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AEDES AEGYPTI SURVIVAL AND DISPERSAL ESTIMATED BY MARK-RELEASE-RECAPTURE IN NORTHERN AUSTRALIA

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Abstract. The survival and dispersal of adult *Aedes aegypti* were estimated in northern Australia where sporadic outbreaks of *Ae. aegypti*-borne dengue viruses have occurred in recent years. Standard mark-release-recapture methods were used. In addition, a new sticky trap was used to capture the mosquitoes. Prior to the field study, the survival and effect of marking *Ae. aegypti* with fluorescent powder were determined in the laboratory. Mortality was age-dependent and the marked cohorts had higher survival rates than the untreated cohorts. Recapture rates of 13.0% and 3.6% over a seven-day period were achieved for two batches of marked *Ae. aegypti* released simultaneously at the field site. More males than females were recaptured although the proportion of females increased with time. The probability of daily survival was 0.91 and 0.86 for the blue- and pink-marked females, respectively, and 0.57 and 0.70 for the blue- and pink-marked and males, respectively. The mean distance traveled of recaptured *Ae. aegypti* was 56 m and 35 m for females and males, respectively. The maximum observed distance traveled of 160 m was the same for both sexes. The warm to hot and dry climatic conditions may have restricted the dispersal of released mosquitoes in this study. The frequency of recaptures at certain trap locations suggested that shade, wind, and the availability of hosts affected the distribution of *Ae. aegypti* within the study site.

Sporadic outbreaks of dengue fever transmitted by the container-breeding mosquito *Aedes aegypti* have occurred in northeastern Australia since 1879.[1, 2] After an absence of 26 years, dengue re-emerged as a public health problem in 1981 with 286 confirmed cases.[3] The most recent outbreak lasted 20 months during 1992–1993 resulting in 896 laboratory-notified cases of dengue-2 virus or untyped dengue virus.[4, 5] Limited transmission of dengue-2 virus occurred in 1995.[6] Currently, dengue is most probably not endemic to Australia; rather, outbreaks occur when dengue viruses are introduced to an area where *Ae. aegypti* are established and other local conditions favor transmission. The distribution of *Ae. aegypti* is confined to the state of Queensland, particularly northern urban areas[3] where dengue activity has been focused since 1981.

Aedes aegypti adult survival plays a key role in dengue virus transmission because vectorial capacity is proportional to the adult population size times $P^n/-\ln P$ where P is the probability of daily survival (PDS) and n is the extrinsic incubation period (EIP) of the virus.[7] The survival of adults depends on many variables including larval and adult nutrition, climate, predation, and genotype. From previous studies, the PDS of *Ae. aegypti* ranged from 0.65[8] to 0.89[9] and from 0.51[8] to 0.88[10] for adult females and males, respectively. The mortality rate increased with age in laboratory cohorts of female *Ae. aegypti;*[11] however, in Kenyan field studies, mortality of adult domestic *Ae. aegypti* was independent of age and their life expectancy was 9.2 days for females and 4.4 days for males.[9] Focks and others[12] have used the latter evidence that mortality is age-independent for their simulation models of the epidemiology of urban dengue fever.

The dispersal of *Ae. aegypti* affects dengue transmission through its influence on human-vector contact. Traditionally, *Ae. aegypti* has been regarded as having limited dispersal.[13] *Aedes aegypti* appears to be a poor flyer, and this, combined with its container-breeding habit, has supported the concept of low dispersal and a clumped distribution around breeding sites. However, adult females disperse sufficiently to use container habitats that are often scattered and ephemeral (short-lived). A wide variety of maximum dispersal distances between 27 m[14] and 1,150 m[15] have been estimated for *Ae. aegypti* from mark-release-recapture studies. However, most studies show that the majority of *Ae. aegypti* disperse < 80 m,[8, 16, 17] an exception being that of Reiter and others,[18] who estimated that gravid females dispersed on average 279 m after five days. Generally, males disperse further than females in the first 24 hr but females disperse longer distances than males during their lifetimes.[9, 10] Factors affecting the pattern of dispersal of *Ae. aegypti* include the availability of cool, dark, resting places and vegetation,[19] oviposition sites,[18] and wind direction.[20] In urban northern Queensland, *Ae. aegypti* immature forms and adults had a clumped distribution centered around key locations;[21] however, recent collections suggested that the distribution of adults was more uniform (Muir L, unpublished data). This paper reports the first estimations of survival and dispersal of *Ae. aegypti* adults in Australia using mark-release-recapture methods.

MATERIALS AND METHODS

Effect of marking with fluorescent dyes on the survivorship of adult *Ae. aegypti* in the laboratory. Two- or three-day-old, colonized *Ae. aegypti* were used. For the controls, 10 groups of 20 males and of 20 females were aspirated into waxed, 135-mm diameter cardboard containers with gauze tops. For the marking with powdered fluorescent pigment (Day-Glo Color Corp., Cleveland, OH), approximately 300 males and 300 females were aspirated into two 215-mm diameter waxed containers with gauze tops and bottoms. A 1-ml syringe with a 22-gauge needle was used as an insulflator. After 1 hr, 10 subsamples of approximately 20 mosquitoes were aspirated into the 135-mm diameter containers as for the controls. After 1–2 hr, the number of dead mosquitoes in each of the smaller containers was counted and this was used as time zero. All mosquitoes were provided with 10% sucrose and fresh apple daily and held at 28°C and a relative humidity of 60–90% The numbers of live mosquitoes were counted daily for 54 days and the percentage survival was plotted against time.

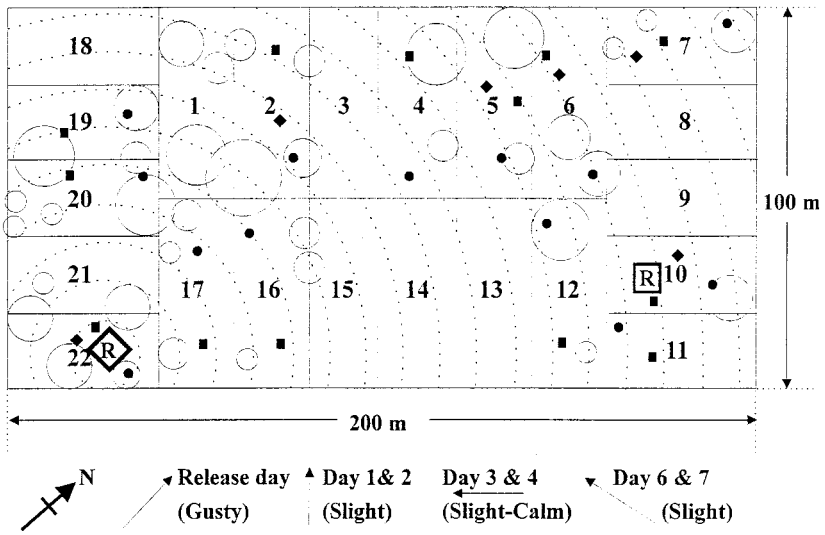

FIGURE 1. Scale diagram of the mark-release-recapture study site at Pentland, north Queensland, Australia, showing the distribution of premises (numbered). Circles = trees; R = release sites; ● = sticky traps placed outdoors, ■ = sticky traps placed peridomestically, ◆ = sticky traps placed indoors. Annuli of 10-m widths centered on the release site of the blue-marked *Aedes aegypti* are shown as dotted lines.

Field study site. Pentland (145°24′E, 20°32′S) (population = 210) is a rural town 240 km inland from the coastal city of Townsville in northeastern Australia. Pentland was chosen as the mark-release-recapture area because *Ae. aegypti* were present without dengue transmission. A block (200 m × 100 m) of 22 premises was chosen as the study site (Figure 1). Each premise consisted of a wooden house elevated 700 mm in the center of a yard delineated by an open, wire fence. Most yards had some shade. The block was surrounded by wide streets and cleared ground. Two vacant premises, one at each end of the block, were chosen for simultaneous release of two cohorts of marked *Ae. aegypti*. The mark-release-recapture was authorized by the relevant health authorities and all householders within the block. The area was surveyed for mosquito breeding prior to the mark-release-recapture experiment and all *Ae. aegypti* breeding sites were removed or treated with 1% temephos (Cyanamid Australia Pty. Ltd., Baulkham Hills, New South Wales, Australia) sand granules at a concentration of 1 g/10 liters of water. Over the experimental period, temperature and relative humidity ranged between 20°C and 34°C and 32% and 54%, respectively. The wind direction varied (Figure 1) and ranged from calm to 15 km/hr. No rain was recorded (Bureau of Meteorology, Brisbane, Australia).

Mosquito rearing and marking procedures. Because there were insufficient *Ae. aegypti* larvae in the study area for a large mark-release-recapture experiment, adults were reared from eggs of *Ae. aegypti* colonized from Townsville in 1990. At Pentland, eggs were hatched in deionized water in plastic containers and larvae were reared on goldfish food flakes. Batches of 2,000 and 1,600 pupae were placed in separate gauze cages. After emergence, adults were provided with 10% sucrose solution. On the morning of the release, 1–2 days after emergence, the majority of each batch of mosquitoes was removed from its cage and placed into a large, cardboard cylinder with gauze at each end. The mosquitoes remaining in the cages were killed, sexed, and counted to determine the sex ratio. The mosquitoes in the cardboard cylinders were dusted with blue or pink fluorescent pigment as described above.

Release and recapture of mosquitoes. Mosquitoes were released with minimum disturbance around noon when *Ae. aegypti* exhibited low activity. The blue-marked *Ae. aegypti* were released indoors at Premise 22, and the pink-marked cohort was released in a semi-enclosed fixture attached to the rear of Premise 10. The number of released mosquitoes was calculated by subtracting the numbers left in the cages and in the release cylinders from the number of pupae placed in the cages.

Prior to releasing the marked mosquitoes, 32 sticky lures were placed within the block (Figure 1). Sticky lures consisted of a black rectangle of cardboard (270 mm × 130 mm) glued to a white backing sheet (330 mm × 180 mm). The black rectangle was coated with a thin layer of polybutylene adhesive (Five Star Japan Co. Pty. Ltd., Kenmore, Queensland, Australia) and a 100 mm × 5 mm strip of cardboard impregnated with a proprietary blend of chemicals was stapled to the center. Sticky lures were placed within 1 m of the ground. Lures were collected each morning for seven days, collected materials were taken to the field laboratory, and marked and unmarked *Ae. aegypti* were counted under a stereomicroscope. Recaptures were stopped after seven days so that the experimental period was less than the shortest likely EIP of dengue viruses.[12] At the end of the experiment, the block was fogged with pyrethrum and each householder given a spray can of insecticide for indoor use.

Survivorship of *Ae. aegypti* in the laboratory. Data of the number of mosquitoes that died each day were analyzed using the product limit method (SAS Version 6.08 for Windows; SAS Institute, Cary, NC). This method constructs a Kaplan-Meier survival curve (distribution function, s(t)) for control and marked cohorts and compares their homogeneity using the Wilcoxon test. The best model of mortality was determined by constructing hazard functions for each treatment and sex following the methods of Clements and Paterson[7] and using the SAS Version 6.08 for Windows. The

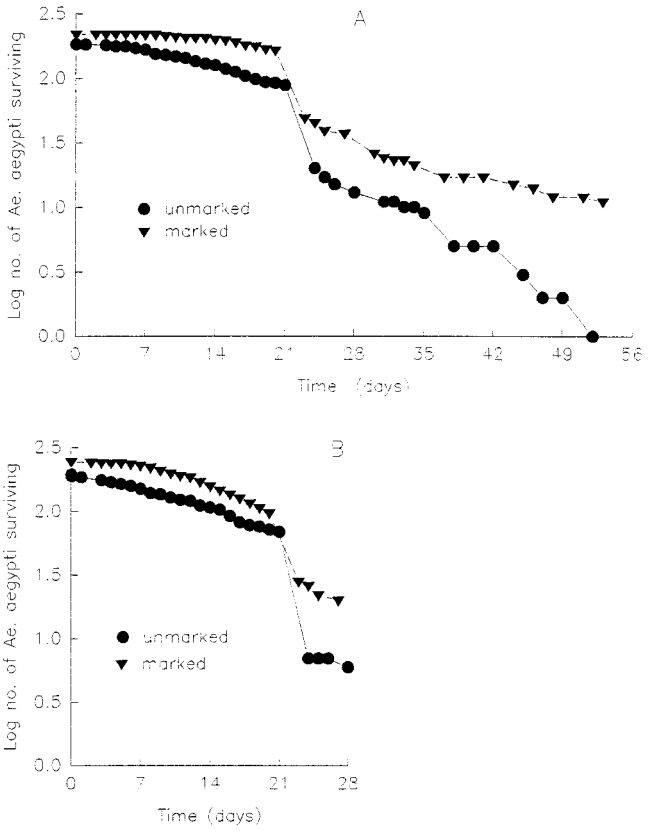

FIGURE 2. Log_{10} number of survivors of **A,** female and **B,** male *Aedes aegypti* untreated and marked with fluorescent powder and kept under laboratory conditions.

hazard function plots the mortality rate applying at any instant in time over the period of the experiment. The log_e of the hazard values plotted against age intervals will approximate a horizontal straight line if the mortality rate is constant for all ages.

Mark-release-recapture data. To test for differences in the proportions of females and males (sex ratio) recaptured compared with the proportions released, the chi-square test with Yates' correction factor was used. The chi-square test also was used to test for differences in the proportions of females and males recaptured each day. The PDS was estimated by regressing $\log_{10}$ (x + 1) of the number of recaptures against the day of recapture where the $antilog_{10}$ of the slope of the regression line is the PDS.[22] Average life expectancy (ALE) was calculated from the PDS as $1/-\log_e PDS$.[23]

Dispersal distances were measured by drawing annuli 10 m apart around the release sites on a scale map featuring the trap positions (Figure 1). The mean distances traveled (MDT) and flight ranges (FR) were calculated according to the methods developed by Lillie and others,[24] White and Morris,[25] and Morris and others.[26] A correction factor (CF) to accommodate unequal trap densities was included in the calculations. The MDT was calculated as Σ (estimated recaptures [ER] × median distance of annulus (for all annuli))/total number of ER, where ER = the number of observed recaptures in an annulus × CF/number of traps in the annulus, and CF = the area of the annulus × the total number of traps in trapping area/total trapping area. The FR was estimated from the linear regression of the cumulative ERs from each annulus (x axis) on the $\log_{10}$ (annulus median distance + 1). The FR_{50} and FR_{90} are calculated from the equation of the regression line as the value of y at 50% and 90%, respectively, of the largest value of x.

TABLE 1

Number of marked *Aedes aegypti* recaptured on each day of the mark-release-recapture study at Pentland, northern Queensland, Australia, February 1994

Day of recapture	Blue-marked		Pink-marked	
	♀	♂	♀	♂
1	18	102	15	27
2	3	43	0	1
3	6	17	0	1
4	5	8	2	0
6	7	4	0	1
7	4	2	2	0
Total	43	176	19	30

RESULTS

Survivorship of *Ae. aegypti* in the laboratory. All mosquitoes treated with fluorescent powder were marked and remained so for the life of the mosquito. The oldest females lived for 54 days and the oldest males for 28 days (Figure 2). Median longevity was 19 days and 14 days for females and males, respectively. The Wilcoxon test of the Kaplan-Meier survival functions of the females over 42 days and over seven days gave a significant difference between the control and marked groups ($\chi^2 = 16.93$, $P < 0.001$); $\chi^2 = 6.47$, $P = 0.011$; respectively); the males showed a significant difference between the groups over seven days ($\chi^2 = 19.64$, $P < 0.001$), but not over 28 days. The marked groups showed higher survival rates. The plot of ln hazard values against age showed that the mortality rate of female and male control and marked groups increased with age ($P < 0.05$). The linear regressions were not horizontal and had slopes of 0.04–0.12.

Release and recapture data. A subsample of the blue-marked *Ae. aegypti* had a female:male ratio of 1.0:2.4 (n = 292). Since 1,688 blue-marked mosquitoes were released at premise 22, by extrapolation, these consisted of 497 females and 1,192 males. At Premise 10, 1,365 pink-marked *Ae. aegypti* were released and a cohort subsample gave a sex ratio of 1.0:0.9 (n = 224); by extrapolation, these mosquitoes consisted of 715 females and 650 males. The number of blue-marked mosquitoes recaptured was 219 (13.0%) (Table 1), consisting of 43 females (8.7%) and 176 males (14.8%); the number of pink-marked mosquitoes was 49 (3.6%), consisting of 19 females (2.7%) and 30 males (4.6%). For the blue-marked cohort, house 22 (the release site) had the highest number of recaptures, 176; house 20, 18; house 2, 15; house 6, three; house 11, two and houses 5, 12, 16, 17, and 19, one recapture each. The most pink-marked *Ae. aegypti*, 41, were recaptured at house 10 (the release site); four at house 20; two at house 11; and one each at houses 7 and 19.

The female:male ratios of recaptured blue- and pink-marked *Ae. aegypti* were 1.0:4.1 and 1.0:1.6, respectively. A chi-square test showed that the proportion of blue-marked

TABLE 2

Components* of regression analyses of the number of marked *Aedes aegypti* recaptured against day of recapture at Pentland, northern Queensland, Australia, February 1994, and the derived probability of daily survival (PDS) and average life expectancy (ALE)

	Blue-marked		Pink-marked	
	♀	♂	♀	♂
n	6	6	6	6
r^2	0.173	0.945	0.110	0.466
r	0.416	0.972	0.331	0.683
a	1.013	2.099	0.620	0.999
b	−0.042	−0.244	−0.068	−0.158
t	0.914	8.298	0.701	1.868
P	0.412	0.001†	0.522	0.135
PDS	0.908	0.570	0.855	0.695
ALE (days)	10.36	1.78	6.38	0.64

* n = sample size; R^2 = coefficient of determination; r = correlation coefficient; a = y-intercept (constant); b = slope of regression; *t* = tests the null hypothesis that the coefficient of the independent variable (day of recapture) is zero; *P* = significance probability.
† Statistically significant.

females to males recaptured was significantly different from the proportions released ($\chi^2 = 8.28$, degrees of freedom [df] = 1, $P < 0.05$), and that proportionally more males than females were recaptured over the study period. However, the proportion of released and recaptured pink-marked females to males was not significantly different. There was a significant relationship between sex ratio and the day of recapture for blue-marked mosquitoes ($\chi^2 = 32.31$, df = 5, $P < 0.001$), and the proportion of females recaptured increased with time ($t = 7.38$, $P < 0.05$).

Survival and dispersal. The regression analyses (Table 2) gave an estimated daily survival of 0.91 and 0.86 for the blue and pink-marked females, respectively, and, 0.57 and 0.70 for the blue and pink-marked males, respectively. The average MDT by recaptured female and male *Ae. aegypti* were 56 m and 35 m, respectively (Table 3). As a group, females dispersed further than males, although the maximum observed distance traveled was similar for both sexes. The flight range of 90% of the released *Ae. aegypti* (FR_{90}) was further for females (108 m) than males (82 m). Daily dispersal, measured as the MDT/day (mean ± SE), was 16.8 ± 4.1 m and 24.7 ± 7.4 m for blue- and pink-marked females, respectively, and 14.7 ± 1.4 m and 18.2 ± 5.3 m for blue- and pink-marked males, respectively. There was no statistically significant difference between the MDT/day of females and males ($P > 0.05$). The daily dispersal of recaptured females, as shown by the blue-marked cohort, was low on the first day post-release (5 m) but increased to its highest level on the second day (69 m) (Figure 3). The daily dispersal of males was relatively constant.

DISCUSSION

This paper describes the first mark-release-recapture of *Ae. aegypti* in Australia, and the first field experiment using an artificial lure to capture adult *Ae. aegypti*. The recapture rates of 13% and 3.6% for the blue-marked and pink-marked cohorts, respectively, are comparable with most mark-release-recapture experiments with *Ae. aegypti*, although recapture rates depend upon the topography of the study site and the number and type of trap used. The lower recapture rate of the pink-marked cohort (released outdoors) may be attributed to gusty winds blowing mosquitoes out of the study site on the day of release. Nayar[8] recovered an average of 5.4% of marked *Ae. aegypti* adults released outdoors in Florida using CO_2-baited suction traps and vacuum collections. Conway and others[27] and Trpis and Hauserman[17] recaptured 12.4% and 40%, respectively, of released *Ae. aegypti* using human-bait collections, and McDonald[20] recovered 37.5% using human-bait collections and exit window traps. Human-bait is the most powerful attractant for host-seeking *Ae. aegypti* and it also attracts males, presumably seeking mates. However, human-bait collections undersample females less than two days old and gravid females. The sticky lures recaptured sufficient numbers of the marked *Ae. aegypti* to estimate the survival and dispersal characteristics of the marked population. Both females and males were captured on the lure. The physiologic condition of the captured females was not routinely determined although at least one was gravid. The number of females recaptured over seven days did not show a periodicity as has occurred for female *Ae. aegypti* captured by human bait,[27] and this could indicate that the lures captured females in all physiologic states.

For the blue-marked mosquitoes, proportionally more males than females were recaptured overall, but the proportion of females recaptured increased with time. This trend could be due to the lures becoming more efficient at captur-

TABLE 3

Mean distance traveled (MDT) from estimated recaptures, observed maximum distance traveled (MAX), and flight ranges (FR) of marked *Aedes aegypti* released at Pentland, northern Queensland, Australia, February 1994

	MDT (m)	MAX (m)	FR_{50}* (m)	FR_{90}* (m)
Blue-marked ♀	58	140	41	108
Pink-marked ♀	53	160	25	107
Blue-marked ♂	44	140	31	100
Pink-marked ♂	25	160	19	63
Average ♀	56	150	33	108
Average ♂	35	150	25	82

* The flight range within which 50% (FR_{50}) or 90% (FR_{90}) of the marked population dispersed.

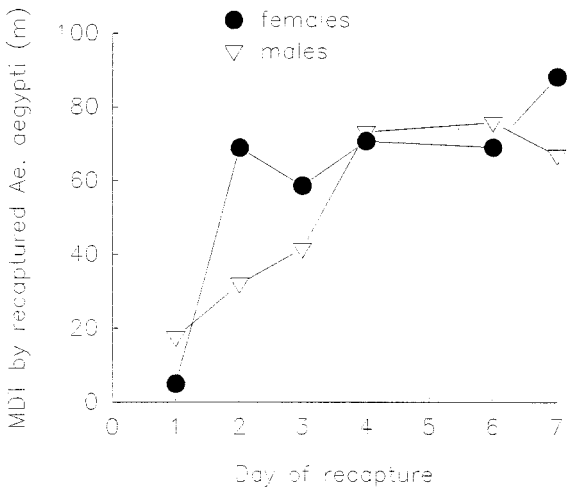

FIGURE 3. Mean distance traveled (MDT) by recaptured blue-marked *Aedes aegypti* for each day of the mark-release-recapture study at Pentland, northern Queensland, Australia.

ing aging females due to their increased likelihood of beginning appetitive flights,[28] or because the mortality rate for females was not as high as for males proportionally more females were available for capture as time progressed.

In the laboratory, marked mosquitoes had higher survival rates than unmarked mosquitoes, so the estimated PDS for marked and recaptured *Ae. aegypti* in this study may be higher than the natural population. We cannot explain why marking improved survival, but this was the case for both females and males in all replicates. Perhaps the fluorescent powder was toxic to pathogens that would otherwise have infected the adults. The mortality rate of colonized *Ae. aegypti* held in the laboratory increased with age, as has been reported previously by Clements and Paterson,[7] who reanalyzed the data of Putnam and Shannon.[11] We cannot determine whether the same model of mortality was appropriate for our field recaptured *Ae. aegypti.* Our regression analysis of $\log_{10}$ recaptures over time for blue-marked males suggested that mortality in the field was constant from one to seven days post-release, but the sample size and time period were limited.

The PDS of blue-marked females of 0.91 is slightly higher than previously reported but is close to 0.89 estimated by McDonald.[9] The PDS of 0.57 for blue-marked males is the same as that calculated by Nayar[8] using the same method. Trpis and Hauserman[17] estimated the daily survival of males was 0.53 using the Jolly-Seber stochastic method while Sheppard and others[10] used a modification of the Fisher and Ford deterministic model to estimate male survival rates of 0.554–0.873 over a one-year period. McDonald[9] calculated a male survival rate of 0.77 by comparing observed survivorship curves with estimated ones.

The MDT by the recaptured *Ae. aegypti* of 56 m for females and 35 m for males were similar to other reports in which 95% of marked individuals remained within 40 m[20] of the release site and where 84% of released *Ae. aegypti* were recaptured within 66 m.[8] Daily dispersal is a better indication of the dispersal characteristics of the cohort than the overall MDT for the entire study period, especially when combined with the life expectancy of the population. Daily dispersal of recaptured *Ae. aegypti* at Pentland was somewhat less than the dispersal rates estimated in other studies; [10, 16, 17] however, dispersal would depend on the physical characteristics of the study site (for example, urban or village), climate, and the physiologic state of the mosquitoes on a given day. Low relative humidity at Pentland may have restricted the dispersal of *Ae. aegypti*.

Females remained close to the release site for the first 24 hr and then dispersed the furthest during the next 24 hr. Females were less than two days old when released, so their dispersal may have been influenced by physiologic readiness to seek hosts. Ovaries of female *Ae. aegypti* undergo a maturation period of approximately 2.5 days[29] following emergence and during which the female does not blood feed. Dispersal and appetitive flights during this time would increase the female's chance of being damaged or killed without increased reproductive success;[28] therefore, it would be selectively advantageous for females to remain near release sites (and breeding sites) until ready to blood feed. Dispersal of females was relatively low from days 2 to 6 of the study with a second increase in dispersal around day 7. This second increase may have been associated with the search for oviposition sites. In contrast to females, males dispersed at a relatively constant daily rate for the first four days after which dispersal was low.

Since the daily dispersal of female *Ae. aegypti* increased during the last day of our study, the maximum observed distance dispersed (160 m) may have been greater if recaptures continued for more than seven days. Because the estimated ALE of females was up to 10 days, using a daily dispersal rate of 19 m (the MDT by blue-marked females between day 6 and 7) and assuming that there were no barriers to dispersal, released females could have dispersed an additional 57 m during their lifetime, giving a maximum distance of 217 m. The flight range within which 90% of the marked population dispersed (FR_{90}), 108 m and 82 m for females and males, respectively, gives an effective flight distance for the population as a whole and is a useful operational limit of dispersal.

Our study has demonstrated limited dispersal by *Ae. aegypti* in northern Australia during warm and dry climatic conditions. In premises where *Ae. aegypti* were captured most frequently, a shady habitat and easily accessible hosts were characteristic features. The difference in recapture rates between the blue- and pink-marked cohorts suggests that wind direction also influences *Ae. aegypti* dispersal. The blue-marked cohort was released indoors whereas the pink-marked cohort was released in a peridomestic situation so its dispersion would more likely have been influenced by prevailing wind. The dispersion and distribution of *Ae. aegypti* within houses and the urban environment will be the subject of a future report.

When a suspected case of dengue virus is reported to the public health authorities in northern Queensland, vector control officers respond by performing intensive control of larvae and adults within a 200–300-m radius of the point of suspected transmission. Given the dispersal distances estimated in our study, this focal area would seem appropriate for control activities especially if control was initiated within four days (one gonotrophic cycle of *Ae. aegypti*) of the suspected case becoming viremic or entering the area. With a PDS of 0.85–0.91 for released females, assuming the constant mortality model, 14–32% of the female cohort would have survived an extrinsic incubation period of 10 days for dengue virus[12] under the temperature conditions of this study, assuming the females fed on a viremic host when two days old. Therefore, sufficient infected females would survive to transmit the virus to nonimmune hosts. Given the multiple feeding habit of *Ae. aegypti*, a few such females could maintain transmission.

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