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Mark–release–recapture study to measure dispersal of the mosquito *Aedes aegypti* in Cairns, Queensland, Australia

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Abstract. In Queensland, Australia, in response to isolated cases of dengue infection, larval control of the vector *Aedes aegypti* (L.) (Diptera: Culicidae) is targeted at breeding sites within 200 m of a case and interior spraying with a pyrethroid adulticide is targeted at premises within 100 m. To ascertain whether these limits are appropriate, we conducted a mark–release–recapture study to measure the dispersal of female *Ae. aegypti* in the city of Cairns where transmission occurs. Female mosquitoes reared from wild collected eggs were differentially marked with fluorescent dust depending on whether they were to be released blood-fed or non-blood-fed, and a total of 1948 females was released. A total of 132 sticky ovitraps was set at 64 premises within a 200 m radius and collections of trapped adults were made at 5–15 days post-release. Sixty-seven females (3.4%) were recaptured, with the furthest being caught 200 m from the release point, and the mean distance travelled was 78 m. Overall, 23.1% of the recaptures outside the release site were taken beyond 100 m by day 15. Dispersal was comparable for both blood-fed and non-blood-fed releases. There was a significant tendency for dispersal to be in a north-westerly direction, probably because of the presence of numerous containers and heavy shading by trees in this direction and a busy road to the south of the release point that appeared to inhibit dispersal. The results suggest that adulticiding may have to be extended beyond 100 m if more than 8 days have elapsed since female *Ae. aegypti* could have fed upon a viraemic dengue case. The study also shows that dispersal is not random, and that it may be possible to maximize vector control by taking into account environmental factors that affect the direction of female mosquito flight.

Key words. *Aedes aegypti*, arbovirus, Dengue, dispersal, vector, Australia.

Introduction

Dengue viruses imported to Queensland, Australia have caused a series of outbreaks since 1994 (Ritchie *et al.*, 2002). The health department of Queensland has developed a Dengue Fever Management Plan (DFMP) that emphasizes surveillance and control of the vector *Aedes aegypti* (L.) and the local transmission of the dengue viruses (Ritchie *et al.*, 2002). The DFMP advocates source reduction and larviciding within 200 m of a dengue case and spraying of interior furniture with an adulticidal pyrethroid within 100 m.

We wished to know if a significant proportion of female *Ae. aegypti* that may have fed on a viraemic case could disperse beyond the 100-m adulticiding zone before they were able to transmit the virus (typically within 10 days after blood-feeding (Rodhain & Rosen, 1997)). We were

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concerned as to whether wind strength and direction, vegetation, and roads might affect dispersal, and whether particular premises were more likely to attract and retain the mosquito.

There are widely different estimates of the distance that *Ae. aegypti* disperses. This has been thought to be minimal if feeding and oviposition resources are available nearby (Teesdale, 1955). Sheppard *et al.* (1969) estimated that females moved an average of 37 m daily within a Bangkok study area over 3 weeks but found none dispersed beyond 75 m from the release point, Harrington *et al.* (2001) estimated a total range of 79 m in Puerto Rico and Thailand, and Getis *et al.* (2003) found that the species was strongly clustered within houses and weakly clustered to a distance of 30 m from households in Peru. By contrast, Reiter *et al.* (1995) reported much greater movement of up to 279 m over 5 days in Puerto Rico, and Liew & Curtis (2004) reported rapid dispersal up to 320 m over 4 days in Singapore (although their released mosquitoes had their probosces glued-up to prevent them from acting as vectors and this may have affected their behaviour).

The only such dispersal study in Australia was undertaken in the relatively dry inland environment of Pentland in northern Queensland where there was no dengue transmission, and the mean distance travelled per day by female *Ae. aegypti* over 7 days was found to be only 16.8 m and 24.7 m for indoor and outdoor releases, respectively, with a maximum of 160 m recorded (Muir & Kay, 1998). Most dengue transmission in Queensland takes place in northern coastal towns with generally more humid climates, so to investigate the dispersal behaviour of *Ae. aegypti* in an urban environment where dengue transmission occurs almost annually, a mark–release–recapture study was undertaken in the city of Cairns during the early part of the 2004/2005 wet season, using the locally developed sticky ovitrap (Ritchie *et al.*, 2003). This trap has been shown to be sensitive in detecting the presence of *Ae. aegypti* (Ritchie *et al.*, 2003, 2004), and effective in investigating its oviposition behaviour and dispersal (Russell & Ritchie, 2004).

Materials and methods

Study area

A private 'Queenslander-style' house (raised on pillars and with unscreened louvred windows all round), in a suburban area of Cairns where there was known activity of *Ae. aegypti*, was selected as the central release site, and a study area of 200 m radius from the house property boundaries was defined on a local authority street and property map (Fig. 1). The area was subdivided into NW, NE, SE and SW quadrants. The area contained eight suburban streets and the NW and NE quadrants were separated from the SW and SE quadrants by a major road. Based on radii at 50, 100, 150 and 200 m from the boundary of the release property, 64 sampling areas of approximately 2250 m^2 each were established, encompassing a total area of 144 000 m^2, and within each a single property was chosen, with permission, for setting two ovitraps.

The study was undertaken in the early part of the wet season during December 2004. The protocol received ethical approval from the appropriate academic and health authorities, and extensive community publicity preceded the investigation. All houses in the study area were offered larval control with methoprene to minimize adult populations of *Ae. aegypti* (a condition of the ethics approval for the study), and this treatment was known to not have a negative impact on oviposition (Ritchie & Long, 2003). Those residents volunteering for trap placement were offered free insect repellent and provided with gift vouchers for use at local grocery stores.

Rearing, marking and release

To provide adults for release, *Ae. aegypti* eggs were collected from ovitraps placed variously within the Cairns urban area. The adults reared from the eggs were caged for 3 days for mating and they were either (a) provided with 10% sugar solution only, or (b) provided with a bloodmeal from a human arm.

Bulb-dusters were used to apply fluorescent dusts to the males and females for release. The blood-fed and non-blood-fed cohorts were marked differentially with Magenta and Orange-Yellow dust (Radglo RS18 and Radglo RS12, HCA Colours Australia Pty. Ltd., Kingsgrove, Australia), respectively.

To minimize lengthy 'escape dispersal', releases were made at night when *Ae. aegypti* is inactive. A total of 856 non-blood-fed females was released together with 1181 males in the backyard outside the house, and a total of 1092 blood-fed females was released together with 1008 males in an upstairs room with open windows.

Trap deployment, collection and examination

Sticky ovitraps were prepared as described by Ritchie *et al.* (2003, 2004) and Russell & Ritchie (2004), with 33% hay infusion water and one alfalfa pellet added per trap to make the traps more attractive to *Ae. aegypti* (Ritchie, 2001).

On day 3 following the release, two traps were deployed separately in sheltered positions in each property, including the property where the releases had been made (Fig. 1). The traps were collected and replaced with new traps on days 5, 8, 11 and 15 following the release. The collected sticky strips were searched for mosquitoes, which were identified and examined under ultraviolet microscopy for fluorescent markings.

The wing length of marked recaptured specimens was compared with that of unmarked *Ae. aegypti* collected in the ovitraps, as this may indicate the relative 'fitness' of the laboratory reared and wild *Ae. aegypti* (Nasci, 1986).

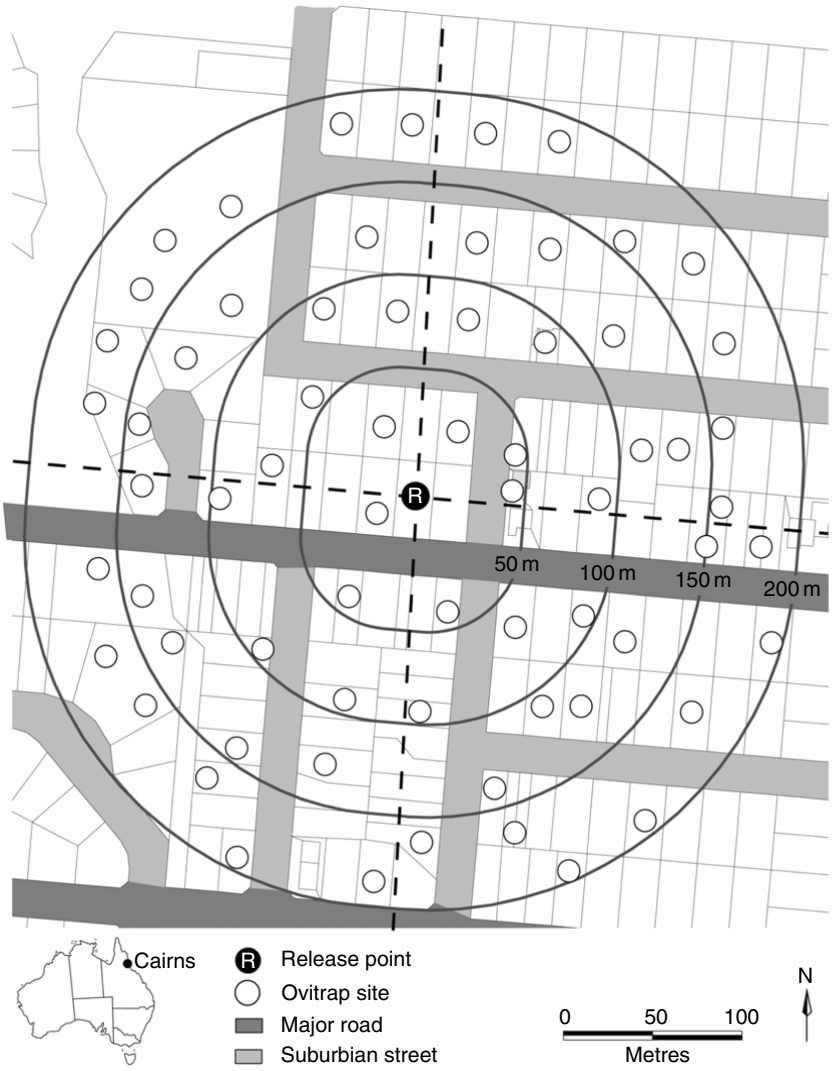

Fig. 1. The location of each premise where ovitraps were deployed in each quadrant to the north-west, north-east, south-west and south-east of the release property in Cairns, Queensland, December 2004. Each annulus is 50 m consecutively further from the boundary of the property (R) where the *Aedes aegypti* were released.

Data recording and analysis

Immediately prior to the release of the marked mosquitoes, premises within the study area were surveyed for larvae and the House Index and Breteau Index (WHO, 1986) were calculated for each quadrant of the study area to assess the distribution and abundance of breeding sites within the four quadrants.

Dispersal of the released mosquitoes was calculated as the Mean Distance Travelled (MDT) (Morris *et al*., 1991), with compensation for unequal trap densities within each annulus (Lillie *et al*., 1985). The numbers of recaptured mosquitoes were $\ln(x + 1)$ transformed and the regression of numbers recaptured on distance from release property was tested for significance. The direction of dispersal was analysed by means of circular descriptive statistics (Zar, 1999). The mean angle (a) of dispersion from the release property was then calculated for blood-fed and non-blood-fed cohorts, for each trapping period. For each mean angle, the length of the mean vector (r) was calculated. The value of r is a measure of the concentration of dispersion directions, and varies from 0 (non-directional dispersion) to 1 (unidirectional dispersion). To determine whether the dispersion differed significantly from non-directional uniformity, the Watson one sample U^2 test (Zar, 1999) was applied.

Certain environmental data (wind, temperature and humidity) were obtained from the official meteorological station at the Cairns Airport, 3.2 km from the release site, and rainfall was measured at the release property.

Results

The environmental conditions were all favourable before and during the course of the study. Within the 2 weeks prior to the release of mosquitoes there was 86 mm of rainfall, and a total of 62 mm fell on 6 of the 15 days of the study. The mean daily minimum and maximum temperatures were 24.4°C and 31.1°C, respectively, and the

Table 1. The *Aedes aegypti* House Index* and Breteau Index† for the four quadrants in the study area based on larval surveys prior to the release of marked mosquitoes at Cairns, Queensland, December 2004

Quadrant	*n*	House Index	Breteau Index
NW	19	31.6	42.1
NE	36	30.6	61.1
SW	42	11.9	11.9
SE	40	15.0	22.5
Total	137	20.4	32.1

*House Index = percentage of houses with one or more containers positive for *Ae. aegypti* larvae.
†Breteau Index = number of *Ae. aegypti* positive containers per 100 houses.

average RH was 71.1% and 67.9% at 09.00 hours and 15.00 hours, respectively. For the first 11 days following release, the winds were light from the NW to NE but they turned to being fresh from the SE for the last 4 days of the trial.

The study area included 164 premises and, from surveys of 137 of these, the House and Breteau Indices for the NW, NE, SW and SE quadrants are shown in Table 1. A total of 132 sticky ovitraps was set in 64 of the premises (Fig. 1). Of the 1948 females released, a total of 67 was recaptured; 39 (4.56%) had been released non-blood-fed and 28 (2.56%) had been released blood-fed. Fifteen of the 67 recaptures had been released within the release property; 11 were released blood-fed and four were released non-blood-fed. Out of the 52 females recaptured outside the release property, 42.3% were caught within 50 m and 63.5% within 100 m of the release site by day 8, and only 23.1% were caught $>$ 100 m over the whole period. Contingency table testing using the χ^2 statistic with Yates' continuity correction (Zar, 1999) revealed no significant difference in the frequency of each female cohort recaptured at the release property ($\chi^2 = 2.4$, $P = 0.12$). Of the 52 recaptures outside the release property, 17 were released blood-fed, whereas 35 were released non-blood-fed. Contingency table testing showed this trend to be significant ($\chi^2 = 6.23$, $P = 0.01$), and thus there was a greater propensity for dispersion by non-blood-feds. No marked males were collected by the sticky ovitraps, but females of six species other than *Ae. aegypti* were collected.

Figure 2 shows the distribution of recaptures in time and space, with the number of recaptures declining over the period of the study. The maximum distance travelled by a recaptured female was 200 m from the boundary of the release property, and the overall MDT was 77.8 m for the blood-feds and 77.6 m for the non-blood-feds. Table 2 suggests that the mean distance travelled tended to increase over the successive days after release. There was a negative geometric relationship between distance and the numbers of recaptured mosquitoes, and significantly so for the non-blood-feds ($P = 0.016$).

Mean angle calculations indicated a general trend in dispersal towards the NW for both non-blood-fed and blood-fed mosquitoes, which was maintained throughout the study (Table 3). The directional trend was significantly non-random ($P < 0.001$) for both cohorts after the 15 days. No analysis was conducted using recapture data from days 5, 8 and 11, due to insufficient numbers. The overall mean direction angles for blood-fed and non-blood-fed mosquitoes after 15 days could not be separated by 95% confidence intervals.

There were no significant differences ($F_{2,79} = 0.65$, $P = 0.52$) in the mean wing length of the recaptured mosquitoes that had been released blood-fed (mean $\pm$ SD = 2.83 $\pm$ 0.13 mm) or non-blood-fed (2.80 $\pm$ 0.15 mm) and the unmarked (2.76 $\pm$ 0.22 mm) *Ae. aegypti* females collected in ovitraps. Therefore, the released mosquitoes were presumed to be as fit as the local wild *Ae. aegypti* during the course of the trial.

Discussion

The recovery of marked females (overall 3.4%) in the traps was lower than is generally reported in the literature (e.g. Conway *et al.*, 1974 = 12.4%; McDonald, 1977 = 37.5%; Trpis & Hauserman, 1986 = 40%), although comparable recapture rates have also been reported (e.g. Nayar, 1981 = 5.4%). However, these other investigations used different recapture techniques (e.g. aspiration of resting adults or light-trap collection of host-seeking adults), making comparisons problematic. Sticky ovitraps identical to those in this Cairns study were used by Russell & Ritchie (2004) in a mark–release–recapture of *Ae. aegypti* in Moorea, French Polynesia and 19–26% of released females were recaptured. In that study, however, the traps were concentrated within 50 m of the release points. In the present study, the recaptures would have been limited by the relatively low proportion of properties in the study area (64/164 or 39%) that were allocated ovitraps, and many of the other properties provided alternative oviposition sites.

Nonetheless, sufficient marked mosquitoes were collected to show several trends. First, dispersal was generally $<$ 100 m within 8 days, but by day 15 releases were recaptured out to 200 m. Second, although both blood-fed and non-blood-fed releases were recaptured in each of the four quadrants, the overall dispersal trend was to the NW. Third, although *Ae. aegypti* females readily crossed some quieter streets, significantly fewer were found across the busy major road immediately south of the release point.

The overall MDT was virtually the same for the blood-fed (77.8 m) and non-blood-fed (77.6 m) releases. In the

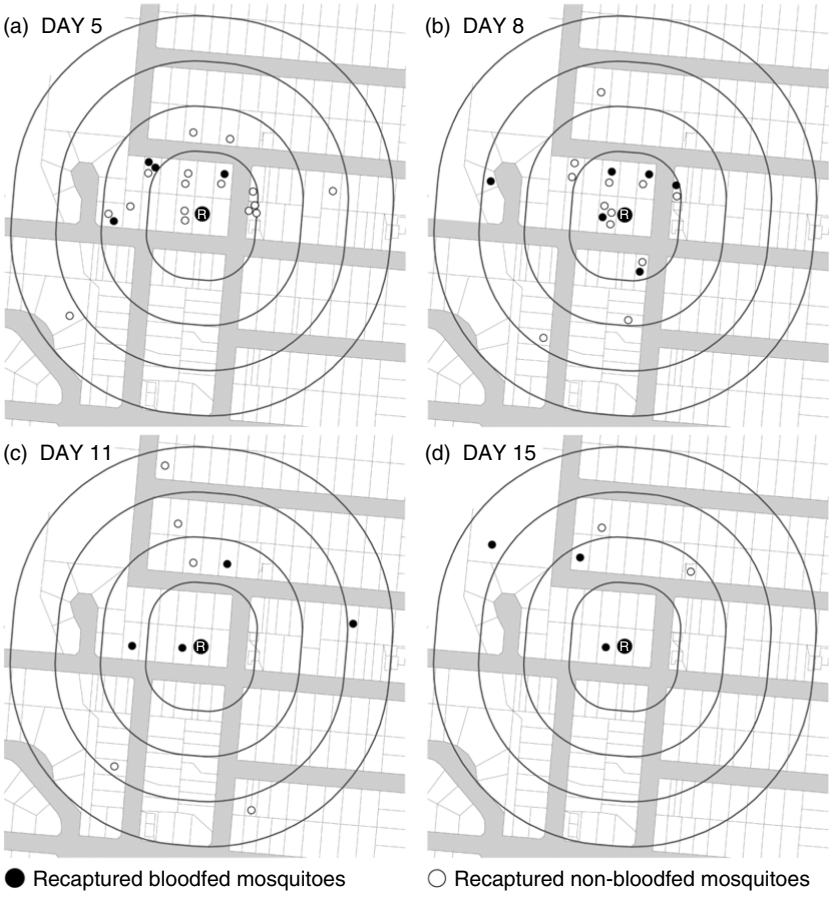

Fig. 2. Total number of marked blood-fed (●) and non-blood-fed (○) *Aedes aegypti* recaptured per collection day following release at Cairns, Queensland, December 2004. Other details are as for Fig. 1, with each annulus being 50 m consecutively further from the boundary of the property (R) where the *Aedes aegypti* were released.

only methodologically similar investigation, Muir & Kay (1998) found the mean distance travelled per day by females over 7 days was 16.8 and 24.7 m for indoor and outdoor releases, respectively, but this was in much drier and arguably less favourable conditions in Queensland. The distance travelled by mosquitoes seeking oviposition sites will depend on the duration of the gonotrophic cycle and the availability and proximity of oviposition sites near to blood sources. The duration of the *Ae. aegypti* gonotrophic cycle has been reported to vary from less than 2 days to more than 5 days, although at 25–30°C in laboratory trials in Malaysia almost 90% had oviposited their first batch within 5 days (Macdonald, 1956). Thus, with an average daily temperature of 27.8°C during the study, we would expect oviposition by the marked blood-feds by day 5 post-release.

Table 2. Mean distance travelled (MDT) in metres for each cohort of *Aedes aegypti* for each of the four quadrants on each collection day at Cairns, Queensland, December 2004

		Distance (m) travelled by collection day after release			
Quadrant	Status when released	Day 5	Day 8	Day 11	Day 15
NW	Non-blood-fed	55.0	75.0	125.0	125.0
	Blood-fed	75.0	75.0	75.0	150.0
NE	Non-blood-fed	58.3	25.0	NR*	75.0
	Blood-fed	25.0	25.0	125.0	NR*
SW	Non-blood-fed	96.1	65.0	125.0	NR
	Blood-fed	75.0	25.0	25.0	25.0
SE	Non-blood-fed	NR*	50.0	175.0	NR
	Blood-fed	NR	25.0	NR	NR
Total	Non-blood-fed	69.8	53.8	141.7	100.0
	Blood-fed	58.3	37.5	75.0	87.5

*NR = no marked mosquitoes recaptured.

Table 3. Mean direction angles, *a* (compass directions), and vectors *r* (see Zar, 1999) for recaptured *Aedes aegypti* females dispersing from the release property at Cairns, Queensland, December 2004

	Released non-blood-fed		Released blood-fed		Combined	
Trap date	*a*	*r*	*a*	*r*	*a*	*r*
Day 5	347° (NNW)	0.26	306° (NW)	0.76	329° (NW)	0.33
Day 8	283° (WNW)	0.30	295° (WNW)	0.29	287° (WNW)	0.30
Day 11	317° (NW)	0.29	297° (WNW)	0.11	313° (NW)	0.21
Day 15	18° (NNE)	0.88	306° (NW)	0.93	332° (NNW)	0.75
Overall	328° (NW)	0.25	303° (NW)	0.46	316° (NW)	0.48
	CI_{95}257°; 39°		CI_{95} 260°; 346°		CI_{95} 293°; 355°	

Mark–release–recapture investigations intended to 'track' blood-fed females seeking an oviposition site following their release are complicated, however, by the fact that *Ae. aegypti* females are well known to feed more than once in each gonotrophic cycle (Macdonald, 1956; Scott *et al.*, 1993) and there can be some secondary host-seeking activity prior to their capture at the ovitrap, precluding simple interpretations of results. Furthermore, when considering vector activity during periods of dengue transmission, it is unclear whether the flight capability of virus infected *Ae. aegypti* is different from that of non-infected blood-fed females. However, it is clear in the present investigation that, over time, mosquitoes continued to move away from the release site, although there was a definite decrease in recaptures associated with time and distance from the release point.

The apparent low number of recaptures across the busy road to the south of the release point deserves comment. Females crossed relatively quiet streets that carried infrequent local-traffic in the study area, but only 7/67 (10%) of the recaptured mosquitoes were collected south of the busy road adjacent to the release site that carried almost constant through-traffic during the daytime and early evening. Contingency table testing using the χ^2 statistic with expected frequencies based on the proportion of traps set either side of the road showed that this trend was statistically significant ($\chi^2 = 38.81$, $P < 0.0001$). There are several possible reasons for this. First, the four premises immediately NW and NE of the release premise were well-vegetated with trees, with a mean Shade Index (Tun-Lin *et al.*, 1995) of 2.25, whereas the four immediately to the south all had open yards with $< 25\%$ shade (Shade Index = 1). The House Index suggests that this area is favourable for *Ae. aegypti* breeding; the greatest proportion of houses with *Ae. aegypti* larvae present were in the northern quadrants. Muir *et al.* (1992) demonstrated that Australian female *Ae. aegypti* were most attracted to black objects, and the dispersing females may have been attracted to the dark shady properties immediately NW and NE of the release site. This suggests that female *Ae. aegypti* may prefer to disperse via quiet, well-shaded vegetated areas rather than cross busy unshaded roads.

Second, the quadrants north of the release site also had the highest proportion of breeding sites, as shown by the relatively high Breteau Indices for these quadrants. The NW to NE winds from days 0–10 post-release would have blown over areas rich with breeding sites, bringing attractive odours for *Ae. aegypti* seeking to oviposit. The *r*-value indicates that there was a significant trend for upwind flight. Edman *et al.* (1998) found that dispersion of female *Ae. aegypti* was reduced when oviposition sites were available, but high dispersal rates have been observed where few oviposition sites were available (Reiter *et al.*, 1995; Liew & Curtis, 2004).

Recaptures within the release property suggest that either some females remained within or near the release property for that length of time, or that movement brought them back to the release site over time. The overall recapture rate outside the release property's boundaries was particularly low for blood-fed females compared to non-blood-fed females. The release of blood-fed mosquitoes from inside a second storey room may have inhibited their dispersal away from the property because they would not have responded to host-seeking cues as early as non-blood-fed females would have. The interior release site for the blood-fed mosquitoes was deliberately chosen to represent a potential feeding situation within a typical north Queensland house with unscreened louvred windows all around to provide ventilation. The mosquitoes could easily exit through the continuously open windows, and indeed blood-fed females released indoors did eventually reach the 200 m annulus by day 11, along with the non-blood-fed females released outdoors.

Relatively large numbers of unmarked mosquitoes were captured overall, especially in the outer annuli later in the study period. This reflects not only the amount of local breeding of *Ae. aegypti*, but also indicated dispersal into the study area from beyond the 200 m perimeter where there was no larval control, and where the frequent rainfall and favourable temperatures during the study period would have initiated egg hatching, promoted larval development, increased adult productivity and enhanced adult survival. For the area in general, the winds were relatively light during the study and, because of the relatively protective housing and tree space environment, likely did not influence the overall movement of adult mosquitoes adversely.

The results indicate that *Ae. aegypti* in Cairns can move through relatively open and heavily vegetated areas in all directions up to 200 m within 11 days, and these results have several operational implications. They support the DFMP's practice of limiting adulticiding to premises within 100 m of a dengue case, provided that the spraying occurs

within 8 days of the person becoming infective. However, adulticiding should be expanded beyond 100 m when there is reason to believe that the case could have been infective to mosquitoes for some time before spraying begins. Busy roads or unshaded areas may serve as barriers to movement and thus treatments could be targeted away from areas bounded by these features, and areas with a higher degree of shade and water-holding containers should be targeted for more intensive adulticiding.

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