected to mix with the wild flies immediately instead of having first to search for the areas containing hosts and flies.

Sterile flies must be quickly separable from native flies when they are captured, since the necessary overflooding ratios can be most easily determined by examining the ratio of sterile to wild flies. Dyes or the

methods used to apply them may injure flies. Moreover, some dyes may be transferred from marked to native flies in dry traps or during mating or may fade and become unrecognizable.

We have been testing many dyes for toxicity, permanence, transfer possibilities, and effects in the laboratory on longevity. Although it may not be possible to obtain 100% marking and 100% identification of dyed flies, Calco Oil Blue RA and Red 1700 (American Cyanamid Co.) and several fluorescent 'Da-Glo' (Switzer Bros., Inc.) colours have had no significantly adverse effect on the longevity of released flies.

7.2. The male annihilation method of eradication

Poisoned male attractants with short residual effectiveness might make it possible to use the method of male annihilation during one generation. After large populations of flies have been reduced sufficiently, the method of sterile fly release could be used. Male annihilation involves the application of 5-10 lb or more of male lure-toxicant formulation per square mile, usually on a two-week schedule, until all fertile females have died and all males have been killed before any reach sexual maturity (3). Our tests indicate that when sterile Medfly males are released into a population in which the females are already responding to the male lure because of the scarcity of males, the response of those females to the male lure terminates as soon as the released males reach sexual maturity. Male annihilation may be helpful in areas of concentrated, heavy infestations that are surrounded by much larger areas of low infestation where sterile fly releases could be made.

The effectiveness of male lures can be extended by using a formulation containing a thickening agent and 5% naled [4], and applying it aerially as large droplets to foliage located on widely spaced (500 ft to 1000 ft) flight lines (unpublished data). However, both trimedlure and medlure are too volatile for this method, and we are still searching for a better Medfly lure and for better extenders and toxicants.

A 19:1 formulation of trimedlure and naled has been used as bait in stations made from 2 in. × 2 in. × 1/2 in. cane fiberboard. When these baits are suspended at the rate of one or more per acre, they produced substantial reductions in the male population. In addition, many tests have indicated that the Medfly cannot be poisoned as easily by baited materials placed on the ground as by the same baits suspended in the air (unpublished data).

Tests are being made of the feasibility of using the male annihilation method on Terceira in the Portuguese Azores where most of the Medfly hosts are dooryard fruit plantings within the villages.

7.3. Improvement in bait sprays

Bait sprays should be applied as large droplets that provide concentrations of poisoned protein hydrolysate which are more attractive than fresh droplets of honey dew. Since these sprays usually attract only tephritids and require less poison than conventional, full-coverage sprays, they leave less residue and kill few beneficial insects.

About two years ago we began to develop low-volume protein hydrolysate bait sprays (unpublished data). These should not be confused with ultra-low-volume sprays. Instead of ultra-fine droplets, we use droplets of about 500 - 1000 μm that spread out to 2 - 3 mm on foliage. Such sprays require a liquid protein hydrolysate that contains about 50% solids and a technical organic phosphate such as malathion or naled in mixtures that contain from 5 - 20% toxicant and to which no water or emulsifier is added. Because of the low content of moisture of the droplets, the sprays can be applied by aircraft from elevations of 100 - 500 ft, depending on wind velocity, at almost any temperature and with the flight lines as much as 500 ft apart. Nozzles with 10/64 disk openings and pressures of about 25 lb/in^2 are used to obtain the large droplet size. A 4-to-1 (protein-to-insecticide) formulation at 15 ounces (avoirdupois) per acre was used to eradicate a recent Medfly outbreak in Brownsville, Texas [5]. In Hawaii, a similar mixture at 10 ounces gave excellent control of the melon fly on cantaloupe, one of the most difficult crops to protect.

In our research, we have tested applications of different formulations at different swath spacings and elevations to more than 40 plots of one square mile each. The amount of protein hydrolysate per acre and the spacing of the swaths determine the time required to attract all flies between the lines; the amount of toxicant determines the length of residual effectiveness and whether or not flies will be killed if they are not attracted within one day. Effective bait sprays of this type would offer a rapid and efficient method of quickly eliminating fertile females in high fly density areas ahead of a sterile release program without leaving residues that would kill released flies in a sterile fly eradication program initiated a few days later.

This paper has reviewed some of the research under way at the Department of Agriculture's Hawaiian laboratory relating to the method of sterile fly releases. Methods of integrating male annihilation and bait sprays with sterile fly releases will be receiving increasing attention as each technique is improved. New problems can be expected to arise wherever new methods are tried, and these will continue to require additional research.

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ETUDES SUR LA MOUCHE MEDITERRANEENNE DES FRUITS EN TUNISIE

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Abstract — Résumé

STUDIES ON THE MEDITERRANEAN FRUIT FLY IN TUNISIA. The work performed by Soria, Sigwalt and Yana of INRAT has provided some valuable basic knowledge of the ecology of Ceratitis capitata in Tunisia and of the efficacy of the different methods of study. A list of host-plants was established and this has contributed to crop protection; the eradication of certain dangerous plants reduced the rate of increase of the flies at certain times of the year. The release-recapture method with flies labelled with ^{32}P has permitted the authors to estimate the population level, which is quite low in winter (10 to 100 males per hectare). Various trapping methods (permanent traps, discontinuous and continuous trapping and release-recapture) have, in addition, contributed toward a better understanding of the variations in the population of this insect.

ETUDES SUR LA MOUCHE MEDITERRANEENNE DES FRUITS EN TUNISIE. Les travaux de Soria, Sigwalt et Yana, de l'INRAT, ont apporté des connaissances de base sérieuses sur l'écologie de Ceratitis capitata en Tunisie, et sur la valeur de différentes méthodes d'étude. La liste des plantes-hôtes, cultivées ou non, a été établie et a permis une application intéressante de lutte culturale; la suppression de certaines plantes dangereuses a réduit le taux de croissance de la population de mouches à certaines époques. La méthode des lâchers-recaptures après marquage au ^{32}P a permis une estimation du niveau de population, qui est assez bas en hiver (10 à 100 mâles par hectare). Différentes méthodes de piégeage (postes permanents, piégeage discontinu, piégeage continu, piégeage pour lâchers-recaptures) ont permis de mieux comprendre les variations de population de l'insecte.

IMPORTANCE DU PROBLEME

Les pertes moyennes annuelles dues à Ceratitis capitata ont été estimées à $500 000. Pour la campagne 1965-66, qui a vu une très forte attaque, les pertes ont dépassé 2 millions de dollars.

Les travaux présentés sont ceux de M.M. Soria, Sigwalt et Yana, chercheurs de l'Institut national de la recherche agronomique de Tunisie (INRAT).

RESULTATS ANTERIEURS A 1966

a) La liste des plantes-hôtes, cultivées ou non, a été établie avec leurs époques d'infestation et leur importance relative dans la pullulation de C. capitata.

b) L'importance de certaines plantes-hôtes secondaires a été mise en évidence: Lycium subglobosum, Opuntia ficus-indica, bigaradiers (orange amère).

c) Des études de population ont été conduites par la technique des lâchers-recapture et indice de Lincoln, après marquage au ^{32}P (opérations conduites sur 1 ha - lâcher de mouches marquées - piégeage 6 h après, pendant 24 h). Les résultats ont montré que le minimum de population se situe de décembre à mai, avec, suivant les hivers, de 10 à 100 mâles par hectare. La remontée est très brusque en juin (environ 1000 mâles/ha) et se poursuit jusqu'en août (5000 mâles/ha), puis il y a diminution. La dispersion des mouches marquées est faible (maximum 460 m/jour, 600 m en 6 jours).

TRAVAUX DE 1966 à 1967

L'effort principal a porté sur le verger de la Soukra, voisin de l'INRAT: environ 700 ha d'agrumes, quelques vergers mélangés et plantations de figuiers.

Lutte culturale

- Arrachage des haies de Lycium subglobosum
- Arrachage de 40 km de haies d'Opuntia
- Elimination des oranges amères
- Traitement insecticide particulier des plantations de figuiers.

Le résultat a été une chute spectaculaire des captures à la fin d'août (avant les premieres attaques sur agrumes).

Les différentes méthodes de piégeage (au trimedlure)

a) Postes permanents

Des postes de 10 pièges sont placés chacun sur un arbre d'espèce différente: clémentinier, bigaradier, oranger tardif valencia, pomelo, néflier, abricotier, figuier, pêcher, poirier, opuntia.

Les pièges sont relevés deux fois par semaine.

Intérêt: détection des premières présences de mouches sur différentes espèces; avertissement de printemps intéressant particulièrement pour l'abricotier.

b) Piégeage discontinu

Cent pièges sont placés le matin et retirés à midi (le maximum de captures se fait pendant les 3 premières heures, et l'activité sexuelle est maximale en début de journée); ils sont disposés à raison d'un piège tous les trois arbres dans les deux sens. Une équipe place ainsi un poste chaque matin dans un verger différent, avec rotation de 7 à 10 jours.

Intérêt: surveillance d'un vaste territoire et bonne méthode d'avertissement pour les traitements; mise en évidence de façon très nette des remontées de populations.

c) Piégeage continu

Un piège par arbre est placé sur 12 X 12 arbres au milieu d'un verger homogène; ils sont relevés chaque jour.

Ce dispositif d'étude permet de mettre en évidence les variations de population.

Exemple pour un verger de figuier en 1966:

- du 18 mai au 4 juin, peu de captures, répartition des mouches au hasard (loi de Poisson); le piégeage continu provoque un effet de vidange ou d'éradication de la parcelle, les mouches disparaissent
- du 5 au 13 juin, effet de bordure, pression de population extérieure (première génération sur abricotier)
- du 14 au 27 juin, réinvasion des mouches, ou répartition contagieuse (les figuiers deviennent attractifs)
- de fin juin à septembre, disparition de l'effet de bordure, apparition d'un effet de centre (éclosions sur la parcelle), toujours répartition contagieuse
- à partir d'octobre on revient à une répartition suivant la loi de Poisson.

d) Piégeage pour lâchers-recaptures

- Vidange par piégeage continu d'une parcelle de 230 arbres
- Piégeage de bordure pour éviter la réinvasion (efficacité vérifiée)
- Lâchers de mouches d'élevage ou sauvages, marquées (au ^{32}P) ou non sur 1 arbre; recapture sur les 8 arbres voisins (constituant un bloc).

RESULTATS

Le marquage ne modifie pas la mortalité des mouches d'élevage. Les mouches sauvages ont une vitalité plus forte mais semblent mal supporter le marquage.

Le marquage ne modifie pas le taux de recapture (mouches d'élevage), donc ne modifie pas le comportement.

Les recaptures représentent environ 46% des mouches d'élevage lâchées; résultats très homogènes d'un bloc à l'autre, très hétérogènes d'un arbre à l'autre.

Les recaptures de mouches sauvages sont inférieures (20%) à celles des mouches d'élevage; il y aurait une différence de comportement.

Ces résultats amènent à interpréter avec prudence les données obtenues par la méthode de lâchers-recaptures.

Il faut tenir compte d'une différence possible de comportement entre mouches d'élevage et mouches sauvages et également des conditions idéales des essais réalisés: les mouches sauvages et d'élevage avaient en effet le même âge et le même état sexuel. En pratique, lors des études de population peut-être faudrait-il lâcher une population de mouches marquées aussi hétérogène que possible en âge.

Les différences de réaction des mouches au piège au trimedlure sont encore insuffisamment connues. Beaucoup de pièges ne prennent pas de mouches; l'observation directe montre que beaucoup de mouches viennent aux pièges mais qu'une certaine proportion (50%?) seulement est capturée.

Des essais analogues seront repris avec le marquage coloré par la méthode Steiner.

REGULATORY ASPECT OF INSECT POPULATION DYNAMICS

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Abstract

REGULATORY ASPECT OF INSECT POPULATION DYNAMICS. Populations are to some extent regulated and to some extent just fluctuate. The main causes of variation in abundance can be identified by comparing the mortality from different factors with the total mortality, in successive generations. Regulation is also variable because of the influence of weather and many other factors upon it. Nevertheless, it is possible, and highly desirable for a better understanding of insect populations, to detect the presence of regulation and to estimate its power. Methods available for this purpose include (a) observing the trend towards 'normal' after a disturbance of the numbers (but not of the habitat), (b) assessing how mortality, reproduction and net increase are related to abundance, and (c) plotting the logarithmic regression of numbers in successive generations or at successive intervals within a generation. Logically the next step is to identify the regulatory factor(s) or process(es) and to estimate the degree of density dependence of each. The means of doing this include (a) making a quantitative comparison, by observation, of the effect of particular factors on population density, (b) interfering experimentally with a factor, thought to be density dependent, to find how the population will react, (c) graphical factor analysis, and (d) assessing, from a series of one-generation 'life-tables', variation from generation to generation at different stages in the life cycle. Most of these methods can be adapted to show delayed density relationships.

1. INTRODUCTION

The study of the population dynamics of insects in the field will probably always be difficult, because of sampling problems and the intricate complex of varying influences to which such populations are subject. Another difficulty has been the obscurity and uncertainty of how best to go about such studies. Without claiming that the conceptual difficulties have been entirely overcome, I think we may recognize that some useful preliminary steps and a few solid advances have been achieved, especially in the past 10 years or so. We now have instructive examples of new ways of investigating the causes of variation in abundance and the regulatory influences tending to restrict such variation.

No-one has ever doubted the value of studying the causes of variation in abundance. It is also important to understand how numbers are regulated. The development towards integrated control arose from a recognition of the necessity of respecting the natural regulatory factors operating against pests. To exploit these factors or processes, we must first investigate and learn to understand them. The new methods help us to see what should be done. No doubt they will be improved or outgrown, and further new ones will be introduced. Meanwhile we should strive to clarify our thoughts on these matters and to bring the available methods to the attention of all investigators of insect populations. As a contribution towards this end, it is here proposed to enumerate the methods and to comment on some of them, following approximately the lines of a more extensive discussion [1]

which may be consulted for more complete information, together with the other referenecs quoted. For the sake of brevity, consideration of some relevant topics such as the ranges of variation in abundance of various insects, genetic and physiological changes, and the use of mathematical models is omitted.

Regulation is, of course, intimately connected with variation in numbers and cannot be studied apart from it. Furthermore, the regulatory processes come inevitably under the influence of non-regulatory variables such as the weather. Nevertheless, we shall concentrate first on regulation itself as far as this is practicable.

2. DETECTING AND ASSESSING REGULATION

A natural beginning to the study of the regulatory aspects of the population dynamics of an insect is to try to detect the presence of regulation and to assess its range and power. Some possible approaches are listed below.

(a) Studying how the rates of mortality, reproduction, dispersal or net increase or decrease are related to population density

This is the direct approach to the detection and assessment of density-dependent processes, which are responsible for regulation. Such processes differ among themselves in the contribution they make to regulation, and some are unimportant in this connection.

(b) Testing the tendency of numbers to return towards 'normal' after a disturbance

This approach, which is perhaps a special case of (a), can be attempted by examining the responses of a population to natural disturbances, i.e., we may observe whether a population reduced below its average numbers tends to increase and a swollen population to decline. Klomp [2] gave an example of this simple test with a population of Bupalus piniarius. It can only be expected to succeed with a closely regulated population having a stable mean level of abundance.

As has often been pointed out, and occasionally demonstrated in practice, there is scope for field experimentation along these lines. Populations may be artificially increased or reduced and the subsequent changes compared with those of unaltered populations.

(c) Logarithmic regression analysis of the relationship between numbers in successive generations

This method, which is also a special case of (a), was introduced by Morris [3, 4] and can be explained in the following way. The dots in Fig. 1 represent a succession of population estimates to which a curve can be drawn, the form of which indicates (on the logarithmic scale) that the geometric rate of increase from generation to generation declines as density rises. If the rate of increase had remained approximately constant (density

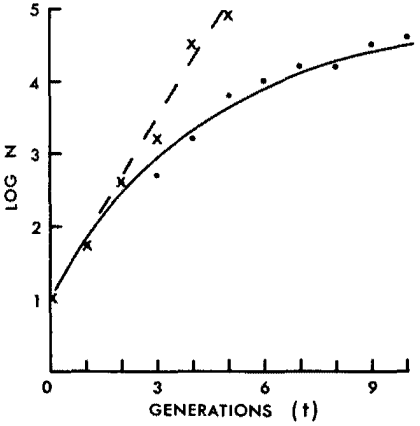

FIG. 1. Geometric rate of population increase compared with constant (density independent) rate of increase.

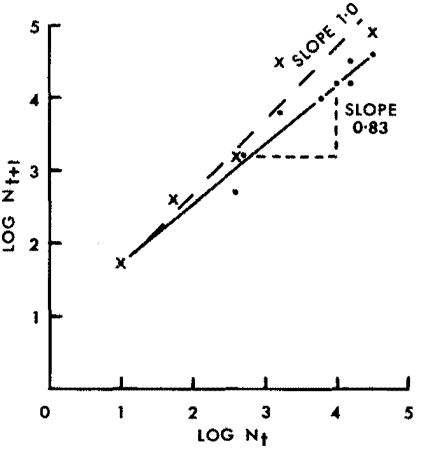

FIG. 2. Graph of log N_{t+1} against log N_t to illustrate the degree of density dependence.

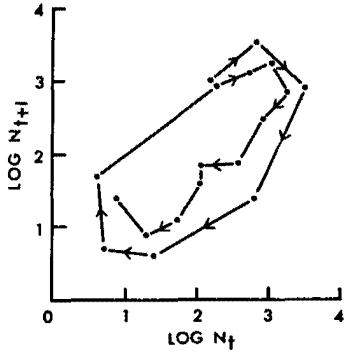

FIG. 3. Oval pattern resulting from application of the logarithmic regression method to a population with cyclic oscillations (based on diagrams by Miller [5] and Morris [6]).

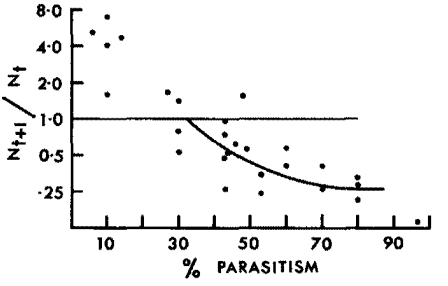

FIG. 4. Relationship between annual rate of population change and per cent parasitism (Miller [5]).

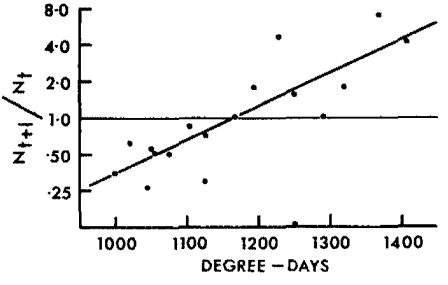

FIG. 5. Relationship between annual rate of population change and degree-days (Miller [5]).

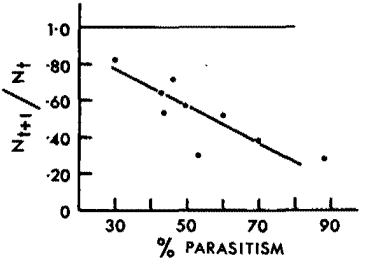

FIG. 6. Relationship between N_{t+1}/N_t and per cent parasitism at one particular level of degree-days (Miller [5]).

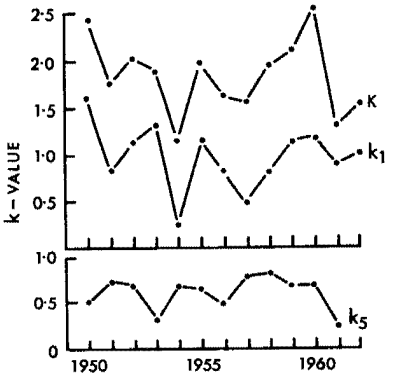

FIG. 7. Results produced by plotting the k-values for a succession of generations (Varley and Gradwell [9]).

independent), the points would have followed a straight line, as do the crosses in Fig. 1. If we now graph log N_{t+1} against log N_t, as in Fig. 2, straight lines can be drawn to each set of points. Since the ratio of the log numbers in successive generations remains approximately constant, the slope of the line drawn to the crosses in Fig. 2 will be about 1.0. In the case of the lower line, however, the ratio of log numbers in successive generations declines as density rises (cf. Fig. 1), hence the slope will be less than 1.0. The deviation of the slope from 1.0 is a measure of the degree of density dependence. (If the slope is >1, the density relationship is inverse.)

Morris used this method for successive population counts of forest insects, taking decreases as well as increases and treating the points as a scatter diagram. It seems preferable, however, to distinguish between the two [1, 5].

Morris used logarithmic scales to equalize the variance, so that valid regression analyses could be carried out; a definite value could then be attributed to the slope of the line and the significance of the difference of the slope from 1.0 could be tested.

It may be possible to use this procedure to detect a change in the equilibrium level about which a population is fluctuating [1], or to detect a density relationship which may be obscured by fluctuations imposed by weather or other density-independent factors [1, 5].

When Morris [6] applied the logarithmic regression method to a population undergoing cyclic oscillations in a delayed density-dependent relationship with parasites, the points formed an oval pattern in the manner of Fig. 3 (this has been extended by reference to the further data of Miller [5]).

In describing the logarithmic regression method, Morris went on to study the improved regression, between the numbers of each generation and the next, after one or more factors had operated, so assessing the contribution of these factors to the variation. In the present scheme this is a separate matter, to which we shall return later.

(d) Inferring regulation from correlations between density and weather indices

It has been argued, notably by Klomp [2] and Nicholson [7], that if a good correlation is found to exist between a weather index and density,

it is because the weather effect operates on a population starting at a sufficiently constant level of abundance in each generation; this implies a regulatory mechanism bringing the successive generations to about the same level before the variable weather factor operates. This argument suggests that we should go on to determine what the relatively constant level is, and how it is determined.

3. ASSESSING THE ROLE OF PARTICULAR FACTORS IN VARIATION AND REGULATION

(a) Assessing the influence of particular factors on the rate of increase or decrease

A good example of how this may be done was given by Miller [5] in a study of the tortricid Acleris variana in Eastern Canada. He plotted the rates of population change between successive annual generations (N_{t+1}/N_t) against the per cent parasitism, somewhat as in Fig. 4, and also the relationship between N_{t+1}/N_t and a weather index (the number of degree-days above developmental zero), in the manner of Fig. 5. To eliminate the effect of variations in the temperature factor, he also graphed the relationship between N_{t+1}/N_t and per cent parasitism at one particular level of degree-days, in the manner of Fig. 6.

The same sort of study, whether involving an index of population change or a comparison of population densities before and after treatment, can be made experimentally. In California, DeBach and his colleagues, in experiments described in a series of papers from 1949 to 1958, assessed the effects of natural enemies of scale insects and mites by artificially reducing or excluding them. Others have described similar experiments.

(b) Factor analysis: estimating the contributions of particular factors to the total of population variation

(1) The first type of factor analysis to be formally developed was that used by Morris [3, 4] for estimating the effects of what he called 'key factors'. Key factors are simply the chief causes of variation in abundance. This should be emphasized, for one comes across signs of confusion on the matter; perhaps the name carries a suggestion that key factors are important in regulation, whereas this is not necessarily so at all—they are distinguished solely by their contribution to variation.

The simplest form of the method is that called by Morris 'single-factor analysis' [6], in which he first constructs a graph of log N_{t+1} against log N_t, as in Fig. 2, for numbers at the same stage in each generation. Then, in a second graph, the log numbers in generation t+1 are plotted against the log numbers remaining in generation t after the suspected key factor has acted. The improved correlation achieved in this way gives a measure (r^2) of the extent to which the mortality due to the suspected key factor accounts for the variation in numbers of the following generation.

If the mortalities due to other factors are also known, the above process can be continued; the proportion surviving after these mortalities have acted shows an improved correlation with N_{t+1}, and r^2 approaches

more closely to 1.0, the value it would have if all the mortalities were allowed for [4, 8].

(2) Varley and Gradwell [9] introduced a graphical method of detecting key factors. They estimated the mortalities due to a succession of different factors or sets of factors through the life cycle of the winter moth, Operophtera brumata, and plotted the killing powers of these factors for each generation. Killing power, or k-value, is the logarithm of the proportionate reduction caused by a factor. For example, if a factor kills 70% of the individuals surviving to that stage, its k-value is log (100/30), or 0.52. When the k-values of all the mortalities in the life cycle are added, the total is the K-value for that generation. The graph produced by plotting the k-values for a succession of generations is like that in Fig. 7, which is simplified by the omission of minor mortalities. It will be seen that k_1, representing the whole set of mortalities operating during the adult and growing larval stages, follows a course roughly parallel to that of the K-value for the whole generation, and comprises a considerable fraction of it. It follows that k_1 includes the key factor or factors. The line for k_5, representing losses of pupae by predation, seems on the whole to fluctuate in an opposite way to K, as if tending to reduce the variations in the mortality of the earlier stages. It was, in fact, considered that predation of pupae was density dependent. Thus the method can, in some circumstances at least, reveal the key factors and prominent regulatory factors, or show where they come in the life cycle.

(3) A step towards determining where the chief regulatory influences come in the life cycle is Klomp's application [10] of the Morris logarithmic regression method to successive stages in the life cycle. The procedure is the same as in plotting log N_{t+1} against log N_t, except that one plots the number of pupae against the number of larvae in the same generation, or the number of early larvae against the late larvae and so on, with one point for each generation. Again, the slope of the regression line indicates the degree of density dependence operating between the two chosen stages.

(4) Another method of detecting where regulation occurs in the life cycle is by the compilation and study of life tables. In recent years a great deal of effort has been devoted to the building up of such tables for various insects. They are frequently published in the form of mean life tables, i.e. the population is followed through a number of generations, the successive mortalities during the life cycle are recorded, and usually the fecundity and fertility as well; for publication, however, the differences from generation to generation are omitted, and only average values are given. This greatly reduces the value of life tables for the study of population dynamics. To identify the key factors and the regulatory factors and to assess their importance, we must examine to what extent they are responsible for variations in abundance from generation to generation (key factors), or how they react to differences in the level of abundance in successive generations (regulatory factors). For this purpose we need a series of generation life tables, each expressing the course of events in a particular generation; and of course we need to know the actual numbers of animals covered, not just percentage values.

If generation life tables are available, we may compare each of the different mortalities with the total mortality, in successive generations, to identify key factors. We may examine the numerical variability, through a number of generations, of different stages in the life cycle, and so infer where the significant regulatory influences come in [1].

Harcourt [11] used generation life tables to test where in the life cycle there is the most variance from generation to generation. He examined the variance in the "trend index", N_{t+1}/N_t (eggs).

(c) Further remarks on key factors and regulatory factors

Although the ideas of key factors (causing variation) and regulatory factors (restricting variation) are opposite, in practice the two functions may be combined. Morris [6] showed that Acleris variana was involved in a delayed density-dependent cycle with its parasites, which were responsible for its regulation but also for the chief variation in abundance, which was that due to the cyclic oscillations.

Even when key and regulatory factors are different, they may come at the same stage in the life cycle, so that regulatory effects may be submerged in the key factor mortality. This seems to have been the case when Klomp [12] applied the graphical analysis of Varley and Gradwell to his data for Bupalus piniarius.

It is sometimes assumed that there is only a single important regulatory factor and a single key factor in the life cycle of a species. There is no basis for such an assumption. Although examples of the dominant role of a single factor in bringing about regulation or variation are certainly known, there are also examples of two or more factors playing an important part. An analysis of the changes in variation from generation to generation in successive stages in the life cycle of the broom beetle Phytodecta olivacea, using the data of Richards and Waloff [13], suggested the incidence of regulation at several different points in the life cycle, and this was supported by a comparison of the mortalities with the current population densities [1].

4. CONCLUDING REMARKS

This account has been an attempt to explain and classify rather than to criticize. It has been confined to the elementary aspects of each approach and has ignored some more sophisticated developments of some of them, especially by Morris and his colleagues.

We began with some optimistic remarks about the value of the new methods of studying population dynamics. They do represent a considerable advance, and it is to be hoped that all entomologists who study population dynamics will examine carefully the relevant papers by Morris, Klomp, Varley and Gradwell, and others. But perhaps we should conclude with some reservations. These methods are inapplicable if the data have not been collected in the way that is appropriate to them. When they are applicable, they tend to take one only part of the way towards a satisfactory analysis. They may need modification or development to meet the demands of a particular field study. They should be regarded as stimulating examples of approaches to population dynamics, not simply as ready-made methods. Often the chief difficulty in applying them is that the data are not complete

enough, especially if not continued over enough generations. The field work and the methods of analysis are mutually dependent.

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RECOMMENDATIONS OF THE PANEL

1. INTRODUCTION

The Panel recognizes the need for reliable ecological studies whenever and wherever the sterile-male technique is employed for control of pest insects and related forms, such as ticks and mites. Although information on ecology is important in any insect control program, the specific requirements for the sterile-male technique have distinctive characteristics which need to be recognized to provide a satisfactory and efficient approach to the execution of the control program. With these features in mind the following recommendations are made.

2. THE NEEDS OF ECOLOGICAL STUDY BEFORE, DURING AND AFTER THE USE OF STERILE-MALE CONTROL

Population ecology represents today one of the essential components of any operation pertaining to the control of pest insects.

It follows that investigations involving the use of sterilized organisms require the participation of competent ecologists in planning, execution, and evaluation.

In formulating our recommendations, we have assumed that preliminary investigations had established the possibility of:

(a) developing an effective method to obtain adequate numbers of sterilized individuals of the species under review, which would perform in nature in a manner consistent with the purpose of the project; and
(b) procuring sufficient means in personnel, facilities, and finance to carry out an effective feasibility study in the field.

Our recommendations should be regarded as guide lines to be interpreted according to circumstances. They do not include details of ecological methodology, since these are provided in the literature. It is understood that much of the initial information to which the recommendations allude will need to be obtained either from published work, or by preliminary studies whenever data essential for the planning of an intended investigation are lacking.

The chronological sub-division used in the recommendations is arbitrary; planning, execution, and evaluation of field studies constitute a dynamic process, the stages of which must be integrated in the light of acquired experience.

The main points to be considered at each successive stage of a field study of the sterile-release method are defined below.

2.1. The needs of ecological study before the use of sterile-male control

2.1.1. An attempt should be made to define the position occupied in its ecosystem by the species under review:

(a) in relation to potential niche competitors;
(b) in relation to the changes which its suppression might induce in natural food chains.

2.1.2. The pest status of the species should be assessed according to:

(a) its importance in relation to other pests of the same and related crops:

- (i) from an economic viewpoint, accounting for current losses and cost of pest control,
- (ii) considering the limitations and eventual side-effects of current control procedures, and
- (iii) considering the proposed interventions in relation to the current control of other pests;

(b) the eventual injuriousness of released individuals and possibilities of minimizing their damage.

2.1.3. Information is needed on the population ecology of the proposed target species, i.e.:

(a) an adequate definition should be given of the 'population units' formed by the species, as it concerns the proposed investigation (dispersion);
(b) the patterns of change affecting the abundance of the species in time and space should be established;
(c) attention should be paid to the availability of supplementary means that could serve before, during or after the intended operations to reduce further the numbers of the target population.

2.1.4. Appropriate study areas should be defined and selected.

2.1.5. Appropriate sampling methods and means of estimating population abundance (particularly at low levels) should be developed.

2.1.6. The feasibility of the proposed operations should be evaluated in the light of the foregoing considerations.

2.1.7. The final step in the preparation should include the statement of aims and the formulation of procedures, including the definition of the end-point of the intervention (release operations), and the determination of the follow-up work intended (survey and quarantine measures).

2.1.8. To recapitulate, the initial phase of the study should seek to clarify successively the following points, which must be considered

basic to the conception and planning of any work involving the evaluation of a control strategy in the field:

(a) Systematic status and intra-specific variability of the target pest.
(b) Economic importance of the pest in the area considered, and need for control beyond that currently feasible.
(c) General biology of the species, including distribution, rates of reproduction and mortality.
(d) The ecological niche occupied by the target pest, and the relations of the pest to other species.
(e) Methods for estimating the abundance of target populations (including low and very low densities).
(f) Requirements of the target species with regard to physical resources, including temperature, humidity, etc.
(g) Quantitative information on the distribution, dispersal, and variation in abundance of the target species, and similar information on the host organism, as far as is relevant.
(h) Determination of the chief causes of fluctuation and of the regulatory mechanisms, on a quantitative basis.
(i) If possible, development of a model of the population dynamics.

2.2. The needs of ecological study during the use of sterile-male control

Execution of the study should cover the following points:

2.2.1. Population records

(a) Estimates of changes induced in the pattern of abundance of the target population (detection and measurement).
(b) Assessment of the adequacy of the release procedures, including considerations of flushing effects, predator-prey interactions, etc.
(c) Estimates of changes induced in the actual injuriousness of the target species.
(d) Reassessment of the adequacy of original premises and assumptions on the biology, etc., of the target species – in particular as they relate to the objectives of operation (changes in the characteristics of the target species, probability of reinfestation, etc.).
(e) Detection and estimates of changes induced in the ecosystem generally.

2.2.2. Periodic evaluation of the performance and of the characteristics of the released organisms

(a) Adequacy of the supply of environmental requisites to support the released contingents.
(b) Comparative performance and compatibility of released and native forms (especially longevity).

2.3. The needs of ecological study after the use of sterile-male control

The termination of the project should entail:

2.3.1. The implementation of planned follow-up procedures (some initiated eventually before the end-point of operations, e.g. surveys and regulatory measures).

2.3.2. Final analysis and interpretation of all results.

2.3.3. The recommendation of further steps to hold and exploit the gains achieved, to ensure the continuation of relevant investigations, to improve the strategy of control, and to expand the use of the tested procedures, if justified.

2.3.4. Publication

3. COMMENTS ON THE ORGANIZATION OF AN EVALUATION STUDY OF A STRATEGY OF INSECT PEST CONTROL IN THE FIELD

Appropriate organization and personnel would be essential to the success of such an undertaking, and to its success within a reasonable span of time. It was understood that the following steps (1-6) would be part of established practice:

1. A member of the Agency staff, or a consultant, would make a preliminary survey on the spot, considering both biological and organizational aspects of the intended work.

2. One or two Agency staff members would be recruited, or assigned, to take charge of the enterprise.

3. Local entomologists, if any, would be drawn into the project as far as possible, e.g. members of the Department of Agriculture or of the University.

4. Collaboration would be sought with appropriate research institutes, especially in the region of study.

5. Financial support for the fuller participation of local scientists in the projects would be mobilized, e.g. to provide or attract funds for research grants, fellowships, temporary appointments, etc. However, this would be conditional on suitable people being available.

6. Efforts would be made to draw in competent workers on secondment for limited periods.

In view of the difficulty of carrying out good ecological research in the field, we recommend that special attention be paid to planning, and to the formation of a team of adequate quality, as follows:

1. An ecologist of established reputation and experience in carrying out field investigations should be engaged for a few months as consultant in connection with the project concerned. In collaboration with the project team, he should consider the proposals, inspect the intended locations (or alternative sites), and draw up a plan including statements on the definition of the project, the reasons for undertaking it, its aims (i.e. the questions to be answered), and the steps by which it should be carried out. As far as the testing of the sterile-release method is concerned, it would be desirable to state in the plan the criteria to be used in assessing success, partial success, or failure of the attempt.

If possible, the same consultant (or another of the same calibre) should periodically assess progress, and make a report on the final outcome.

2. A leading member of the team should be experienced in field ecology.

3. A biometrician should be included in the team, or, failing that, arrangements should be made for a biometrician to take a continuing interest in the project and to be available for frequent consultation.

It is further recommended that:

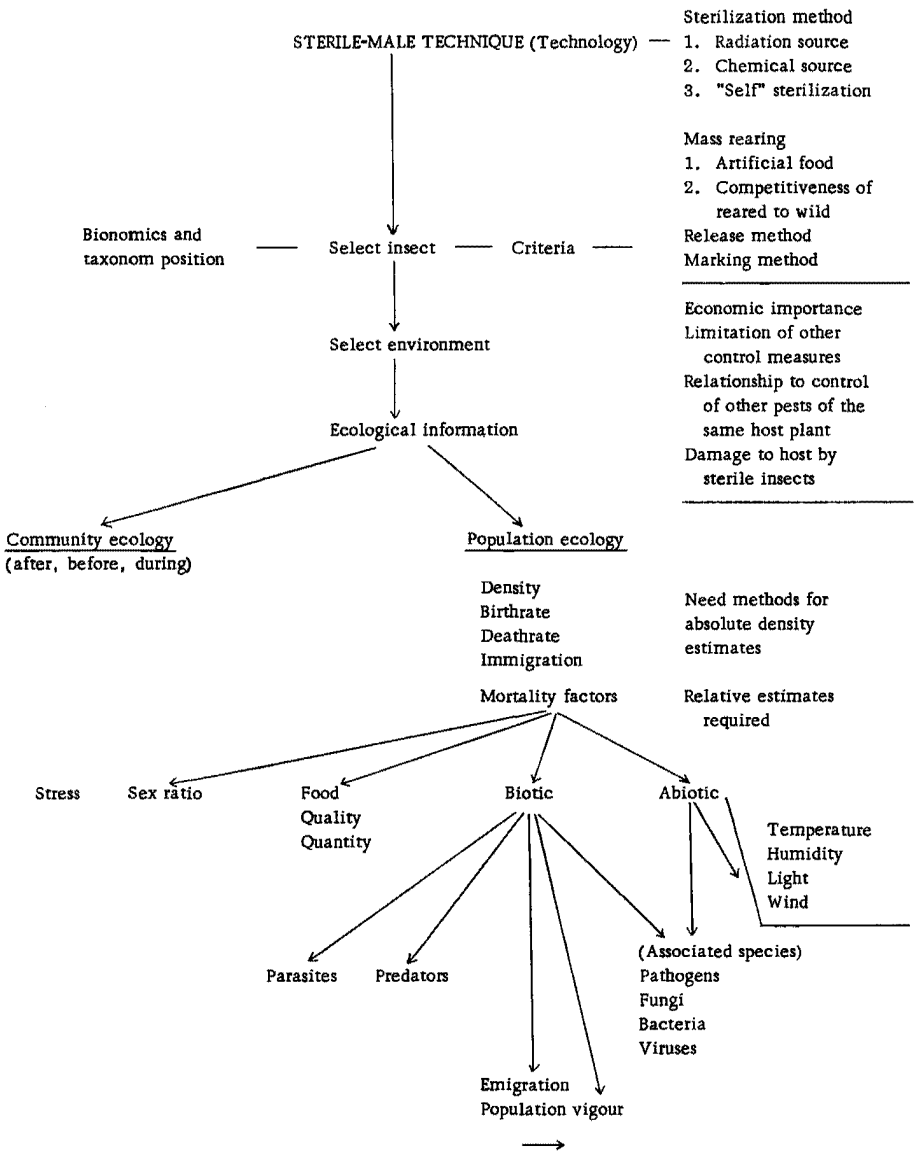
1. The team should try to 'farm out' any segments of the project that are readily detachable, especially to local research centres when available. Such items might be problems of behaviour, diapause, systematics of associated animals, etc.

2. On completion of the project, someone, preferably local, should remain responsible for making periodic checks and reports on the situation.

Finally, the Panel recommends that, whenever possible, efforts should be made to derive from studies of this kind maximum information of fundamental interest to population biology. This would imply, in certain circumstances, a deliberate shift of emphasis from exclusively technological applications to goals of a more scientific nature.

The views of the Panel on the ideal structure of an evaluation study in the field are summarized diagrammatically in Table I.

TABLE I. DIAGRAMMATIC SUMMARY OF PANEL RECOMMENDATIONS FOR FIELD STUDIES



Time factor: Minimum 3 generations or one year before and during sterile insect release
After: Emphasis shifts from "Population Ecology" to "Community ecology"

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