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Horizontal and vertical dispersal of dengue vector mosquitoes, *Aedes aegypti and Aedes albopictus*, in Singapore

C. LIEW[1] and C. F. CURTIS[2]

[1]Environmental Health Institute, National Environment Agency, Singapore and [2]London School of Hygiene and Tropical Medicine, London, U.K.

Abstract. To study the dispersal of dengue vector mosquitoes in Singapore, females of *Aedes aegypti* (L.) and *Aedes albopictus* (Skuse) (Diptera: Culicidae) were fed blood containing rubidium (Rb), which was detectable in their eggs by means of Graphite Furnace Atomic Absorption Spectrophotometry (GFAAS). Laboratory calibration of the Rb reading, for a range of egg numbers from Rb-fed females, indicated a reasonably linear relationship and an unequivocal distinction between results with zero and one marked egg. Rb-marked female *Aedes* mosquitoes aged 3–5 days were released in semi-rural and urbanized parts of Singapore, with an array of ovitraps extending to a radius of 320 m from the release point. Subsequently, Rb-marked *Aedes* eggs were detected throughout the array, with similar distributions on each of the 4 days after release. More Rb was detected nearer the release point. However, when correction was made for the greater areas of zones further from the release point (and therefore presumably existence of more alternative oviposition sites), there were no significant differences in the numbers of marked eggs per ovitrap in the zones nearer or further from the release points. It is concluded that females of both these *Aedes (Stegomyia)* species could disperse easily and quickly throughout areas of radius 320 m in search of oviposition sites. This contrasts with the general belief that *Ae. aegypti* seldom flies more than 50 m and that control operations can safely be based on such an assumption. Releases on level 12 of a 21-storey apartment block, with ovitraps on each storey, showed similar easy and rapid dispersal to the top and bottom of the block.

Key words. *Aedes aegypti*, *Ae. albopictus*, dengue vectors, flight range, mosquito dispersal, multi-storey building, ovitrap, rubidium chloride, Singapore.

Introduction

Dengue often spreads in explosive epidemics (Gubler, 1988; Reiter *et al.* 1995; Reiter, 1996), suggesting the importance of vector flight range in the dynamics of disease transmission (Newton & Reiter, 1992). For the main vector of dengue, *Aedes (Stegomyia) aegypti*, the general belief has been that females have a maximum flight range of only 50–100 m during their entire lifetime (PAHO, 1994), yet this species is known to colonize new areas rapidly.

Reiter *et al.* (1995) marked adult female *Ae. aegypti* with rubidium (Rb, a rare alkali metal), released them and detected this element in the eggs that they laid hundreds of metres away. In the present study, the dispersal of the two dengue vectors in Singapore, *Ae. aegypti* and *Ae. albopictus* (Goh, 1998), and their vertical dispersion in a multi-storey building are reported for the first time. Such knowledge is especially valuable in light of the recent recrudescence of the disease in Singapore, despite the stringent control efforts maintained. Furthermore, Singapore has undergone many

Correspondence: Dr Christina Liew, Environmental Health Institute, National Environment Agency, Singapore Science Park II, Singapore 117610. Tel: +65 6771 9116; fax: +65 6777 8029; e-mail: Christina_LIEW@nea.gov.sg

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environmental changes in recent years, particularly in housing type and population density, and there is a need for up-to-date information to guide current control methods.

Materials and methods

Study sites

Three different sites in Singapore were chosen for the mark–release–recapture studies. The first site was rural Bidadari Christian Cemetery – open terrain of $\sim$207 400 m^2 with abundant greenery. The second site was urban Geylang – a dengue-sensitive locality of $\sim$135 000 m^2, densely populated with mixed types of premises. The third site was an apartment block at the 'Gillman Heights' condominium – a vacant building comprising 21 storeys and 114 residential units, with virtually no standing water where mosquitoes could breed as the toilets and cisterns had been drained.

Preparation of Aedes *females for release*

Using laboratory-reared *Aedes* of local strains (originating from pooled families of each species, collected during 1992–1993 from various parts of Singapore), nulliparous females aged 3–5 days (and presumably inseminated) were starved for 24 h, then fed on blood laced with rubidium chloride (RbCl) marker. Those not fully blood-fed were discarded.

The blood-feeding system was based on that of Rutledge *et al.* (1964), comprising a glass feeder with a stretched membrane of 'M' Parafilm® (American National Can Co., Chicago, IL, U.S.A.) and a jacket of circulating warm water to maintain 37.5 °C temperature for fresh pig blood containing anticoagulant (150 ml per L blood) plus RbCl tracer 0.045 M rubidium chloride. Anticoagulant was freshly prepared by dissolving the following ingredients in 1 L distilled water: 0.28 g adenine, 3 g citric acid (anhydrous), 31.7 g dextrose (monohydrate), 26.4 g sodium citrate (dehydrate) and 2.2 g sodium phosphate (monohydrate). All chemicals were purchased from Sino Chemical Co., Singapore).

Three days after blood-feeding and just prior to release, *Aedes* females were anaesthetized with chloroform and their mouthparts sealed with a drop of Supa Glue® (Selleys Pty Ltd, Padstow, N.S.W., Australia) placed on the tip of a sharp needle and delicately applied to the proboscis. This was to render them unable to bite, thus avoiding possible criticism of the releases adding to the potential dengue vector population.

From the bloodmeal, Rb was translocated to and incorporated into the desiccation-resistant eggs of the females (Reiter *et al.*, 1995). Marked eggs could then be retrieved in ovitraps, following oviposition by the females after their release.

Mark–release–recapture methods

Each study site was first cleared of discarded receptacles and other removable breeding habitats to increase the proportion of total oviposition in the ovitraps. A known number of ovitraps (68 at the first site, 31 at the second and 38 at the third) were placed singly at suitable locations throughout the areas at distances of up to 320 m from the release point. One hundred healthy prepared *Aedes* females, now gravid and ready to oviposit, were released at the centre of each study site. Every 24 h for the following 4 days, the hardboard paddles from the ovitraps set out were collected and replaced with fresh ones, brought back to the laboratory and examined for eggs. Physical environmental parameters were monitored daily.

The eggs from each ovitrap were counted, pooled together and digested in acid. The method used by Reiter *et al.* (1995) for the detection of Rb in *Aedes* eggs was found to be not feasible here. Instead, analysis was carried out using Graphite Furnace Atomic Absorption Spectrophotometry (GFAAS) (Minoia & Caroli, 1992; Sneddon, 1992, 1995). Calibration was carried out relating Rb score to number of marked eggs: from 0, 1, 2, up to 300. Further calibration was done by mixing known numbers of marked and unmarked eggs.

Three replicate trials were carried out for each *Aedes* species at each study site, except at the first site where only *Ae. albopictus* was present and thus only this species was released. Releases for each replicate trial were not made until 2 weeks after the last collection day of the previous trial, to ensure that all females of one release had died before beginning the next.

Results

Supaglue application to the proboscis of Aedes *females*

Application of Supaglue to the proboscis of each female *Aedes* did not appear to immediately affect their general behaviour, nor the number of eggs laid in the next oviposition, as confirmed by laboratory studies. However, the mean lifespan of these treated females was reduced to an average of 4 days, presumably because of their inability to feed. Therefore, egg collection in the field was undertaken for only 4 days.

Rubidium calibration lines

Twelve tests consisting of only unmarked eggs gave Rb scores of zero, indicating that false positives did not occur. For *Ae. albopictus* (Fig. 1), the calibration line was satisfactorily linear, but this appeared to be somewhat less true for *Ae. aegypti* (Fig. 2). Nevertheless for both species, linear regressions were fitted and, because of the above evidence from tests with unmarked eggs, the regression lines were forced through the origin. The regression coefficients indicated that the Rb score per egg was 4.66

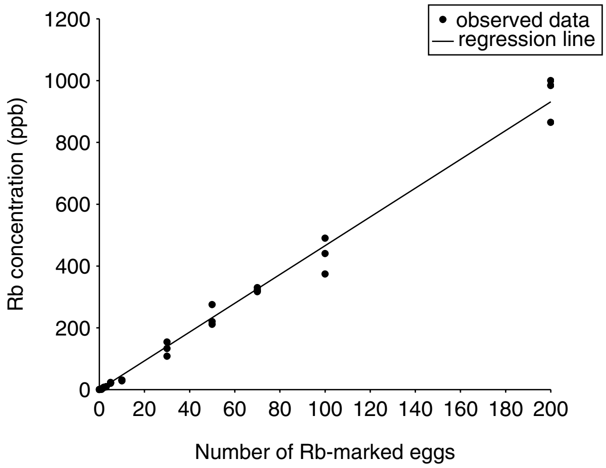

Fig. 1. Calibration line for *Aedes albopictus*: the relationship between number of rubidium (Rb)-marked eggs and Rb concentration. Line was forced through the origin. Very significant fit to this model.

for *Ae. albopictus* (SE = 0.069; $t = 68.0$; $P << 0.001$) and 2.56 for *Ae. aegypti* (SE = 0.13; $t = 19.1$; $P << 0.001$).

A separate series of tests in which marked eggs were mixed with unmarked eggs gave the data shown in Table 1. As indicated, there was no significant relationship between the mean Rb score per marked egg and the numbers of unmarked eggs mixed with them, for both *Aedes* species. Therefore, we feel confident in taking the Rb scores from field ovitraps as measures of numbers of eggs laid by released females, regardless of their admixture with eggs from wild females. Only in the study on the distribution of numbers of eggs from released females per ovitrap was it considered necessary to convert Rb scores to estimated numbers of marked eggs; in other cases results are quoted in terms of Rb scores.

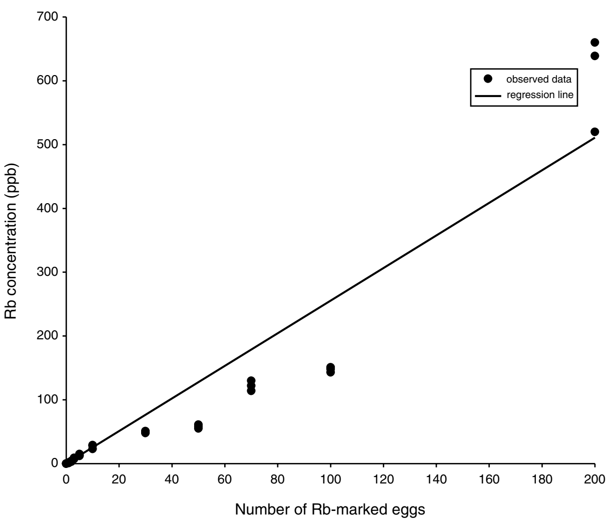

Fig. 2. Calibration line for *Aedes aegypti*: the relationship between number of rubidium (Rb)-marked eggs and Rb concentration. Line was forced through the origin. Very significant fit to this model.

Distribution of ovitraps with rubidium-marked eggs at site 1: rural Bidadari Christian Cemetery

Figure 3 represents the Bidadari Christian Cemetery site, showing circles drawn with radii increasing in steps of 80 m and illustrating the distribution of ovitraps relative to the central release point of *Ae. albopictus* females. Every ovitrap throughout the circle of radius 320 m yielded some marked eggs, as indicated by all the dots being coloured black, showing that such flight distances are common. The total Rb score in each ovitrap from the three replicate trials is categorized by dot size on an approximately logarithmic scale. The greatest Rb concentrations detected in any of the ovitraps ($\geq$ 1000 p.p.b.) were found in two ovitraps in zone 1 near the release point.

Distribution of ovitraps with rubidium-marked eggs at site 2: urban Geylang

Figures 4(a) and (b) show the results for separate releases of *Ae. albopictus* and *Ae. aegypti*, respectively, at Geylang, with concentric rings marked as in Fig. 3. In these cases, there were several ovitraps negative for marked eggs and with lower Rb scores than in Fig. 3. This is probably because there are more competing oviposition sites in the urban site compared to the rural site. However, despite these low scores at the urban site, evidence of movement of some released individuals to at least 280 m was obtained. For both species, positive ovitraps were found predominantly westwards of the release point, where there are more shop–houses and vegetation providing shade.

Distribution of ovitraps with rubidium-marked eggs at site 3: 'Gillman Heights' condominium

Figures 5(a) and (b) show the results for *Ae. albopictus* and *Ae. aegypti*, respectively, at the 'Gillman Heights' condominium site. The ovitraps were located two per storey, on both sides of the 21-storey and 60-metre high building. Storey 3 was taken as the first level for the study, as it was not feasible to place ovitraps on the first two very exposed storeys. Females were released at the middle of the building, on storey 12. The greatest Rb concentrations were found on the release storey and on some storeys above it, including at the top of the building.

Frequency distributions of rubidium-marked eggs per ovitrap

Using the calibration lines in Figs 1 and 2, Rb scores were converted to estimated numbers of Rb-marked eggs, and frequency distributions (combined for replicate trials) of ovitraps with the indicated numbers of Rb-marked eggs, for both *Aedes* species at each site, are shown in Fig. 6(a–c). The most common numbers of marked eggs found in individual ovitraps were 1, 2, 3, 4 and 5, with 1 and 2

Table 1. Laboratory controls. Summary of mean (of three replicates) rubidium (Rb) scores per Rb-marked egg, in varying combinations of marked and unmarked eggs

		Mean Rb score per Rb-marked egg			
		Number of unmarked eggs			
Species	Number of Rb-marked eggs	1	50	100	200
Aedes aegypti	1	1.33	2.00	1.67	2.33
	5	1.93	2.60	2.00	1.67
	10	2.87	3.13	2.47	2.50
Aedes albopictus	1	2.00	3.00	3.00	3.00
	5	3.00	3.13	3.13	3.33
	10	2.90	3.40	2.37	3.43

Regression of mean Rb score per Rb-marked egg on ratio of Rb-marked to unmarked eggs. For *Ae. aegypti*: regression coefficient = 0.044; SE = 0.053; $t = 0.834$; $P = 0.43$. For *Ae. albopictus*: regression coefficient = −0.015; SE = 0.043; $t = -0.343$; $P = 0.74$.
Regression of mean Rb score per Rb-marked egg on number of unmarked eggs. For *Ae. aegypti*: regression coefficient = 0.000; SE = 0.002; $t = -0.132$; $P = 0.90$. For *Ae. albopictus*: regression coefficient = 0.002; SE = 0.002; $t = 1.55$; $P = 0.15$.

being the most frequent. Higher counts of marked eggs were rare, with a maximum of 146 in a single ovitrap.

Regression analysis of data from rural and urban situations

To assess whether or not significantly more marked eggs were laid near the release point, regression of the Rb scores from each of the three replicate trials on the four zones (shown in Figs 3 and 4) was carried out.

One was added to all Rb values before taking natural logs, to allow inclusion of any zeros (i.e. no Rb detected in the egg sample from the ovitrap) in the data set.

For *Ae. albopictus*, there were significant negative relationships between Rb score and zone number (i.e. distance from the release point). The small numbers of *Ae. aegypti* eggs yielded a negative regression, but this was not significant (Table 2).

As an alternative type of analysis, corrections to the totals of the Rb scores were made on the hypothesis that a smaller number of Rb-marked eggs (and thus a lower Rb concentration) would be retrieved from ovitraps in the zones further away from the release point, simply because there was greater area in these zones and thus more likelihood of females finding oviposition sites other than the ovitraps. The correction factors used were the areas of each zone or annulus in Figs 3 and 4. The Rb scores were multiplied by the area of the zone in which each ovitrap was located (20.10 for zone 1; 60.29 for zone 2; 100.48 for zone 3; and 140.67 for zone 4). When the correction factor and log transformation were applied, there was found to be no significant relationship of Rb score to zone number (Table 2).

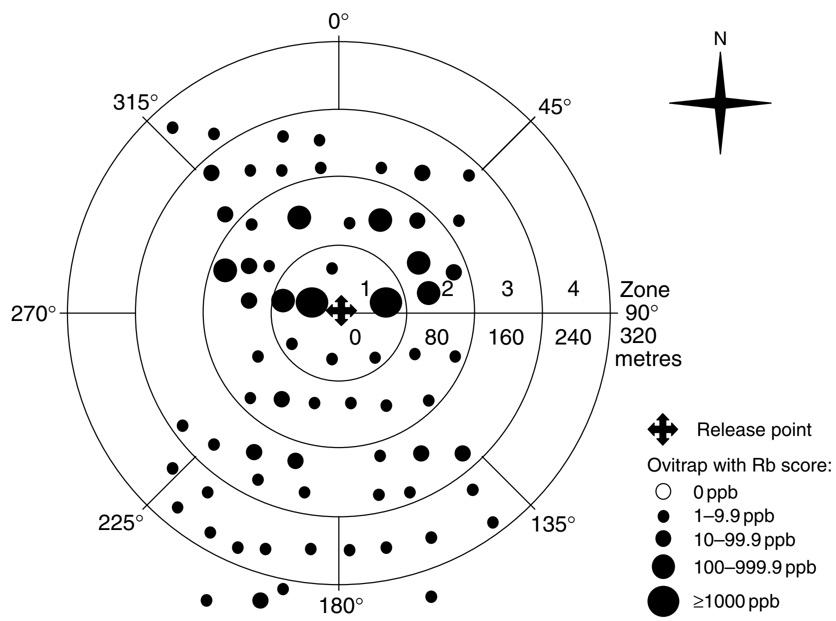

Fig. 3. *Aedes albopictus* at Bidadari Christian Cemetery: distribution of ovitraps where rubidium (Rb)-marked eggs were deposited, following release of RbCl-blood-fed female mosquitoes in the centre. Each dot represents an ovitrap: black where Rb was detected; white where no Rb was detected. Concentric rings delineate zones of 80-m intervals. Rb scores shown were cumulative over the four collection days, and combined for the three replicate trials.

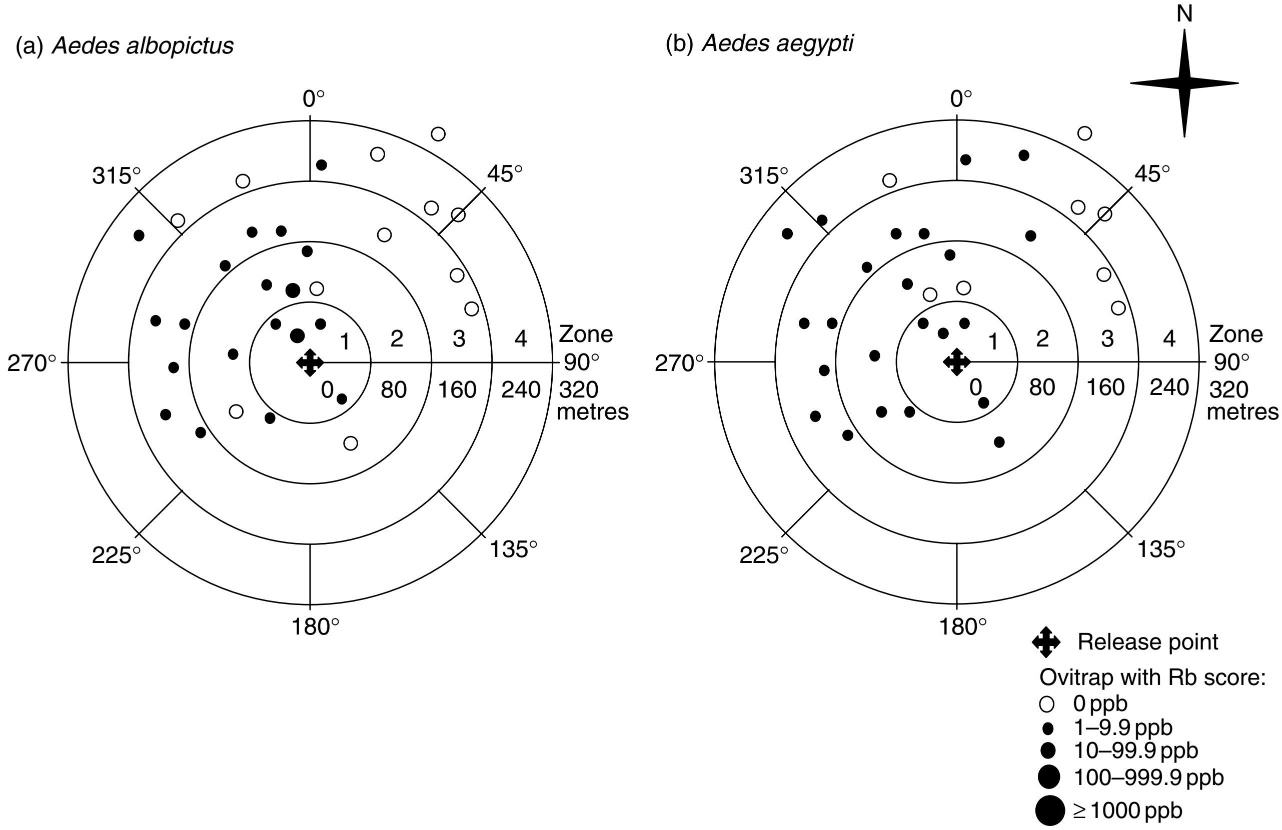

Fig. 4. Distribution of ovitraps where rubidium (Rb)-marked eggs were deposited at Geylang for (a) *Aedes albopictus* and (b) *Aedes aegypti*. Symbols as in Fig. 3.

Regression analysis of data from the multi-storey apartment

The results of the apartment block study were divided up according to storey. The directions upward and downward from the release point at storey 12 were subjected separately to regression analysis of Rb score against number of storeys away from the release level. Rb score was tested after adding 1 and transforming to natural logarithms. Correcting for area as in the above studies on horizontal movement was not necessary here, as each storey was of the same area. Presumably there were few or no other oviposition sites here apart from the ovitraps, as this was a vacant block of flats with no residual stores of water in the locked-up residential units.

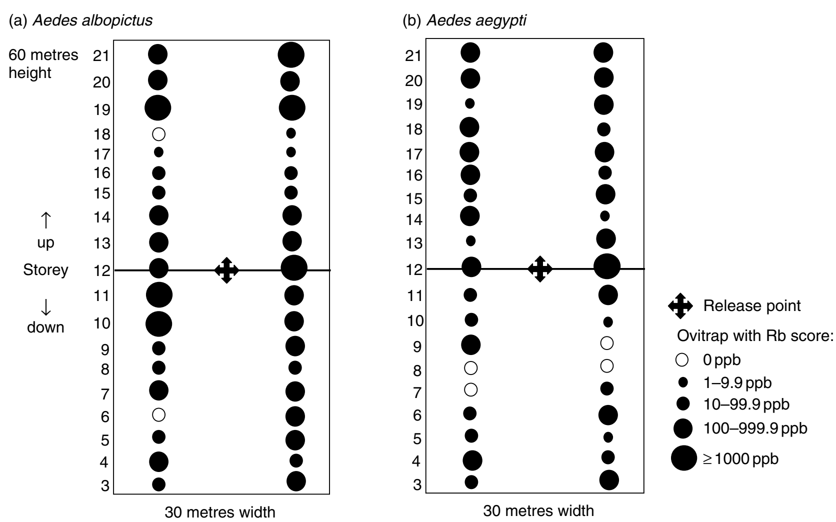

Fig. 5. Distribution of ovitraps where rubidium (Rb)-marked eggs were deposited at 'Gillman Heights' condominium, for (a) *Aedes albopictus* and (b) *Aedes aegypti*.

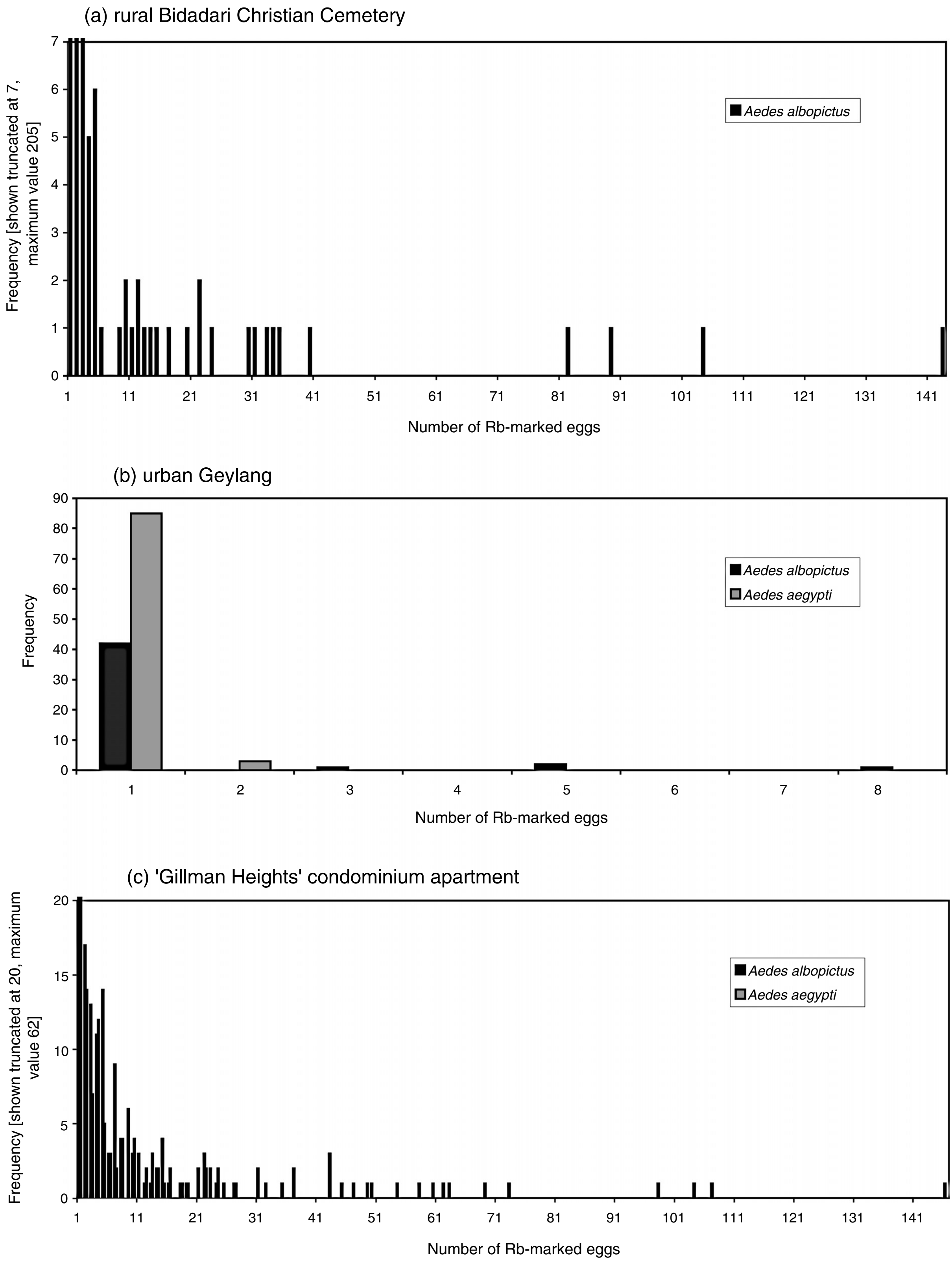

Fig. 6. Frequency distributions of ovitraps with indicated numbers of rubidium (Rb)-marked eggs. Frequencies were combined for replicate trials: separately for each *Aedes* species at each site: (a) rural Bidadari Christian Cemetery, (b) urban Geylang and (c) 'Gillman Heights' condominium apartment.

Table 2. Computation of regression lines to compare the relationship between zone number and rubidium (Rb) score, at the Bidadari Christian Cemetery (rural) and Geylang (urban) sites

Species and site	Regression analysis	Coefficients	SE	*t* stat	*P*-value
Aedes albopictus	'ln(1 + total)'	−0.680	0.165	−4.122	< 0.001
(Bidadari Christian Cemetery)	'ln(1 + corrected total)'	−0.175	0.180	−0.972	0.334
Aedes albopictus	'ln(1 + total)'	−0.418	0.162	−2.574	0.015
(Geylang)	'ln(1 + corrected total)'	−0.830	0.487	−1.704	0.099
Aedes aegypti	'ln(1 + total)'	−0.160	0.140	−1.146	0.261
(Geylang)	'ln(1 + corrected total)'	−0.232	0.483	−0.481	0.634

SE, standard error.

Analysis of Rb scores for *Ae. albopictus* in the storeys upward from the release storey showed that the observed data did not fit to a linear regression (Table 3). In fact the data could be fitted to a v-shaped relationship, indicating concentration at the release storey and top of the building with relative sparsity in-between. Downwards, there was a significant decline in marked eggs as one progressed towards ground level.

With *Ae. aegypti*, for both storeys upward and downward from the release point, there was found to be no significant trend with storey number (Table 3).

Rubidium scores weighted by zone or storey on successive collection days

Further analyses were carried out to examine the rate of dispersal of the gravid females over the four collection days, by examining when marked eggs were laid in the ovitraps in each zone or storey. Thus tests were made of whether the females moved progressively over the 4 days or readily reached the furthest ovitraps from the release point by day 1.

Weighted means (for zones or storeys, depending on the study site) were calculated for each day of each trial in the following manner.

1. The weighted zone or storey score was calculated for each zone or storey. The Rb score was multiplied by the distance away from the release point, with the release zone at 0 or storey at 12, and the furthest zone or storey away from this having the highest value.
2. The values from (1) for all zones or storeys were added together to give the total weighted zone or storey score, for a particular day.
3. The total Rb score was calculated by adding together all the Rb scores found in all zones or storeys on that day.
4. The weighted mean zone or storey was calculated by dividing (2) by (3), giving the mean zone or storey in which Rb-marked eggs were found on that day.

Table 4 shows calculated weighted means for all 4 days of the replicate trials. The weighted means were calculated with Rb score data corrected according to zone area, as done previously. Linear regression analyses showed no significant relationship between weighted means and day, either for Bidadari Christian Cemetery or Geylang, for both *Aedes* species.

Similarly, there were no significant regressions of these weighted means on storey at 'Gillman Heights' condominium, except marginally for *Ae. aegypti* downward from the release storey (Table 5).

Discussion

Mosquito dispersal, particularly over long distances, contributes crucially to the dynamics of dengue transmission (Newton & Reiter, 1992) and the devising of efficient control strategies. The general assumption is that *Ae. aegypti* females do not fly more than 50–100 m in their whole lifetime (PAHO, 1994). However, this claim is predominantly based on studies carried out in restricted sites where natural boundaries limited dispersal and where the mosquitoes were searching for bloodmeals and not oviposition sites.

The only reported study so far on dispersal in search of oviposition sites was conducted with *Ae. aegypti* by Reiter

Table 3. Computation of regression lines to compare the relationship between storey upwards and downwards from the release point and rubidium (Rb) score, at the 'Gillman Heights' condominium (apartment block) site

Species	Direction from release point	Regression analysis	Coefficients	SE	*t* stat	*P*-value
Aedes albopictus	Up	Linear: 'ln(1 + total)', 'storey'	−0.079	0.194	−0.408	0.688
	Down		−0.303	0.129	−2.344	0.031
Aedes aegypti	Up		0.107	0.162	0.663	0.516
	Down		−0.194	0.190	−1.022	0.320

SE, standard error.

Table 4. Calculated daily weighted mean zones, from rubidium (Rb) scores corrected for zone area plus one and transformed to natural logarithms, at the Bidadari Christian Cemetery (rural) and Geylang (urban) sites. t and P-values of the regression coefficients of weighted mean on day are also shown (d.f. = 11 in each case)

Species and site	Day	Weighted mean zone			t stat	P-value
		Trial I	Trial II	Trial III		
Aedes albopictus	1	1.410	2.068	1.406		
(Bidadari Christian Cemetery)	2	1.549	2.794	1.618	−0.890	0.394
	3	1.551	1.707	1.091		
	4	1.347	1.835	1.184		
		Trial I	Trial II	Trial III		
Aedes albopictus	1	0.576	1.857	2.000		
(Geylang)	2	1.045	0.000	0.000	1.081	0.305
	3	1.986	2.000	2.682		
	4	1.666	1.688	1.539		
		Trial IV	Trial V	Trial VI		
Aedes aegypti	1	2.211	1.214	2.000		
(Geylang)	2	2.035	2.518	2.000	−1.295	0.225
	3	1.792	1.772	1.562		
	4	1.528	1.389	1.802		

and colleagues in urban Puerto Rico, using Rb as a marker. The flight activity was found to cover an area at least 420 m in radius (Reiter *et al.*, 1995; Reiter, 1996).

The present study has demonstrated the rapid and extensive horizontal ovipositional dispersal of the two *Aedes* vectors in Singapore, establishing much greater flight ranges than generally assumed. Rb score per ovitrap decreased significantly with increasing distance from the release point at both the rural (Fig. 3) and urban (Fig. 4) sites. However, if zone size was corrected for, there was actually no significant difference between the Rb scores (and thus number of marked eggs deposited) in the ovitraps nearest the release point compared to those in the outermost ovitraps (Table 2). Daily records showed rapid dispersal of the gravid females at both the rural and urban sites. Regression analyses indicated that dispersal was so rapid that the distribution of Rb recorded on day 4 was not significantly different from that on day 1 (Table 4).

In addition to movement in a horizontal plane, vertical dispersion of *Aedes* was studied for the first time. An extensive three-dimensional flight pattern was observed throughout an entire apartment block, giving an interesting insight into the likely spread of dengue throughout a multi-storey building. Clearly, the females do move about extensively and the potential for virus dissemination in a building is great. This aspect has particular relevance to Singapore, where, today, over 85% of the population dwell in high-rise apartment blocks. In fact, it has been suggested that the

Table 5. Calculated daily weighted mean storeys, upwards and downwards from the release point, at the Gillman Heights' condominium (apartment block) site. t and P-values of the regression coefficients of weighted mean on day are also shown (d.f. = 11 in each case)

Species	Direction from release point	Day	Weighted mean storey			t stat	P-value
			Trial I	Trial II	Trial VI		
Aedes albopictus	Up	1	16.572	14.105	13.765		
		2	17.829	17.839	18.090	0.135	0.895
		3	17.661	15.324	16.230		
		4	14.211	14.447	17.924		
	Down	1	9.377	8.307	10.039		
		2	10.413	7.004	8.658	−1.163	0.272
		3	9.313	7.659	6.833		
		4	9.693	8.033	7.095		
			Trial III	Trial IV	Trial V		
Aedes aegypti	Up	1	20.605	14.991	17.703		
		2	16.026	16.487	17.271	−0.986	0.347
		3	16.965	14.048	19.688		
		4	14.969	14.091	18.545		
	Down	1	3.000	9.489	9.468		
		2	10.363	10.537	11.970	2.273	0.046
		3	12.000	10.171	9.333		
		4	11.000	11.650	12.000		

apartment block scenario could be a reasonably close fit to a very simplified model of dengue transmission (Reiter, 1998). This assumes that each mosquito has an equal chance of biting each person in a community. As a block comprises more than 100 homes, and our data show that to a mosquito the vertical distance of a few tens of metres constitutes almost no barrier to movement, a community of several hundred people in such a block approximates to Reiter's model.

Data from the Ministry of the Environment in Singapore (ENV) show that in high-rise government Housing and Development Board (HDB) flats, children living on the ground floor had a significantly higher rate of dengue infection than those living on higher floors (Goh, 1998). This was explained by the fact that most *Aedes* breeding habitats were found around the common areas, as opposed to within the flats. However, the present study has demonstrated the extensive movement of ovipositing females, which are also likely to seek their next bloodmeal near to where they have oviposited.

For further research, it would be worthwhile to set up ovitraps around the vicinity of apartment blocks where releases are to be made, and in neighbouring blocks, to examine the potential for movement from one building to another. Thus it would be possible to determine whether an infected female in one high-rise building is likely to give rise to disease cases in a neighbouring one. (In the case of the present study it was not possible to explore this aspect, as permission was granted strictly for work in the vacant block alone.)

A common feature observed in the frequency distribution of ovitraps with marked eggs, for both *Aedes* species and at all three sites, was that small numbers of these marked eggs were found in most ovitraps, with a mode of 1 (Fig. 6). *Aedes aegypti* distributes its eggs among several oviposition sites in each gonotrophic cycle (Christophers, 1960), and more recent studies using molecular techniques have confirmed this (Reiter, 1996). In the present work, the extreme sensitivity of the GFAAS technique was therefore crucial in order that single marked eggs could be detected.

Attempts at reducing disease transmission by source reduction or the elimination of breeding sites could drive mosquitoes to search for oviposition sites over longer distances, resulting in the enhanced dissemination of virus-infected mosquitoes (Reiter *et al.*, 1995; Reiter, 1996, 1998). The suppressed mosquito population in Singapore today could well be much more efficient at dengue dispersal than the same vector was previously, when the population and premise index were much higher (Reiter, 1998).

Oviposition activity in a single gonotrophic cycle has been reported to last several days (Reiter *et al.*, 1995; Reiter, 1996). The present study confirmed this, as marked eggs were collected in the field for 4 days following release. Longevity of the females and perhaps their ovipositional activity would have been longer if Supaglue had not been applied to their probosces, thus preventing them from feeding and resulting in their mortality after a few days.

Guidelines for the *Ae. aegypti* eradication campaign in the Americas state that, following an initial survey to determine foci in houses, insecticide application by perifocal treatment or residual intradomiciliary spraying should be administered to all houses in the infested area, and to those located within a 100-m radius of that area (PAHO, 1971). In Singapore, however, regions or transmission foci are intensively targeted where at least two cases are found less than 200 m apart and within two incubation periods of each other (Chan, 1985; Tan & Teo, 1998). Source reduction and mass fogging are then carried out, with the aim of rapidly terminating transmission. However, it has been found that 60–70% of the notified dengue infections are actually transmitted outside these focus areas (Tan & Teo, 1998).

If the extensive flight ranges determined from the present study are taken into consideration, it is clear that these target area sizes recommended for control are too small. Indeed, Gubler (1989) and Reiter *et al.* (1995) stated that the current recommendation of controlling dengue transmission during urban outbreaks by focal spraying of insecticides and other area-limited responses at 50–100 m around presumed or confirmed cases is probably ineffective.

Chan (1973) was the first to document the use of the ovitrap for control in a 1969 study in which *Ae. aegypti* was successfully eradicated from the Singapore Paya Lebar International Airport after 1 year. Data from the present study show that only small percentages of marked eggs that the released females could potentially have laid were retrieved. Thus killing their progeny would not make much impression on the population. However, data on the high frequency of single marked eggs found in the ovitraps strongly support the concept of a trap that captures the ovipositing females. Such a gravid female trap has been devised for *Culex* mosquitoes by Reiter (1983). If every female that entered an ovitrap had been captured, thus preventing it from going to any other oviposition sites, this would probably have caused a major reduction in the population.

There seems good reason to consider the use of the sterile insect technique (SIT) as a possible means of eradicating *Aedes* mosquitoes from the island of Singapore, as intensive control efforts by conventional means have not eliminated the dengue problem, and indeed the recorded number of dengue cases has increased since the 1970s (Goh, 1998). Methods for mass rearing, sex separation, sterilization, mass release, and testing mating competitiveness of sterile males in an urban area were developed almost 30 years ago, with a view to eradication of an urban population of *Ae. aegypti* (Ansari *et al.*, 1975; Grover *et al.*, 1976; Reuben *et al.*, 1976; Grover, 1985). Sex separation and sterilization could probably now be much improved with transgenic technology (Thomas *et al.*, 2000). Information on the dispersal of both released males and already mated females into the sterile male release area is important for the successful application of SIT. The methodology described in the present study could be applicable to these questions, at least regarding the mated females.

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