MEASURING MOSQUITO DISPERSAL FOR CONTROL PROGRAMS[1]

C. D. MORRIS, V. L. LARSON AND L. P. LOUNIBOS

Florida Medical Entomology Laboratory, IFAS-University of Florida, 200 9th Street SE, Vero Beach, FL 32962

ABSTRACT. Simple and economic methods were developed for control programs to demonstrate the movement of mosquitoes from a breeding source to residential areas. Using mark-release-recapture methods and examples, mean, median and maximum distances traveled were estimated or observed and compared for 11 species produced in a wastewater treatment facility near Lakeland, FL. The applicability of these methods and data interpretation for operational mosquito control programs are discussed.

INTRODUCTION

As social pressures increase for mosquito control operations to curtail pesticide use, it becomes more important to demonstrate that chemical control is necessary and effective. This requires more information about mosquito biology and its application to insecticide management decisions.

One issue faced by mosquito control programs is proving that mosquitoes produced in one location create a problem elsewhere. A case in point is a 600 acre (243 ha) wastewater treatment facility located near Lakeland, FL. Previous monitoring showed that this site produced large numbers of mosquitoes that presumably became pests in nearby residential areas. The operators of the facility did not accept the local mosquito control program's evaluation. To convince the wastewater management operators to modify their procedures or subsidize mosquito control, it became necessary to prove that mosquitoes found in nearby residential areas came from this source. One way to do this was to conduct mark-release-recapture studies on the mosquitoes breeding in the treatment facility.

Past mark-release studies were concerned with describing the bionomics of mosquitoes (Dow et al. 1965, Gillies 1961, Provost 1952, Yasuno et al. 1973). Research dealt with questions concerning where and how far mosquitoes travel and the environmental and physiological conditions that influence their flights. These studies released minimally handled and lightly marked mosquitoes of a known age from single points and then used a surrounding network of recapture traps to monitor movements in time and space as a function of weather. Such procedures were complex and expensive.

Our major objective was to develop simple mark-release-recapture methods that could be used by mosquito control programs to determine if mosquitoes produced in one location were flying to residential areas. During these studies, we found we could also make useful, albeit conservative, estimates of mean and maximum distances traveled. Both the methods and the results of our studies are presented in this report.

MATERIALS AND METHODS

Since the primary objective was to show that mosquitoes could fly from one location to another, rather than to quantify flight dynamics, the age and condition of the released mosquitoes was less critical. We relied on collecting, marking and releasing as many mosquitoes as possible. And, rather than have one release site and numerous recapture sites surrounding it, we chose to have 3 release sites at differing distances from 2 residential areas and concentrate recapture sites near those areas.

Two mark-release-recapture experiments were performed during May and July of 1987 at the wastewater treatment facility located between Lakeland and Mulberry, FL (Fig. 1).

Mosquitoes were collected in CO_2-baited CDC light traps operated overnight. The catch chambers were modified to accommodate the 5,000–15,000 mosquitoes per trap that we anticipated collecting. We joined the tops of two 1-gallon (3.8 liter) ice cream cartons and secured them with duct tape. Three openings were cut in the sides and covered with screen to maintain trap efficiency and increase air circulation during dusting. An opening cut in the top was fitted with a 12 inch (30.5 cm) cloth sleeve which was placed over the bottom of the trap body and held with rubber bands. In studies conducted later, but not reported here, we placed accor-

[1] Institute of Food and Agricultural Sciences, University of Florida Experiment Stations Journal Series Number R-01522.

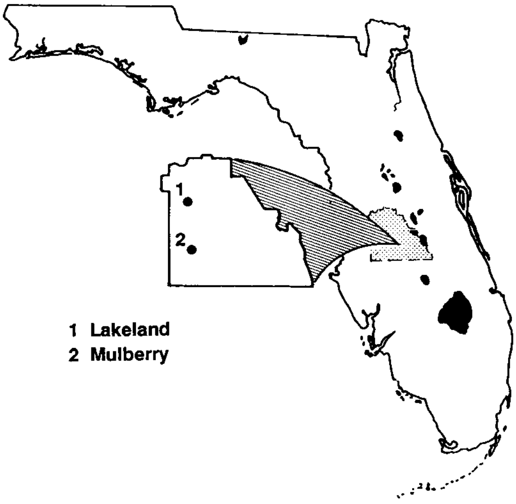

Fig. 1. Location of study sites in Polk County, FL.

dion-folded screening inside the catch chambers to provide more resting surface for the mosquitoes, reduce mortality and increase marking efficiency.

Collecting and handling mosquitoes: Forty traps were positioned at 0.1 mile (about 0.16 km) intervals along the dikes between wetlands and operated overnight on May 12 and 14 and July 7 and 9 of 1987 (Fig. 2). At dawn on the following mornings, mosquitoes in 37 traps were dusted with an orange, blue or green fluorescent dust and released from 3 sites (Fig. 2), one color per site. The remaining 3 trap collections were used to estimate the species composition and numbers released.

Mosquitoes were marked by injecting dust through the sleeve opening in the trap catch chamber with a 50 ml syringe fitted with a 16 gauge needle broken off at the base. The force of the injection created a cloud of dust that covered the mosquitoes with enough pigment to allow their color to be determined with the naked eye. After all chambers at a site were dusted, they were opened and the collections dumped out on the ground. Many of those marked never recovered.

Recapture traps were operated at 44 sites: 10 to the southwest along the perimeter of the city of Mulberry, 10 to the north near Lakeland and 24 within the wetlands (the 20 sites used to collect mosquitoes for marking and 3 on-going collection sites used by Polk County mosquito control (Fig. 2). Collections were made on the nights of May 13 and 15 and July 8 and 10. Traps were retrieved the following morning, collections frozen and, after thawing, examined under UV light to detect marked mosquitoes. Magnification was not required to identify dusted mosquitoes. Dusted mosquitoes were identified to species.

Analyses: Annuli separated by 0.4 km (0.25 mi) were drawn around the release points to estimate dispersal distances. A correction factor (CF) was calculated (after Lillie et al. 1981, 1985, White and Morris 1985) to accommodate unequal trap densities.

$$\text{Annulus CF} = \frac{\text{Area of annulus}}{\text{Total trapping area}} \times \text{total number of traps}$$

The estimated recaptures (ER) for each annulus were calculated as:

$$\text{ER} = \frac{\text{Number of observed recaptures in annulus}}{\text{Number of traps in annulus}} \times \text{CF}$$

$$\text{Annulus distance} = \frac{\text{Inner radius} + \text{outer radius}}{2}$$

The mean distance traveled (MDT) was calculated as:

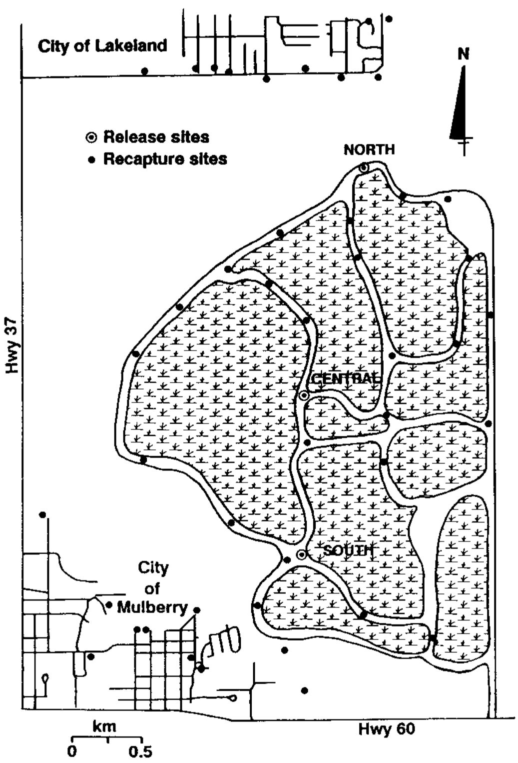

Fig. 2. Locations of 3 release sites and 40 recapture sites at the Lakeland study area.

$$\text{MDT} = \frac{\text{Sum (ER} \times \text{distance) for all annuli}}{\text{Total number of ER}}$$

Corrected data, i.e., ER, were also used to calculate regressions of the cumulative number of recaptures against log-transformed distance. The regression line estimates the flight range (FR) of various proportions of marked populations (e.g., Gillies 1961, White and Morris 1985).

RESULTS

May: An estimated 235,000 mosquitoes were marked and released on May 13 and 15. Five species, *Anopheles crucians* Wied., *Culex salinarius* (Coq)., *Cx. nigripalpus* Theobald, *Mansonia titillans* (Walker) and *Coquillettidia perturbans* (Walker), accounted for 98.7% of the mosquitoes collected for estimating species composition of the specimens marked (Table 1). The same 5 species accounted for 98.9% of dusted recaptures; *Cx. salinarius* comprising over 50% of both counts.

Data manipulation, an example: The data were adjusted for the number of traps in each annulus and the area of the annulus to calculate the MDT and FRs. There are several steps to the data conversion, but the mathematics is elementary. For instructional purposes, we present all steps required to calculate ER and its use in calculating MDT and FRs. The example uses *Cx. nigripalpus* data from the May release (Fig. 3, Table 2). The ER for the May release of *Cx. nigripalpus* consists of the sum of the ERs for the 6 releases (3 release sites, 2 dates). Here, we present the detailed calculations for only the May 12 release from the central site.

On a scale drawing of the study area (Fig. 3), we drew evenly spaced concentric circles around the release site. While we used 0.4 km (0.25 mi) for the annulus spacing, any distance can be used as long as there is at least one recapture site in each annulus. The inner and outer radii of each annulus are recorded as A and B, respectively, in Table 2. Next, we determine the area of each of the 8 annuli (10 for the north and south release sites); this is the area of the circle using the outer radius (B) minus the area of the circle using the inner radius (A). Area is recorded as C and the sum of the areas as D in Table 2.

Count the number of recapture sites in each annulus. If a trap site falls on the line dividing annuli, count the trap as 1/2 in each annulus (there are 5 such sites in the example). Record the number of traps in each annulus as E; the total number of traps is F.

Calculate the correction factor (CF) for each annulus by dividing the area of the annulus (C) by the area of the study area (D), and then multiply this value by the total number of traps in the study (F); e.g., for annulus 1: $(1/64.34) \times 43 = 0.67$. Now count the number of *Cx. nigripalpus* recaptured in each annulus (see Fig. 3) and record as H, observed recaptures.

The estimated recaptures (ER) for each annulus is determined by dividing the observed recaptures in the annulus (H) by the number of

Table 1. Estimated species composition of mosquitoes marked and released and species composition of recaptured mosquitoes during May and July, 1987.

Species	May 13 and 15		July 8 and 10	
	Est. % of released*	Percent of recaptures	Est. % of released*	Percent of recaptures
Culex salinarius Coquillett	54.6	70.2	7.2	27.5
Culex nigripalpus (Theobald)	16.1	17.5	69.5	55.6
Anopheles crucians Wiedemann	15.7	5.1	6.7	1.4
Mansonia titillans (Walker)	8.4	3.6	5.7	0.7
Coquillettidia perturbans (Walker)	3.9	2.5	2.0	2.1
Aedes vexans (Meigen)	1.6	0.1	0.8	0.0
Mansonia dyari Belkin, Heinemann and Page	0.7	0.0	2.2	0.0
Culex erraticus (Dyar and Knab)	0.5	0.7	4.0	2.1
Psorophora columbiae Dyar and Knab	0.4	0.2	2.7	8.5
Aedes infirmatus Dyar and Knab	0.3	0.1	0.0	0.7
Aedes atlanticus Dyar and Knab	0.0	0.1	—	—
Anopheles quadrimaculatus Say	<0.1	0.0	—	—
Psorophora howardii Coquillett	<0.1	0.0	0.3	0.0
Psorophora columbiae Dyar and Knab	<0.1	0.0	0.5	0.0
Uranotaenia sapphirina (Osten Sacken)	<0.1	0.0	0.2	0.0
Number of specimens	35,228	1,692	32,434	142

* Average percent of 6 collections.

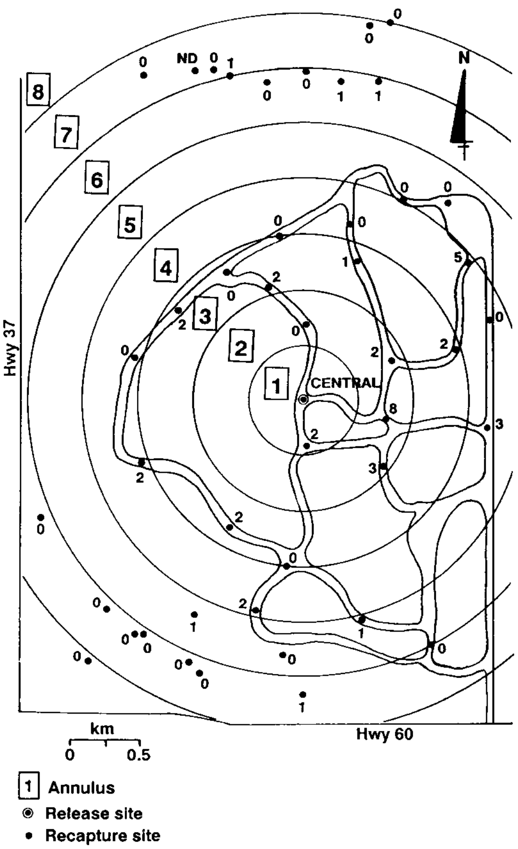

Fig. 3. Location of trap sites (●) and annuli (numbers in squares), and number of *Culex nigripalpus* (numbers beside ●) recaptured on May 12–13 used to determine ER, MDT and FRs of *Cx. nigripalpus* released from the central site on May 12.

traps in the annulus (E) and then multiplying this number by CF and round to the nearest whole number; e.g., for annulus 1: (2.0/1.0) × 0.67 = 1.34, rounded to 1. Sum the ERs for all annuli; 24 in our example. This completes the data conversion for the May 12 release from the central site.

The same procedures were used to calculate the ERs for the other 5 date and release site combinations in May (items I2 through I6 in Table 2). These were then added for each annulus (e.g., annulus 1, 47 in Table 2) and the annuli sums totaled (K = 102 in Table 2). Next, the median distance of each annulus (L) was calculated by adding the inner radius (A) and outer radius (B) and dividing the total by 2. Median distance (L) was then multiplied by its respective J and the Js summed (N). We are now ready to calculate MDT for the May release of *Cx. nigripalpus* by dividing K by N: 77.2/102 = 0.76 km (0.47 mi). The same procedures were used to calculate MDTs for the other species (Table 3).

Flight distances: The MDTs of *Cx. salinarius* and *An. crucians* were similar to that of *Cx. nigripalpus* and all 3 were significantly lower than those of *Cq. perturbans* and *Ma. titillans.* Insufficient numbers of *Cx. erraticus* were recaptured to compare its MDT with the others.

The regressions of mean number of mosquitoes (log scale) of all species recaptured per trap, per annulus, plotted against distance (linear scale) were highly significant for both nights (Fig. 4A; $R^2 = 0.78$, $P < 0.001$ for May 12–13 and $R^2 = 0.62$, $P < 0.004$ for May 14–15). The slopes were not significantly different ($t = -1.17$, $P = 0.26$). One can assume the same relationship is true for individual species.

Special attention was paid to the traps situated in the residential areas to the north (Lakeland) and southwest (Mulberry) of the release sites (Fig. 2). As expected from the regression, the mean number of dusted mosquitoes collected at residential sites decreased with the distance from the release sites (Tables 4 and 5).

The cumulative number of expected recaptures of all species as distance increased was fitted to a linear regression (Fig. 5A; $y = 0.002X - 0.47$; $P < 0.001$) which accounted for 91% of the variance. Using this equation, the 50% and 90% flight ranges for all species combined were calculated at 0.20 km (0.12 mi) and 2.27 km (1.4 mi), respectively (Fig. 5A).

July: An estimated 216,000 mosquitoes were marked and released on July 8 and 10. Seven species accounted for 97.8% of mosquitoes marked and released and 97.9% of marked recaptures (Table 1). In July, as in May, the MDTs of *Cx. nigripalpus* and *Cx. salinarius* were not significantly different (Table 3; $t = 1.29$, $P = 0.203$, df = 46). Insufficient numbers of the other species were recaptured to compare their MDTs. The maximum observed distances traveled (Table 3) were less for 5 species than in May, similar for one species and greater for two.

The linear regressions of log-transformed recapture numbers on distance from the release sites were significant for both July 7–8 (Fig. 4B; $R^2 = 0.60$, $P = 0.005$) and July 9–10 ($R^2 = 0.62$, $P = 0.004$). The two July slopes were not significantly different from each other ($t = -0.68$, $P = 0.58$), but both were significantly different from the May slopes ($t = -4.10$, $P = 0.002$).

The regression equation $y = 0.13X - 0.24$ ($P < 0.001$), which accounted for 94% of the variance, was used to calculate the July flight ranges for all species combined, at 0.48 km (0.30 mi) for 50% and 2.11 km (1.31 mi) for 90% of the mosquitoes (Fig. 5B).

Table 2. An example of calculating mean distance travelled (MDT) using May *Culex nigripalpus* data.

	Annulus											
	1	2	3	4	5	6	7	8	9	10	11	Sum
Radius (km)												
A. Inner	0.0	0.4	0.8	1.2	1.6	2.0	2.4	2.8				
B. Outer	0.4	0.8	1.2	1.6	2.0	2.4	2.8	3.2				
C. Area (km)	1.00	3.02	5.03	7.04	9.05	11.06	13.07	15.08				D = 64.34
E. Number of traps	1.0	4.0	7.0	8.0	5.5	12.0	5.0	0.5				F = 43.0
G. CF = (C/D) × F	0.67	2.02	3.36	4.70	6.05	7.39	8.73	10.08				
H. Obs. recaptures	2.0	13.0	9.0	12.0	2.0	3.5	0.5	0.0				
I. ER = (H/E) × G	1	7	4	7	2	2	1	0	—	—	—	24
(Items I2. through I6. are the estimated recaptures (ER) for the other 5 site/date combinations in May.)												
I2. Cent., May 14	10	9	6	2	1	2	2	0	—	—	—	32
I3. South, May 12	0	2	1	0	0	0	0	0	1	0	0	4
I4. South, May 14	0	0	0	0	0	0	0	0	0	0	0	0
I5. North, May 12	4	1	1	0	0	0	0	0	0	1	0	7
I6. North, May 14	32	2	0	1	0	0	0	0	0	0	0	35
J. Sum of I. to I6.	47	21	12	10	3	4	3	0	1	1	0	K = 102
L. Distance (A + B)/2	0.2	0.6	1.0	1.4	1.8	2.2	2.6	3.0	3.4	3.8	4.2	
M. J × L	9.4	12.6	12.0	14.0	5.4	8.8	7.8	0.0	3.4	3.8	0.0	N = 77.2

MDT for *Cx. nigripalpus* for May = K/N = 77.2/102 = 0.757 km.

Table 3. Mean distance (km) traveled (MDT) from estimated recaptures (ER) and observed maximum distance (km) traveled (Max.).

	May 1987			July 1987		
Species	ER	MDT ± SD*	Max.	ER	MDT ± SD	Max.
Ae. atlanticus	1	2.20	2.2	—	—	—
Ae. infirmatus	—	—	0.2	—	—	1.4
Ae. vexans	1	1.40	1.4	—	—	—
An. crucians	19	0.45 ± 0.60b	2.6	1	0.20	0.2
Cq. perturbans	21	1.67 ± 1.05a	3.4	1	1.80	1.8
Cx. erraticus	3	0.73 ± 0.61	1.4	1	2.20	2.2
Cx. nigripalpus	102	0.76 ± 0.76b	3.8	32	0.94 ± 0.87a	3.4
Cx. salinarius	475	0.84 ± 0.77b	4.2	16	0.68 ± 0.53a	2.2
Ma. titillans	25	1.30 ± 1.00a	3.4	1	1.80	1.8
Ps. ciliata	—	—	—	—	—	0.6
Ps. columbiae	—	—	1.0	2	0.20	1.0
All species	266	0.82	4.2	64	0.91	3.4

* Column means followed by different letters are significantly different ($P < 0.05$); no letter indicates no testing. October and July interspecies comparisons done by *t*-tests (two-tailed), May by Duncan's Multiple Range Test (alpha = 0.05) which followed a one way ANOVA ($F_{(4,637)} = 9.43$, $P < 0.0001$).

As in May, the number of dusted mosquitoes collected at residential sites in July decreased with the distance from the release site (Tables 4 and 5).

DISCUSSION

The major objective of this study was to develop simple mark-release-recapture methods that could be used by mosquito control programs to determine if mosquitoes produced in one location were creating problems in residential areas. We were able to do this using mosquito control field personnel and readily available materials: CDC traps and fluorescent dusts. The methods were successful with low (studies not reported here) and high mosquito population densities.

Trap set-up and collection and specimen marking and release required 2 people working five 10-h days. Specimen examination and identification were done immediately in the lab by 4 additional people. Once frozen, however, specimens could be examined at a later time by the field staff.

It was not necessary to arrange recapture traps in a strict configuration about the release sites. Rather than have one release site and

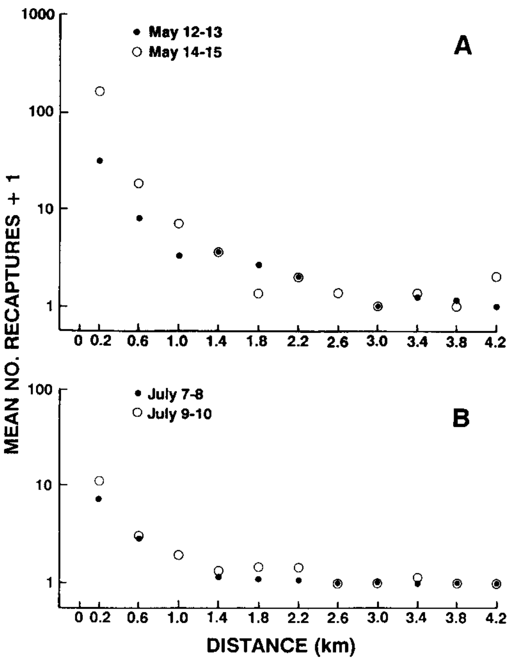

Fig. 4. Numbers of mosquitoes recaptured as a function of distance from the release sites, and the fitted regressions for May (A) and July (B).

recapture specimens at numerous sites, we used multiple release sites at differing distances from residential areas where retrapping was concentrated. The species composition of the recaptured mosquitoes were similar to those marked and released, despite the harsh treatment.

We were also able to consistently estimate relative flight ranges among species by using standard analytical methods without knowing the precise numbers of marked mosquitoes released, although such data could have been used in other analyses. Because the specimens in this study were stressed, i.e., spent the night in crowded catch chambers, were heavily dusted and then released during the day to find their own diurnal refuges, our flight ranges may underestimate substantially the dispersal capability of the species examined.

Furthermore, most recaptures were taken only one night after release, thus not allowing for greater movement that may have occurred over several days. In follow-up studies not reported here, we made releases from multiple sites on one day and retrapped for 4 consecutive nights in nearby residential areas. Nevertheless, our results here corroborate other studies on the relative dispersal among species, e.g., that *Cq. perturbans* ranges considerably farther than *Cx. nigripalpus* (Table 3 of Dow 1971, McNeel 1932).

The lights of the 2 residential areas, particularly the City of Mulberry, may have acted as an attractant for these phototrophic species, further biasing the data. In this case, however, the bias would tend to extend the dispersion range.

The MDT is a useful parameter for assessing and comparing dispersal capacities of different species under different environmental conditions. The FR_{50} is, mathematically, the median distance traveled and, therefore, another measure of the mean distance traveled. It can be compared to the MDT.

In this study the differences between MDT and FR_{50} were 0.60 km (0.37 mi) for May and 0.43 km (0.27 mi) for July. Operationally, these differences are not great. Differences between MDTs and FR_{50}s will be greater and of more importance for different population densities or under different environmental conditions than differences between the 2 measures under the same conditions. The FR_{90} is a useful estimate of the operational upper-limit of dispersion beyond which the mosquitoes would not create a problem.

The methods described herein can also be used to evaluate the relative contribution of different breeding sites to the mosquito problems in a given area. In this case, it becomes important to know the wind direction and the numbers of marked mosquitoes released from each site.

Data interpretation: Using MDTs, we conclude that *Cq. perturbans* and *Ma. titillans* move considerably further than *Cx. nigripalpus* and *Cx. salinarius*, independent of their relative densities. Both groups moved further, as expected, than *An. crucians*. This is important operationally because *Coquillettidia* and *Mansonia* are more severe pests than either *Culex* species in central Florida (Morris, unpublished data).

While it is important and desirable to work with species data, mosquito pest problems are the sum of all the man-biting mosquitoes that occur in an area; citizens as well as mosquito adulticiding operations do not care which species is biting. The observed movement of marked mosquitoes from all 3 release sites confirms, unequivocally, that mosquitoes can fly from all parts of the wetlands into both residential areas. This fact alone is very useful. We can, however, learn more about the nature of the mosquitoes using MDT and FRs.

Using the average MDTs for all species (0.82 km or 0.51 mi in May, 0.91 km or 0.56 mi in July) overlaid on the study area map we estimate that approximately half the mosquitoes produced at the northern and southern perimeters of the wetlands would disperse into the nearby

Table 4. Mosquitoes recaptured at 10 sites north of the Lakeland study area.

Observed recaptures:

	May 12–13			May 14–15			
	Release point			Release point			
Species	North	Central	South	North	Central	South	Total
An. crucians	1	0	0	7	1	0	9
Cq. perturbans	1	0	0	3	1	1	6
Cx. nigripalpus	3	3	1	6	4	0	17
Cx. salinarius	6	4	0	47	3	1	60
Ma. titillans	2	0	0	0	0	0	2
Total	13	7	1	63	9	2	94

	July 7–8			July 9–10			
	Release point			Release point			
Species	North	Central	South	North	Central	South	Total
Ae. infirmatus	0	0	0	1	0	0	1
Cx. erraticus	0	0	0	1	0	0	1
Cx. nigripalpus	6	1	0	5	0	0	12
Cx. salinarius	3	0	0	3	0	0	6
Ps. columbiae	0	0	0	1	0	0	1
Total	9	1	0	11	0	0	21

Mean number of recaptures per trap:

Distance from release site	May 12–13	May 14–15	July 7–8	July 9–10
1.04 km	1.4	6.3	1.1	1.1
2.20 km	0.8	0.9	0.1	0.0
3.24 km	0.1	0.2	0.0	0.0

Table 5. Mosquitoes recaptured at 10 sites south of the Lakeland study area.

Observed recaptures:

	May 12–13			May 14–15			
	Release point			Release point			
Species	North	Central	South	North	Central	South	Total
Cq. perturbans	0	1	2	0	0	2	5
Cx. nigripalpus	1	2	2	0	1	2	8
Cx. salinarius	1	3	3	0	9	9	25
Ma. titillans	0	0	0	0	0	1	1
Total	2	6	7	0	10	14	39

	July 7–8			July 9–10			
	Release point			Release point			
Species	North	Central	South	North	Central	South	Total
Cx. nigripalpus	0	1	1	0	0	2	4
Cx. salinarius	0	0	0	0	1	0	1
Total	0	1	1	0	1	2	5

Mean number of recaptures per trap:

Distance from release site	May 12–13	May 14–15	July 7–8	July 9–10
1.22 km	0.7	1.4	0.1	0.3
1.94 km	0.6	1.0	0.1	0.1
3.70 km	0.2	0.0	0.0	0.0

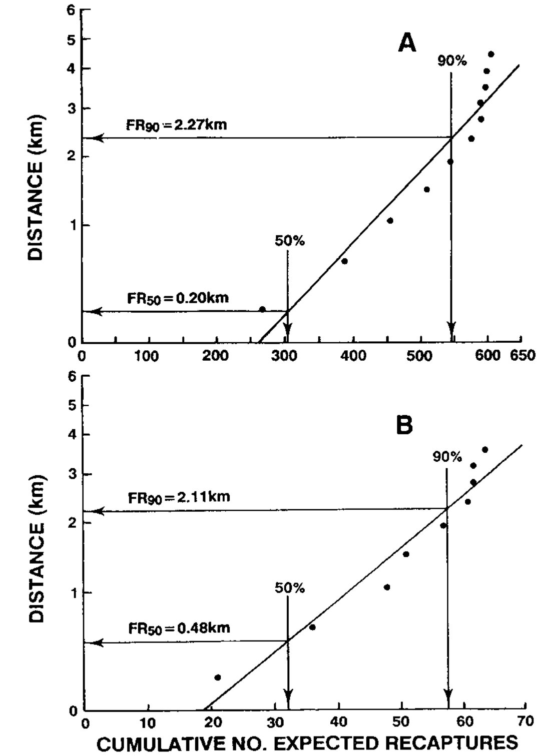

Fig. 5. Cumulative number of recaptures as a function of distance from the release sites for May (A) and July (B). FR_{50} and FR_{90} are the estimated flight ranges (km) of 50 and 90%, respectively, of the recaptured mosquitoes.

residential areas. Remembering that we collected an average of over 5,000 mosquitoes per trap per night indicates that the numbers moving into residential areas are substantial.

Overlaying the FR_{90}s for all species combined (2.27 km or 1.41 mi in May, 2.11 km or 1.31 mi in July) on the map further suggests that both Lakeland and Mulberry are within flight range of at least 10% of the mosquitoes produced in the center of the wetland, where mosquito densities are highest. Even 10% of our 5,000 per trap average is a substantial number of mosquitoes. By using these 3 parameters, observed recaptures, MDT and FR_{90} we have a much better idea of the contribution of each part of the wetland to the mosquito problem in the 2 residential areas and where control efforts would provide the greatest benefit.

The results of this study were used in the development of a local interagency agreement between the operators of the sewage treatment facility and the local mosquito control program to prevent mosquito production in the facility.

ACKNOWLEDGMENTS

The authors gratefully recognize Hampton Lewis, Sheryl Ayler, John Haefner, Lottie Jordan and Nancy Aker of Polk County Environmental Services, Bartow, FL, for assisting with this project. This work was made possible, in part, by grant #LD801 from the Florida Department of Health and Rehabilitative Services, Jacksonville.

REFERENCES CITED

Dow, R. P. 1971. The dispersal of *Culex nigripalpus* marked with high concentrations of radiophosphorus. J. Med. Entomol. 8:353–363.

Dow, R. P., W. C. Reeves and R. E. Bellamy. 1965. Dispersal of female *Culex tarsalis* into a larvicided area. Am. J. Trop. Med. Hyg. 14:656–670.

Gillies, M. T. 1961. Studies on the dispersion and survival of *Anopheles gambiae* Giles in East Africa, by means of marking and release experiments. Bull. Entomol. Res. 52:99–127.

Lillie, T. H., W. C. Marquardt and R. H. Jones. 1981. The flight range of *Culicoides variipennis*. Can. Entomol. 113:419–426.

Lillie, T. H., D. L. Kline and D. W. Hall. 1985. The dispersal of *Culicoides mississippiensis* (Diptera: Ceratopogonidae) in a salt marsh near Yankeetown, Florida. J. Am. Mosq. Control Assoc. 2:68–72.

McNeel, T. E. 1932. Observations on the biology of *Mansonia perturbans* (Walk.) Diptera, Culicidae. Proc. N. J. Mosq. Exterm. Assoc. 19:91–96.

Provost, M. W. 1952. The dispersal of *Aedes taeniorhynchus*. I. Preliminary studies. Mosq. News 12:174–190.

White, D. J. and C. D. Morris. 1985. Bionomics of anthropophilic Simuliidae (Diptera) from the Adirondack Mountains of New York State, USA. J. Med. Entomol. 22:190–199.

Yasuno, M., P. K. Rajagopalan, S. Russel and G. C. LaBrecque. 1973. Influence of seasonal changes in climate on dispersal of released *Culex pipiens fatigans*. A study in villages in Delhi Union Territory, India. Bull. W.H.O. 48:317–321.