STUDIES ON THE DISPERSION AND SURVIVAL OF *ANOPHELES GAMBIAE* GILES IN EAST AFRICA, BY MEANS OF MARKING AND RELEASE EXPERIMENTS.

By M. T. Gillies

East African Institute of Malaria and Vector-borne Diseases, Amani, Tanga, Tanganyika.

(Plates I & II.)

Despite their importance as vectors of disease, we know very little at present about the movements or flight range of most tropical mosquitos. In Africa, small-scale observations were made by De Meillon (1937) and Adams (1940) on *Anopheles gambiae* Giles in Northern Rhodesia, who found maximal flights of one to four miles. Apart from this work, our knowledge is mainly limited to the observations of those concerned with control of breeding sites in small towns, whose general impressions may be summed up by the view that, provided the surrounding areas are not totally unpopulated, a controlled zone of one to one and a half miles renders a township relatively malaria-free. More precise information is essential therefore to understanding not only particular problems of malaria control but also wider aspects of the biology of this important species.

The study of the expectation of life of mosquitos has received much stimulus from recent advances in age-grouping techniques, as developed by Soviet workers. However, the technical difficulties have not yet been solved for most of the vectors of malaria in the tropics, and complementary information on their survival in nature obtained by other methods cannot fail to be of value. An attempt was accordingly made to study the movements and survival under natural conditions of *A. gambiae* in the humid coastal belt of Tanganyika. The method employed was the release and recapture of marked, insectary-reared mosquitos. The first aim was to determine flight range, with reference to general behaviour rather than to occasional flights of exceptional length made by individual insects. Secondly, we set out to study dispersion in relation to age, and ultimately, if it was found that there was little or no progressive loss of mosquitos by emigration as the population aged, to obtain some picture of longevity and mortality. These objectives were partially fulfilled, and this paper is an account of the two different marking methods used, of the flight range of recaptured mosquitos, the effect of prevailing winds, the relationship of age to dispersion, and the pattern of survival of marked mosquitos.

Methods and material.

Labelling technique.

By painting.—As already reported, Gillies (1958*a*), the topical application of paint was used as a marking method for the study of the duration of the first gonotrophic cycle in *A. gambiae*.

A field insectary was established in the centre of the experimental area. The rearing technique used was that devised by Shute (1956). The eggs used were derived from locally caught females, with occasional supplements of eggs from the colony at Amani. On emergence, the adults were isolated and offered sugar solution. Releases were made three times a week, the mosquitos at the time of marking being 16–40 hours old, except for those marked on Monday mornings, which included some that had emerged on the Friday evening.

Artists' poster paint, mixed with a little water to the right consistency, was applied with a micro-loop made from gauge ·0024 plated copper wire. These lengths of wire were fixed to the ends of matchsticks with candle wax, each forming a delicate instrument with which it was impossible to exert more than the lightest pressure. The mosquitos were caught five at a time in a sucking tube, into which just sufficient chloroform vapour was sucked or poured to knock them down. The moment they were anaesthetised they were tipped out on to a strip of cork, gently flipped over with a dissecting needle so as to lie dorsal side up, and the cork was placed under a wide-field, low-power magnifier for painting. By gently touching each mosquito in the centre of the mesonotum with the tip of the loop, it was possible to lift them up just off the cork. A slight tap of the hand holding the loop would cause the insect to fall back again, leaving a discrete spot of paint at the site of contact. The cork was transferred to the release cage until the mosquitos recovered, which took between 5 and 30 minutes. As the paint dried in about a minute, it was essential to make certain that the mosquitos did not roll over and become stuck to the cork. A useful modification to the technique was the use of a dilute solution of Teepol. If the loop was dipped into this and then into the paint, a smaller spot remained on the insect than if the paint alone was used.

Fifteen different colours or blends were used which, at the rate of three releases a week, allowed for an interval of five weeks before the same colour recurred. Only females were marked. An output of 1,000 mosquitos a week was aimed at, which worked out in practice at between 200 and 400 a morning. Under field conditions, two assistants could handle about 150 mosquitos in an hour, although in the main laboratory considerably faster rates of painting could be achieved. One mosquito was heavily painted, pinned, and kept as an example of the exact colour used on that day. All recaptured mosquitos were examined individually with a hand lens, and any marked specimens compared with the reference series. Assistants did the preliminary sorting, but with the exception of one small series, the actual matching of the colours was always checked by myself. It was found that certain colours in the cream or buff range had to be avoided, since they could be confused with the spots of excreta occasionally ejected by mosquitos after knockdown and accidentally transferred to the thorax from one specimen to another when lying in the storage tins before sorting.

With radioisotopes.—Radioactive tracers have been widely used for marking mosquitos, and in the experiments described here no departures from established practice were introduced, apart from the serial use of two different isotopes. The eggs were derived more or less equally from wild-caught females, from a recently established colony of the local strain of *A. gambiae*, and from a long-established strain originally obtained from Kenya. The isotopes used were ^{32}P, supplied as a solution of orthophosphate, and ^{35}S, supplied as sulphate, both obtained from the Radiochemical Centre, Amersham. The solution containing isotope was introduced into the breeding pans two to three days before pupation, in the third or early fourth instar. A dose of 5 microcuries of ^{32}P, or of 15 microcuries of ^{35}S per litre in the breeding pans gave rise to high enough levels of radioactivity in the emerging adults to be easily detected. No attempt was made to do any quantitative estimations of radioactivity, and the only counter in use was a simple monitoring instrument for checking contamination after handling active solutions.

Labelled mosquitos were detected by means of autoradiography. The insects to be tested were attached to cellulose tape, stretched over a numbered grid (see Pl. I), details of the catch being attached to the end of the tape. These were applied to strips of X-ray film (Ilford, Industrial G, 29 × 280 mm.) in a dark-room, and normally exposed over two nights, that is for about 40 hours. To distinguish insects labelled with the two different isotopes, use was made of the technique of energy discrimination, as described by Gillies (1958*b*). In most instances there was no possibility of confusing the diffuse fogging, produced by mosquitos labelled with ^{32}P, with the sharp images of those labelled with ^{35}S. These differences are illustrated in Plate II. But in every instance in which there was any doubt, the mosquitos were re-exposed on double layers of film when, in contrast to the effect of ^{32}P, those with ^{35}S only left an image on the strip of film in immediate contact with them. Use was also made of the observation by Duncombe (1959) that, when using X-ray film which is normally coated with emulsion on both sides, objects labelled with ^{35}S leave an image on *one side* only of the film.

Evaluation of labelling technique.

In addition to simplicity and cheapness, a satisfactory marking method must be recognisable throughout the life of the insect, and be without obvious harmful effects. Both these criteria were studied, with the following results.

Persistence of labels.—It was not easy to check the permanence of the mark in mosquitos that had been painted, except in caged specimens. Once dried, poster paints show no tendency to crack or chip, and it seems unlikely that in nature the mesonotum of a mosquito would be subjected to either abrasion or wetting. It should be pointed out that the mesonotal scales, themselves extremely delicate objects, are seldom rubbed or missing in wild-caught mosquitos at the time of capture. In fact, the greatest risk to any ornamentation on a mosquito, whether natural or applied, lies in its treatment after capture, and steps to minimise this risk were incorporated in our recapture routine.

With radioactive tags, there are two main sources of loss of activity that could lead to difficulty or doubt in recognising long-lived specimens. These are decay, and elimination of labelled material during formation and deposition of eggs.

It might be thought that decay would be an important factor when using ^{32}P, since, with a half-life of 14·3 days, three-quarters of the radioactivity will have been lost by the end of a month. However, ^{32}P is taken up so readily by developing mosquitos, and its effect on photographic plates so intense, that radiation is easily detected in marked specimens up to 7–8 weeks after emergence. ^{35}S has a half-life of over 12 weeks, and there is, correspondingly, relatively little loss through decay.

Loss of radioactivity through the eggs is less easy to assess. There was substantial loss after the first few egg-batches, particularly in the case of radiosulphur. The rate of loss is likely to fall off in older, less fertile females, but it was not possible to follow this in the laboratory. In females recaptured in the third or fourth week after release, doubtfully positive specimens were not encountered. However, the possibility of missing feebly radioactive females remained and, to minimise this risk, the exposure time of all catches was extended to 3–4 days during periods when old markings might have appeared in the catches.

A further practical point should be mentioned. With ^{35}S, internal absorption of low-energy beta-particles can be an important source of loss of detectable radiation, particularly in females distended with blood. When spreading the mosquitos out on the cellulose tape for testing, it was necessary to squash each specimen and also to apply very firm pressure to the film holders to make certain that the insects were in close contact with the surface of the film.

Perhaps the best illustration of the over-all effect of these sources of loss is provided by the autoradiographs shown in Plate II, in which actual recaptures of old marked mosquitos are compared with those of freshly emerged specimens. This shows very clearly both the reduction in radioactivity of the older mosquitos and its recognisable persistence at an advanced age.

One needs also to be reassured that no radioactivity is passed on through the eggs to act as an unintended label in the next generation. In laboratory tests it was found that batches of eggs from females labelled with ^{32}P showed up faintly on X-ray film when first laid; but in the fourth-stage larvae, and adults reared from them, no radioactivity could be detected. With ^{35}S not even the eggs affected the film.

Biological side-effects.—Preliminary tests on the effects of labelling on the survival of mosquitos were carried out in the laboratory. Since the application of paint involves some handling of the mosquitos, as well as the administration of anaesthetic, it was to be expected that this might affect their longevity. The pigment used in any of the paints might also have been specifically toxic to mosquitos. Survival tests using insects marked with paint alone, or treated with Teepol with or without paint, or subjected to anaesthetic without painting, all resulted in a slightly higher mortality during the first 24 hours after marking; but, beyond that age, no difference in survival rates could be detected between any of these categories of mosquitos and those used as controls.

When using radioisotopes, there was virtually no handling of the mosquitos and, apart from unknown defects in rearing conditions, the only factor that could have any adverse effect was the presence of radioactivity. Survival tests in the laboratory on over 1,100 mosquitos gave the following results: mean age of controls, males 10·3 days, females 10·0 days; ^{32}P at 5 microcuries per litre, males 9·9 days, females 10·5 days; ^{35}S at 15 microcuries per litre, males 10·3 days, females 10·9 days. Thus it is clear that rearing in these solutions, at the dosage used, had no adverse effect on the subsequent survival of the adults. The labelled mosquitos were also fully fertile, and normal development of their progeny was observed.

Validity of experimental method.—Since it was planned to study the dispersion of mosquitos at all ages, it was essential to employ a marking method that would persist throughout the life of the insect. Some of the techniques that have been used in the past, such as dusting, or spraying with dyes, have been primarily intended for short-term experiments, and were not thought suitable for the present work. For this reason the topical application of paint was chosen, despite the extra handling involved. The method is particularly useful for small-scale releases where insectary facilities or opportunities for collecting larvae in nature are limited. Moreover, with careful blending and matching of colours a wide variety of different marks can be employed, such as are required when daily variations in behaviour are being studied.

The use of radioisotopes has the obvious advantage that large numbers can be released without handling. Its main limitations are those of expense and the difficulty of distinguishing different batches of marked insects. This is particularly serious where serial releases are planned and the exact age of the recaptures is required to be known. Both disadvantages were largely overcome by the autoradiographic technique used in these experiments.

A further word should be said about the two uncertainties mentioned above; namely, the possible harmful effects of painting, and the risk that the older isotope-labelled females were being missed. The latter possibility was very much in the front of our minds, and any strips of mosquitos that produced doubtful shadows on the film—and they were quite common—were re-exposed for longer periods. In no case did any turn out to be due to radioactivity. Any remaining doubts about the validity of the techniques used are further dispelled when the results of the two methods are compared. As is recorded below, the average ages at recapture in the parallel series of releases of painted and isotope-labelled mosquitos were identical. Thus, one must postulate either that the respective failings of the two methods matched each other exactly, or that they were of negligible importance. The latter seems by far the most likely explanation.

There remains one outstanding limitation in the experimental method adopted: the use of artificially-reared insects. This difficulty is almost insuperable with a mosquito like *A. gambiae*, whose small, scattered, temporary breeding sites make it virtually impossible to collect adequate numbers of wild larvae. Consequently, as regards flight range, we cannot be quite certain that a natural population would have behaved in the same way, although the differences may not be great. But, when it comes to longevity, there is fairly good evidence from the incidence of malaria infection among the recaptured females that their span of life was unnaturally short. And as described below, estimation of mortality rates must be confined to the pattern of survival after release, that is to changes in mortality with age.

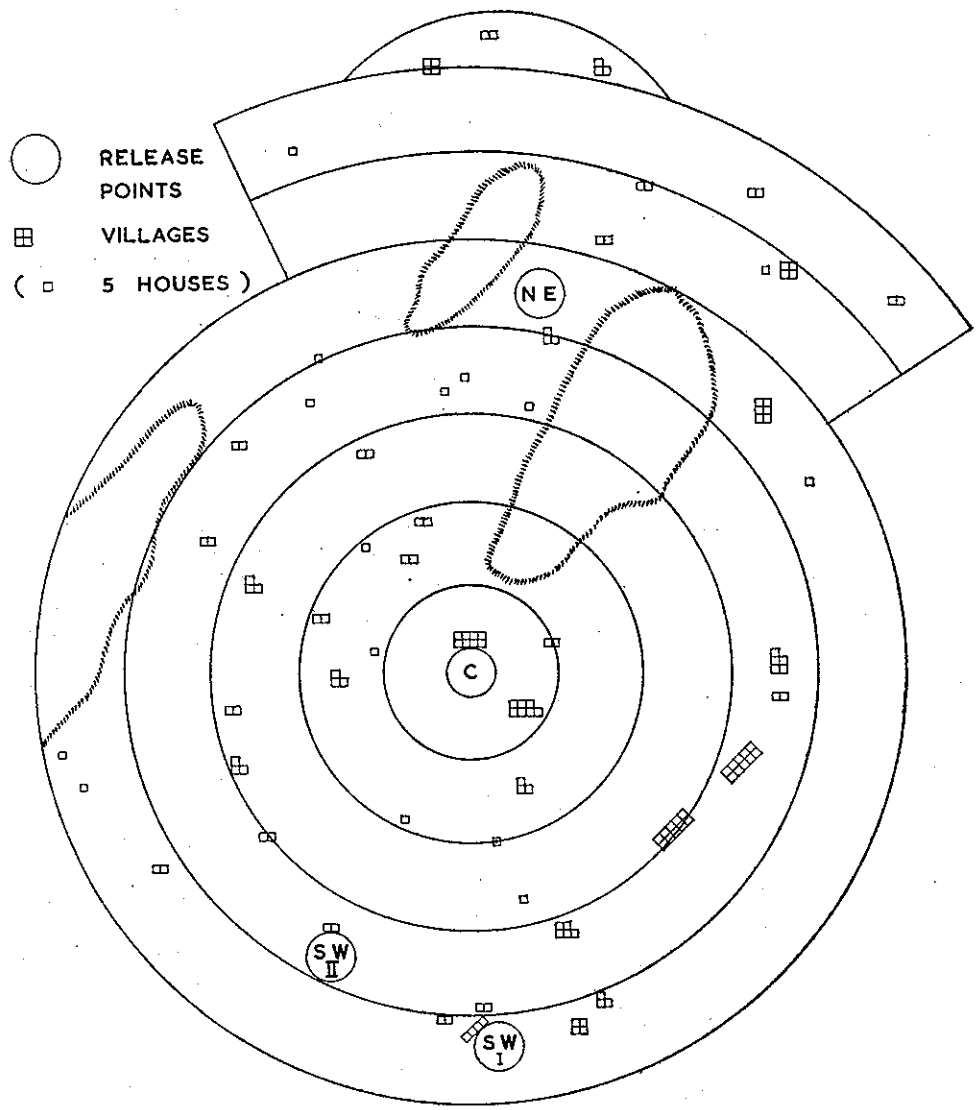

Fig. 1.—Sketch map of experimental area to show distribution and density of houses. The concentric circles are at quarter-mile intervals.

Release and recapture procedure.

Experimental area.—The area chosen for the experiments lay in the well-watered foothills of the Eastern Usambara Mountains. Accounts of the region have already been published by Gillies (1954, 1955). The area is moderately densely populated, and the people live in small villages or scattered family groups of houses. The distribution and density of houses in the experimental area, which consisted of a circle of radius one and a quarter miles, with an extension in one sector up to one and three quarter miles from the centre, is shown in fig. 1.

Releasing procedure.—The main bulk of the larvae pupated over a period of three days. In the experiments with radioisotopes, pupae were collected from the rearing pans and transferred to distilled water in waxed paper cups, at a density of 100 per cup. Ten to fifteen cups were put into each release cage, which was fitted with a sliding lid, and sugar-water was provided for the adults when they emerged. A count was made afterwards of dead pupae, trapped adults and dead adults remaining in the cages, from which the total number released was calculated. The sex ratio was found to approximate to 1 : 1, males tending to be more numerous on the first day of emergence. Adults emerged 24 hours after pupation, and were released as soon as practicable. About one-third were released within 18 hours of emergence, one-half during the second 24 hours, and a small number during the third day of adult life.

Four different points within the experimental area were used for the releases. The central release point was an experimental hut with wide, open eaves. The peripheral releases were made either from unoccupied and partly broken-down huts, or from box shelters of the type normally used for the capture of outdoor-resting mosquitos. The cages were put in position on ant-proof trays at around midday, and the lids carefully slid off. The few mosquitos that were disturbed by this action would fly out and settle on the adjacent walls. But most stayed inside the cages until the last hour of daylight when, after a period of mounting activity and of brief preparatory flights towards the failing light, continuing up till 10 to 20 minutes after sunset, a mass exodus through the eaves took place. A certain amount of predation occurred at this time. On one occasion geckos were seen patrolling the eaves and picking off the mosquitos that rested there before their final departure. On another, a Salticid spider, caught in the vicinity of the release cages, was found to be strongly radioactive when tested. On several evenings, mosquitos were seen streaming out from the release points and forming typical swarms in adjacent open spaces. Of 300 males netted and tested from one such swarm, 267 were found to be labelled.

Recapture routine.—Catching stations were maintained in one house out of five once a week within the one-and-a-quarter-mile radius of the experimental area. In addition, catches were extended out to a mile and three quarters in one sector, referred to from now on as the ' extension area ', at a frequency of one house in five once a fortnight. Mosquitos were collected by spray-catching, that is to say, cotton sheets were spread over all horizontal surfaces and the room then sprayed with 0·1 per cent. pyrethrins in kerosene. Only bedrooms were used for the catches, and since in some houses there were several rooms, only one of which was sprayed, the fraction of the total house population collected from each catching station varied quite widely. Some elasticity in the choice of catching stations was allowed so that the actual house chosen in each group of five was not necessarily the same every time.

There were four spray teams for the main area, each consisting of two or three men, and one for the extension area, operating on a strict routine five days a week. Each had its own sector, and the villages visited on any particular day were as far as possible spread over the different parts of the sector. The total number of occupied houses within the one-and-a-quarter-mile radius fluctuated round 600, 120 of them being used at catching stations in each week. In the extension area there were 12 catching stations in operation during the latter half of the experiments. The catches were maintained continuously throughout each series and for one month after the last release regardless of the place of release. Thus, apart from other factors, the chance of recapture at any particular point remained constant throughout the experiments.

Distribution of release points in relation to recapture area.—Releases were initially all made from the centre of the area. But after the first two series of experiments it became apparent that catches would have to be extended beyond the mile-and-a-quarter radius originally planned. The resources available did not permit an extension of the area up to two miles without a drastic reduction of the proportion of houses used as catching stations, and the recapture rate. So, to avoid this difficulty, it was decided to leave the recapture area as it stood, and to shift the release point to the perimeter instead. In this way, while those mosquitos that flew in one general direction would leave the area almost at once, the others would be available for recapture at any distance up to two and a quarter miles from the point of release. Two peripheral release points were accordingly set up near the north-eastern and south-western perimeter, and releases made alternately from the different points. After a short period it became necessary to move the south-western point to another village about half a mile away. Hence, four different release points were used, as shown in fig. 1. Releases of painted mosquitos were alternated more or less regularly from one point to another. The isotope-labelled insects were released in nearly equal numbers from the centre and from the periphery.

The peripheral releases raise some problems of interpretation when the density of recaptures in relation to distance flown is assessed. The difficulties are most readily to be comprehended by reference to fig. 2, which shows, in a diagrammatic

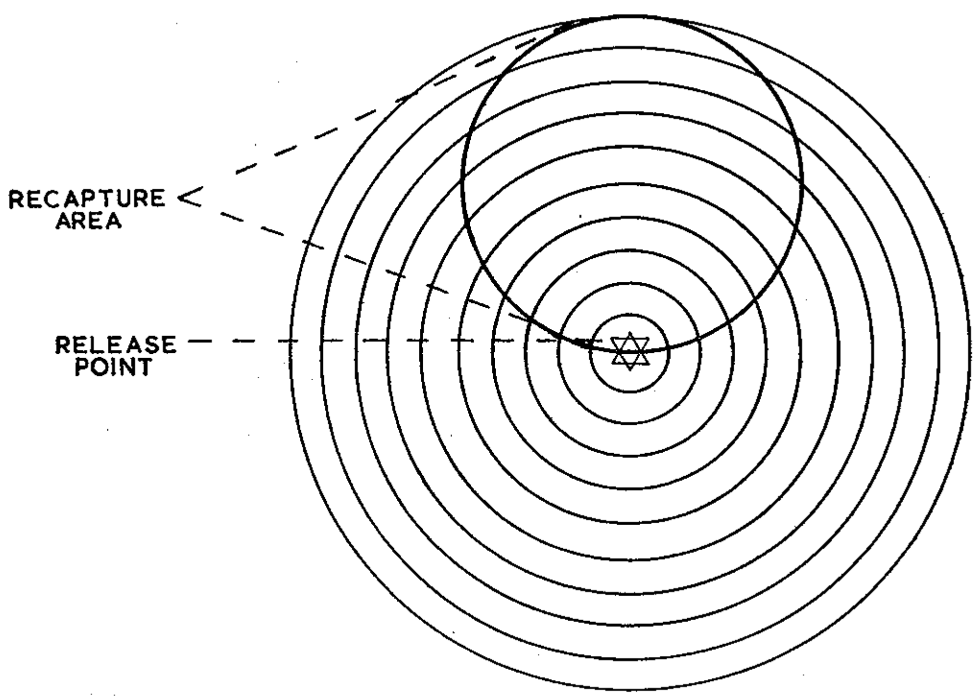

Fig. 2.—Diagram to show geometric relationship of recapture area to peripheral releases.

TABLE I.

Summary of results of all releases and recaptures.

Period	Method of labelling	Numbers released	Sex of releases	Trapping range	Proportion of houses used as catching stations (%)	Numbers recaptured		Per cent. recaptured		Total number trapped	
						Males	Females	Males	Females	Males	Females
March–June, 1956	Paint	3500	Females	600 yd.	27	—	66	—	1·9	—	14750
Jan.–Feb., 1957	Paint	3200	Females	¼ mile	67	—	121	—	3·8	—	6100
March–July, 1957	Paint	13800	Females	1¼ miles	20	—	55	—	0·4	—	32300
Oct., 57–Oct., 58	Paint	49250	Females	1¼–2¼ miles	20	—	324	—	0·7	—	95500
Total	Paint	69750	Females			—	566	—	0·81	—	
July–Oct., 1958	Isotopes	8550	Males, females	1¼–1¾ miles	20	36	64	0·8	1·5	1230	—
Jan.–June, 1959	Isotopes	54150	Males, females	1¼–2¼ miles	20	120	233	0·4	0·9	14810	65350
Total	Isotopes	62700	Males, females			156	297	0·5	0·95	—	—
Total ..	All releases	132450				156	863			16040	214000

way, the geometry of the problem. From this diagram it is clear that, with each increase in range from the release point, the recapture area covers a smaller proportion of the potential area of dispersion at that range. For example, the whole of the ¼-mile zone round the north-eastern release point was covered by routine catches; whereas only about one-seventh of the 2¼-mile zone was included in the recapture area. It follows that this factor must be taken into consideration in estimating the effect of distance on density. The appropriate correction factors have been calculated geometrically, and are set out in the second column of Table VII.

Results.

Summary of releases and recaptures.

The results of all the releases are summarised in Table I. Of the successive series, the first was of a preliminary nature to test the painting technique and to find out what sort of recapture rate would be obtained. The second was designed to study the duration of the first gonotrophic cycle, and catches were accordingly concentrated in the vicinity of the release point. This resulted in a relatively high recapture rate, made up for the most part of young mosquitos (see Table III in Gillies, 1958*a*). In all the later series the recapture routine remained constant and the numbers of recoveries largely depended on the siting of the release points, whether in the centre or the periphery of the experimental area. In the case of the isotope-labelled releases, the recapture rate of the males was approximately half that of the females, a difference that presumably reflected the less domestic resting habits of male mosquitos.

Dispersion.

For the analysis of dispersion, only those series of releases in which the recapture area extended up to 1¼ miles and over are considered. The recoveries of marked mosquitos from the central releases, in which, as already explained, catches were made in all sectors up to a range of 1¼ miles and, for part of the period, up to 1¾ miles in the sector that included the extension area, are shown in Table II. The table gives the total numbers recaptured and the percentage of the total at each range, so that we are considering here the mean dispersion up to a distance of 1¼ miles, regardless of age. Within these limits it will be seen that recaptures of both sexes fell off steadily with increasing range, although there

TABLE II.

Recaptures of marked mosquitos from central release point.

Range (miles)	Numbers recaptured				Per cent. recaptured			
	Painted females	Isotope females	Isotope males	All females	Painted females	Isotope females	Isotope males	All females
0–¼	64	65	59	129	36	38	55	37
¼–½	39	45	19	84	22	26	18	24
½–¾	30	31	12	61	17	18	11	18
¾–1	32	14	10	46	18	8	9	13
1–1¼	12	17	7	29	7	10	7	8
1¼–1½*	—	1	—	1	*Extension area: incomplete series, catches made on one quarter of perimeter only.			
1½–1¾*	1	1	—	2				
1¾–2*	—	—	1	—				
Total	178	174	108	352				

is a marked concentration of males round the release point. The regression of density on distance for the recaptures of both sexes plotted on a semi-logarithmic scale is shown in fig. 3. Regression coefficients for males and females in the isotope releases are $-0{\cdot}21$ and $-0{\cdot}17$, respectively. The same coefficient for all recaptured females is $-0{\cdot}16$. If one assumes that dispersion beyond the limits of the experimental area continued at the same rate, it is found (by extrapolation from the regression line corresponding to $-0{\cdot}16$) that 78 per cent. of the mosquitos flew less than one mile, 18 per cent. from one to two miles, and only 4 per cent.

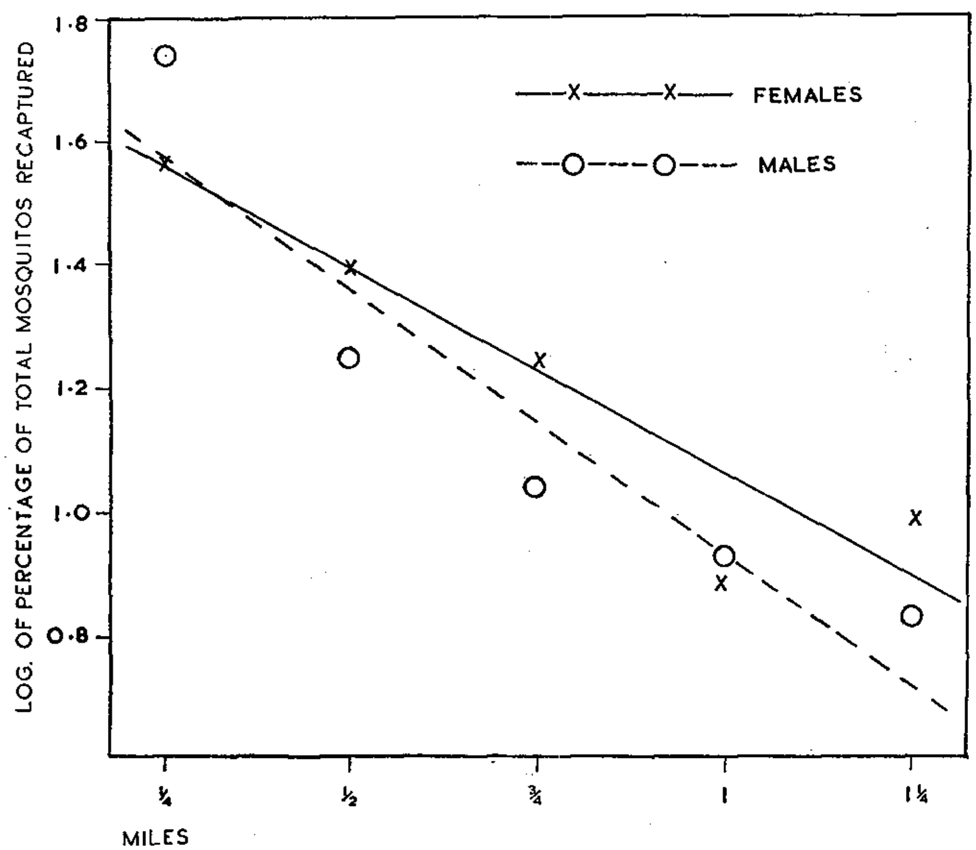

Fig. 3.—Regression lines of recaptures (expressed as log percentage of total recaptured) of isotope-labelled males and females in relation to distance (central releases).

more than two miles. On the same basis, the mean flight range of females is found to be 0·76 mile and of males 0·64 mile. However, recaptures were made at any point within each zone. Thus, the mean flight range is in reality ⅛th of a mile less than that calculated, and the figures given here should be—females, 0·64 mile, and males, 0·52 mile.

The recoveries from the peripheral releases, in which the recapture area extended in one direction up to a maximum of 2½ miles, are shown in Table III. The left-hand section of the table shows the numbers recaptured, while the remaining part shows the estimated distribution at the different ranges. Details of the calculation of this estimate are shown in Table VII (all catches), which takes into consideration the geometry of the recapture area (see figs. 1 and 2). The differences in the closer ranges between the painted and isotope-labelled females is largely due to differences in the frequency with which the various release points were used. In the isotope series the north-eastern point, which was situated in open country, was more frequently used than the south-western points, whereas the reverse was true for the painted releases.

TABLE III.

Recaptures of marked mosquitos from peripheral release points.

Range (miles)	Numbers recaptured			Estimated distribution*			Estimated distribution as percentages		
	Painted females	Isotope females	Isotope males	All females	Isotope females	Isotope males	All females	Isotope females	Isotope males
0– ¼	34	10	9	48	10	9	8	4	10
¼– ½	60	4	5	75	6	8	12	2	9
½– ¾	39	43	22	117	67	36	19	25	40
¾– 1	15	13	3	64	30	7	11	11	8
1–1¼	27	34	5	158	88	13	26	33	14
1¼–1½	13	10	1	68	30	3	11	11	3
1½–1¾	3	6	1	31	21	3	5	8	3
1¾–2	4	1	1	23	5	5	4	2	5
2–2¼	1	2	1	20	7	7	3	3	8
Total	196	123	48	—	—	—	—	—	—

* See Table VII for method of calculation.

The pattern of dispersion from the peripheral releases is shown graphically in fig. 4. The most obvious features of this distribution are the relative scarcity of recaptures in the ¼-mile zone, the somewhat uneven dispersion between ½ and 1½ miles, and the very small numbers captured beyond this range. This pattern is readily explained if the number of catching stations, and hence the density of human population, at the different ranges is taken into account. The break-down

TABLE IV.

Estimated density of recaptures from peripheral release points, in relation to number of catching stations at different ranges (females only).

Range (miles)	North-eastern			South-western (I)			South-western (II)			Total per station	Per cent.
	Density	No. of stations	Density per station	Density	No. of stations	Density per station	Density	No. of stations	Density per station		
¼	20	3	6·7	12	2	6·0	16	12	1·3	14·0	25
½	61	5	12·2	5	7	0·7	9	9	1·0	13·9	24
¾	95	20	4·7	18	23	0·8	4	4	1·0	6·5	11
1	41	6·5	6·3	21	28	0·7	2	22	0·1	7·1	13
1¼	143	26	5·5	7	18	0·4	8	32	0·2	6·1	11
1½	36	16	2·2	20	20	1·0	12	14	0·9	4·1	7
1¾	24	15	1·6	7	12	0·6	—	9	—	2·2	4
2	23	12	1·9	—	10	—	—	13	—	1·9	3
2¼	20	17	1·2	—	2	—	—	4	—	1·2	2

of estimated recaptures from the different release points, together with the numbers of catching stations at successive distances from them, are given in Table IV. Inspection of the table indicates the paucity of houses in the nearer zones, and their concentration in the middle zones, of the experimental area. In the table, the numbers recaptured per station have also been calculated, and in fig. 5 the logarithm of these values has been plotted against distance. This

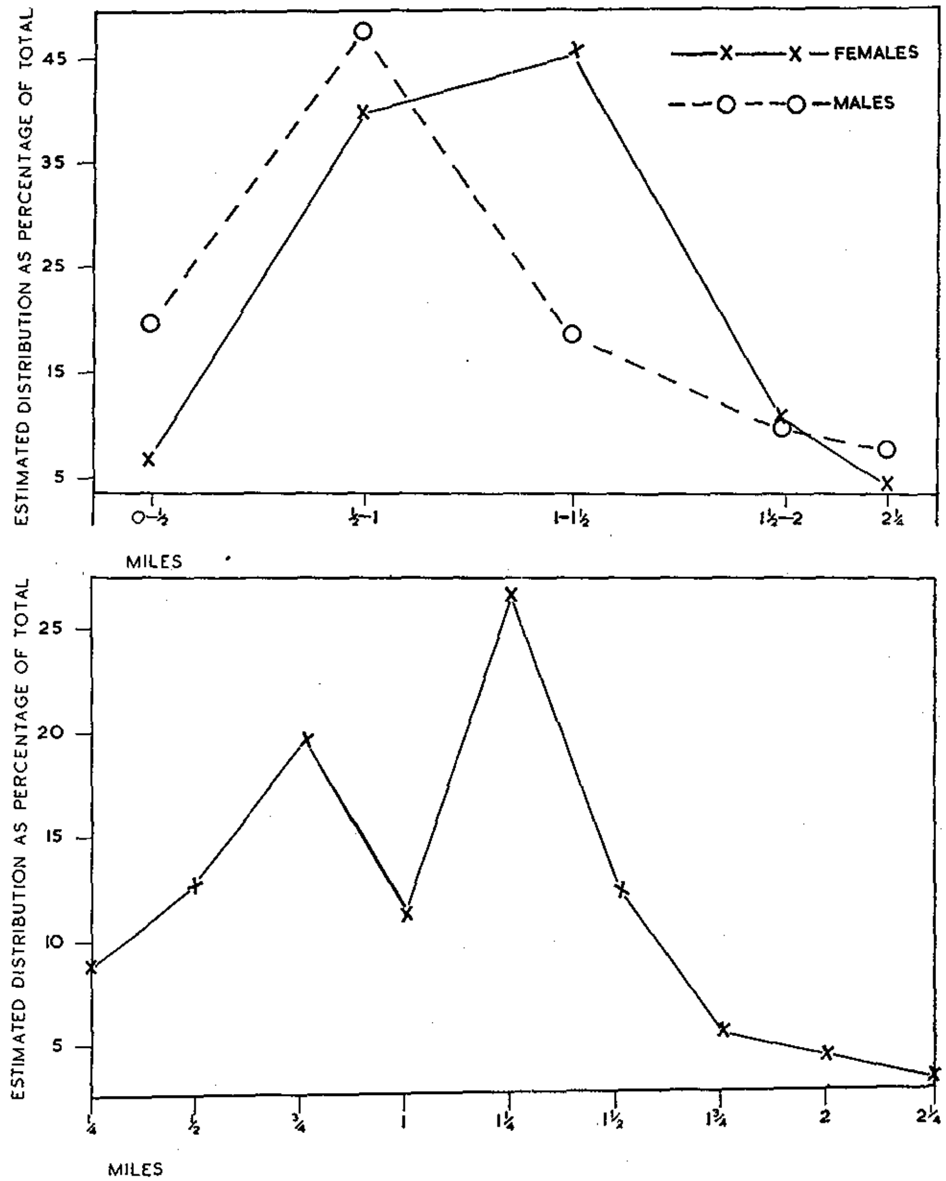

Fig. 4.—Estimated dispersion of marked mosquitos from peripheral release points, expressed as percentage of total recaptured. Above, isotope releases. Below, all females combined.

clearly shows a more or less straight-line distribution, the numbers recaptured falling off steeply with increasing distance. In other words, the irregular pattern of dispersion from these release points can be largely explained by the uneven distribution of villages within the experimental area.

An estimate of the flight range of the whole population released from the peripheral points is not easily obtained. But if the second part of the curve shown in fig. 4 is considered, in which the fall in density is more or less regular, and if the 1- to $1\frac{1}{4}$-mile zone is taken as the starting point, the logarithm of the number of recaptures is found to decline at a rate of 0·23 per $\frac{1}{4}$ mile. If this regression is assumed to have continued beyond the limits of the experimental area, it can be calculated * that 50 per cent. of females flew less than one mile, 44 per cent. from one to two miles, and about 6 per cent. more than two miles. This gives a value of 1·1, or 0·98 miles if measured from the middle of each zone, as the mean flight range of the whole female population. The sample of males recaptured was too small for accurate estimation of flight range, but the upper part of fig. 4 shows very distinctly the more restricted range, although the pattern

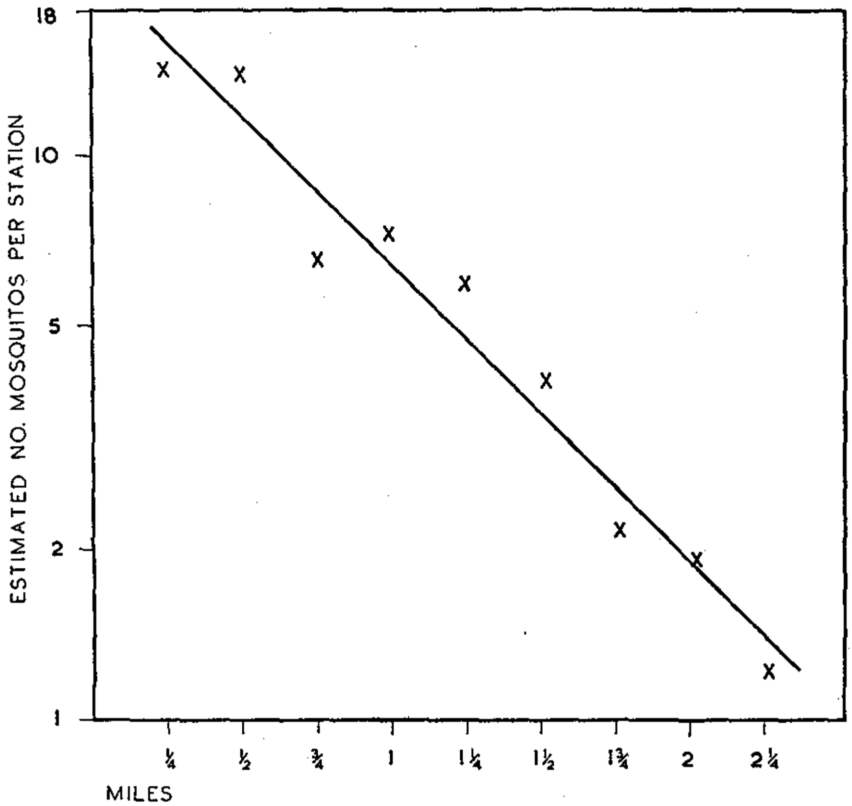

Fig. 5.—Density of recaptures per catching station in relation to distance.

* By giving the $1\frac{3}{4}$-mile zone the value of antilog. 0·85, which is the mean value of the series of recaptures, expressed as percentages, from the $1\frac{1}{4}$- to $2\frac{1}{4}$-mile zones, and the $1\frac{1}{4}$-mile zone the value of antilog. $0{\cdot}85 + 2 \times 0{\cdot}23 = 1{\cdot}31$ or 20·4 per cent., and so on.

of dispersion was similar to the females. It should also be noted that individual males were recaptured at all ranges up to 2¼ miles.

To summarise these results, there is first of all an obvious relationship between flight range and density of human population. In the particular area chosen for the releases the dispersion of mosquitos from the centre, where the concentration of houses was high, was less than from the more sparsely populated peripheral areas. It also appears that, once the peripheral releases had spread into the centre of the area, their further dispersion was similar to those originally released in the centre. In other words, the somewhat greater flight range of the peripheral releases was not primarily due to the greater distance up to which recaptures were possible (2¼ as opposed to 1¼ miles), but to the fact that they had further to go before coming under the influence of the central villages. It should also be noted that the distribution of breeding sites, as well as food sources, may have been significant. This could have been particularly important in the dry season, since the central area lay at a lower level than most of the outlying sectors where the surface water in the valley bottoms was less permanent.

These experiments have served to emphasise the limited meaning of the term 'flight range' as applied to a particular species. The actual movements of a mosquito population are clearly the product of the influence of topographical factors on its intrinsic flight characteristics, and the detailed results obtained here only refer to the flight range of *A. gambiae* in the type of country and with the density of human settlement described.

The effect of prevailing winds on dispersion.

Precise observations on the effect of wind on the movement of low-flying insects are always hindered by the presence of eddies and turbulence in the air stream, created by local irregularities in the terrain. In the present instance the situation was further complicated by the hilly nature of the experimental area. Consequently no attempt was made to measure the importance of local air currents on the flight of *A. gambiae*. On the other hand, the seasonal changes in the trade winds on the East African coast are regular and well defined, and it is possible to recognise two periods in the year, corresponding to the N-E. and S-E. monsoons, when the general wind direction remains constant for several months on end, with only short-term fluctuations in the vicinity of storms. An attempt was made, therefore, to assess the effect of this prevailing wind on the dispersion

TABLE V.

Mean flight range (in miles) of recaptures in relation to prevailing wind.

Release point	N-E. monsoon			S-E. monsoon		
	Males	Isotope females	All females	Males	Isotope females	All females
Central (northern sectors)	0·31	0·38	0·38	0·41	0·42	0·48
Central (southern sectors)	0·47	0·62	0·62	0·39	0·39	0·4
North-eastern (southern sectors only)	1·0	1·22	0·93	0·69	0·97	0·92

of mosquitos. In the experimental area the proximity of mountains had some influence on the movement of the air stream, as judged by the movement of low clouds, so that the locally effective direction of the S-E. monsoon, from late April to late October, fluctuated from West of South to a few degrees East of South. From mid-December to mid-March the wind blew steadily from the North-East. (It should be noted that the daily swing in direction, so noticeable on the coast itself, was of minor importance in the area studied.)

The average flight range of recaptured mosquitos in relation to the seasons as defined above is shown in Table V. Only the recaptures from the north-eastern and central release points are shown, since the south-western point was not in use all round the year. The results may be summarised as follows:

(a) Of the mosquitos released in the centre of the area during the N-E. monsoon, dispersion against the wind (northern sectors) was appreciably less than in the southern sectors. The difference in the numbers flying over or under half a mile, to the south or north of the release point, is highly significant ($\chi^2 = 32{\cdot}6$, $P = 0{\cdot}01$). On the other hand, this difference disappeared during the S-E. monsoon.

(b) From the north-eastern release point, there was no seasonal change in the over-all flight range of female mosquitos, although, if the isotope females are taken alone, there is a small but significant difference ($\chi^2 = 5{\cdot}43$, $P = 0{\cdot}02$) when the numbers flying under and over three-quarters of a mile are compared. Too few males were recaptured for further analysis.

These small differences are brought out more clearly if the recaptures are plotted diagrammatically, as in fig. 6. In particular, the numbers flying downwind from the north-eastern release point into the extension area, during the S-E. monsoon, are clearly shown. The general impression given by these observations is that, in a populous and hilly region such as the experimental area, wind direction was a minor factor in aiding the dispersion of mosquitos.

TABLE VI.

Recaptures from central release point, showing dispersion in relation to age (females only).

Range (miles)	Day 1		Day 2		Days 3–9		Days 10+		All catches	
	Catch	Per cent.	Catch	Per cent.	Catch	Per cent.	Catch	Per cent.	Catch	Per cent.
¼	28·5	59	27·8	61	54	29	18·7	27	129	37
½	10	21	6	13	53	28	15	22	84	24
¾	5	10	4·5	10	35·5	19	16	23	61	18
1	1	2	6	13	26	14	13	19	46	13
1¼	4	8	1	2	18	10	6	9	29	8
Mean range (miles)	0·45		0·45		0·62		0·65		0·58	

Dispersion in relation to age.

Up till now we have considered the flight range of marked mosquitos regardless of the time interval between release and recapture. It is important, however, to know what relationship exists between dispersion and age. For this purpose, four age-groups have been selected, representing those aged one day, two days, three to nine days and ten days and over, at the time of recapture. These groupings have been chosen since it was clear from the data that the movements of the population during the first two days after release were generally different from those during the rest of the period over which mosquitos were recovered. The results are set out in Tables VI–VIII. It will be noted that in certain places the catches recorded are not whole numbers. As explained on p. 119, this results from the occasional use of the same mark on more than one day.

The distribution of recaptures up to $1\frac{1}{4}$ miles from the central release point for

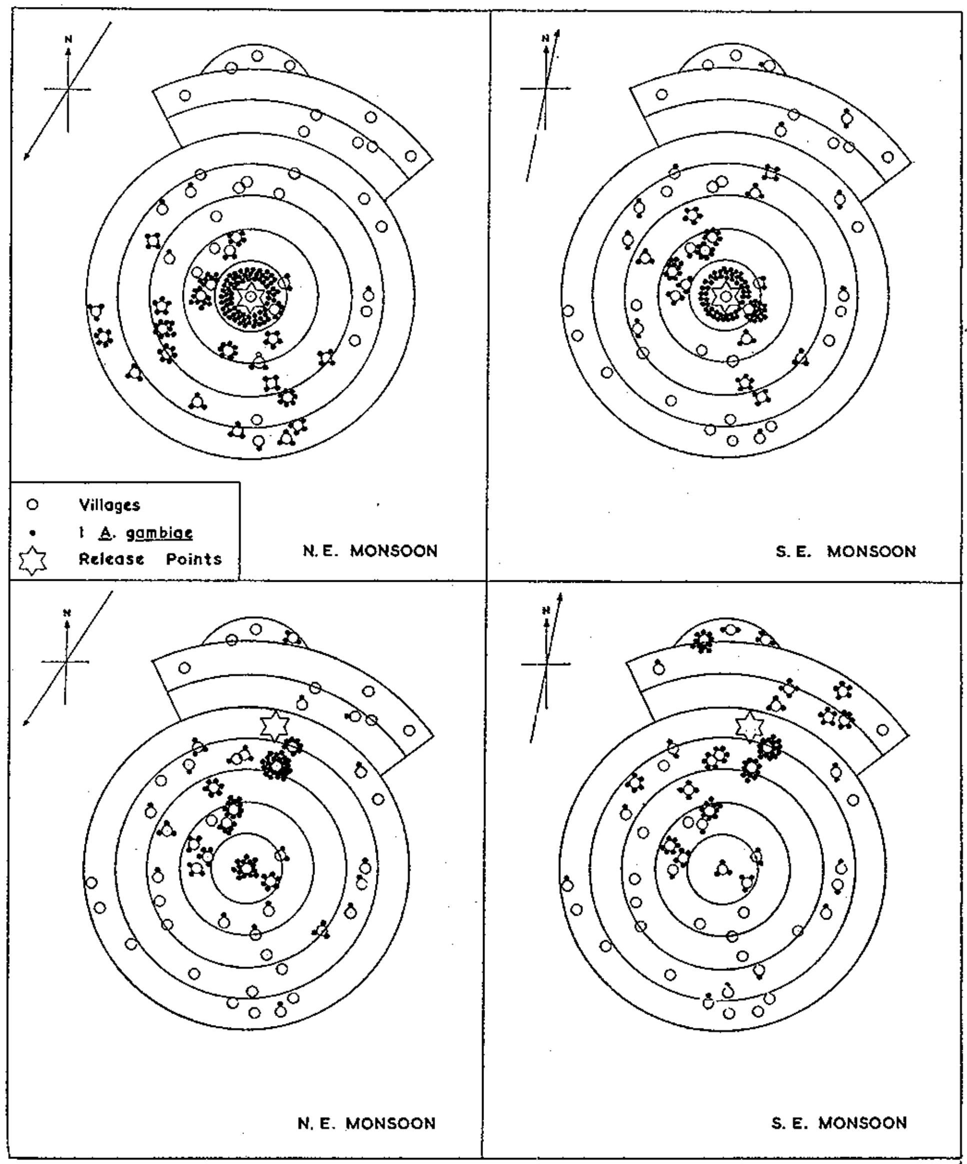

Fig. 6.—Dispersion of marked mosquitos in relation to prevailing wind. Each dot represents one individual of *A. gambiae* recaptured.

the four age-groups is illustrated in fig. 7. This shows very clearly that there are two phases of distribution, first, a period covering the initial two days after release, and secondly, the rest of the recorded life of marked mosquitos. In the first phase, marked females were mainly concentrated within a quarter of a mile of the release point, while in the second phase they were spread out throughout the

TABLE VII.

Recaptures and estimated dispersion from peripheral release points in relation to age (females only).

North-eastern release point

Range (miles)	Area factor	Day 1		Day 2		Days 3–9		Days 10+		All catches	
		Catch	Estimated density	Catch	Estimated density	Catch	Estimated density	Catch	Estimated density	Catch	Estimated density
¼	1	—	—	1	1	12	12	7	7	20	20
½	1*	35	37	1	1	14·1	16·2	5·9	6·8	56	61
¾	1*	7·3	8·3	13·1	15·5	31·6	47·2	17	24	69	95
1	2·4	3	7·2	2	4·8	8	19·2	4	9·6	17	40·8
1¼	2·6	2·2	5·7	17·8	46·3	25	65	10	26	55	143
1½	3·0	1	3	—	—	10	30	1	3	12	36
1¾	3·5	1	3·5	2	7	3	10·5	1	3·5	7	24·5
2	4·6	—	—	—	—	5	23	—	—	5	23
2¼	6·7	1	6·7	1	6·7	—	—	1	6·7	3	20·1

South-western (I) release point

Range (miles)	Area factor	Day 1 Catch	Day 1 Estimated density	Day 2 Catch	Day 2 Estimated density	Days 3–9 Catch	Days 3–9 Estimated density	Days 10+ Catch	Days 10+ Estimated density	All catches Catch	All catches Estimated density
¼	1	—	—	9	9	3	3	—	—	12	12
½	1·2	—	—	—	—	4	4·8	—	—	4	4·8
¾	1·6	1	1·6	1	1·6	9	14·4	—	—	11	17·6
1	2·1	—	—	4	8·4	5	10·5	1	2·1	10	21
1¼	2·4	—	—	—	—	1	2·4	2	4·8	3	7·2
1½	2·9	1	2·9	—	—	3	8·7	3	8·7	7	20·3
1¾	3·5	—	—	—	—	1	3·5	1	3·5	2	7·0

South-western (II) release point

Range (miles)	Area factor	Day 1 Catch	Day 1 Estimated density	Day 2 Catch	Day 2 Estimated density	Days 3–9 Catch	Days 3–9 Estimated density	Days 10+ Catch	Days 10+ Estimated density	All catches Catch	All catches Estimated density
¼	1·3	—	—	5	6·5	7	9·1	—	—	12	15·6
½	1·8	1	1·8	1	1·8	2	3·6	1	1·8	5	9
¾	2	—	—	1	2	1	2	—	—	2	4
1	2·4	1	2·4	—	—	—	—	—	—	1	2·4
1¼	2·6	—	—	1	2·6	1	2·6	1	2·6	3	7·8
1½	3	—	—	—	—	3	9	1	3	4	12

* Catches from the extension area have been multiplied by 2.

experimental area, but decreasing in density as its outer limits were approached. There is no significant difference in this pattern between the two older age-groups, a fact which suggests that, once the initial dispersion had taken place, mosquitos tended to be restricted to the same general area for feeding or oviposition. It also suggests that any continuing emigration of older mosquitos was at too low a level to be detected. In this series of releases, however, recaptures were made only up to 1¼ miles, and it is possible that the existence of a movement of this sort was masked by the limited area of recapture. Closer inspection is required, therefore, of the recoveries from the peripheral releases.

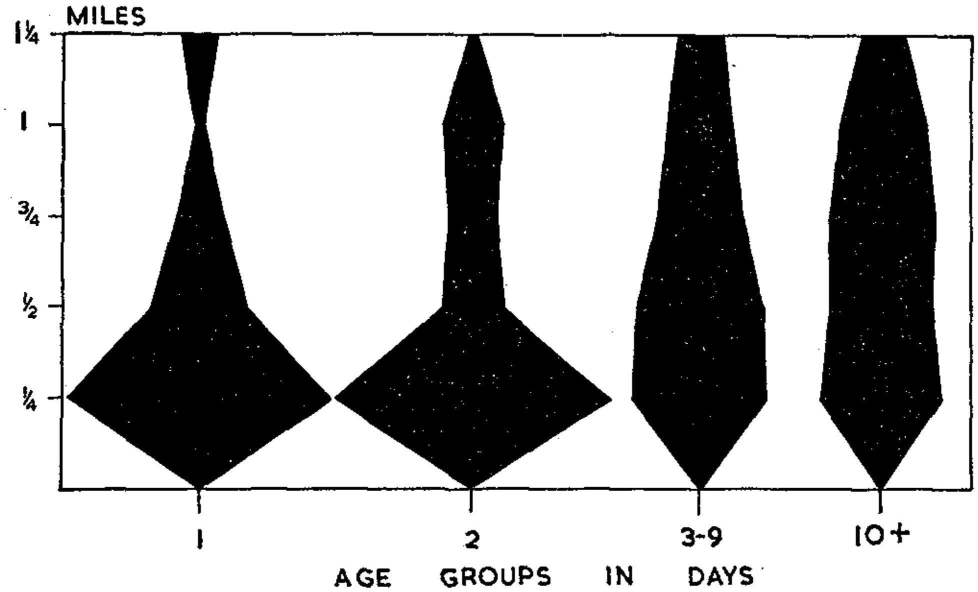

Fig. 7.—Dispersion from central release point by age-groups.

TABLE VIII.

Estimated dispersion of recaptures for all peripheral releases in relation to age (females only).

Range (miles)	Day 1		Day 2		Days 3–9		Days 10+		All catches	
	Density	Per cent.	Density	Per cent.	Density	Per cent.	Density	Per cent.	Density	Per cent.
¼	—	—	16·5	14	24·1	8	7	6	47·6	8
½	38·8	48	2·8	2	24·6	8	8·6	8	74·8	12
¾	9·9	12	19·1	17	63·6	21	24	21	116·6	19
1	9·6	12	13·2	12	29·7	10	11·7	10	64·2	11
1¼	5·7	7	48·9	43	70	24	33·4	30	158	26
1½	5·9	7	—	—	47·7	16	14·7	13	68·3	11
1¾	3·5	4	7	6	14	5	7	6	31·5	5
2	—	—	—	—	23	8	—	—	23	4
2¼	6·7	8	6·7	6	—	—	6·7	6	20·1	3
Mean range (miles)	0·9		1·07		1·1		1·12		1·07	

The data in Table VII show the numbers recaptured and the estimated dispersion up to 2¼ miles for the same four age-groups. The estimated dispersion from all peripheral releases in relation to age, together with the mean flight range for each group, is shown in Table VIII. The same distribution is illustrated graphically in fig. 8. As was found for the central releases (fig. 7), both the two older groups show an essentially unchanged pattern. Only in the recoveries from the south-western (I) release point is there any suggestion that the oldest group had an excess of females in the outer recapture stations; and here unfortunately the size of the sample was very small. With this exception, the findings from the recaptures of older mosquitos up to 2¼ miles parallel those up to 1¼ miles.

There is, however, one clear difference between the recoveries from the north-eastern release point and the central releases when the distribution on the second

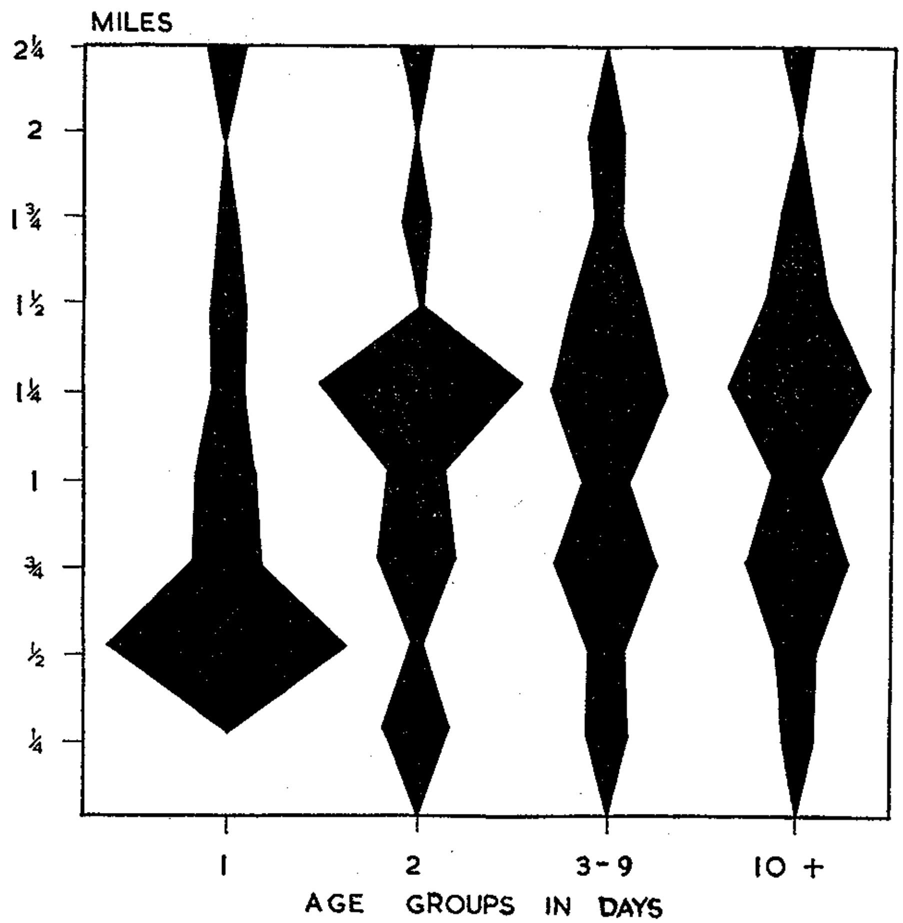

Fig. 8.—Dispersion from peripheral release points by age-groups.

day is considered. The dispersion of the latter group was virtually unchanged between the first and second days, whereas the mosquitos from the north-eastern point had already spread quite widely throughout the area by this time. The difference probably reflects the difference in density of houses and inhabitants in the two areas, although it was also influenced by the scarcity of catching stations in the vicinity of the peripheral point and consequent difficulty in ensuring adequate randomisation of catches on both days.

To recapitulate these findings, there is, first, a period of reduced dispersion lasting either one or two days. Its termination coincides approximately with the

TABLE IX.

Distribution by age of all mosquitos recaptured.

Age in days		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Painted	females	119·5	89	73	44·5	31·5	36·5	48	24	17	12	10	10	8	9·5	10	
Isotope ..	females	44	54·1	22	20	16·9	34·8	24	11·3	15·6	4·6	4	2·7	13·2	5·9	2·7	
Isotope ..	males	18·6	31·8	12·6	13·3	12·2	11·7	11·3	9·4	4·5	5·7	—	3·4	2·1	3·5	4·1	
All ..	females	163·5	143·1	95	64·5	48·4	71·3	72	35·3	32·6	16·6	14	12·7	21·2	15·4	12·7	
Age in days		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Total
Painted	females	4·5	4	2	5	3	3	0·5	1·5	—	—	—	—	—	—	—	566
Isotope ..	females	4·4	0·8	3	1·1	5·4	2·7	2·2	1·6	—	—	—	—	—	—	—	297
Isotope	males	4·8	1	—	1·4	1·6	0·2	0·8	—	—	—	0·4	—	0·6	—	1	156
All ..	females	8·9	4·8	5	6·1	8·4	5·7	2·7	3·1	—	—	—	—	—	—	—	863

Trapping continued up to 35 days after each release. Where releases with the same mark were made on more than one day, recaptures have been divided between the two possible ages.

first egg-laying flight. The second phase covers the rest of the observed life-span of marked mosquitos, and is characterised by an irregular distribution up to the limits of the recapture area. No change in the over-all distribution of the marked population between the earlier and later stages of this phase was detected, and no evidence was afforded therefore of a progressive dispersion with age. The existence of a continuing emigration from the experimental area on a small scale cannot, however, be excluded.

Age distribution of recaptures.

The distribution by age of all recaptures is set out in Table IX. In a number of releases the same label was used on two consecutive days or, more rarely, after an interval of one day. Consequently, mosquitos recaptured with such marks might have belonged to either day's releases. In setting out the results by age, such insects have been allocated fractionally to two different days. For example, in Table IX it will be seen that 0·4 males were recaptured on day 26 and 0·6 on day 28. Both refer to one specimen caught on August 20th, belonging to an unusually small rearing released in two batches of 500 and 300 on July 23rd and 25th, respectively. Since the chances are approximately 6:4 that the mosquito belonged to the earlier release, the recapture has been apportioned to the two days in the appropriate ratio.

A further correction has been applied to make allowance for the effect of interruptions of the recapture routine caused by weekends and holidays. The calculation is laborious and is not shown here. But one example will serve to explain the method. In the second series of isotope experiments there were eight releases. Routine catching was carried out on day 1 after seven out of eight releases, on day 2 after all eight, on day 3 after five, on day 4 after six, and so on. The method of working is shown in Table X. The third line of the table gives the number of recaptures per catching day, which provides the best value for the true age composition of the recaptured sample. However, there were several series of releases, each with different recapture rates. Since we want to combine all the series together again after correction, it is necessary to re-convert the corrected total of each series back to the original total, as shown in the lowest line of the table. The corrections have been made to all the series (see Table XI), and these figures are used in all further discussions on the age structure of recaptures.

TABLE X.

Method of correction for number of catching days; second series of isotope experiments (8 releases) (females only).

Age in days	1	2	3	4	5	6	7	8–23	Total
Total catch ..	35	45·8	20·2	17	9·2	25·8	14·6	65·4	233
No. of catching days (max.=8)	7	8	5	6	6	7	6	–	–
Mosquitos per catching day ..	5	5·72	4·04	2·83	1·53	3·69	2·43	9·7	34·94
ditto × weighting factor (233÷34·94=6·67)	33·4	38·1	27	18·9	10·2	24·6	16·2	64·6	233

Detailed working is only shown for first 7 days after release. The weighting factor is applied so as to convert the total of corrected daily catches back to the original number recaptured.

TABLE XI.

Distribution by age of all mosquitos recaptured, after correction for number of catching days.

Age in days		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Painted	females	129·2	89·9	77·2	45·2	32·8	35·5	35·5	23·9	17·5	11·4	10·4	9·8	7	7·6	10	
Isotope ..	females	42·6	48·9	31·3	23·3	15·7	31	23·3	11·1	15·8	5·1	5·4	2·7	10·8	5·9	2·7	
Isotope ..	males	17·8	27·9	17·5	14·6	12·1	10·3	11	9·2	4·9	6·8	—	3·3	1·7	3·3	3·9	
All ..	females	171·8	138·8	108·5	68·5	48·5	66·5	58·8	35	33·3	16·5	15·8	12·5	17·8	13·5	12·7	
Age in days		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Total
Painted	females	4·1	3·8	1·5	5·7	2	2·2	0·3	3·5	—	—	—	—	—	—	—	566
Isotope ..	females	4·7	0·9	3·3	1·1	5·1	2·4	2·1	1·8	—	—	—	—	—	—	—	297
Isotope ..	males	4·8	1·3	—	1·5	1·5	0·2	0·7	—	—	—	0·3	—	0·3	—	1·1	156
All ..	females	8·8	4·7	4·8	6·8	7·1	4·6	2·4	5·3	—	—	—	—	—	—	—	863

The general pattern of age distribution shown is one of a regular and moderately steep decline in numbers with increasing age. From Table XI it can be calculated that 77 per cent. of all females were caught during the first week after release (36% during the first two days), 17 per cent. during the second week, 6 per cent. during the third week, and just under 1 per cent. during the fourth week. No females older than 23 days were recaptured. The results of the two different marking methods are broadly similar. Regression coefficients for the logarithm of the numbers recaptured per two-day period (excluding days 1 and 2) are $-0{\cdot}09$ and $-0{\cdot}067$ for the paint and isotope releases, respectively. While suggestive, this difference is not significant at the 5 per cent. level ($t=1{\cdot}9$). The two series of results have therefore been combined, and in fig. 9 the density of all recaptured females has been plotted on a semi-logarithmic scale in relation to age. The regression coefficient for this curve is $-0{\cdot}075$, which corresponds to a daily loss of mosquitos of 16 per cent.*

The age distribution of male mosquitos is also shown in Table XI. The regression coefficient for log density on age for males, for the period from 3–4 to 21–22 days, is $-0{\cdot}084$, which corresponds to a daily mortality of about 18 per cent. This is an unexpectedly low figure. It is commonly thought that males are short-lived insects. Yet their survival rate to 22 days is only slightly lower

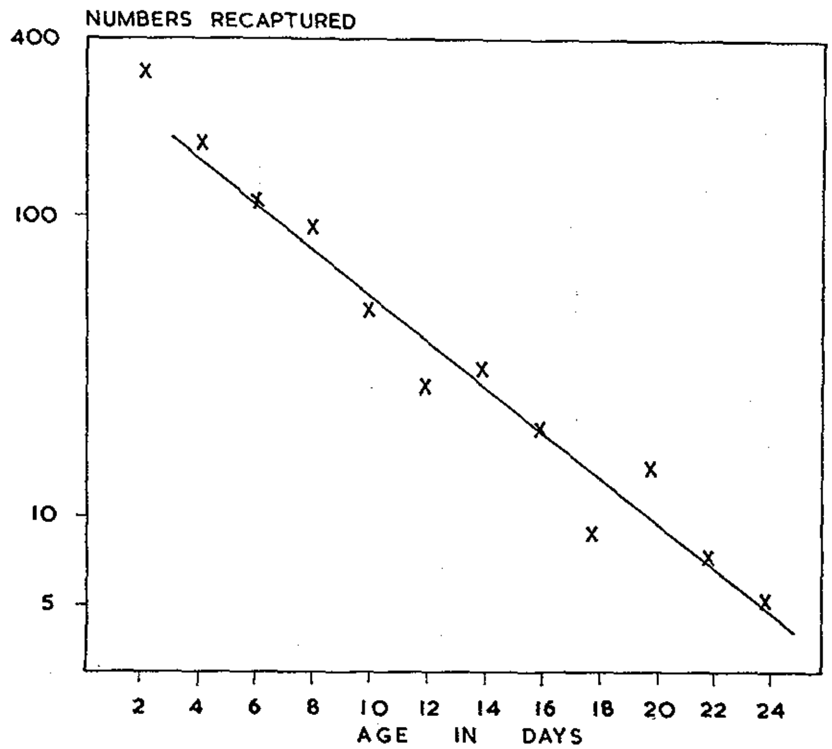

Fig. 9.—Numbers of recaptured mosquitos in relation to age.

* At age 3-4 days the expected catch is 159·6, and at 23-24 days it is 5; the decrease in 20 days is therefore 96·9 per cent., and 3·1 per cent. survive. Hence, if P is the chance of survival through one day, P^{20}, the chance of survival through 20 days, is 0·031, and $P = 0{\cdot}841$. The chance of dying in one day is $1 - P = 0.159$, hence the percentage daily mortality is 15·9.

TABLE XII.

Results of gland dissections of marked mosquitos, showing numbers negative and positive for sporozoites.

Age in days	3–9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total (12–23)
Negative dissections	—	7	3·5	11·5	10	10	10·5	6	3·5	—	5	5·5	3	2	2·5	69·5
Positive dissections	—	—	—	0·5	1	0·5	—	—	—	—	0·5	—	0·5	—	—	3
Not dissected ..	366·5	7	6·5	1	6·5	3	1	2·5	—	4	1	2	2	—	—	23
Total ..	366·5	14	10	—	—	—	—	—	—	—	—	—	—	—	—	95·5

than that of the females, and, even more surprisingly, the oldest two mosquitos caught were both males, recaptured at 30 and 26 or 28 days after release.

Mortality rates of marked population.

As already pointed out, the slope of the curve in fig. 9 corresponds to the rate of loss of marked mosquitos from the experimental area. This loss may be the product of three factors, death, emigration, or failure of the marking technique. Evidence has already been adduced to suggest that the last factor was of negligible importance, and we are left, therefore, with the question of emigration. It is obvious from the spatial distribution of recoveries that a proportion of the insects was flying beyond the limits of the experimental area, even when released in the centre; and it is even more obvious that the peripheral releases must have resulted in an immediate substantial loss. The question to be answered is, how much did this loss continue to deplete the population, and to what extent did it vary with age? From fig. 7 it is clear that the first two days after release represented a phase of reduced emigration, and catches on these days should be excluded from the present discussion. But thereafter, although recaptures continued to be made up to the limits of the area, no change in their distribution could be detected. This indicates that the population had become stabilised after the first two or three days; and that, while there must have been a steady and continuing loss through emigration, this was at too low a level to have materially affected the distribution of mosquitos within the experimental area. That it was probably of minor importance is also suggested by the estimates of dispersion beyond the recapture area made in the section on dispersion in relation to age of recaptures. But it remains as one factor contributing to the rate of loss indicated by fig. 9. It cannot be assessed quantitatively from these data, and the ' mortality ' rate of 16 per cent. derived from them refers to the combined loss through emigration as well as through death.

If the slope of the curve gives us only a limited amount of information, its shape, on the other hand, is of considerable interest. The densities of recaptures shown in fig. 9 have been plotted on a semi-log scale, and it will be seen that the points from day 4 to day 24 fall more or less on a straight line. This means that the rate of loss remained constant for all the age-groups shown; and unless, as seems highly improbable, the emigration rate fortuitously compensated exactly for any changes in survival rate, it must be concluded that the death-rate also remained stable throughout this period. It is possible that beyond this age the mortality rate may have risen, since recaptures of females ceased rather abruptly at 23 days. From the regression line shown in fig. 9 a total catch of some 8–10 mosquitos older than 24 days would have been expected. Their absence may have been due to a combination of the effects of chance together with a sharply reduced survival rate, or, less probably, to the simultaneous failure of persistence of both marking techniques. The implications of these tentative conclusions are discussed below.

Malaria infections in marked mosquitos.

Additional evidence on the survival of the population comes from the malaria infection rate among recaptured mosquitos. No malaria control measures were carried out in the experimental area, where the sporozoite rate in wild-caught *A. gambiae* averaged over all seasons 5–7 per cent. Since the chance of acquiring infection was the same for the marked as for the natural population, the sporozoite rate for the former should also be the same. However, of the limited number of gland dissections carried out, only three marked specimens positive for sporozoites were found. The results of the dissections are shown in Table XII.

Of those old enough to have mature sporozoites, that is, those aged 12 days and over, only 3 out of 72·5 were positive. (For an explanation of the presence of fractions in these figures, see p. 119). A further 23 belonging to the same age-groups were not dissected, making an expected total of positives of 4 out of 95·5. In the same series of catches there were 390·5 mosquitos recaptured at an age below that at which malaria infection could be manifested. Hence the sporozoite rate of the whole population (aged three days and over) was 4 out of 486, or $0{\cdot}8 \pm 0{\cdot}5$ per cent. Recaptures aged one and two days have been omitted for the reasons given on p. 123. Had they been included, the infection rate would have been lower still. Thus, comparison of the infection rates in natural and marked mosquitos gives a further demonstration of the abnormally low survival rate of the released mosquitos within the experimental area.

Discussion.

The use of laboratory-reared mosquitos for marking and release experiments places an immediate limitation on the application of the results, particularly those relating to longevity. It may have some effect also on flight range, although, in view of the importance of the distribution of sources of food and oviposition sites in influencing the movements of the population, the use of reared mosquitos is unlikely to have affected the results to any very great extent. But as regards survival, it has already been pointed out that the rate at which females disappeared from catches amounted to 16 per cent. per day, the greatest part of this loss being attributed to mortality. Earlier work in the same district, Gillies (1958*a*) and Davidson & Draper (1953), had indicated that an average mortality rate of 7–8 per cent. per day would account for the age structure and malaria infection rate found in natural populations of *A. gambiae.* Thus, the figure obtained from marking and release experiments is too high by a factor of 2; and the most likely explanation of the discrepancy must be the condition of the mosquitos used. It would seem that this represents a major difficulty in any experiments to determine the longevity of *A. gambiae*, except perhaps in those places where larvae can be collected from natural waters in great numbers. However, comparison of the behaviour of artificially reared mosquitos, released in different areas and situations, may give valuable results, particularly in relation to dispersion.

When analysing the movements of insects it is important to distinguish between the decline in density with distance and the total numbers reaching any particular range. The density (numbers per unit area) will, of course, tend to fall owing to the increasing area over which they are spread. If a population is distributed at random, as pointed out by Russell & others (1944), the density will decrease regularly with distance, but the total numbers distributed at each range will be the same, provided a sufficient interval of time has elapsed. Under these conditions, the mean dispersion of the population will vary as the square root of the time (D. Yeo, The dispersal of insects—a theoretical model based upon random movement.—*Misc. Rep. colon. Pest. Res. Unit, Arusha* no. 249, 1959). It is doubtful whether many insects disperse from a localised focus in this manner, except over a very limited fraction of their total range, and the data obtained in these observations on *A. gambiae* confirm the conclusion of Russell & others (*op. cit.*), for *A. culicifacies* Giles, that dispersion is non-random. The alternative type of movement is that of flight within an ambit, in which the spread of the population is restricted by particular features of the environment.

It seems fairly clear from the present work that the movements of the marked mosquitos conformed to the latter pattern, the restricting features presumably being the concentrations of villages and breeding sites within the area. It would appear unlikely that the boundaries of such an ambit would be particularly sharply defined, as they may be for instance in the case of tsetse flies (Jackson, 1940), and a certain amount of exchange between adjacent localities must obviously occur. The size of the ambit will vary according to the nature of the terrain.

In open and sparsely inhabited country, mosquitos may range over a wide area with little in the way of recognisable limits. However, the subject has been little explored up till now, and it is not possible to describe the dispersion of tropical mosquitos with any degree of precision.

Some further discussion is needed on the question of mortality, the pattern of which, in the present experiments, led to the conclusion that the death-rate remained unchanged between the ages of 4 and 24 days. This implies that aging processes are unimportant in a wild population, and that the causes of death must be largely external, the result of accident or predation. As already remarked, however, it is possible that, beyond this age, physiological changes may have become important. The shape of the survivorship curve is of particular interest in relation to the epidemiology of malaria. If the mortality rate is constant, then as was demonstrated by Macdonald (1952, and later papers), the mathematical analysis of malaria transmission becomes greatly simplified. The point at present remains unsettled. Much of the evidence on it comes from studies on the survival of caged mosquitos, the results of which are somewhat conflicting and not wholly relevant. Field studies are scarce, and are mostly the work of Russian authors on *A. maculipennis* Mg. using advanced age-grouping techniques (see Gillies, 1958*c*). Of these, the most complete series is that of Detinova (1953), who found a steadily rising mortality rate among the older mosquitos. Her results, however, were not uniformly confirmed by workers in other parts of the Soviet Union. More recently, Zalutskaya (1959) has reported a study of the age condition of populations of *A. minimus* Theo. and *A. vagus* Dön. in North Vietnam. Closer examination of her results shows that, in both species, the mortality rate remained constant throughout the period of adult life for which detailed analysis can be made (age-groups " 2-parous " to " 6-parous "). In the case of *A. vagus*, of which a very large number of specimens were dissected, the fit is particularly close. Females that had laid more than six egg-batches, however, were less common than would be expected if the death-rate had remained the same. Thus, both Zalutskaya's work and the present findings with *A. gambiae* give some measure of support to the type of mortality pattern postulated by Macdonald. It suggests the possibility that, under tropical conditions, the importance of predation pressure may outweigh other factors in just the same way that the lethal effect of insecticides falls on young and old mosquitos alike. On the other hand, in cooler climates, they may be sufficiently long-lived for aging changes to become apparent.

Summary.

An account is given of marking and release experiments with *Anopheles gambiae* Giles in a coastal area of Tanganyika. Laboratory-reared mosquitos were used, labelled either by the topical application of paint or by the introduction of radioisotopes into the larval breeding pans. Two different isotopes were used, ^{32}P and ^{35}S, and recaptures were recognised by autoradiography.

Routine catching stations were established within a circle of radius of 1¼ miles. Releases were made either in the centre or near the periphery of the experimental area, so that recaptures were possible up to a maximum of 2¼ miles.

The following results were obtained:

1. Of 132,000 mosquitos released, 1,019 were recaptured.
2. The mean flight range of females released in the centre was estimated to be 0·64 mile, and of males 0·52 mile. Of females released on the periphery, the mean range of dispersion was estimated to be 0·98 mile. Individuals of both sexes were caught at the maximum range of 2¼ miles.

3. The dispersion of recaptured mosquitos was shown to be non-random and to be related primarily to the distribution of human settlements.
4. In certain series of releases the direction of the prevailing wind had a definite effect on the dispersal of mosquitos. But in general this was a minor factor.
5. Dispersion during the first day or, in many instances, during the first two days after release was more restricted, compared with that of older mosquitos. But no difference in the distribution of catches was detected between those aged three–nine days and those more than nine days old.
6. Marked females were recaptured up to 23 days after release. Apart from the first two days, the regression of density on age amounted to a daily loss of 16 per cent. of mosquitos from the experimental area. The effect of emigration could not be assessed quantitatively, but it was held to be a minor component of the total daily loss. The relatively high level of mortality suggested by these figures is attributed to the use of laboratory-reared mosquitos.
7. The corrected sporozoite rate in marked females at the time of recapture was 0·8 per cent.
8. The survival of males was only slightly lower than that of females.
9. It is concluded from the survivorship curve that the mortality rate remained constant throughout the period in which marked females were recovered.

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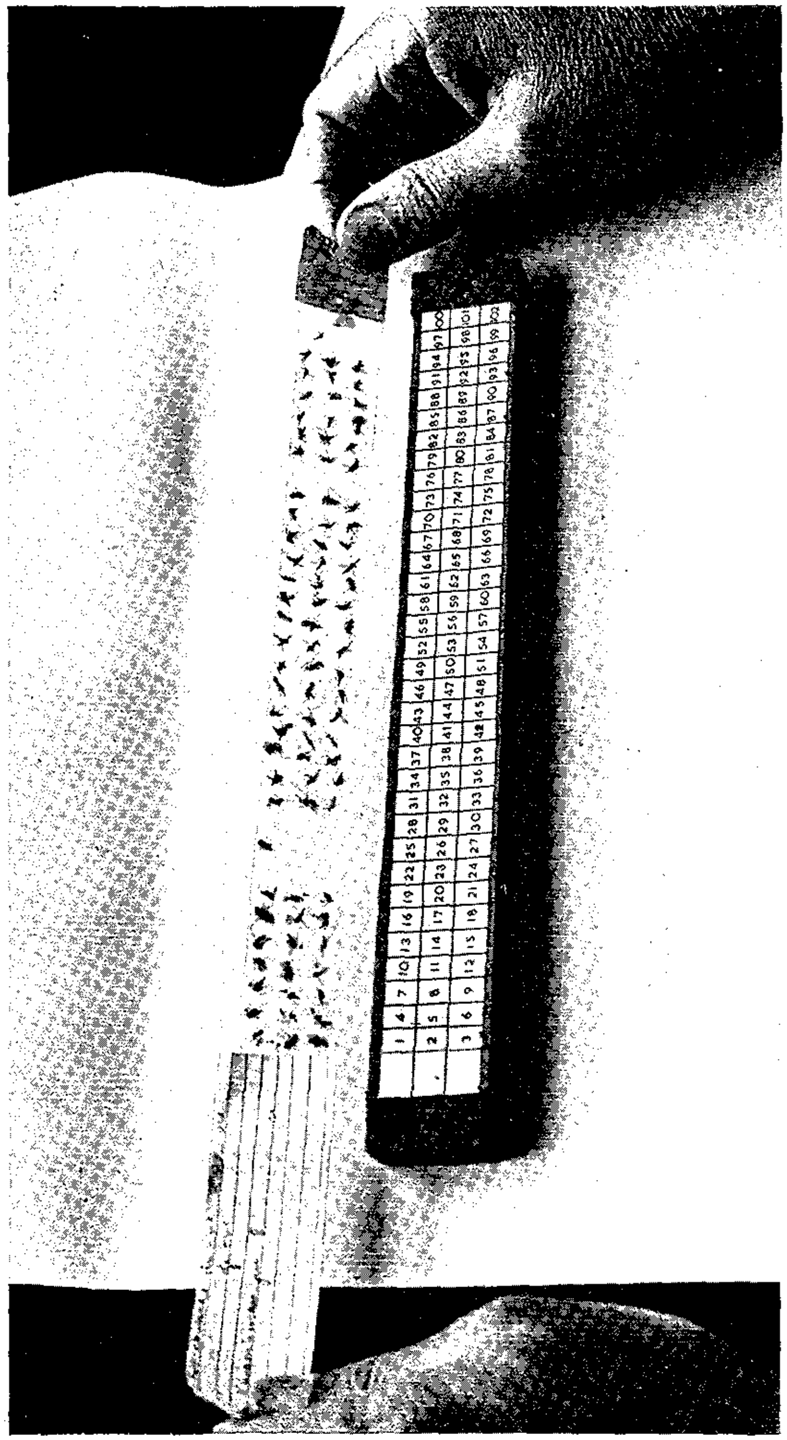

Numbered grid used for checking origin of recaptured radioactive mosquitos.

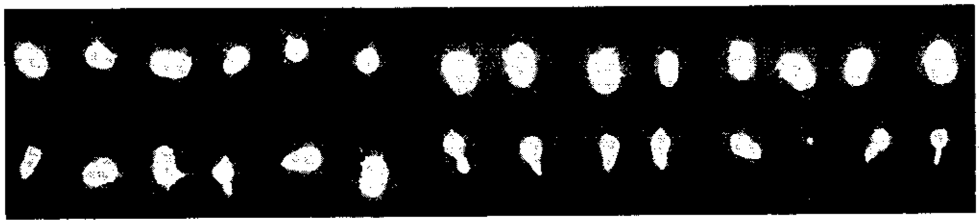

FIG. 1. Newly emerged mosquitos labelled with ^{32}P.

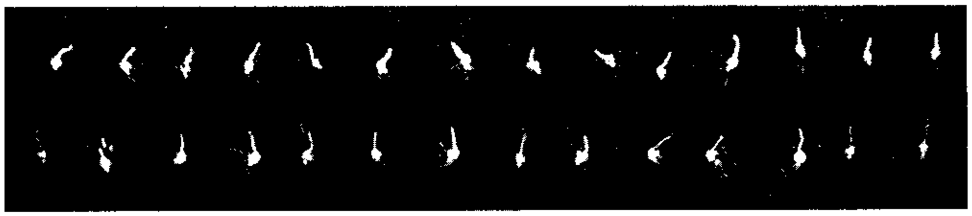

FIG. 2. Newly emerged mosquitos labelled with ^{35}S.

FIGS. 3-7 (left to right). 3. A male, labelled with ^{35}S, recaptured after 30 days. 4. A female, labelled with ^{35}S, recaptured after 19-21 days. 5. A female, labelled with ^{35}S, recaptured after 18 days. 6. A male, labelled with ^{32}P, recaptured after 21-22 days. 7. A female, labelled with ^{32}P, recaptured after 20 days.

AUTORADIOGRAPHS OF SPECIMENS OF *A. GAMBIAE* LABELLED WITH RADIOISOTOPES (NATURAL SIZE).