

Dispersion Studies of *Culex pipiens fatigans* Tagged with ^{32}P in the Kemmendine Area of Rangoon, Burma*

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The flight range and the dispersion of a vector are important factors when control or eradication measures are being considered and when general biological information is desired. The present work on Culex pipiens fatigans was carried out under conditions where breeding is intensive and housing congested. The radioactive tagging method adopted seemed to be harmless to the mosquito and gave excellent results.

Radioactive adults emerging under normal conditions from larvae collected in the centre of the Kemmendine Experimental Area did not appear to differ in flight behaviour from radioactive adults released at one time in the centre. Mosquitos of both sexes dispersed fairly evenly in all directions from the release point; this fact is likely to be of practical value in control and biological experiments. Some mosquitos even crossed a river over one-third of a mile (500 m) wide and specimens were collected by hand more than 1/2 mile (800 m) from the release point without the use of lures or traps.

The method also yielded valuable data on the daily mortality of adults and on the total mosquito population in the area. There seems little doubt that the radioisotope tagging technique can be a most valuable weapon in the hands of the biologist or epidemicologist.

In order to devise satisfactory and economical measures for controlling insects, it is necessary to know their dispersion habits. The use of radioactive materials has greatly facilitated studies of the dispersion of many species of insects during the past 15 years. It was decided to undertake a study of the dispersion habits of *Culex pipiens fatigans*, the vector of filariasis, under very congested housing conditions in the Kemmendine area of Rangoon, Burma, utilizing ^{32}P as a marker for released mosquitos. When the present work began, the WHO Filariasis Research Unit (FRU) had already made extensive studies in Kemmendine on the ecology

of *C. p. fatigans*. The main objective of the present research was to obtain information on: (1) the distance both sexes travel, (2) the distribution of released mosquitos over the study area, (3) the direction and speed of travel, and (4) any other biological aspects.

FIRST FIELD EXPERIMENT: RELEASE OF LARVAE

The study area

The flight-study locality was in the Kemmendine Experimental Area of Rangoon,¹ which has been intensively studied for two years by the WHO Filariasis Research Unit. The area covers approximately one square mile (2.6 km²) and has a population of about 40 000 (1961 census). It is bounded on the west by the Rangoon river, which is one-third of a mile (500 m) wide. The land is nearly level and the only possible barriers to the migration or dispersion of mosquitos are the numerous houses, trees and stone walls. Most of the streets are lined with mango and jackfruit trees and smaller types of

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¹ For a map of the area, see the paper on page 67 of this issue.

vegetation. Large tropical trees abound along some streets and in the monasteries.

The streets west of Kemmendine Avenue are all paved. They are for the most part narrow and measure 25 ft (7.6 m) from drain to drain. On both sides of the streets there are 1-ft (0.3-m)-wide concrete drains which carry off rainwater, domestic water, public-washing water from street stand-pipes and any other waste water. These drains become clogged with trash, filth and soil, causing the water to move sluggishly or not at all. This creates perfect conditions for the breeding of enormous numbers of *C. p. fatigans* throughout the area. In addition to the streets, there are narrow—10-foot- (3-m)-wide—unimproved alleys with concrete drains behind the houses.

The eastern section has earth streets with earth drains. The houses are smaller, of poorer construction and made mainly of bamboo lattice; they have thatched roofs. Sanitation is poorer than in the western section.

The houses throughout the area are typically Burmese, being of wood and bamboo-lattice construction with sheet-iron or thatched roofs. They are separated from each other by at most 2 ft (0.6 m). In height they range from 15 to 20 ft (4.6 to 6.1 m). Two to four families, depending on their size, live in each house and the living quarters per family range from 200 ft² to 600 ft² (18.6 m² to 55.7 m²). According to a census made by FRU there are about 3700 houses in the FRU Kemmendine experimental area, which is slightly smaller than the area in which the flight experiments were carried out.

Also in the area are four large *pongyi kyaungs* (monasteries) with house compounds surrounded by stone or brick walls 10-12 ft (3.05-3.65 m) high. In addition there are the Bishop Bigandet Home, a large school compound, a leper asylum and a football field, the latter two surrounded by high stone walls. Markets abound along several of the streets.

The conditions under which this experiment was done differ greatly from those in the swamps and large uninhabited areas where Bidlingmayer & Schoof (1957) and Provost (1952, 1957) studied the dispersion of *Aedes taeniorhynchus* in Georgia and Florida, USA. They also differ considerably from those in the site where Gillies (1961) studied the dispersion of *Anopheles gambiae* in the foothills of the Eastern Usambara Mountains in Africa; that area was moderately populated and contained about 600 houses scattered over a 1¼-mile (2-km) radius. Afridi & Abdul Majid (1938) studied the dispersion

of *C. p. fatigans* in New Delhi, India, where a sewage farm outside the city was the source of enormous breeding. These mosquitos traversed 1¼ miles (2 km) of open land to the nearest inhabited part of New Delhi and caused considerable annoyance to the people. The authors used coloured dust as a marker on *C. p. fatigans*, which were released at the sewage farm. Collecting stations were scattered over New Delhi. One coloured specimen was caught in the northern part of the city, 5500 yd (5 km) from the sewage farm. Here also the conditions were different from those in the present experiment.

The chief characteristics of the Kemmendine area therefore are the thousands of houses, high stone fences around the monasteries, hospitals and football field, heavy *C. p. fatigans* breeding and a dense human population. The average number of people per acre of occupied land in 80, giving 531 ft² (49.3 m²) per person, including roads, alleys, lanes, gardens and so on. Because of the numerous breeding sites available, the plants providing shade and nectar, and the dense human population for blood-meals, it seems that *C. p. fatigans* has no need to fly more than a few feet to fulfil all its biological requirements.

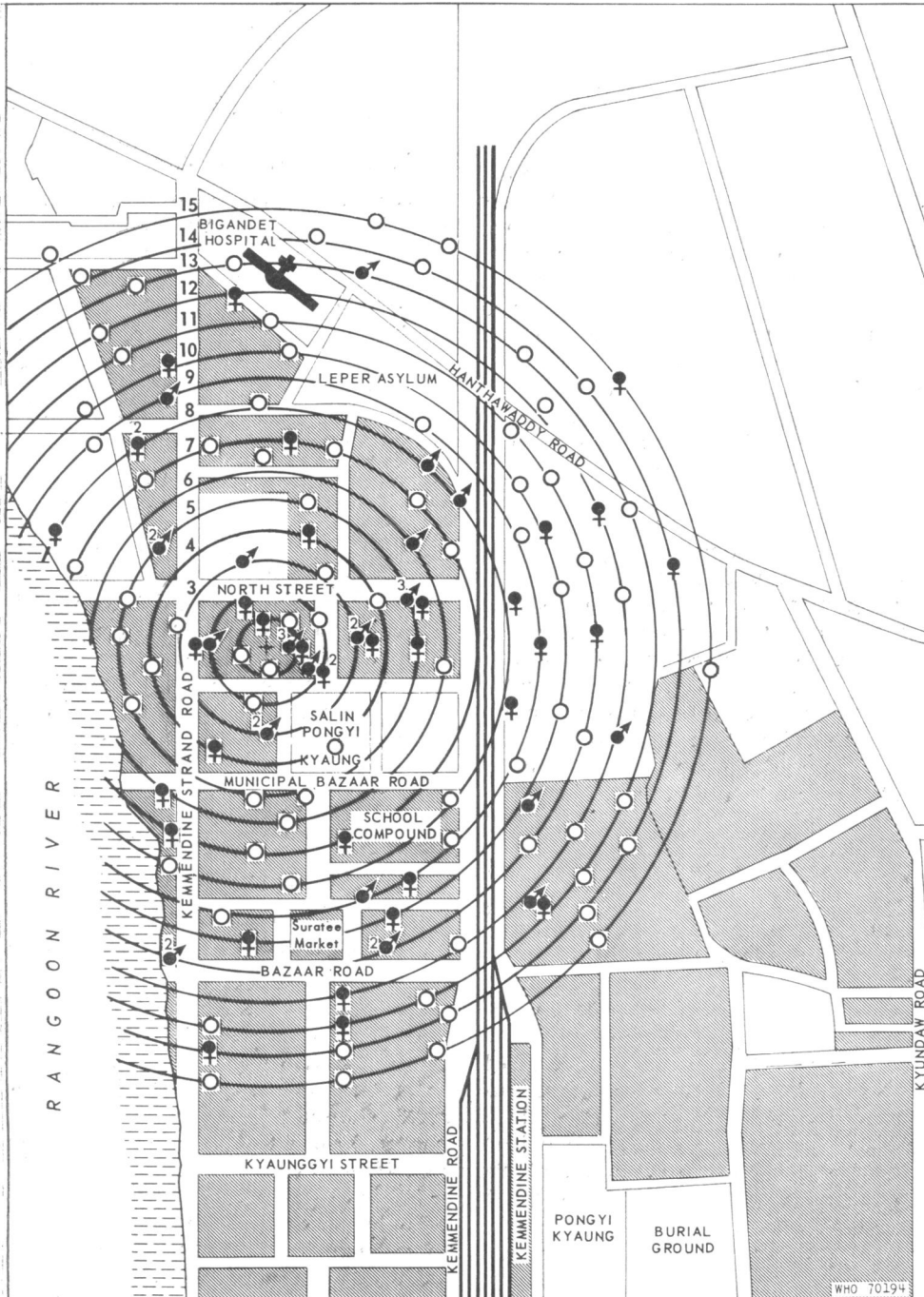
General plan

As it was not known how far *C. p. fatigans* might disperse under congested conditions and as the number of collectors was inadequate, the first experiment was designed somewhat differently from the usual type of flight study. Usually traps or insect collectors are set up at various distances from the release point and operate on a daily basis for the duration of the experiment.

In the present experiment concentric circles 150 ft (46 m) apart were laid out over a map of the Kemmendine area. Approximately one-sixth of the outermost circle (No. 15) extended over the Rangoon river and the circle also extended beyond the confines of the regular FRU study area to the south and north-east. Catching stations were plotted on the circles, as indicated in Fig. 1. The first six circles had five stations each but the remaining nine circles had 10 stations each.

The general plan was to start collecting along the inner circles but to move outward each day. Only 10 trained mosquito collectors were available. Since the first six circles had only five stations each, the men collected there on two circles each day, but

FIG. 1

LOCATION OF COLLECTING STATIONS AND RECAPTURED TAGGED *C. P. FATIGANS* IN FIRST FIELD EXPERIMENT^a^a The male or female sign without a number against it indicates a single recaptured specimen.

after reaching circle No. 7, which had 10 stations, they moved outward one circle per day.

Rearing and release

The larvae used in both field experiments were third- and fourth-stage larvae collected only a few feet from the release point. By this procedure, no new mosquitos were introduced into the population when they were subsequently released. The buckets of collected larvae and water were brought to the laboratory for the numbers to be estimated; several methods were tried and the most satisfactory was weighing after straining the larvae through a screen and placing them on filter-paper. This treatment did not appear to injure the larvae.

Between 60 000 and 70 000 larvae were placed in sheet-iron vats of dimensions 30 in \times 24 in \times 5 in (76 cm \times 61 cm \times 13 cm). Tap water (17.4 litres) was added to each of four vats, together with ground dog-biscuits for larval food. Radioactive phosphoric acid (^{32}P) was added at a concentration of 0.05 $\mu\text{Ci/ml}$ of water on 13 January. Reports in the literature indicate that ^{32}P at this concentration is usually adequate to tag various species of mosquito larvae. Preliminary laboratory tests with *C. p. fatigans* were made at this concentration as well as at 0.025 $\mu\text{Ci/ml}$ and 0.1 $\mu\text{Ci/ml}$ of water. The uptake of ^{32}P by the larvae depends on the length of time they are exposed in the water to the radioisotope; it is also influenced by the number of larvae present, the amount of organic matter in the water and the type of container used.

Because the larvae were of different ages at the start, they showed a variation in the counts per minute recorded on the scaler. However, the adult mosquitos emerging from the treated larvae were tagged sufficiently for the purpose of this experiment. Counts per minute on the scaler ranged from 400 to 1900 for the females and 300 to 1300 for the males.

On 15 January, larvae and pupae were removed from the vat by straining the water through screens and were transported to the release centre, where they were placed in Pegu jars (earthenware jars) 20 in (51 cm) in diameter located in a specially built bamboo-lattice structure against the front of a house. Emergence of mosquitos commenced during the night of 15 January. Two similar cultures of larvae were prepared but the concentration of ^{32}P was increased to 0.075 $\mu\text{Ci/ml}$ of water in the vats. The approximate numbers of larvae released were:

Released	
15 January	271 000
20 January	300 000
21 January	157 000
	<u>728 000</u>
Removed on 27 January	145 000
Total released	<u>583 000</u>

Collection of adult mosquitos

Collection of the adult mosquitos was done by hand in houses. Spreading sheets on the floor and using pyrethrum aerosols to knock down the mosquitos was not practical because the houses were not tightly constructed. The use of boxes inside the houses to serve as traps for *C. p. fatigans* was not promising in a preliminary test but should be investigated further.

Each station actually consisted of three or more adjacent houses and the men usually worked in teams of two, collecting for a total of four hours, beginning at 07.00 hours; occasionally a man would be absent or an extra man available, in which case the number of hours at one or two stations would be altered. The number of *C. p. fatigans* collected per man-hour could thus be calculated. One three-hour collection was made on 29 January in the village of Setkale across the Rangoon river.

When two consecutive days of collecting on circle No. 15 yielded no radioactive *C. p. fatigans*, search was resumed on the inner circles, as indicated in Table 1.

The collectors placed the mosquitos in Barraud cages, which were then brought to the laboratory, where the mosquitos were killed and examined for radioactivity on the portable five-decade battery-operated scaler. The scaling unit was a Type 1287 A unit (Dynatron Radio) and the Geiger-Müller tube a Type M \times 108/01 with a window thickness of 1.5-2.5 mg/cm² located in a closed hard-wood box. The end-window opened to the bottom of the box over a built-in slide tray. This was designed originally for exposing blood specimens on 1 \times 3 glass slides, but it was found that individual mosquitos could be taped on to a slide or a piece of paper and inserted for counting. The specimen was approximately 1/8 in (3 mm) from the window of the Geiger-Müller tube.

To detect radioactive mosquitos in large samples, an ordinary 1-in (2.5-cm) Monel Metal planchet was mounted on supports so as to bring the mosquito sample to within 5/8 in (16 mm) of the tube. The number of counts per minute was lower than that

obtained from the slide-mounted specimens, but the planchet method was suitable for scanning 100 or more mosquitos at a time and for the subsequent counting of individual specimens to obtain comparative values.

Results

Weather conditions. The average daily maximum temperature during January was 30.6°C (87.3°F) and the average daily minimum 19.0°C (66.9°F). These are 1.5degC (2.8degF) and 0.8degC (1.5degF), respectively, below the 10-year average from 1950 onwards. From 1 to 13 February (when the experiment was terminated) the temperature was close to normal. The weather was bright and seldom cloudy, with no rain; it was generally calm or with light winds, with an average speed of 4 mi/h (6.4 km/h).

Emergence of released C. p. fatigans. After the release of larvae it was observed during mid-morning that, if the numerous *C. p. fatigans* around the Pegu jars at the release point were disturbed, they would fly upwards for 20 ft-25 ft (6 m-7½ m) and then fly away over the trees and housetops. No doubt some of the mosquitos flew horizontally and followed the streets, but it is significant that those observed flew upwards; de Meillon (1937), working with *A. gambiae* in Northern Rhodesia (now Zambia), observed the same phenomenon. This first upward flight probably accounts for the speed and distance of travel observed. Emergence of mosquitos continued daily over a 13-day period and averaged about 45 000 per day.

Number of C. p. fatigans caught. In all, 46 275 *C. p. fatigans*, almost equally divided as to sex, were caught over the 23-day period of collecting (Table 1). This is an average of 50 per man-hour of collecting. They were caught at 225 sites, several of which were visited twice during the period. The data in Table 1 also include the total number of *C. p. fatigans* collected in each circle each day and the ratio of tagged to untagged for each day. The number caught per circle per day varies somewhat, but in general is fairly uniform.¹ *C. p. fatigans* represented over 99% of the total catch, the other species being *Aedes aegypti* and *Lutzia* sp.

Tagged C. p. fatigans recaptured. Of the *C. p. fatigans* caught, 31 males and 36 females were radio-

active. 0.011% of the released mosquitos were recaptured. The total of 67 radioactive mosquitos represents 0.14% of the total number of *C. p. fatigans* caught in the houses.

In view of the small number of houses examined each day, the recovery rate was very satisfactory and also indicated an even distribution of tagged mosquitos over the area. Furthermore, the collectors could take only a small fraction of the total mosquitos in a house. In addition, vast numbers of *C. p. fatigans* rest on vegetation, in containers, jars, boxes and in underground drains, which were generally not sampled; a few collections on vegetation yielded two radioactive specimens.²

The ratio of tagged to untagged mosquitos averaged 1:691 for the period of collecting but ranged from 1:100 to 1:1359. It can be stated that under the conditions of this experiment there was an average of approximately one radioactive *C. p. fatigans* for each 700 caught in houses.

A total of 51 stations or 22.7% of the total number of stations (225) yielded tagged *C. p. fatigans*. This is a surprisingly high percentage of positive stations.

Distribution. Table 1 and Fig. 1 show that *C. p. fatigans* dispersed in all directions from the release point in a remarkably uniform pattern. Both males and females were distributed over the area. The effect of wind on distribution cannot be determined because of the low wind speed and the shifting of the wind from north to south each day or two. However, in this experiment there appeared to be a tendency for *C. p. fatigans* to move south in greater numbers than either east or north. If the number of positive stations from circle No. 8 (Table 1 and Fig. 1) outward is examined, it is noted that there were 11 to the east, nine to the south and seven to the north. Collections were made from a total of 30 stations to the east, 19 to the south and 20 to the north. The ratio of positive stations to the total number of mosquitos captured in each direction (beyond circle 8) is 1:909 in the east, 1:443 in the south and 1:1018 in the north.

Distance travelled. To determine the maximum distance that any insect will fly or travel is very difficult. A great number of traps or collectors would be required. In this experiment only an approximation of the distance travelled could be made. The fact that two *C. p. fatigans* males and one female were caught across the Rangoon river, a distance of 0.55 mile (880 m) from the release

¹ A detailed breakdown of these figures, giving the number of tagged and untagged mosquitos caught at each station each day, is included as Table 2 in the unpublished document WHO/Vector Control/157.65, available, on request, from Vector Biology and Control, World Health Organization, Geneva, Switzerland.

² See the paper on page 67 of this issue.

TABLE 1
SUMMARY OF TAGGED AND UNTAGGED C. P. FATIGANS COLLECTED IN HOUSES DURING FIRST FIELD EXPERIMENT

Date of collection	Circle no.	Stations	Distance from centre (yd) ^a	No. caught		Total males and females	No. of mosquitoes per man-hour		No. radioactive		No. of stations positive	Ratio tagged to untagged		% of catch radio-active
				Males	Females		Males	Females	Males	Females		Both sexes		
January														
18	1 & 2	1-10	50-100	1 567	1 062	2 629	66	5	6	1:313	5	1:177	1:239	0.42
19	3 & 4	11-20	150-200	1 499	1 056	2 555	64	5	3	1:300	5	1:352	1:319	0.31
20	5 & 6	21-30	250-300	1 405	739	2 144	56	2	2	1:702	4	1:369	1:536	0.19
21	7	31-40	350	1 387	827	2 214	55	0	3	—	3	1:276	1:738	0.14
22	8	41-50	400	1 485	1 108	2 593	65	0	0	—	4	1:554	1:1297	0.08
23	9	51-60	450	1 148	1 151	2 299	52	2	2	1:574	4	1:576	1:575	0.18
25	10	61-70	500	624	773	1 397	35	1	4	1:624	5	1:193	1:279	0.36
26	11	71-80	550	849	980	1 829	42	1	1	1:849	2	1:980	1:914	0.11
27	12	81-90	600	956	1 585	2 541	63	1	4	1:956	4	1:396	1:508	0.20
28	13	91-100	650	1 021	1 116	2 137	49	1	1	1:1021	2	1:1116	1:1068	0.09
29	Across river	(1-10)	975	199	715	914	23	2	1	1:100	2	1:715	1:305	0.33
30	14	101-110	700	544	793	1 337	30	0	2	—	2	1:396	1:668	0.15
February														
1	15	111-120	750	346	554	900	23	0	0	—	0	—	—	—
Subtotal		130		13 030	12 459	25 489	47	20	31	1:652	39	1:402	1:500	0.20
February														
2	15	111-120	750	626	942	1 568	39	0	0	—	0	—	—	—
3	11	71-80	550	1 032	1 045	2 077	52	3	3	1:344	2	—	1:692	0.14
4	8	41-50	400	1 397	1 405	2 802	70	2	3	1:698	5	1:468	1:560	0.18
5	5	21A-25A	250	1 367	1 273	2 640	66	4	1	1:342	2	1:1273	1:528	0.19
6	15	111-120	750	528	687	1 215	30	0	1	1:579	1	1:667	1:1215	0.08
8	12	81-90	600	579	780	1 359	42	0	0	—	1	—	1:1359	0.07
9	10	61-70	500	1 089	1 203	2 292	57	0	0	—	0	—	—	—
10	7	31-40	350	1 441	1 510	2 951	74	0	0	—	0	—	—	—
11	3	11-15	150	876	778	1 654	69	0	0	1:876	1	—	1:1654	0.06
13	4	16-20A	200	1 205	1 023	2 228	70	0	0	—	0	—	—	—
Subtotal		95		10 140	10 646	20 786	55	11	5	1:922	12	1:2129	1:1299	0.08
Total		225		23 170	23 105	46 275	50	31	36	1:748	51	1:642	1:691	0.14

^a 1 yard = 0.914 metre.

point, indicates that at least some of the population will travel over water as well as over land. A point of interest is that when collections were made at Setkale, across the Rangoon river from Kemmendine, no breeding of *C. p. fatigans* was observed in the village. However, 914 *C. p. fatigans* (23 per man-hour) were recovered. Since on the west Setkale is adjacent to rice-paddy fields (which do not produce the species), it seems likely that most of these mosquitos came across the river from the dense breeding areas in Kemmendine.

Only one radioactive specimen, a female, was captured on circle No. 15 over the land area to the east, almost 0.25 mile (400 m) from the centre. It is recognized that if more men had been stationed farther out, radioactive mosquitos would probably have been collected.

The fact that males travelled in good numbers as far as 0.20 mile (320 m) or more is encouraging if experimental work is initiated on the possible control of *C. p. fatigans* by the release of sterile males. Distribution of released sterile males would be efficient because of the distance they fly.

It is clear that, to give absolute protection to an inner area, insecticide-treated barrier zones must be of considerable width, probably at least one mile or more. However, the percentage of *C. p. fatigans* that travel over a mile is exceedingly small, perhaps less than 5%, so that the risk of reinfestation of a clean area becomes increasingly less with the distance.

SECOND FIELD EXPERIMENT: RELEASE OF ADULTS

General plan

Twenty additional men were provided by the Rangoon Corporation for the second field test. These men had been previously trained as mosquito collectors by FRU. Thirty stations were therefore established on five concentric circles 200 yd (183 m) apart (Fig. 2). A major difference in this experiment was that adult *C. p. fatigans* were released. The larval releases had led to considerable complaints of excessive numbers of mosquitos from the householders adjacent to the release point, even though immense natural breeding occurred at the very doors of the houses. There were no vacant houses or open areas that could be used for a release point, so the adults were released in a street.

Rearing, release and collection of adults

Larvae were collected and handled as before, except that several smaller vats were employed, each

of which was covered by a cage to hold the adults, which were fed a sugar-water solution; ³²P was added to the vats at a concentration of 0.075 μ Ci/ml of water late on 11 February. Approximately 280 000 adult *C. p. fatigans* 1-3 days old were released on the street at twilight (18.30 hours) on 16 February. It was observed that the mosquitos flew upwards for about 25 ft (7½ m), beyond which they could not be seen. Soon typical mating swarms appeared. As in the first experiment, this upward flight probably accounted for the observed speed and distance of flight. The experiment was terminated on 27 February after 10 days of collecting; this time there were no complaints from the householders.

Results

Weather conditions. The average daily maximum temperature during the period of this test was 35.6°C (96.1°F) and the average daily minimum 20°C (68°F). The maximum was 1.8degC (3.4degF) above normal, and the minimum 0.5degC (1.1degF) below normal. There was no rain and the weather was bright, with no or only light wind.

Number of C. p. fatigans caught. Altogether 64 695 *C. p. fatigans* were collected in houses during 10 days at the 30 stations (Tables 2-4);¹ 58% were females. The number of collections was 300. The average number of mosquitos caught per man-hour was 53. Again *C. p. fatigans* represented over 99% of the total catch. It will be noted that the number of mosquitos caught at the stations varied considerably (Tables 2 and 3). This is because the number of mosquitos in houses varied and because the collectors differed in skill and energy. However, it is seen from Fig. 3 that the daily number of captures per station followed a rather similar pattern on the successive circles, although, constantly, more mosquitos were collected per station on the second circle (radius 400 yd (366 m)). A particularly large number of mosquitos were collected on the last day in the second and fifth circles.

Tagged C. p. fatigans recaptured. The total number of radioactive *C. p. fatigans* recaptured was 117—34 males and 83 females. The percentage of males (29%) is considerably less than in the first experiment. Of the mosquitos released 0.042% were recaptured, a considerably higher percentage than in the first experiment. The number recaptured

¹ A detailed breakdown of the figures in Table 2, giving the number of tagged and untagged mosquitos caught at each station each day, is included as Table 3 in the unpublished document WHO/Vector Control/157.65.

FIG. 2
 LOCATION OF COLLECTING STATIONS AND NUMBERS OF RECAPTURED *C. P. FATIGANS*
 IN SECOND FIELD EXPERIMENT

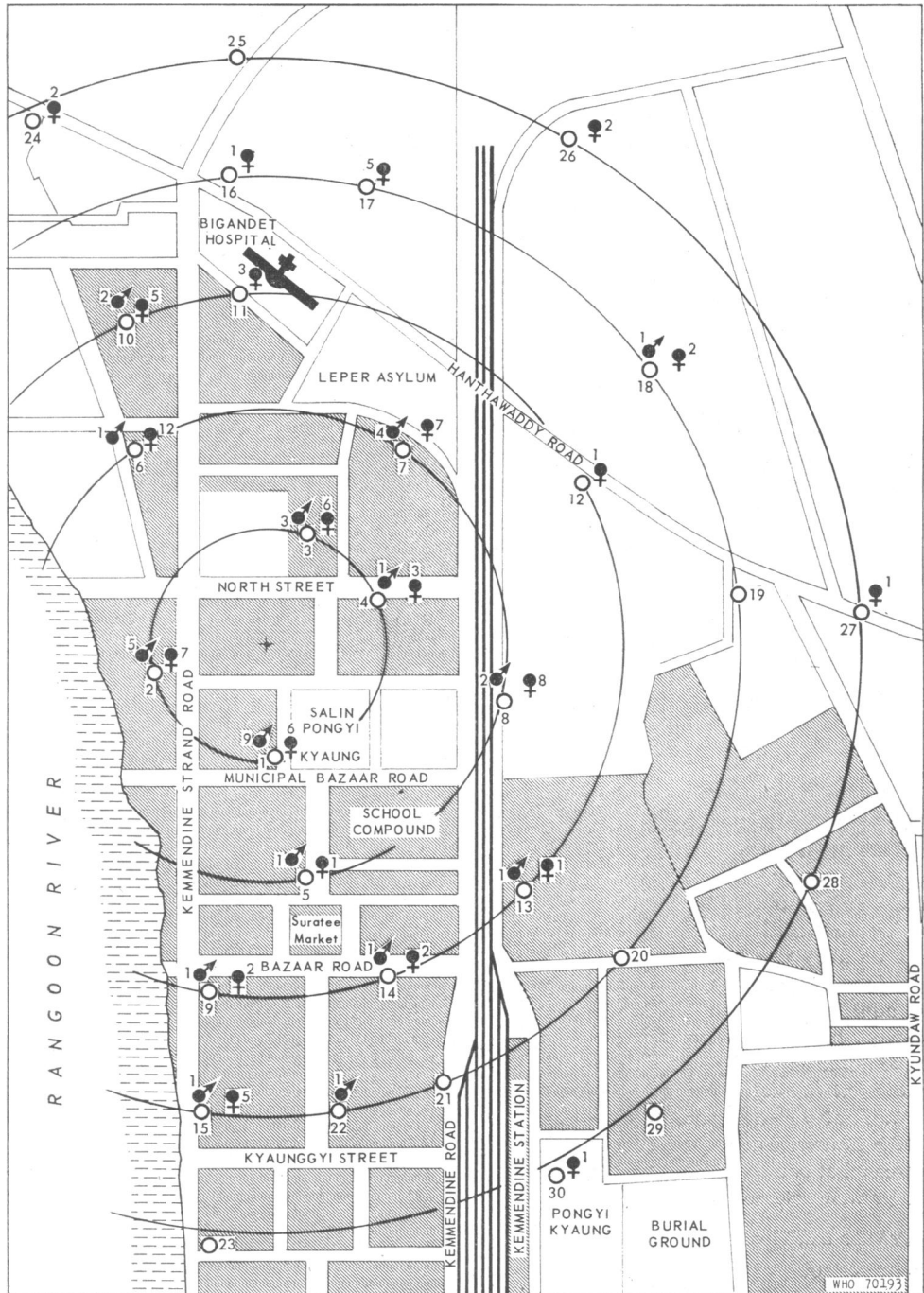


TABLE 2
NUMBER OF TAGGED AND UNTAGGED *C. P. FATIGANS* COLLECTED IN EACH CIRCLE EACH DAY DURING THE SECOND FIELD EXPERIMENT

Date of collection	Circle no.	Stations	Distance from centre (yd) α	No. caught		Total males and females	No. of mosquitoes per man-hour	No. radioactive		No. of stations positive	Ratio tagged to untagged			% of catch radio-active
				Males	Females			Males	Females		Males	Females	Both sexes	
17 Feb.	1	1-4	200	231	235	466	29	3	5	4	1:77	1:35	1:58	1.71
	2	5-8	400	531	493	1 024	64	2	5	3	1:266	1:99	1:146	0.68
	3	9-14	600	372	417	789	33	0	3	2	—	1:139	1:263	0.38
	4	15-22	800	279	483	762	24	0	2	2	—	1:242	1:381	0.26
	5	23-30	1 000	546	703	1 249	39	0	0	0	—	—	—	—
Total		30		1 959	2 331	4 290	36	5	15	11	1:392	1:155	1:215	0.47
18 Feb.	1	1-4	200	194	285	479	30	1	3	3	1:194	1:95	1:120	0.83
	2	5-8	400	608	709	1 317	67	1	6	3	1:608	1:122	1:191	0.52
	3	9-14	600	603	573	1 176	59	1	2	3	1:603	1:267	1:392	0.26
	4	15-22	800	373	607	980	61	1	3	2	1:373	1:202	1:245	0.41
	5	23-30	1 000	770	1 119	1 889	59	0	3	2	—	1:373	1:630	0.16
Total		30		2 548	3 313	5 861	51	4	17	13	1:637	1:195	1:279	0.36
19 Feb.	1	1-4	200	356	421	777	48	1	3	3	1:356	1:140	1:194	0.51
	2	5-8	400	524	770	1 294	81	0	5	3	—	1:154	1:259	0.39
	3	9-14	600	562	597	1 159	48	0	0	0	—	—	—	—
	4	15-22	800	346	940	1 286	40	0	4	2	—	1:235	1:322	0.31
	5	23-30	1 000	730	1 003	1 733	54	0	1	1	—	1:1003	1:1733	0.06
Total		30		2 518	3 731	6 249	52	1	13	9	1:2518	1:287	1:518	0.22
20 Feb.	1	1-4	200	687	487	1 174	59	9	1	3	1:76	1:487	1:117	0.85
	2	5-8	400	470	730	1 200	60	1	3	3	1:470	1:243	1:300	0.33
	3	9-14	600	681	695	1 376	49	1	2	2	1:681	1:348	1:459	0.22
	4	15-22	800	392	836	1 228	34	0	0	0	—	—	—	—
	5	23-30	1 000	842	1 117	1 959	61	0	0	0	—	—	—	—
Total		30		3 072	3 865	6 937	61	11	6	8	1:279	1:644	1:408	0.25
22 Feb.	1	1-4	200	356	630	986	62	1	2	2	1:356	1:315	1:329	0.30
	2	5-8	400	791	895	1 686	105	0	4	1	—	1:448	1:843	0.12
	3	9-14	600	581	809	1 390	38	0	2	2	—	1:202	1:348	0.28
	4	15-22	800	365	820	1 185	37	0	2	2	—	1:410	1:593	0.17
	5	23-30	1 000	671	1 049	1 720	54	0	0	0	—	—	—	—
Total		30		2 764	4 203	6 967	58	1	10	7	1:2764	1:420	1:633	0.16

α 1 yd = 0.914 metre.

TABLE 2 (continued)
 NUMBER OF TAGGED AND UNTAGGED C. P. FATIGANS COLLECTED IN EACH CIRCLE EACH DAY DURING THE SECOND FIELD EXPERIMENT

Date of collection	Circle no.	Stations	Distance from centre (yd) ^a	No. caught		Total males and females	No. of mosquitoes per man-hour	No. radioactive		No. of stations positive	Ratio tagged to untagged			% of catch radio-active
				Males	Females			Males	Females		Males	Females	Both sexes	
23 Feb.	1	1-4	200	407	430	837	70	2	4	3	1:204	1:108	1:140	0.72
	2	5-8	400	596	551	1147	71	3	3	3	1:199	1:184	1:191	0.52
	3	9-14	600	580	602	1182	49	0	1	1	—	1:602	1:1182	0.08
	4	15-22	800	478	882	1360	42	0	1	1	—	1:882	1:1360	0.07
	5	23-30	1 000	561	1 006	1 567	49	0	0	0	—	—	—	—
Total		30		2 622	3 471	6 093	53	5	9	8	1:524	1:386	1:435	0.23
24 Feb.	1	1-4	200	246	485	731	46	1	2	2	1:246	1:243	1:244	0.41
	2	5-8	400	530	614	1 144	71	0	2	1	—	1:307	1:572	0.17
	3	9-14	600	285	400	685	28	1	0	1	1:285	—	1:685	0.15
	4	15-22	800	471	889	1 360	42	0	0	0	—	—	—	—
	5	23-30	1 000	1 031	1 154	2 185	79	0	0	0	—	—	—	—
Total		30		2 563	3 542	6 105	53	2	4	4	1:1282	1:886	1:1018	0.10
25 Feb.	1	1-4	200	452	551	1 003	63	0	2	2	—	1:276	1:502	0.20
	2	5-8	400	612	837	1 449	91	1	2	2	1:612	1:419	1:483	0.21
	3	9-14	600	452	685	1 137	47	0	0	0	—	—	—	—
	4	15-22	800	333	997	1 330	42	1	1	2	1:333	1:997	1:665	0.15
	5	23-30	1 000	784	1 112	1 896	59	0	0	0	—	—	—	—
Total		30		2 633	4 182	6 815	57	2	5	6	1:1317	1:836	1:974	0.10
26 Feb.	1	1-4	200	403	710	1 113	70	0	0	0	—	—	—	—
	2	5-8	400	749	882	1 631	102	0	0	0	—	—	—	—
	3	9-14	600	343	494	837	35	2	1	2	1:172	1:494	1:279	0.36
	4	15-22	800	689	874	1 543	48	1	0	1	1:669	1:884	1:1543	0.06
	5	23-30	1 000	803	884	1 687	52	0	1	1	—	1:884	1:1687	0.06
Total		30		2 967	3 844	6 811	57	3	2	4	1:989	1:1922	1:1362	0.07
27 Feb.	1	1-4	200	653	1 073	1 726	108	0	0	0	—	—	—	—
	2	5-8	400	667	896	1 563	98	0	0	0	—	—	—	—
	3	9-14	600	539	642	1 181	49	0	1	1	—	1:642	1:1181	0.08
	4	15-22	800	433	871	1 304	41	0	0	0	—	—	—	—
	5	23-30	1 000	1 584	1 209	2 793	87	0	1	1	—	1:1209	1:2793	0.04
Total		30		3 876	4 691	8 567	71	0	2	2	—	1:2346	1:4284	0.02

^a 1 yd = 0.914 metre.

TABLE 3
TOTAL *C. P. FATIGANS* CAUGHT AT EACH STATION DURING SECOND
FIELD EXPERIMENT

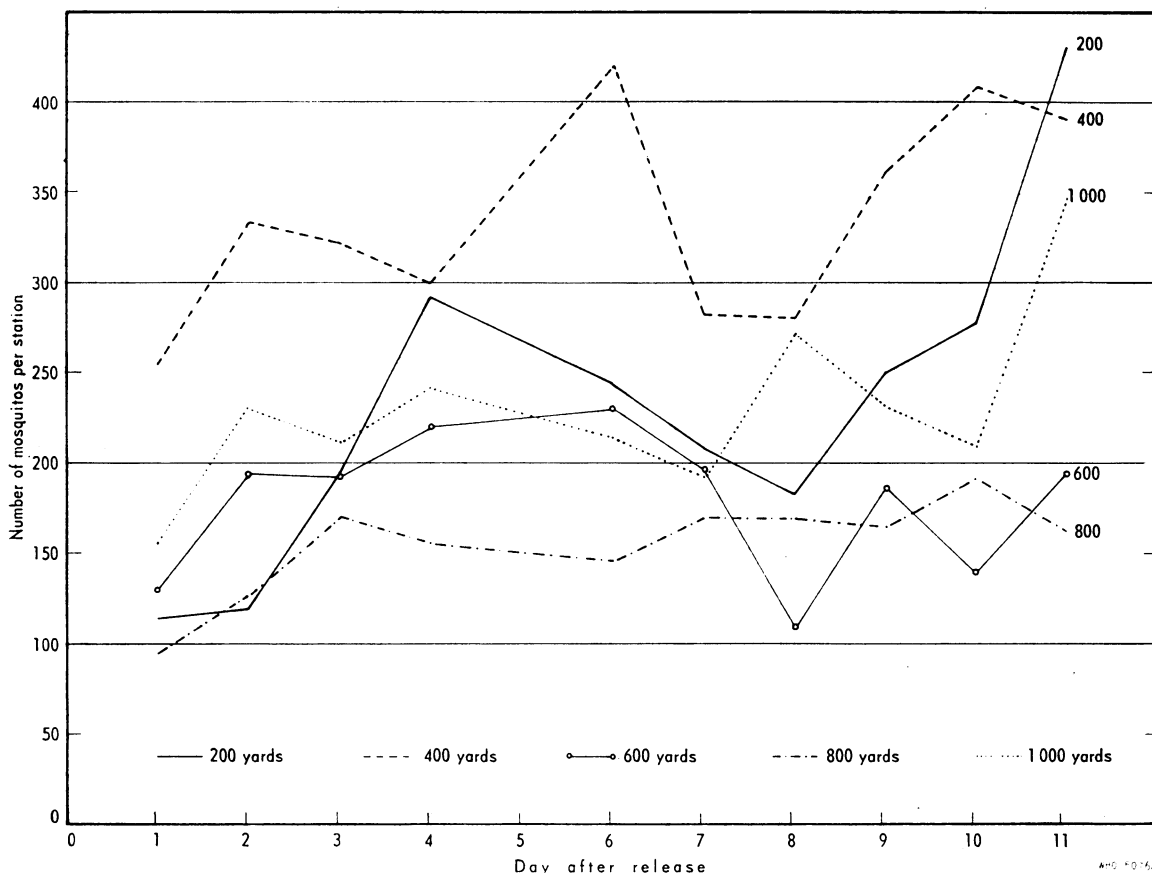
Circle no.	Station no.	No. caught		Total no. males and females	No. radioactive	
		Males	Females		Males	Females
1	1	1 353	1 390	2 743	9	6
	2	1 022	1 751	2 773	5	7
	3	727	1 218	1 945	3	6
	4	883	948	1 831	1	3
2	5	1 394	1 756	3 150	1	1
	6	2 310	2 664	4 974	1	12
	7	1 336	1 867	3 203	4	7
	8	1 038	1 110	2 148	2	8
3	9	658	1 287	1 945	1	2
	10	1 387	974	2 361	2	5
	11	1 566	1 790	3 356	0	3
	12	287	503	790	0	1
	13	762	867	1 629	1	1
	14	338	493	831	1	2
4	15	352	1 535	1 887	1	5
	16	1 599	1 144	2 743	0	1
	17	606	1 476	2 082	0	5
	18	468	1 776	2 244	1	2
	19	179	488	667	0	0
	20	456	611	1 067	0	0
	21	219	506	725	0	0
	22	260	663	923	1	0
5	23	464	852	1 316	0	0
	24	964	1 594	2 558	0	2
	25	678	658	1 336	0	0
	26	901	1 094	1 995	0	2
	27	1 628	1 838	3 466	0	1
	28	331	580	911	0	0
	29	650	999	1 649	0	0
	30	2 706	2 741	5 447	0	1
Total		27 522	37 173	64 695	34	83

TABLE 4
TOTAL CATCH OF *C. P. FATIGANS* IN EACH CIRCLE DURING SECOND FIELD EXPERIMENT

Circle no.	Stations	Distance from centre (yd) ^a	No. caught		Total males and females	No. of mosquitos per man-hour	No. radioactive		No. of stations positive	Ratio tagged to untagged			% of catch radioactive
			Males	Females			Males	Females		Males	Females	Both sexes	
1	1-4	200	3 985	5 307	9 292	55	18	22	4	1 : 221	1 : 241	1 : 232	0.43
2	5-8	400	6 078	7 397	13 475	80	8	28	4	1 : 760	1 : 264	1 : 374	0.27
3	9-14	600	4 998	5 914	10 912	45	5	14	6	1 : 1000	1 : 429	1 : 574	0.17
4	15-22	800	4 139	8 199	12 338	38	3	13	5	1 : 1380	1 : 631	1 : 771	0.13
5	23-30	1 000	8 322	10 356	18 678	58	0	6	4	—	1 : 1726	1 : 3113	0.03
Total			27 522	37 173	64 695	53	34	83	23	1 : 809	1 : 448	1 : 553	0.18

^a 1 yd = 0.914 metre.

FIG. 3
DAILY NUMBER OF MOSQUITOS CAUGHT PER STATION, SEPARATELY FOR EACH RING



represents 0.18% of all of those caught in houses. This somewhat higher recovery than in the first experiment was no doubt caused by the daily collections at all stations. The stations nearest the release point yielded the greatest numbers of tagged mosquitos.

The ratio of tagged to untagged mosquitos for each circle averaged 1 : 553 for 10 days collecting, but ranged from 1 : 221 to 1 : 3113 (Tables 2 and 4). Of the 30 stations, 23 (77%) yielded radioactive mosquitos. The total number of tagged *C. p. fatigans* diminished, and the ratio of tagged to untagged mosquitos increased, on going from inner to outer circles (Table 4).

Distribution. Tables 2 and Fig. 2 show that *C. p. fatigans* dispersed in all directions from the point of release. Both sexes were fairly evenly distributed, but the males did not range as far as in the first experiment. Of special interest is the fact that the concentration of released mosquitos was greatest within the first three circles, which is in line with most previously reported observations on flies and mosquitos.

The distribution of the 117 tagged *C. p. fatigans* collected on the five circles is shown in Table 5.

TABLE 5
DISTRIBUTION OF RADIOACTIVE *C. P. FATIGANS*
COLLECTED IN SECOND EXPERIMENT

Circle no.	Tagged mosquitos collected	
	Number	% of total tagged collected
1	40	34
2	36	31
3	19	16
4	16	14
5	6	5

It is clear that approximately 8% of the *C. p. fatigans* were located within a radius of 600 yd (550 m). In this experiment the males tended to concentrate within the first circle or 200 yd (183 m). Eighteen (53%) of the males caught were located in the four stations on circle No. 1; eight (24%) were caught in circle No. 2 and the remaining 23% in circles No. 3 and 4. No males were caught beyond circle No. 4, i.e., 800 yd (730 m). In the first experiment males were caught across the Rangoon river,

0.55 mile (880 m) from the release point and at points up to 650 yd (595 m) over the land area of Kemmendine.

The fact that both sexes distribute themselves evenly for considerable distances from emergence or release points suggests that localized strains or populations of *C. p. fatigans*, e.g., ones that show differences in susceptibility to insecticides, would not be able to maintain themselves for any length of time. It seems certain that, eventually, the entire population of an area would become mixed and small differences would be smoothed out.

No further tagged mosquitos were taken after day 11 from release. In the first experiment one male and one female were captured 15 days after the last possible day of emergence from the Pegu jars.

Distance and speed of travel. Since the farthestmost collecting stations were set up 1000 yd (915 m) from the centre and tagged *C. p. fatigans* were caught at this distance, the maximum flight range was not determined directly. However, six tagged females were caught at four of the eight stations at the 1000-yd (915-m) circle.

The speed with which *C. p. fatigans* travelled is interesting. On the first collecting day, about 12 hours after release, a female was caught at each of stations No. 17 and 18 on circle No. 4, a distance of 800 yd (730 m). On the second day, or approximately 36 hours after release, two tagged females were recaptured at station No. 24 and one at No. 26, both on circle No. 5, a distance of 1000 yd (915 m) from the centre.

It is interesting to speculate on why the mosquitos should travel more than a few feet. At the emergence and release centre and only a few feet away there are ample sources of nectar, blood-meals and suitable water for oviposition. These conditions prevail over the entire area. Yet the data show that some of the mosquitos travel up to 1000 yd (915 m) in 36 hours while great numbers flew up to 600 yd (550 m) in between 12 and 36 hours.

It appears that the first flight is the response to a migrational instinct, at least in some of the population. The migration may, as Provost (1952, 1957) has postulated in regard to *A. taeniorhynchus*, be non-appetential in character, since the mosquito is flying not in direct response to feeding, mating or oviposition stimuli but more from an "urge to flight".

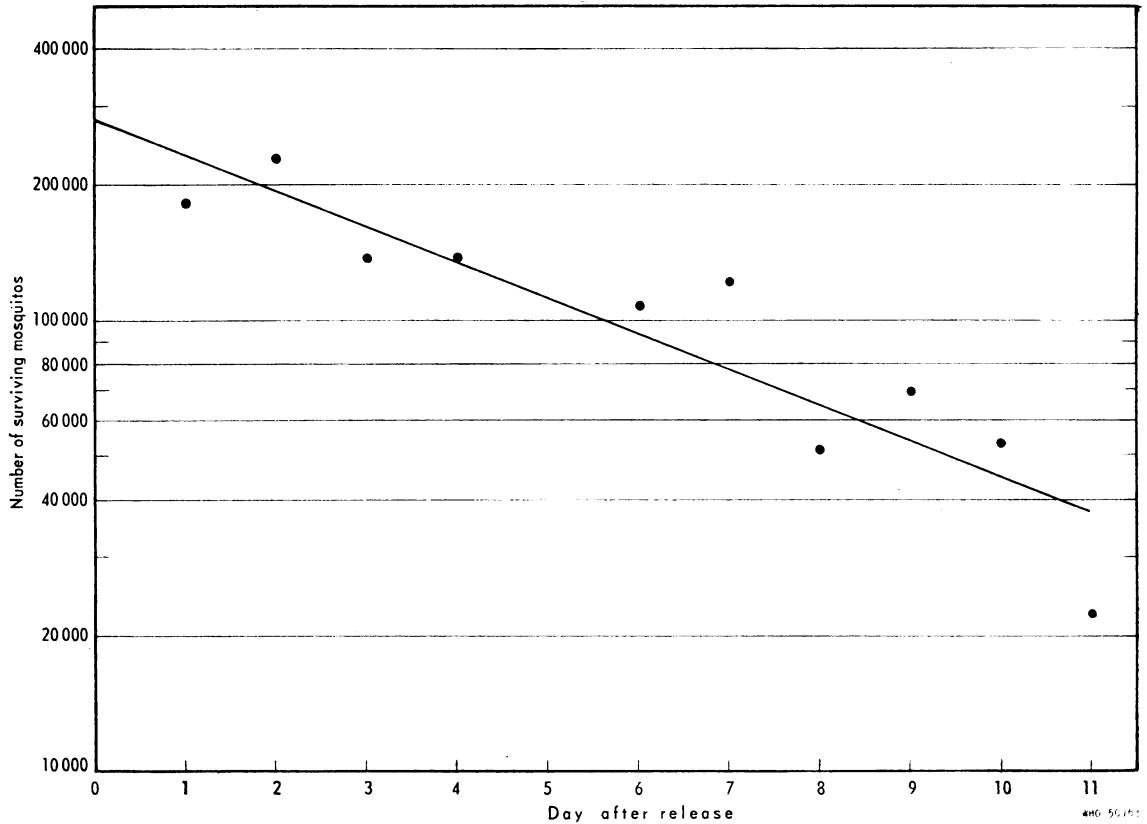
Population size. The total size of an insect population can be estimated from the proportion of marked

TABLE 6. DAILY NUMBER OF SURVIVING TAGGED MOSQUITOS AND ESTIMATE OF TOTAL *C. P. FATIGANS* POPULATION IN THE AREA

Day after release	Surviving tagged mosquitos		Total population		Statistical weight ($\times 10^{18}$)
	Estimated from recapture (in thousands)	Expected number (in thousands)	Estimated size (in millions)	Standard error of estimate (in millions)	
0	280.0	280.0	—	—	—
1	181.8	233.3	61.4	24.5	1 667
2	220.9	194.5	60.0	16.6	3 649
3	137.0	162.1	83.3	33.3	901
4	137.3	135.1	74.4	32.3	956
5	—	112.6	—	—	—
6	109.1	93.8	65.8	26.0	1 476
7	124.5	78.2	42.4	24.8	1 625
8	51.4	65.2	87.0	66.6	225
9	69.9	54.3	58.4	26.0	1 482
10	53.9	45.3	63.2	29.7	1 134
11	22.2	37.7	161.0	114.3	77

FIG. 4

NUMBER OF TAGGED MOSQUITOS SURVIVING ON EACH OF THE 11 DAYS FOLLOWING RELEASE ^a



^a Estimated from the daily recaptures.

specimens recaptured by means of the so-called capture-recapture method (Lincoln, 1930; Jackson 1933; Bailey, 1951).

In the second experiment, mosquito samples were collected on 11 successive days (except on the fifth day) following the release of 280 000 tagged *C. p. fatigans*. The total population can be estimated independently on each day from the daily proportion of tagged specimens recaptured, provided that due allowance is made for the mortality amongst the released mosquitos, which is known to be rather high (about 20% per day). The statistical approach applicable in the present situation is described in the annex.

On the basis of the data obtained in the second experiment, the daily survival rate was found to be 83% (with 95% confidence limits of 78% and 89%), which is in good agreement with the generally accepted rate. The numbers of surviving tagged mosquitos, as estimated from daily recaptures and as derived from the regression line fitted by the least-square method, are given in the second and third columns of Table 6. It is clear from Fig. 4 that the number of survivors tends to decrease linearly when plotted on a semi-log scale against the day of sampling, indicating that the daily mortality was approximately constant.

The daily estimates of the total population of *C. p. fatigans* in the area have been computed with the help of equations 5 and 6 of the annex and are shown in the fourth column of Table 6. The large

variability observed among these estimates is essentially due to the low number of tagged mosquitos recaptured on successive days; in particular, the aberrant estimate of 161 million on the eleventh day was based on the recapture of two tagged mosquitos only. However, as the associated standard errors derived from equation 9 of the annex (and given in the fifth column of Table 6) are also very large, the χ^2 test for heterogeneity did not reveal a significant lack of homogeneity between the 10 different estimates of total population. Therefore, a consolidated weighted estimate was computed using the weights shown in the last column of Table 6. The resulting final estimated number of *C. p. fatigans* living in the area was 62.5 million, with 95% confidence limits of 42.5 million and 82.5 million.

This estimate of total population size was derived on the assumption that the proportion of released mosquitos flying out of the survey area was negligible. A study of the available data, however, suggests that the proportion of such mosquitos may have been as high as 30% (see footnote in annex). This proportion was obtained by extrapolating beyond the survey area the relationship between the density of tagged mosquitos and the distance from the release point, and its reliability is arguable.

Nevertheless, if we may assume that only 70% of the released mosquitos stayed in the survey area, the estimated total number of *C. p. fatigans* would be 43.7 million, with 95% confidence limits of 29.7 million and 57.7 million.

Annex

STATISTICAL NOTE ON CAPTURE-RECAPTURE METHOD

In the case of recapture of a single random sample of n mosquitos, the total mosquito population N is estimated by the formula:

$$N = \frac{n}{r} a \quad (1)$$

where a is the total number of tagged and released mosquitos and r is the number of mosquitos found to be tagged in the sample (Bailey, 1951).

In the second experiment, specimens of *C. p. fatigans* were collected simultaneously at 30 capture stations located on five concentric circles 200 yd (180 m) apart, around the point of release. The mosquito population in the ring area demarcated

by the two circles of radius $(d - 100)$ yd and $(d + 100)$ yd may each be estimated from:

$$N_d = \frac{na}{ra} a_d \quad (2)$$

where the suffix d refers to the ring area with mean radius d .

Certain hypotheses are needed to assess the number of tagged and released mosquitos, a_d , actually present in the ring area at the time of sampling.

First of all, we shall assume that the number of released mosquitos not flying more than 100 yd (90 m) or flying more than 1100 yd (1000 m) on a

straight line from the point of release is small enough to be neglected. In other words, we shall take for granted that all released mosquitos are living in the area limited by the two circles with radii of 100 yd and 1100 yd respectively.¹

An equally important assumption to be adopted is that on the distribution of the population density throughout the area. Although the number of mosquitos captured depends on the skill of the collectors, as well as on the efforts made, we may consider that this number reflects essentially the mosquito density at the point of collection (see Fig. 3). Consequently, we shall assume that the number of mosquitos in the ring area with mean radius d is proportional to $(n_a/k_a)d$, where k_a is the number of capture stations in the ring; then the number of tagged mosquitos (a_a) existing in this ring area is proportional to $(r_a/k_a)a$, and the total number of tagged and released mosquitos (a) is proportional to the sum-total of this quantity over all the ring areas. Therefore, an estimate of a_a is obtained from the equation:

$$a_a = \frac{a(r_a/k_a)d}{\sum (r_a/k_a)d} \quad (3)$$

assuming that none of the tagged mosquitos died from the day of release to the day of capture.

However, the daily mortality rate (q) of *C. p. fatigans* is known to be about 20% and cannot be ignored when the time interval between release and capture exceeds a few days. Equation 3 should then be adjusted by the factor p^x , where p is the daily survival rate (assumed to be constant) and x is the number of days elapsed from the time of release, i.e.:

¹ This assumption may not be entirely valid. An attempt was therefore made to find a mathematical relation between the density of tagged mosquitos and the distance from the point of release, in order to estimate by extrapolation the proportion of released mosquitos that were outside the study area. On the basis of the observed average proportion of tagged mosquitos recaptured in each of the successive ring areas, this mathematical relationship was found to be:

$$y = 0.8042e^{-0.0036 \cdot 1 \cdot x}$$

where y is the number of tagged mosquitos per 100 mosquitos captured and x is the distance (in yards) between the release point and the capture station. The proportion of released mosquitos staying between 100 yd and 1100 yd from the release point was therefore estimated by:

$$\int_{100}^{1100} y \cdot dx \bigg/ \int_0^{\infty} y \cdot dx = 0.713$$

Thus the proportion of released mosquitos staying outside the survey area was estimated at roughly 30%. The total population size estimated on this basis is discussed on page 35.

$$a_a(x) = \frac{ap^x (r_a/k_a)d}{\sum (r_a/k_a)d} \quad (4)$$

An estimate of the daily survival rate (p) is obtained by studying the quantity $\frac{\sum (r_a/k_a)d}{d}$, which is proportional to the number of tagged mosquitos alive on each successive day of observation, on semi-log graph paper. In fact, p is the anti-log of the slope of the least-square regression line fitted to the points representing $\log \frac{\sum (r_a/k_a)d}{d}$ plotted against the day x .

Replacing a_a in equation 2 by the value of $a_a(x)$, we obtain an estimated total mosquito population in the ring area d on day x —namely,

$$N_a(x) = \frac{n_a}{r_a} \cdot \frac{ap^x (r_a/k_a)d}{\sum (r_a/k_a)d} \quad (5)$$

Thus, the whole population on day x is given by:

$$N(x) = \sum N_a(x) \quad (6)$$

Assuming that the population is stable over the period of observation, a weighted consolidated estimate of the population is obtained by averaging the daily estimates, each weighted by the reciprocal of its respective variance. The square root of the reciprocal of the total weight will then provide the standard error of the combined population estimate. The variance for a single-sample estimate of the population is given by (Bailey, 1951):

$$V(N) = \frac{n(n-r)}{r^3} a^2 \quad (7)$$

As a first approximation, this formula may be applied to the population estimated in each ring area, and the variance of the total population in the whole area as estimated on any particular day may be obtained by using the formula:

$$V(N(x)) = \sum \frac{n_a(n_a-r_a)}{r_a^3} \left[\frac{ap^x (r_a/k_a)d}{\sum (r_a/k_a)d} \right]^2 \quad (8)$$

or, more simply:

$$V(N(x)) = \sum \frac{(n_a-r_a)}{n_a r_a} N_a^2(x) \quad (9)$$

In applying the above equations to the actual data, it was noted that no tagged mosquitos were recaptured in some ring areas. Consequently, in these cases it was necessary to aggregate results obtained in two or three adjacent ring areas.

RÉSUMÉ

La région de Kemmendine, Rangoon, Birmanie, a été choisie pour l'étude expérimentale du vol et de la dispersion de *Culex pipiens fatigans*. Cette région est très peuplée, les constructions y abondent et elle offre au moustique d'innombrables possibilités d'installation de gîtes larvaires.

Pour la première expérience, des larves de *C. p. fatigans* ont été recueillies en très grand nombre sur les lieux mêmes et élevées dans un milieu contenant une certaine quantité d'acide phosphorique radioactif (^{32}P). Peu avant la date de l'éclosion imaginale, les larves et les nymphes ainsi marquées ont été transportées à l'endroit choisi. La libération des insectes s'est poursuivie pendant 13 jours à raison de 45 000 individus environ par jour. Au total, 583 000 moustiques ont été mis en circulation. Des stations de capture disposées concentriquement par rapport au point de libération des moustiques ont permis de récolter en 23 jours un total de 46 275 *Culex p. fatigans* dont la radioactivité a été recherchée au laboratoire. Sur l'ensemble des captures, 31 mâles et 36 femelles radioactifs ont été identifiés, soit 0,14%, représentant 0,011% du total des insectes marqués. La dispersion de *C. p. fatigans* s'est effectuée dans toutes les directions et on a pu évaluer approximativement la distance maximale parcourue. Deux mâles et une femelle ont été capturés

au-delà du fleuve, à 880 m du point d'envol. Selon les auteurs, le pourcentage de moustiques qui se dispersent sur une distance supérieure à 1600 m est très faible (moins de 5%), et le risque de réinfestation de zones d'où le vecteur a été éliminé décroît très fortement en fonction de leur éloignement.

La seconde expérience a été menée au moyen de *Culex* adultes, également marqués au ^{32}P , dont 280 000 ont été libérés. En 10 jours de capture, on a récolté 64 695 insectes. Parmi eux, on comptait 117 spécimens radioactifs, soit 34 mâles, et 83 femelles, correspondant à 0,042% des *Culex* mis en liberté. La dispersion a eu lieu dans toutes les directions. Aucun mâle n'a été observé au-delà de 730 m, mais 6 femelles marquées ont été capturées à 915 m du point d'envol. Certaines ont parcouru cette distance en 36 heures, et de nombreux moustiques ont volé sur une distance de 550 m en 12 à 36 heures.

Une note statistique, annexée à l'article, analyse les résultats obtenus au cours de cette expérimentation et propose une estimation de la population culicidienne totale journalière d'après la proportion des moustiques marqués et recapturés, ainsi qu'une évaluation du taux quotidien de survie.

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