A STUDY OF DISPERSAL, SURVIVAL AND GONOTROPHIC CYCLE ESTIMATES OF *MANSONIA UNIFORMIS* IN AN OPEN SWAMP ECOTYPE

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INTRODUCTION

Information on dispersal, survival and length of gonotrophic cycle are of considerable interest when studying the ecology of vectors of arthropod-borne diseases, such as filariasis. These important population attributes and other time-related biological phenomenon can be best studied under field conditions by using mark-release-recapture techniques. Such studies have received much attention in recent years and the literature applying this approach to mosquito populations have been reviewed by Johnson (1969), Provost (1974) and Service (1976). Information on flight range and dispersal of a species is important in control programmes as it is essential to know the width of 'barrier zones' needed to prevent the infiltration of adults into an area where control measures are being assessed. The gonotrophic cycle is necessary not only to derive the extrinsic cycle of transmission of diseases or to estimate the survival rate from the parous rate but also to determine the reproductive potential of a population (Macdonald, 1957; Laurence, 1963; Reuben, 1963). The survivorship of a vector population provides information on the potentiality of the vector capable of maintaining transmission of the disease in an area.

To date, there has been no report of field studies on dispersal and survivorship of *Mansonia* using mark-release-recapture techniques. Previous estimates of *Mansonia* flight ranges were based on indirect observations. Wharton (1962) estimated that in the forest, *Ma. bonneae* and *Ma. dives* can travel the considerable distance of 1.6−3.2 km in search of blood-meal hosts. Observations on *Ma. uniformis* suggested that this species is a weak flier (Bicknell *et al.*, 1956; cit in Wharton, 1962). This was confirmed by Bailey and Gould (1975); using CDC light-traps, they found that marked individuals did not fly further than 375 m from the release point. However, the considerable maximum flight speed of this species (Gillies and Wilkes, 1981) would rather suggest stronger flying abilities. Recently, Gass *et al.*, (1983) estimated the dispersal of *Mansonia* in Southern Thailand by direct density measurements in relation to distance from a single breeding pool. Maximum flight ranges of 1000, 1400 and 1700 m were observed for *Ma. annulata*, *Ma. indiana* and *Ma. uniformis* respectively.

The objective of this study was to obtain some baseline information on the natural dispersal, survivorship and the gonotrophic cycle of *Ma. uniformis* in an open swamp ecotype using mark-release-recapture techniques.

Study area

The experimental site is an open swampy area at Batang Berjuntai in Selangor, 40 km from Kuala Lumpur (Fig. 1). The area is a flat terrain of shrubs and tall grasses with little cultivation. It is interspersed with reclaimed tin mining lands for housing projects. A trunk road runs horizontally from east to west. Patches of oil palm and rubber trees are grown on either side of the road separating the swamp forest in the north and south. A river flows from the east to the south.

MATERIALS AND METHODS

Five experiments were carried out between May 1983 and January 1985; three with unfed females and two with blood fed females.

Collection: *Mansonia* mosquitoes are known to be active during the first hour of the night. Making use of this fact, *Mansonia* were caught landing on bare legs of men, from the first bite at dusk till 2100 hours. Four teams of 4 men each collected the mosquitoes within the study area. Mosquitoes were collected individually in 50 × 19 mm vials with moist wadding at the base. This method enabled the identification of the specimens alive. About 25 percent of the catch was identified to determine the proportions of *Mansonia uniformis* and other species present. The mosquitoes were transferred into cages 30 × 30 × 30 cm counting about 500 into each cage. Using techniques similar to those described by Yasuno *et al.*, (1972), fluorescent dusts (different colour daily for 3 consecutive days) were used to mark the mosquitoes by blowing the dust into the cages using an insufflator. Almost all mosquitoes collected by the method above were unfed. For experiments with fed females, the unfed mosquitoes in the cages were allowed to feed on restrained guinea pig in the field for 30−45 minutes. At release time immediately after feeding, 95%

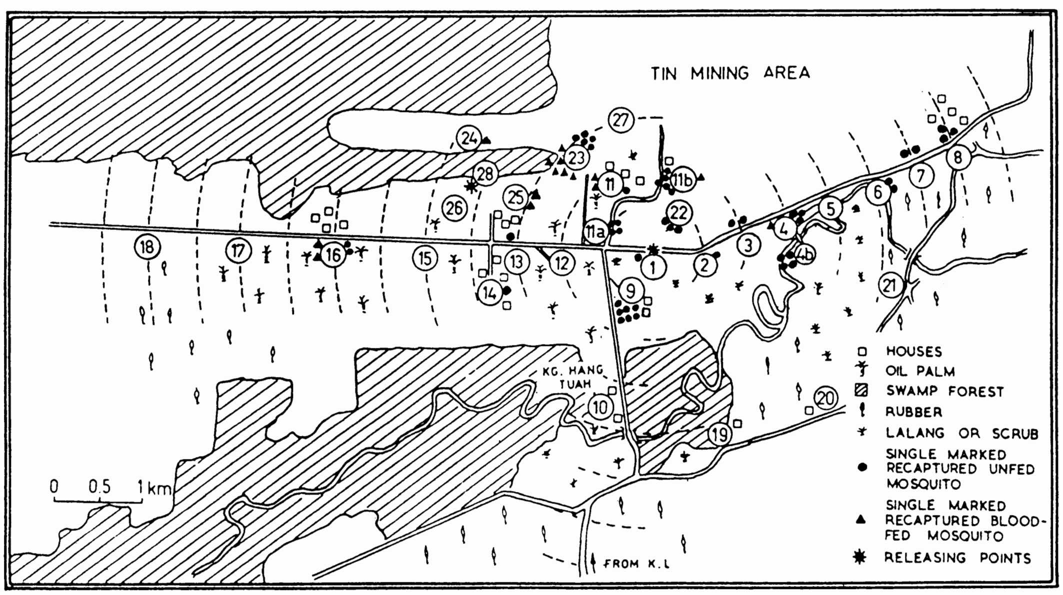

Fig. 1–Map of an area in Batang Berjuntai, Selangor, Malaysia, showing the recapture stations up to 5 km.

of the females had taken a blood meal.

Release: Three consecutive nights' releases of marked mosquitoes were made in each experiment. Release was carried out between 2200 to 2230 hours. There were two release points, Station 1 and 28 (Fig. 1). Station 1 was the release point for three experiments (Expt. 1, 2 & 5) with unfed females and Station 28 for two experiments (Expt. 3 and 4) with blood-fed females. Marked mosquitoes were released by cutting the cotton netting of one side of the cage with a sharp knife. The holding cages after release were collected on the following morning. All dead or immobile mosquitoes remaining in the cages were removed and counted and this number subtracted from the total count to determine the total release.

Recapture: Commencing on the day after the first release, recovery of marked mosquitoes were carried out daily by human bare leg catch during 1800–2100 hours. Adult mosquitoes were collected by eight to twelve teams, each consisting of two collectors, for 10 to 13 days consecutively at catch stations sited at 0.5 km to 5.0 km from the release point (Fig. 1). Each team either spent the whole period at one station or divided the time equally between two adjacent stations. It was possible to cover at least ten stations each day. By a system of rotation all stations were covered at least five times during the course of 10–13 days in each experiment. Another method of collection was aspirating female mosquitoes which were attempting to feed on cattle and those resting in cattle sheds. However, this subsidiary method was confined to two collecting stations, i.e. stations 23 and 9, where there were cattle sheds.

Mosquitoes in vials from each collecting station were placed in polyethylene bags and labelled. All collections were returned to the laboratory alive. The next morning, the mosquitoes were etherised and examined under ultra-violet lamp for fluorescence and some under stereoscopic microscope. The mosquitoes were then sorted to species and counted. All marked and a sample of unmarked female mosquitoes were dissected to determine their physiological age by the Polovodova method of a count of the dilatations of their ovarioles (Detinova, 1962).

RESULTS

Fauna of the study area: Totals of 16,120; 27,349; 16,427; 28,010 and 13,240 female mosquitoes, comprising 31 species in seven genera, were collected during recapture attempts in the five experiments-May 1983 (Expt. 1), October 1983 (Expt. 2), April 1984 (Expt. 3), August 1984 (Expt. 4) and January 1985 (Expt. 5), respectively. *Ma. uniformis* was the most prevalent species comprising 91% to 97% of the total mosquitoes collected (Table 2).

Recapture success: Table 1 shows the number of mosquitoes marked and released and recaptured during the 5 experiments. In the experiments with unfed *Ma. uniformis*, a total of 8,483; 6,480 and 8,147 were marked and released over 3 days each in experiment 1, 2 and 5 with 17 (0.20%), 13 (0.20%) and 19 (0.23%) recaptured respectively. In the experiments with freshly blood-fed/engorged females, of the 9,733 (Expt. 3) and 13,110 (Expt. 4) marked and released, 3 (0.03%) and 12 (0.09%) respectively were recaptured. Recovery of marked mosquitoes was much higher among unfed females.

Dispersal: The mosquitoes dispersed in all direction. The highest recapture rates occurred in stations 23 and 9 near the release sites where there were cattle sheds and 11 (17.2%) and 7 (10.9%) respectively were

Table 1

Summary of releases and recaptures of *Ma. uniformis* in Batang Berjuntai, Selangor.

Experiment No.	Nutrition at release time	Period of experiment	Estimated No. marked and released	No. captured and examined	No. (%) recaptured
1	unfed	9–18 May 1983	8,483	15,677	17 (0.20)
2	unfed	19 Oct.–1 Nov. 1983	6,480	26,438	13 (0.20)
5	unfed	21–30 Jan. 1985	8,147	12,118	19 (0.23)
		Total	23,110	54,233	49 (0.21)
3	blood-fed	5–14 April 1984	9,733	15,366	3 (0.03)
4	blood-fed	31 July–11 Aug. 1984	13,110	17,162	12 (0.09)
		Total	22,840	42,528	15 (0.07)

Table 2

Total number of *Mansonia* & *Coquillettidia* and other species collected during recapture attempts from the five experiments conducted between 1983–1985.

	May 1983 Expt. 1	Oct. 1983 Expt. 2	Jan. 1985 Expt. 5	April 1984 Expt. 3	Aug. 1984 Expt. 4
Mansonia					
uniformis	15,677	26,438	12,118	15,366	27,162
indiana	116	369	393	184	367
bonneae	101	276	366	301	355
dives	15	11	26	28	31
annulifera	5	12	36	35	23
annulata	4	8	2	90	3
Coquillettidia					
crassipes	10	13	0	3	3
hodgkini	1	0	0	0	2
nigrosignata	1	2	0	0	0
Other mosquitoes*	190	220	299	420	64
Total	16,120	27,349	13,240	16,427	28,010

* Includes Anopheline and other Culicine mosquitoes.

recaptured out of the total 64 marked specimens collected in the 5 experiments (Fig. 1). The numbers of unmarked mosquitoes in these two stations during the recaptured periods were also high (19.1% and 14.3% respectively of the total collected).

In all the experiments, more than 70% of all recaptures were taken within a radius of 1.5 km around the point of release and the rest were collected in the surrounding area between a 1.5−3.5 km radius (Table 3).

Table 4 shows the number recaptured in relation to distance from the release point for the 5 experiments. For combined data, 51.0%, 30.6% and 18.4% of the unfed females and 60.0%, 33.3% and 6.7% of the fed females were recovered in the respective range distance of 0−1.0 km, 1.0−2.0 km and 2.0 to 3.5 km from the release site. A declining pattern in the number of marked females recovered with distance was observed. The maximum flight distance was 3.5 km (Table 4). Three marked unfed females were recaptured at station 8; 3.5 km northeast of the release station 1 after 7 days in Expt. 1. In Expt. 2, two marked females were taken at station 16, 3.5 km west of release station 1 after one and four days, respectively. The data suggested that the non-blood fed *Ma. uniformis* was capable of dispersing 3.5 km within 24 hours. In Expt. 4, one female was collected at site 4, 3.5 km east of release station 28 on the fifth day after release. This female fed at the time of release could be returning for a second feed after oviposition. Dissection of the ovaries of this specimen showed contracted ovariole sacs with some degenerated follicles in the ovaries. Oviposition occurred probably in the previous evening, on the fourth day after release.

The mean dispersal distance ($\bar{d}$), calculated from the first day of release to the last day the mosquitoes were recaptured, was highest (1.99 km) in Expt. 1, followed by Expt. 2, Expt. 4, Expt. 5, and the least in Expt. 3 (Table 5). Student's t-test did not show significant difference ($p > 0.05$) among the means of dispersal distance in Expt. 1, 2 and 4, and the between means of dispersal

Table 3

Number of marked females of *Ma. uniformis* released and recaptured in Batang Berjuntai in the five experiments at various distances.

Expt. No.	No. adults released	No. (% released) recovered			% marked adults	
		within 1.5 km	1.5−3.5 km	Total	within 1.5 km	1.5−3.5 km
Unfed						
1	8,483	14 (0.17)	5 (0.06)	19 (0.23)	73.7	26.3
2	6,480	9 (0.14)	4 (0.06)	13 (0.20)	69.2	30.8
5	8,147	17 (0.21)	0 (0)	17 (0.21)	100.0	0
Total	23,110	40 (0.17)	9 (0.04)	49 (0.21)	81.6	18.4
3	9,733	3 (0.03)	0 (0)	3 (0.03)	100.0	0
4	13,110	10 (0.08)	2 (0.02)	12 (0.10)	83.0	17.0
Total	22,843	13 (0.06)	2 (0.01)	15 (0.07)	86.7	13.3

Table 4

Nightly recaptures of marked female *Ma. uniformis* in relation to distance from the release point.

Distance from release point (km)	No. Recaptured						
	Marked unfed				Marked Blood-fed		
	Expt. 1	Expt. 2	Expt. 5	Total	Expt. 3	Expt. 4	Total
0.0	1	0	0	1	0	0	0
0.5	3	3	11	17	2	1	3
1.0	3	0	4	7	1	5	6
1.5	7	6	2	15	0	4	4
2.0	0	0	0	0	0	1	1
2.5	0	2	0	2	0	0	0
3.0	2	0	0	2	0	0	0
3.5	3	2	0	5	0	1	1
4.0	0	0	0	0	0	0	0
4.5	0	0	0	0	0	0	0
5.0	0	0	0	0	0	0	0

Table 5

Mean dispersal distance of *Ma. uniformis* females in Batang Berjuntai, Selangor, in Experiments 1–5.

Nutritional group	Expt. No.	No. recaptured	$\bar{d}$* mean dispersal distance (km)	Overall mean dispersal distance (km)
Unfed	1	19	1.99 ± 1.129	
	2	13	1.31 ± 0.960	1.706 ± 1.03
	5	17	0.88 ± 0.540	
Blood-fed	3	3	0.50 ± 0.289	1.445 ± 1.06
	4	12	1.22 ± 1.135	

* $\bar{d}$ was calculated by the formula, $\bar{d} = \sum_{i=1}^{n} r_i d_i / \sum_{i=1}^{n} r_i$ used previously by Reisen *et al.* (1978) where

r_i = number recaptured at each station (i), d_i = distance in metres of station i from the release point, and n = total number of stations.

distance observed in Expt. 3 and 5. The low dispersal distance in the latter experiments (3 & 5) may have been due to the rainfall which interfered the dispersal of the females and may have contributed to the poor recovery rate. Pooling the data together under the unfed and blood-fed groups, there was no significant difference ($t = 0.853$; $p > 0.05$) in the overall mean dispersal distance of the two groups of females. The data suggested that the unfed and blood-fed females were capable of dispersing to an equal degree.

Gonotrophic cycle: The length of the gonotrophic cycle was determined by the examination of the conditions of the ovaries of recaptured females from the two experiments (3 & 4) on the releases of blood-fed females. The two mosquitoes taken within two days of release (Expt. 3) as shown in Table 6, had partly digested blood in the stomach. The one taken on the first day was while trying to bite the collector. This female would have been seeking an additional blood-meal probably due to insufficient blood taken on the night of release. However, the marked female collected on the second day was recaptured while resting in the cattle shed at station 23, about a km east of the release point. This female was at Stage III–IV ovariole condition or semi-gravid. On the third and fourth day after release (combined data of Expt. 3 and 4 in Table 6), four and six females were recaptured with ovariole sacs in their ovaries. Two even had a few mature eggs left behind in the ovaries indicating they must have oviposited on the same evening they were collected while attempting to take another bloodmeal. The results suggest that the length of the gonotrophic cycle in nature was between 3 to 4 days.

Survivorship: Daily survivorship was estimated for the unfed and blood-fed *Ma. uniformis* females by regressing the numbers of recaptures transformed into ln $(y + 1)$ as a function of time in days after release (Gilles, 1961; Reisen and Aslamkhan, 1979; Reisen *et al.*, 1980). The survivorship was calculated by the expression $S_r = e^b$ where e = base of natural logarithms and b = slope of the fitted regression or the regression coefficient. Initially, survivorship was estimated for each experiment separately, tested by analysis of variance (ANOVA) and then compared by analysis of covariances (ANCOVA). Table 6 shows the number of recaptures in relation to calendar age and the estimated survivorship for the five experiments separately. There were no significant differences among regression coefficients ($p > 0.05$). Since the slopes of the fitted functions did not differ significantly, regressions were fitted to the pooled recaptures to estimate the overall survivorship (S_r) for the unfed and blood-fed females (Fig. 2). The daily survivorship of

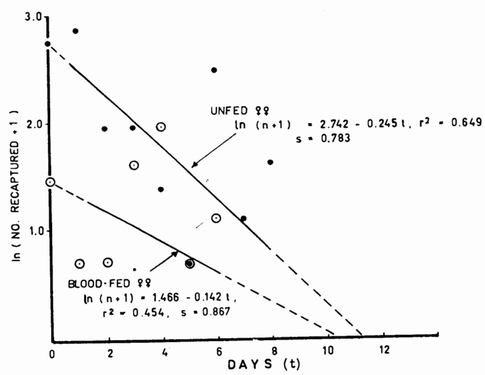

Fig. 2–The pooled number of marked *Ma. uniformis* females unfed (Expt. 1, 2 & 5) and fed (Expt. 3 & 4) transformed to ln $(n + 1)$ and plotted as a function of time in days after release. (r^2 = coefficient of determination, s = vertical survivorship)

0.867 for the blood-fed females was comparable to that of 0.783 for the unfed females. However, maximum longevity observed for blood-fed was six days, while the last marked unfed female was recaptured 8 days after release. Another independent estimate of daily survivorship as shown by Davidson (1954), was derived by dissecting samples of unmarked mosquitoes collected during the recaptured period. The daily survival of the mosquitoes based on the fact that the gonotrophic cycle in the field was 4 days, ranged from 0.751−0.795 for the five experiments. This estimate agreed fairly well with the pooled estimate of unfed females based on the daily recaptures regressed on time but comparable to that of the blood-fed females.

DISCUSSION

In the present study, it was obvious that the number of marked specimens released represented a small part of the relatively

Table 6

Nightly recaptures of marked females of *Ma. uniformis* in relation to calender age and the estimated daily survivorship of the 5 experiments.

Days after release	Marked unfed				Marked blood fed		
	No. recaptured				No. recaptured		
	Expt. 1	Expt. 2	Expt. 5	Total	Expt. 3	Expt. 4	Total
1	1	1	14	16	1	0	1
2	3	2	1	6	1	0	1
3	4	0	2	6	0	4	4
4	1	2	0	3	1	5	6
5	1	0	0	1	0	1	1
6	7	4	0	11	0	2	2
7	2	0	0	2	0	0	0
8	0	4	0	4	0	0	0
9	0	0	0	0	0	0	0
10	–	0	–	0	–	0	0
11	–	0	–	0	–	0	0
12	–	0	–	0	–	–	0
13	–	0	–	0	–	–	0
Daily survivorship S_r^*	0.874	NS	0.837	0.783	0.933	NS	0.867

* Daily survivorship, Sr, estimated by regressing the daily recaptures on time in days after release;

NS = regression coefficient not significantly different from 0 when tested by T-test ($p > 0.05$).

enormous population naturally present in the study area, and that with the personnel available and territory to be covered, the number of recoveries would be relatively small. Out of the approximately 45,950 marked mosquitoes released in the five experiments, only 64 (0.14%) were recovered. This recovery rate is substantially lower than those previously reported for many other species of mosquitoes. The recovery rates were 23.9% and 37.5% for *Anopheles culicifacies* (Curtis and Rawlings, 1980; Rawlings *et al.*, 1981), 16.1% for *An. balabacensis* (Hii and Vun, 1985), 7.13% for females and 4.65% for males of *An. stephensi* (Reisen and Aslamkhan, 1979), 6.32% for females and 1.2% for males of *An. subpictus* (Reisen *et al.*, 1979), 0.11% to 4.7% for *Aedes aegypti* and 0.01% to 7.05% for *Cx. quinquefasciatus* (Service, 1976). However, species like *Ae. taeniorhynchus* (0.02% to 0.13%, see Provost, 1952, 1957) and *Cx. tritaeniorhynchus* (0.03−0.232%, see Wada *et al.*, 1969) was slightly lower or equivalent in recovery.

The nutritional experience prior to release affected the numbers recaptured. When unfed females were released 0.20%−0.23% were recaptured. But when the females were blood-fed, substantially fewer (0.03%−0.09%) were recaptured (Table 1) and most of these were females (83%−100%) that stayed within 1.5 km of the release point (Table 3), indicating that the blood-fed mosquitoes did not disperse widely. These blood-fed females might have already obtained their necessary energy requirements, removing the stress for dispersal. However, the unfed/starved females with their basic energy requirement travelled greater distance in search of blood-meal and this was further demonstrated by the higher overall mean dispersal distance (Table 5).

The present study also revealed remarkable flying ability for *Ma. uniformis*. The maximum flight distance recorded was 3.5 km and this is substantially higher than any reported previously for this species (Bailey and Gould, 1975; Gass *et al.*, 1983). The results of this study suggested that *Ma. uniformis* populations have a wide-range dispersion and tend to move freely out of their own confines. This has relevance to filariasis control measures, especially for subperiodic *B. malayi* which involves the wild animals primarily the monkeys, *Presbytis* spp. that contribute to a large proportion of the infective pool in the forest region. Further studies are needed to determine the movement of the populations of *Ma. uniformis* or other *Mansonia* species between the kampungs and the forest/forest fringe. This is important epidemiologically because the study will provide information on the vectors relating to transmission of filariasis between the sylvatic and the domestic cycle. However, base on the findings of this study, although the recoveries were a bit low, the authors feel that as a tentative practical limit for control measures they should be carried out for a radius of at least 3.5−4.0 km from any human population it is necessary to protect.

The estimate of the length of the gonotrophic cycle of *Ma. uniformis* agreed well with laboratory studies (Chiang, unpublished data; Wharton, 1962).

The daily survival rates of *Ma. uniformis* in the present study varied from 0.783 for the unfed females to 0.867 for the blood-fed females. These horizontal survivorship estimates based on the recapture rates of date-specific marked females agreed fairly well with the survivorship estimated vertically from the dissection of unmarked females (0.751−0.795). The higher survivorship observed for blood-fed females can probably be explained by the nutritional experience prior to release. Similar survival estimated based on regression coefficient have been calculated with other mosquito species and have been summarized by Service (1976); for *Cx. tritaeniorhynchus* as 0.49, for *An. gambiae* as 0.84, for *Cx. p. quinquefasciatus* as 0.83 and for female and male *Ae. aegypti* in Bangkok as 0.81 and 0.70 respectively.

Recent studies with mark-release-recapture methods and using similar method of calculation, the female survivorship of *An. stephensi* was estimated to be 0.808–0.865 (Reisen and Aslamkhan, 1979), of *An. culicifacies* as 0.8294 (Rawlings *et al.*, 1981) and *An. balabacensis* as 0.719–0.787 (Hii and Vun, 1985). The survivorship of *Ma. uniformis* estimated vertically from dissection data in Tanjong Karang (Chiang *et al.*, 1984) was 0.622 which is lower than present estimates. Nevertheless, all these figures suggest that most species of tropical mosquitoes survive from 7 to 14 days in nature and very few, less than 5%, survive beyond 14 days.

SUMMARY

Five mark-release-recapture experiments with wild caught *Ma. uniformis* were conducted in an open swamp area at Batang Berjuntai in Selangor, 40 km from Kuala Lumpur, Malaysia, between May 1983 and January 1985. A total of 64 (0.14%) from the 45,950 females released were recaptured feeding on humans and cattle and resting in cattle-sheds. Substantially fewer (0.03% to 0.09%) females were recaptured from releases of blood-fed females than from releases of unfed females (0.20% to 0.23%). More than 70% of all recaptures were taken within a radius of 1.5 km around the point of release and the longest detected flight was 3.5 km. The mean dispersal distance for blood-fed and unfed females was 1.445 ± 1.06 and 1.706 ± 1.03 km, respectively. However, there was no significant difference in the overall mean dispersal of the two groups of females ($p > 0.05$). The duration of the gonotrophic cycle in the field was between 3 to 4 days. Daily survivorship estimates (0.783–0.867) based on the recapture rates of date specific marked females was comparable to that estimated vertically from the dissection of unmarked females (0.751–0.795). These experiments revealed the remarkable flying ability of *Ma. uniformis* and the importance of reinvasion must be recognized when control operations are restricted to small areas.

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