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DISPERSAL OF THE DENGUE VECTOR *AEDES AEGYPTI* WITHIN AND BETWEEN RURAL COMMUNITIES

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Abstract. Knowledge of mosquito dispersal is critical for vector–borne disease control and prevention strategies and for understanding population structure and pathogen dissemination. We determined *Aedes aegypti* flight range and dispersal patterns from 21 mark-release-recapture experiments conducted over 11 years (1991–2002) in Puerto Rico and Thailand. Dispersal was compared by release location, sex, age, season, and village. For all experiments, the majority of mosquitoes were collected from their release house or adjacent house. Inter-village movement was detected rarely, with a few mosquitoes moving a maximum of 512 meters from one Thai village to the next. Average dispersal distances were similar for males and females and females released indoors versus outdoors. The movement of *Ae. aegypti* was not influenced by season or age, but differed by village. Results demonstrate that adult *Ae. aegypti* disperse relatively short distances, suggesting that people rather than mosquitoes are the primary mode of dengue virus dissemination within and among communities.

INTRODUCTION

Knowledge about flight range and dispersal of mosquito vectors is essential for understanding vector-borne disease transmission dynamics among human populations because flight range and dispersal influence mosquito population dynamics, patterns of genetic structure,[1,2] and pathogen transfer through vector populations. In an applied sense, dispersal is an important factor for determining appropriate control limits necessary to interrupt pathogen transmission and is a fundamental consideration for estimating gene flow in genetic control strategies.[3] With renewed interest in autocidal and genetic control strategies, there is an increased awareness of how little is known about movement of adult mosquito vectors in nature and the importance of gathering that kind of information.[4]

Aedes aegypti is the primary vector of dengue, the most important arboviral human infection worldwide, and urban yellow fever. Approximately 50–100 million cases occur annually and more than 2.5 billion people are at risk of infection.[5] Adult dispersal and flight range for this species have been estimated from results of a few mark-release-recapture studies.[6–18] Those publications cite maximum flight distances for *Ae. aegypti* that range from 154 to 1,207 meters.[7,14] Movement of genetically marked mosquitoes was assessed by some investigators.[19,20] It is not clear, however, if their estimates based on genetic mutants reflect dispersal of wild-type mosquitoes. Reiter and others used the detection of eggs laid by rubidium-labeled females in ovitraps to estimate a maximum flight range of 3,600 meters for *Ae. aegypti* in San Juan, Puerto Rico.[21] Honorio and others similarly reported detection of rubidium-marked eggs up to 800 meters from the release point in Rio de Janeiro, Brazil.[22]

Published studies provide widely variable results and no clear consensus about the patterns of *Ae. aegypti* movement and dispersal. In an effort to contribute more definitive, replicated data, herein we present results for the first part of our analysis of *Ae. aegypti* flight range and dispersal from a series of 21 experiments conducted over a 10-year period in three different field sites where dengue is endemic. Our second article on this topic, which will be published separately, will be an analysis of the probabilities of dispersal from one location (house) to another, which will be compared with conventional methods used in this report for estimating the distance that adult mosquitoes move by flight.

MATERIALS AND METHODS

A summary of the various methods for all experiments is presented in Table 1. Our methods varied among different locations and times because mark-release-recapture experiments were carried out for different reasons. In the conducting those experiments, we gathered the data on *Ae. aegypti* dispersal that we present and analyze herein. Although differences in methodology prohibit a simple explanation of our study design, it adds strength to our overall conclusions because our results are consistent across many different experiments conducted in a variety of regions of the world, using various release and recapture scenarios. We did not attempt to directly compare experiments using different methods. Only when the same methodology was used did we test for statistical differences among or between release-recapture experiments.

This research was conducted in accordance with the following Institutional Review Board approvals: University of Maryland (A-3433), University of California at Davis (200210073), Walter Reed Army Institute of Research (752), Thai Ministry of Health Ethical Review Committee for Research in Human Subjects, University of Massachusetts (M1003), and Cornell University (FWA00004513).

Puerto Rico (January and July 1996). *Field site.* Our release area in Puerto Rico was described in detail by Harrington and others.[18] Briefly, releases were conducted in the village of Yanes III, Florida, a community in north central Puerto Rico (18°21′44″N, 66°33′40″W) consisting of 165 houses surrounded on three sides by limestone hills that appeared to us to be barriers to dispersal (Figure 1).

Mosquitoes. *Aedes aegypti* eggs were collected from ovi-

TABLE 1
Summary of the methods used for mark-release recapture studies*

Location	Date	Release site	Sex	No. of release houses	No. of release days	No. of recapture houses	No. of recapture days	Recapture regimen (days post-release)
HSR, Thailand	March–June 1991	Outdoor	F	1	1	20	12	1–12
HSR, Thailand	March–June 1991	Outdoor	M	1	1	20	12	1–12
HSR, Thailand	January 1992	Indoor	F	12	1	20	10	1–10
HSR, Thailand	January 1995	Indoor	F	6	1	12	8	1–8
HSR, Thailand	July 1995	Indoor	F	8	1	13	9	2–10
Florida, Puerto Rico	January 1996	Indoor	F	6	1	20	10	1–10
Florida, Puerto Rico	July 1996	Indoor	F	6	1	20	10	1–10
Lao Bao, Thailand	February 2000	Indoor	F	10	10	55 (all)	10	†
Lao Bao, Thailand	July 2000	Indoor	F	10	10	55 (all)	10	†
Lao Bao, Thailand	January 2001	Indoor	F	10	10	55 (all)	10	‡
Lao Bao, Thailand	July 2001	Indoor	F	10	10	55 (all)	10	‡
Mae Kasa, Thailand	February 2000	Indoor	F	10	10	60	10	†
Mae Kasa, Thailand	July 2000	Indoor	F	10	10	60	10	†
Mae Kasa, Thailand	January 2001	Indoor	F	10	10	60	10	‡
Mae Kasa, Thailand	July 2001	Indoor	F	10	10	60	10	‡
Pai Lom, Thailand	January 2001	Indoor	F	15	1	38 (all)	4	1–4§
Pai Lom, Thailand	July 2001	Indoor	F	10	1	38 (all)	4	1–4§
Lao Bao, Thailand	January 2002	Indoor	F	12	2	55 (all)	4	1
Lao Bao, Thailand	July 2002	Indoor	F	12	2	55 (all)	4	1
Pai Lom, Thailand	January 2002	Indoor	F	12	2	38 (all)	4	1
Pai Lom, Thailand	July 2002	Indoor	F	12	2	38 (all)	4	1

* HSR = Hua Sam Rong.
† 1–4 days post-release.
‡ 10–14 days post-release.
§ 1, 4, 12, and 13 days post-release in first five houses and 2, 4, 7, and 8 days post-release in second group of five houses.

traps in Yanes III, hatched, and reared in the insectary of the Centers for Disease Control and Prevention in San Juan, as described previously.[17] After eclosion, adults were held in 45-cm^2 cages and allowed access to water but not food.

January–February 1996. Mosquitoes were divided into two cohorts. One was offered a blood meal from one of the investigators' arms one day prior to release when they were 3–4 days old. The other cohort was maintained on water only.

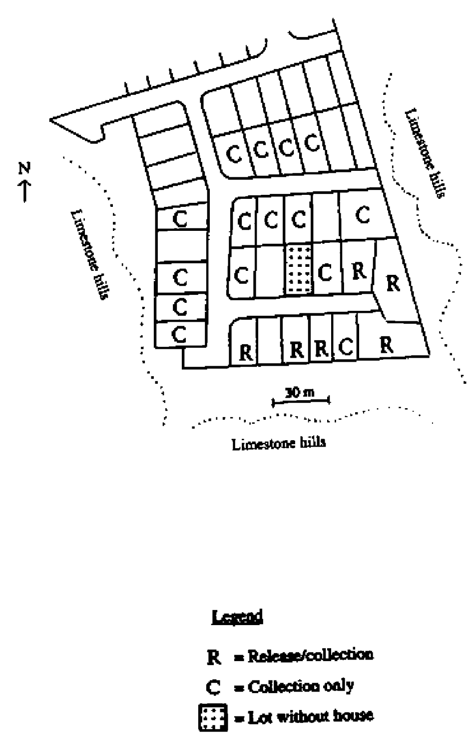

FIGURE 1. Yanes III, Florida, Puerto Rico.

July 1996. A 3- and 13-day-old blood fed cohort was maintained as described previously.[18]

Marking in January–February and July 1996. Female mosquitoes were marked with paint and fluorescent dust following the methods of Edman and others.[17] Paint color–designated release houses were marked with paint one day prior to release and marked with fluorescent dust to designate cohort.

Release. Twenty-five mosquitoes from each cohort (water and blood fed in January–February 1996 and 3- and 13-day-old in July 1996) were released at 5:30 PM inside six houses (total released for both cohorts = 300).

Recapture. Backpack aspirators (John C. Hock Co., Gainesville, FL) were used for approximately 15 minutes per house in an attempt to recapture mosquitoes for 10 days following release inside release houses as well as in 14 adjacent houses in the area.[18]

Thailand, Hua Sam Rong. Releases were conducted in Village Six (13°37′46″N, 101°16′36″E), Hua Sam Rong, Amphur Pleangyao, Chachoengsao Province, located in eastcentral Thailand during March–June 1991, January 1992, January 1995, and July 1995.

Outdoor releases, March–June 1991. The release area for the experiments is described in detail by Harrington and others[18] and was located in the west end of the village and surrounded on three sides by rice paddy (Figure 2). In these experiments, we considered the house next to the release site as the adjacent house.

Mosquitoes. F_1 progeny from wild females collected in the study area were reared at Mahidol University in Bangkok under small (4,000 larvae/jar), medium (2,000 larvae/jar), and large (1,000 larvae/jar) body size diet regimens.[23] In March, April, and June 1991, cohorts of large and small body size were marked and released. In May 1991, large, medium, and small body size cohorts were similarly reared, marked, and released. Adult female wing length averages were 2.26, 2.59 and 2.93 mm for small, medium, and large body size cohorts, respectively.

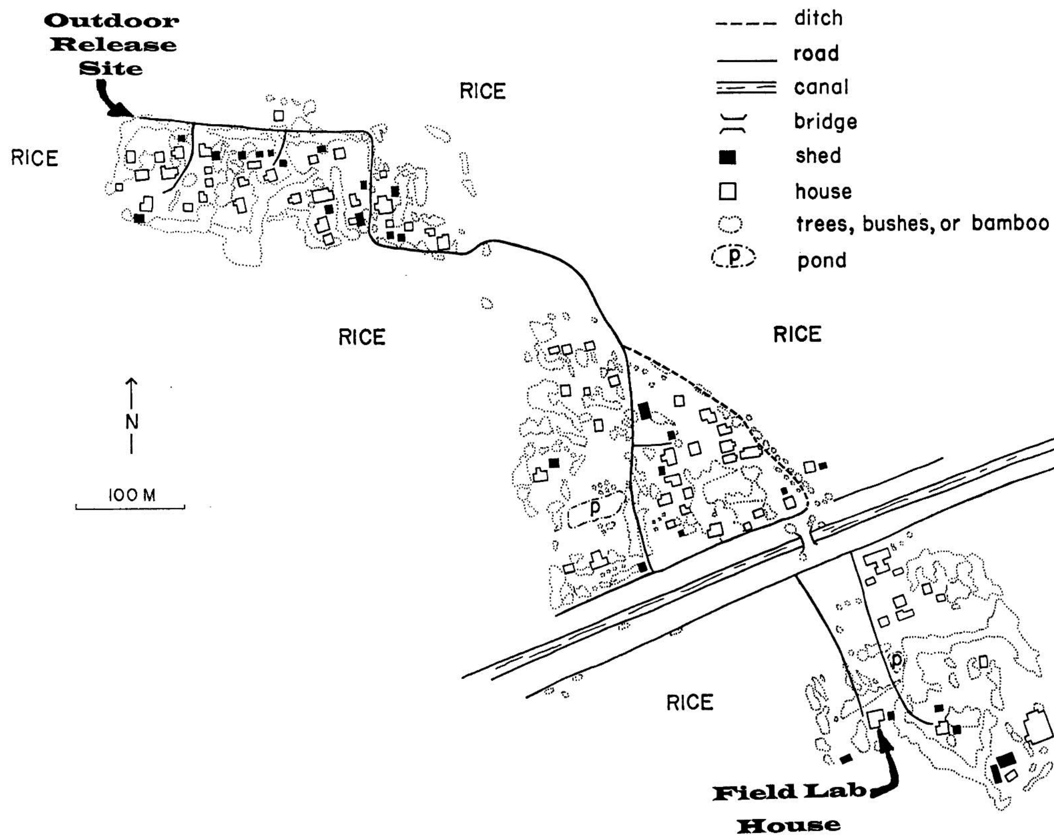

FIGURE 2. Village 6, Hua Sam Rong, Thailand.

Marking. Following the methods of Edman and others,[17] male and female mosquitoes were marked one day prior to or on the morning of release with fluorescent dust to designate each size cohort

Release. Mosquitoes were released between 5:00 PM and 6:00 PM in a bamboo thicket on the edge of the village (Figure 2). In March 1991, 2,000 females and 2,000 males were released. In April 1991, 1,440 females and 1,615 males were released. In May 1991, 2,000 females and 1,500 males were released. In June 1991, 2,235 females and 1,835 males were released. No significant differences ($P < 0.01$) were found in recapture rates among diet cohorts using non-linear regression analysis (PROC IML, PROC NLIN, SAS Institute, Cary, NC) followed by bootstrapping of capture confidence intervals.[24] Consequently, the data were combined for all four months for each sex to evaluate final recapture rates and dispersal distances.

Recapture. Aspirator collections (15–20 minutes/house) using modified vacuum cleaners were carried out for 12 days after release between 9:00 AM and 4:00 PM in 20 houses throughout the village at various distances from the release area. Collected mosquitoes were placed on wet ice and transported to the field laboratory where male and female *Ae. aegypti* were identified to species and examined for dust markings.

Indoor release, January 1992. *Mosquitoes.* Medium and large size larvae were reared outdoors at Mahidol University in Bangkok from Hua Sam Rong colony eggs (20–30 generations in colony).

Marking. Females were marked with a small dot of poster paint on their thorax to designate the house in which they were released.

Release. Fifty females were released inside each of 12 houses at the far west end of Village Six. Mosquitoes were offered a blood meal on one of the investigators' arms just prior to release.

Recapture. Mosquitoes were recaptured with aspirators as described earlier between 9:00 AM and 4:00 PM for 10 consecutive days after release in the 12 release and 8 additional houses located in the western end of the village.

Indoor release, January and July 1995. *Mosquitoes.* Eggs were hatched from a Mahidol University colony derived from adult females captured in Village Eight, Hua Sam Rong. Larvae were reared under a standard diet regimen to obtain medium body size. Emerged adult females were divided into four nutritional groups and offered 1) water only, 2) sugar and water, 3) blood and water, or 4) blood, sugar, and water for three days prior to release.

Marking. Females were marked with different colored dust and paints to designate diet cohort and release house.

Release. One hundred females (25 from each adult diet cohort) were released inside each of six houses (January 1995) and each of eight houses (July 1995) in Village Six as described earlier.

Recapture. In January 1995, mosquitoes were recaptured with aspirators as described earlier between 10:00 AM and 4:00 PM in each of the six release houses and six neighboring houses for eight consecutive days after release. The same recapture method was used in July 1995 with the exception that collections began the second day after release in each of the eight release houses and five neighboring houses for nine consecutive days.

Thailand, Mae Sot. The release villages of Pai Lom (16°45′N, 98°33′E, Figure 3) and Lao Bao (16°45′N, 98°34′E, Figure 4) are located in Mae Pa district 5 km north of Mae Sot city in the westcentral region of Thailand along the Thailand-Myanmar border. The village of Mae Kasa (16°53′N, 98°37′E, Figure 5) is located 20 km north of Mae Sot. All three villages are located in an area where dengue is endemic and transmission of all four dengue virus serotypes occurs. Releases were conducted during the middle of the dry season (January–March) and during the middle of the rainy season (July–August). In addition to climatic differences, these seasons also represented periods of low and high dengue transmission, respectively.[25] A study to determine the efficiency of aspirator collections versus sticky ovitraps[26] for capturing mosquitoes was conducted in Pai Lom during January 2001. An identical release, but only using aspirator collection was carried out in July 2001.

Additional data on dispersal were gathered in Mae Sot during experiments designed to validate a cuticular hydrocarbon age-grading method and to test the hypothesis that survival is age dependent (Harrington LC, Edman JD, Scott TW, unpublished data).[27] Releases were conducted in Pai Lom in January and July 2001 and 2002, in Lao Bao in February and July 2000 and January and July 2001–2002, and in Mae Kasa in February and July 2000 and January and July 2001.

Mosquitoes. *February 2000. Aedes aegypti* pupae were collected from natural development sites in the release villages of Lao Bao and Mae Kasa one month prior to the study, returned to the Armed Forces Research Institute for Medical Sciences Laboratory in Bangkok and held until adult emergence. Females were allowed to mate and were offered a blood meal from an anesthetized hamster (in compliance with National Institutes of Health guidelines for humane use of animals, Armed Forces Research Institute for Medical Sciences Protocol # 03-06). Eggs were collected, conditioned, and transported back to the field laboratory in Mae Pa, Mae Sot where they were hatched in rainwater and adults of uniform body size were reared by placing 2,000 larvae in large clay water jars (50 liters). Larvae were offered a diet of ground fish food (CP brand; Chaleorn Poolaphan Co., Bangkok, Thailand) to obtain mosquitoes of medium body size (mean wing length = 2.59 mm) as described earlier. After emergence, females were placed in four-liter plastic bucket cages with mesh lids. Males were added to cages to

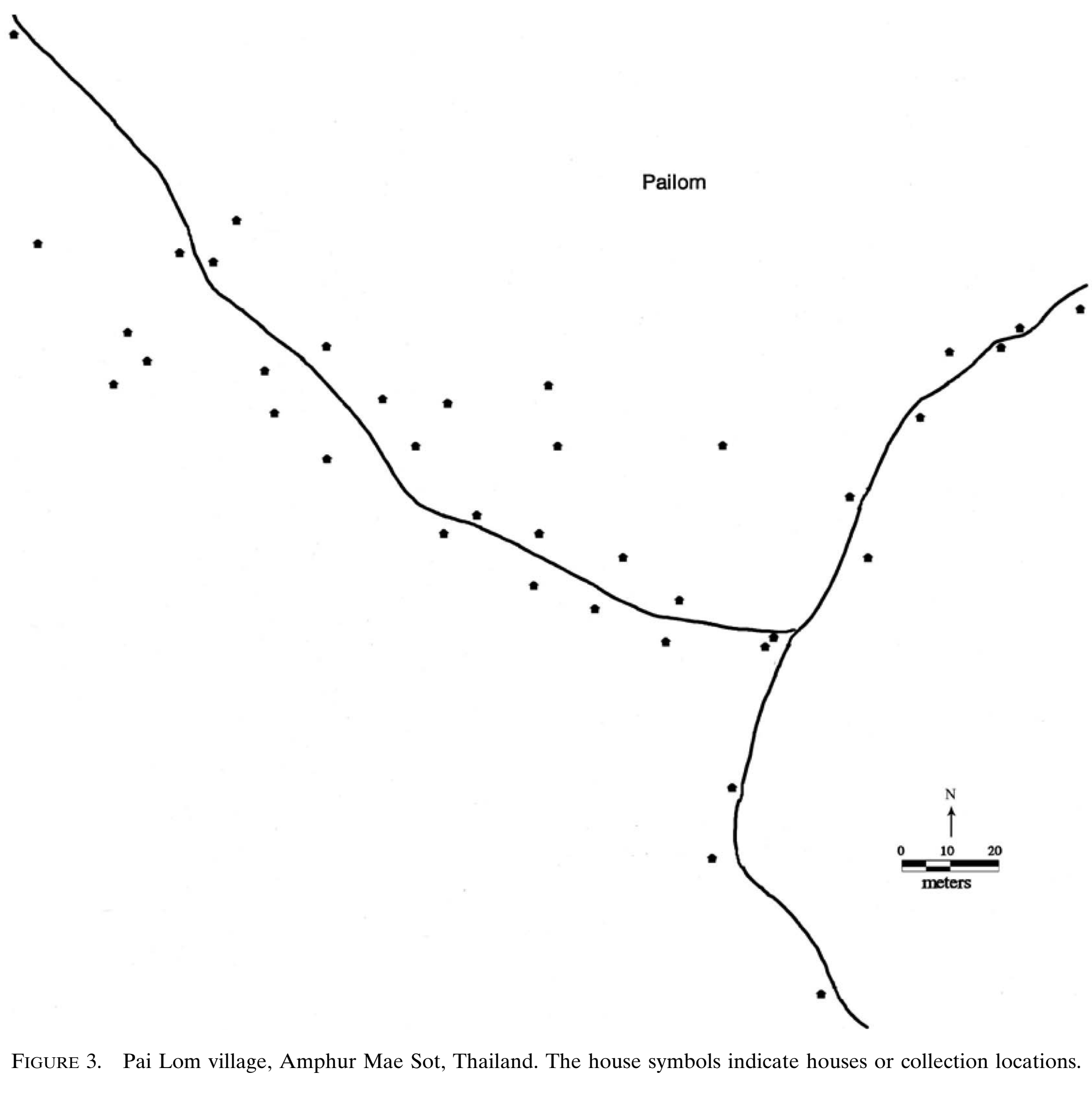

FIGURE 3. Pai Lom village, Amphur Mae Sot, Thailand. The house symbols indicate houses or collection locations.

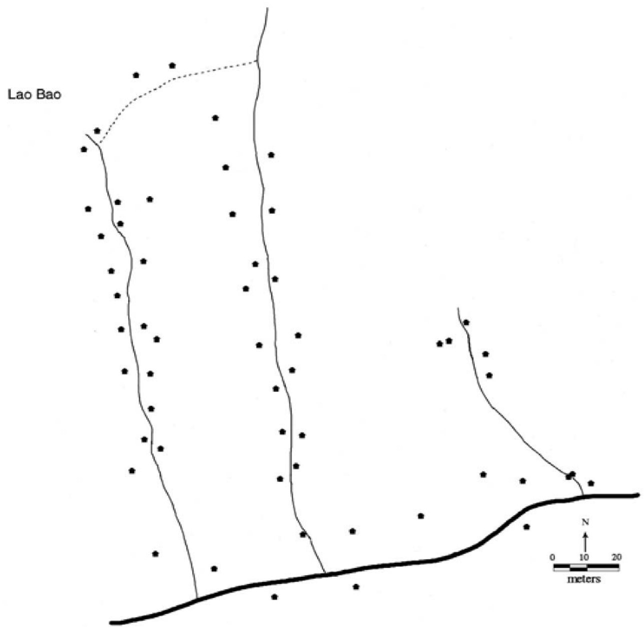

FIGURE 4. Lao Bao village, Amphur Mae Sot, Thailand. The house symbols indicate houses or collection locations.

ensure mating. Females were offered blood from a human arm for 20 minutes daily and water throughout the holding period.

July 2000–July 2002. Pupae were collected from the study villages and held in the field laboratory until emergence, and then placed in four-liter plastic bucket cages and maintained as described earlier.

Marking. Mosquitoes were sedated with wet ice and marked 1–2 days prior to release with paint on the thorax to designate release house and florescent powder on the morning of release to designate release day, following the methods of Edman and others.[17]

Releases in 2000–2001 in Lao Bao and Mae Kasa. *February 2000.* Mosquitoes were released in a maximum of 12 houses per village each day over an 11-day period from January 31 to February 1, 2000 and from February 3 to February 11, 2000 in the villages of Mae Kasa and Lao Bao. All releases during 2000–2001 were conducted between noon and 6:00 PM.

July 2000. Mosquitoes were released from July 16 to July 25, 2000 in the villages of Mae Kasa and Lao Bao as described for February 2000.

January 2001. Mosquitoes were released in two groups in 10 houses (total of 20 houses) from January 14 to January 18 for group 1, and from January 19 to January 23 for group 2.

July 2001. Mosquitoes were released in two groups in 10 different houses from July 13 to July 17.

Releases in 2002 in Lao Bao and Pai Lom. Ten cohorts, each composed of mosquitoes aged at two-day intervals, representing ages 1–2, 3–4, . . . 19–20 days old were simultaneously released in 12 houses in each village on January 31 and again on February 4 during the dry season in 2002. During the rainy season, 10 similar age cohorts were released into 10 houses in each village on August 2 and August 6. All releases were conducted between 10:00 AM and noon.

Recaptures. Since mosquito collections using battery-powered backpack aspirators in northwestern Thailand demonstrated that the majority of *Ae. aegypti* are collected resting inside houses, collections were focused indoors. For all release-recapture experiments in Mae Sot, aspirator collection cartons were placed in plastic bags in a cooler of wet ice in the field and transported to the field laboratory where the mosquitoes were anesthetized with carbon dioxide and placed in tubes on wet ice. Paint and dust colors on marked *Ae. aegypti* were identified with the aid of a dissecting microscope and recorded.

2000–2001 Mae Kasa and Lao Bao. Release houses and approximately 20 neighboring houses were aspirated for 15–20 minutes each between 8:00 AM and 6:00 PM. To obtain the greatest number possible of older mosquitoes, the timing of recaptures was modified as follows. During February 2000, collections were conducted daily on February 11–14 and February 20–24; during July 2000, collections were conducted daily on July 26–29 and on August 5–10; during January 2001 collections were conducted on January 19, 22, 30, and 31 and on February 1 and 2 for group 1 and on January 25, 27, 30, and 31 and on February 1 and 2 for group 2; during July–August 2001, collections were conducted on July 18, 21, 29, 30, and 31 and on August 1 for group 1 and on July 23, 26, 29, 30, and 31 and August 1 for group 2.

2002 Lao Bao and Pai Lom. Recaptures were attempted in all houses in each study village as well as in all houses between the two villages. In the dry season, recaptures were attempted on February 1, 2, 5, and 6, 2002. During the rainy season, recaptures were attempted on August 3, 4, 7, and 8, 2002.

Evaluation of dispersal detection methods. To compare different methods for detecting dispersal and to determine if the aspiration method we had used in previous studies was the best approach, sticky ovitraps versus backpack aspirator collections were compared. In Pai Lom (January–July 2001), mosquitoes were collected as pupae, allowed to emerge in the field laboratory, and held in plastic bucket cages as described earlier for the Mae Sot studies. Females were offered a blood meal from the arm of one of the investigators three days prior to release to ensure that gravid females were marked and released. Mosquitoes were marked with paint and dusts as described earlier for Mae Sot. In the second release, cohorts 1 and 2 were designated with a unique color placed on the thorax next to the dot on their thorax that designated their release house.

January 2001. Sticky ovitraps were prepared by lining the top two-thirds of black plastic four-liter buckets (19 × 19 × 15 cm; Sweda Plastic Co., Bangkok, Thailand) with adhesive (Tangle-Trap™ insect coating; The Tanglefoot Co., Grand Rapids, MI)–coated black paper. Prior to release, three ovitraps per house (total of 105 traps) were placed in every house (two indoors and one outdoors) in the village of Pai Lom. At the time of placement of sticky ovitraps in houses, approximately one liter of water was poured into the bottom of the bucket.

Release 1 was conducted between 5:45 PM and 7:00 PM on January 18, 2001 and release 2 was conducted between 4:00 PM and 5:00 PM on January 31, 2001. A total of 150 marked mosquitoes were released in 15 houses (approximately 0 per house) on one end of Pai Lom for release 1. The same methods were followed for release 2, except that fewer mosquitoes ($n = 60$) were released. The 15 houses selected for release 2 were located on the opposite side of the village from those used in release 1.

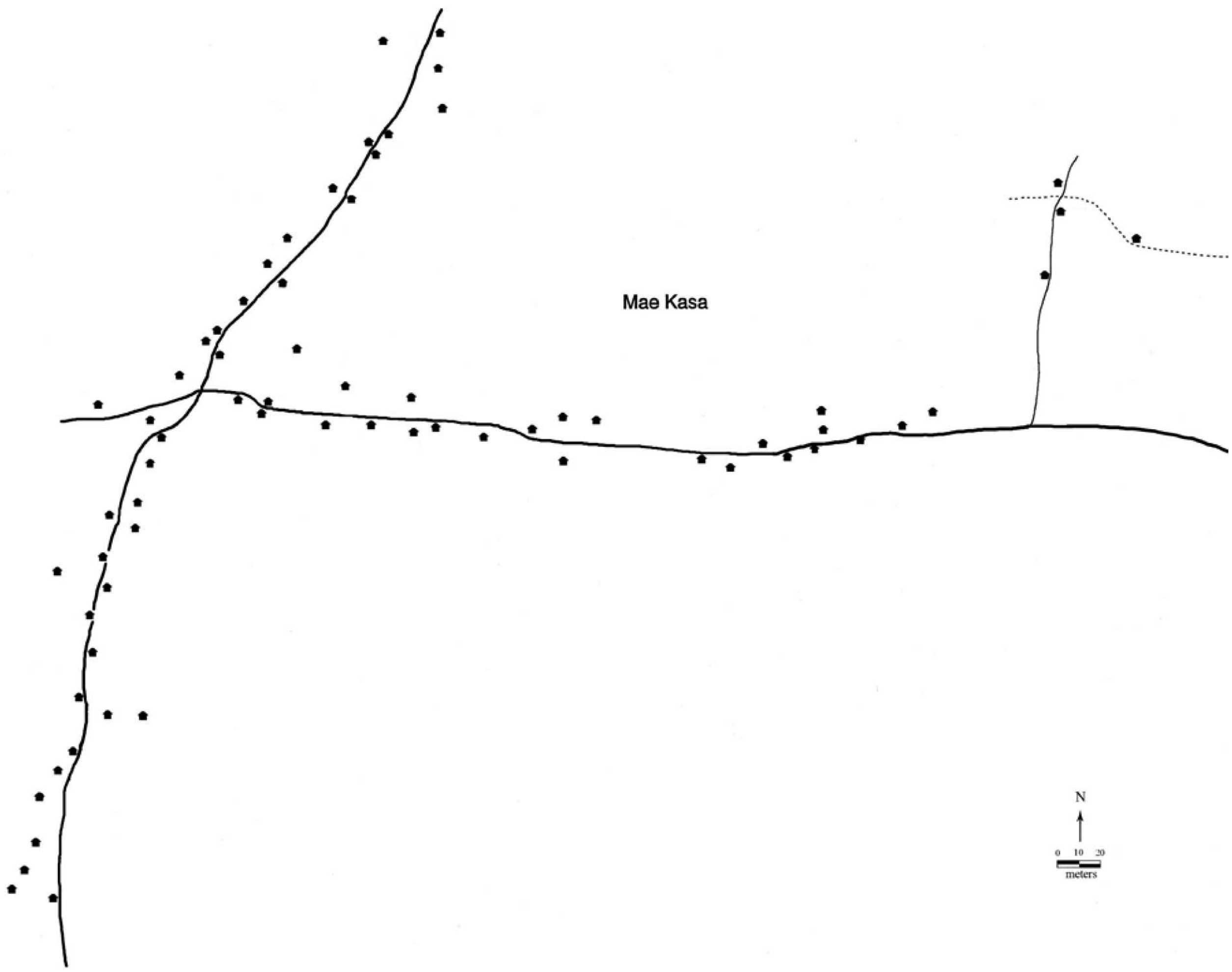

FIGURE 5. Mae Kasa village, Amphur Mae Sot, Thailand. The house symbols indicate houses or collection locations.

July 2001. One release was conducted from 5:00 PM to 6:00 PM on July 19, 2001 to examine the effect of releasing mosquitoes inside versus outside of the house. Mosquitoes were released inside 10 houses in the center of Pai Lom and outside (approximately 10 meters from the back of each release house). A total of 90 and 91 mosquitoes were released indoors and outdoors, respectively.

Recaptures. *January 2001.* Aspirator collections using battery-powered backpack aspirators were carried out to recapture mosquitoes for 15–30 minutes in each house in the village of Pai Lom (n = 35 houses) beginning four days after release. Collections were made from 8:00 AM to 5:00 PM over four consecutive days. Captured mosquitoes were returned to the field laboratory, anesthetized with carbon dioxide, and then placed on wet ice in plastic tubes for at least 30 minutes. Female *Ae. aegypti* were examined carefully under a dissecting microscope for paint and/or fluorescent dust markings. The number of captured marked and wild *Ae. aegypti* was recorded daily for each house.

During the four-day collection period, every sticky ovitrap was examined daily for marked and wild *Ae. aegypti*. Mosquitoes adhering to sticky ovitrap liners were returned to the field laboratory and examined under a dissecting microscope. The same methods were followed for release 2.

One day after the last collection day for release 1, each house in the village, from which consent was obtained, was sprayed with deltacide (deltamethrin/resmethrin; BASF Corp., Limburgerhof, Germany). A four-day interval was allowed between spraying and release 2. Following release 2 and the collection period, all houses in Pai Lom were sprayed again with insecticide.

July 2001. Aspirator collections were conducted in every house in Pai Lom for four consecutive days, beginning four days after release as described for January 2001. After the last collection day, all houses in the village were sprayed with insecticide as described earlier.

Data analysis. Dispersal distances were measured and recorded for each recaptured mosquito as the distance from release to recapture house. Our dispersal estimates do not account for indirect flight patterns, but represent meaningful net movement from house to house. Distances between houses in Puerto Rico and Hua Sam Rong, Thailand were measured manually or within a geographic information system where sites have been geographically referenced. The Thai villages of Lao Bao, Pai Lom, and Mae Kasa were mapped using the geographic information system in MapInfo Professional 7.0 (MapInfo Corp., Troy, NY). Dispersal distances for each mosquito were measured, categorized by the number of houses away from the release site, and recorded. Dispersal distances for different body sized mosquitoes in

TABLE 2

Recapture rates for male and female *Aedes aegypti* released outdoors in Thailand from March to June 1991 (data combined) and indoors in January 1992 and January and July 1995*

	Date	Overall recapture rate	Adjacent or release house†	Recapture rates [total number recaptured by location] (distance from site) 1 house removed	2 houses removed	3 houses removed	4 houses removed	5 houses removed	6 houses removed
♀♀	March–June 1991‡	17%	65% [841]	24% [308] (33–61 m)	7% [90] (60–94 m)	3% [33] (102–144 m)	< 1% [7] (167–228 m)	< 1% [9] (400–456 m)	< 1% [1] (556–594 m)
♂♂	March–June 1991‡	17%	72% [836]	15% [173] (33–61 m)	5% [60] (60–94 m)	6% [75] (102–144 m)	2% [22] (167–228 m)	< 1% [2] (400–456 m)	0% [0] (556–594 m)
♀♀	January 1992§	38%	77% [173]	15% [33] (15 m)¶	6% [14] (32 m)¶	6% [6] (52 m)¶	0% [0] (67 m)¶	0 [0] (> 67 m)¶	–
♀♀	January 1995§	17%	83% [86]	11% [11] (15 m)¶	5% [5] (40 m)¶	2% [2] (48 m)¶	0% [0] (65 m)¶	0% [0] (> 65 m)¶	–
♀♀	July 1995§	16%	53% [67]	24% [30] (15 m)¶	20% [25] (36 m)¶	3% [4] (56 m)¶	0% [0] (68 m)¶	0% [0] (> 68 m)¶	–

* m = meters.
† For outdoor releases this was the house next to the release site.
‡ Released outdoors.
§ Released indoors.
¶ Average distance from release site.

outdoor releases from March to June 1991 and diet cohorts from January to July 1995 were not significantly different ($P < 0.01$) from each other using non-linear regression analysis (PROC IML, PROC NLIN, SAS Institute) followed by bootstrapping of capture confidence intervals.[24] Consequently, those data were combined to augment sample sizes before analysis. Data were analyzed in SAS using PROC GLM with dispersal distance as the independent variable to determine season, village, and age-related differences in dispersal.

In addition to evaluation of dispersal distances, the proportions of mosquitoes captured with sticky traps versus aspirator collections in Pai Lom from January 2001 were compared. Data for release 1 and 2 in Pai Lom, January 2001, were not significantly different ($P > 0.05$) and were combined.

RESULTS

Thailand, Hua Sam Rong. *Outdoor releases of males and females, March–June 1991.* Recapture rates for males and females across all outdoor releases were the same (17%). The majority of males (72%) and females (65%) were captured in the house adjacent to their outdoor release location. Maximum dispersal distance detected was six houses away from the release site (556–594 meters) for females and five houses away for males (400–456 meters) (Table 2).

Indoor releases of females, January 1992. The overall recapture rate for female *Ae. aegypti* released indoors (38%) was greater than for the outdoor releases (1991; 17%; Table 2). The majority of recaptured mosquitoes (77%) were collected in the house from which they were released. The maximum dispersal distance detected was three houses away or 52 meters from the release site (Table 2).

January and July 1995. Recapture rates for indoor released mosquitoes were lower overall in January and July 1995 (16–17%) than in 1992. The majority of females were collected in their release houses and the average maximum dispersal distance detected was similar to the indoor release in January 1992 (48–56 meters) (Table 2).

Puerto Rico, Yanes III. *January 1996.* The overall recapture rate was 34%. Eighty-seven percent of recaptures were collected in the house where they were released and only 1% of recaptures were collected three or more houses from the release point (102 meters) (Table 3).

July 1996. The overall recapture rate was 23%. Eighty percent of recaptures were collected in the house where they were released and only 1% of recaptures were collected three or more houses from the release point (102 meters) (Table 3).

Thailand, Mae Sot Region. *February 2000 and July 2001 releases in Mae Kasa and Lao Bao.* Overall recapture rates were lower for our experiments in northwestern (Mae Sot region) than for those in eastcentral Thailand (Hua Sam Rong region), ranging from 4% to 9%. Differences were most likely due to changes in recapture protocols. Recapture attempts were attenuated and less intensive in the Mae Sot region. Recapture rates in Mae Kasa (4–8%) were consistently lower than in Lao Bao (6–9%) from July 2000 to July 2001 (Table 4). Dispersal rates were similar among seasons (dry season = January and rainy season = July) and within villages. Of the total mosquitoes recaptured, a large proportion in both villages (Mae Kasa = 44–77%, Lao Bao = 50–

TABLE 3

Recapture rates and total numbers for *Aedes aegypti* released indoors in Puerto Rico, January 1996*

Location	Date	Overall recapture rate	Recapture rates (total number recaptured by location) Release house (0 m)	1 house removed (12–30 m)	2 houses removed (43–62 m)	3 houses removed (64–111 m)	> 3 houses removed (102 m)
Puerto Rico	January 1996	34% (101)	87% (88)	5% (5)	4% (4)	3% (3)	1% (1)
Puerto Rico	July 1996	23% (69)	80% (55)	6% (4)	9% (6)	4% (3)	1% (1)

* m = meters.

TABLE 4
Recapture rates for *Aedes aegypti* released indoors in Thailand conducted from 2000 to 2001 in the villages of Lao Bao and Mae Kasa

			% Recaptured of total recaptures by location (total number recaptured by location)				
Location	Date	Overall recapture rate (no.)	Release house (no.)	Adjacent house (no.)	2 houses removed (no.)	3 houses removed (no.)	> 3 houses removed (no.)
Lao Bao	February 2000	9% (62)	66% (41)	11% (7)	10% (6)	2% (1)	11% (7)
Lao Bao	July 2000	9% (83)	70% (58)	12% (10)	13% (11)	2% (2)	2% (2)
Lao Bao	January 2001	7% (68)	50% (34)	20% (13)	13% (9)	6% (4)	12% (8)
Lao Bao	July 2001	7% (69)	65% (44)	15% (11)	10% (7)	3% (2)	7% (5)
Mae Kasa	February 2000	8% (48)	77% (37)	17% (8)	0% (0)	0% (0)	6% (3)
Mae Kasa	July 2000	4% (39)	44% (17)	5% (2)	15% (6)	3% (1)	33% (13)
Mae Kasa	January 2001	4% (35)	57% (20)	29% (10)	6% (2)	6% (2)	3% (1)
Mae Kasa	July 2001	5% (52)	75% (39)	12% (6)	2% (1)	0% (0)	12% (6)

70%) was captured in their release houses. However, a large proportion of recaptures in July 2000 in Mae Kasa (33%) were made greater than three houses from their release sites (Table 4). The mean ± SE dispersal distance in Mae Kasa (75 ± 33 meters for February and 199 ± 29 meters for July 2000) was greater than for mosquitoes recaptured in Lao Bao (71 ± 16 meters for February and 40 ± 5 meters for July 2000) (Table 5). Of those mosquitoes released, the majority was recaptured within 100 meters of their release site (Figure 6). Age of mosquitoes recaptured (Figure 6), season, and year were not significant effects on dispersal. Village was the only significant factor affecting dispersal distance (F = 5.75, degrees of freedom [df] = 21, $P < 0.001$; age F = 1.32, df = 18, $P = 0.171$; season F = 0.90, df = 1, $P = 0.344$; village F = 96.62, df = 1, $P < 0.001$; year F = 1.29, df = 1, $P = 0.257$, by SAS PROC GLM). No interactions were statistically significant. The maximum dispersal distance detected was 566 meters in Mae Kasa (July 2001) and 512 meters in Lao Bao (January 2001).

January–July 2002 releases in Lao Bao and Pai Lom. During 2002 in the Mae Sot region, overall recapture rates were greater during the rainy season (July) than in the dry season (January) in each village (Table 6). Mosquitoes moved farther in the rainy season (mean ± SE = 117 ± 27 meters) than in the dry season (45 ± 6 meters) and in Pai Lom (156 ± 36 meters) than in Lao Bao (68 ± 30 meters) (Table 5). Of those mosquitoes that did move from release houses, the majority was recaptured within 50 meters of their release site (Figure 7). One mosquito released in Pai Lom in July 2002 was collected in a house in Lao Bao 346 meters from its release house. Village (Pai Lom > Lao Bao) was the only significant variable impacting dispersal distances (F = 1.51, df = 22, $P = 0.07$; age F = 1.34, df = 20, $P = 0.16$; season F = 0.84, df = 1, $P = 0.36$; village F = 5.86, df = 1, $P = 0.016$, by SAS PROC GM). No interactions were significant. Age-dependent dispersal effects were not detected (Figure 7), consistent with results from our 2000–2001 release-recapture experiments.

Comparison of dispersal detection methods (Pai Lom). *January 2001.*

Recaptures: release 1 and 2 combined. Twenty-two percent of the marked mosquitoes were recaptured (Table 7). Nearly all of recaptured mosquitoes (n = 44, 21%) were collected with the backpack aspirator method rather than with sticky ovitraps (1%). Only two marked *Ae. aegypti* females and one wild male were found in indoor sticky ovitraps. None were

TABLE 5
Dispersal of *Aedes aegypti* released indoors in Thailand and Puerto Rico from 1992 to 2002*

Location	Total released	Date	No. of mosquitoes moving	Distance traveled (m) Minimum	Maximum	Mean ± SE
Puerto Rico	300	January 1996	13	12	102	†
Puerto Rico	300	July 1996	14	12	102	†
Thailand-Lao Bao	703	February 2000	21	10	344	71 ± 16
Thailand-Mae Kasa	610	February 2000	11	14	304	75 ± 33
Thailand-Lao Bao	937	July 2000	25	3	102	40 ± 5
Thailand-Mae Kasa	988	July 2000	22	11	384	199 ± 29
Thailand-Pai Lom	210	January 2001	24	10	512	124 ± 35
Thailand-Lao Bao	983	January 2001	31	7	512	93 ± 25
Thailand-Mae Kasa	904	January 2001	35	12	365	151 ± 24
Thailand-Pai Lom	181	July 2001	8	11	84 out	40 ± 22 out
			(2 out/6 in)	11	52 in	36 ± 7 in
Thailand-Lao Bao	995	July 2001	25	8	158	45 ± 7
Thailand-Mae Kasa	1,005	July 2001	13	15	566	160 ± 53
Thailand-Lao Bao	1,047	January 2002	33	7	97	31 ± 3
Thailand-Pai Lom	1,067	January 2002	28	6	175	62 ± 12
Thailand-Lao Bao	531	July 2002	8	17	320	68 ± 30
Thailand-Pai Lom	594	July 2002	9	6	346	156 ± 36

* m = meters.
† Distances were recorded in ranges from the release point instead of actual values.

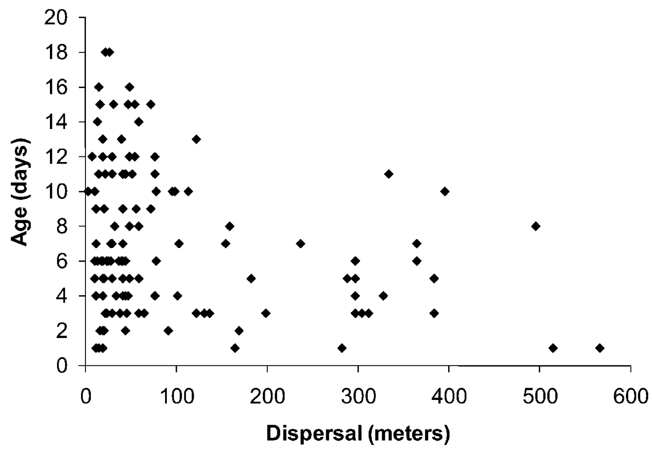

FIGURE 6. Dispersal of *Aedes aegypti* by age since emergence over all seasons and villages in Thailand, February 2000–July 2001.

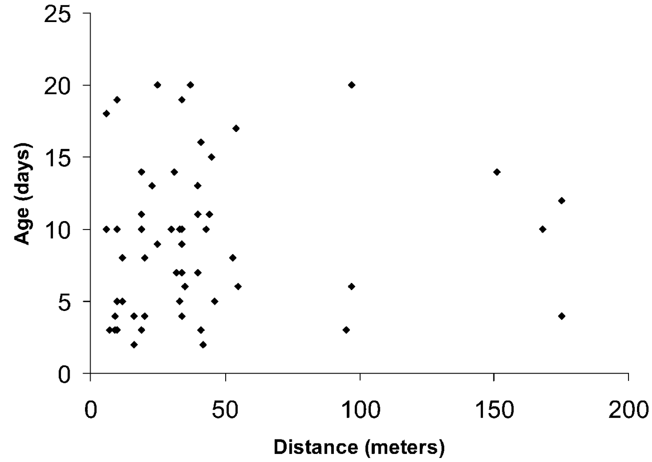

FIGURE 7. Dispersal of *Aedes aegypti* by age since emergence over all seasons and villages in Thailand, January–July 2002.

captured in outdoor sticky traps. The majority (77%) of mosquitoes were collected in their release house or the house adjacent to it (Table 7).

Dispersal: release 1 and 2. The greatest distance that we could detect dispersal within Pai Lom was 290 meters. The mean ± SE dispersal distance of those mosquitoes that moved was 124 ± 35 meters. Three females released in Pai Lom were collected in the neighboring village of Lao Bao (maximum distance = 512 meters, Table 5).

July 2001. ***Recaptures.*** More *Ae. aegypti* from indoor releases were captured (n = 8, 8.8%) than from outdoor releases (n = 5, 5.5%).

Dispersal. The mean ± SE dispersal distances for mosquitoes released outdoors versus indoors were similar (40 ± 22 meters indoors and 36 ± 7 meters outdoors, Table 5). No marked mosquitoes released in Pai Lom were collected in Lao Bao during July 2001.

DISCUSSION

Results from our studies repeatedly indicate limited movement of the dengue vector *Ae. aegypti* regardless of sex (males versus females), release village, release location (indoors versus outdoors), season (high or low dengue transmission season), date, geographic region, or experimental protocol. The majority of released mosquitoes were recaptured in the same house or an adjacent house to where they were released. This pattern in recapture results was consistent among our three different field sites, two in Thailand and one in Puerto Rico. We did not directly assess the effects of marking on mosquito survival and behavior, but other investigators reported no adverse effects from marking with paints[28,29] or Dayglo dusts.[30]

Our comparison of aspirator collections versus sticky ovitraps for assessing dispersal clearly indicated that our aspirator collections were far more efficient. Other investigators have reported higher rates of capture with sticky ovitraps and sticky panels ranging from 3.6% to 13%,[16,26] and sticky ovitraps were an efficient means of capturing wild *Ae. aegypti* in Australia.[31] None of these studies, however, compared ovitraps with the aspirator collection method. Perhaps natural ovipostion sites were less abundant at the study sites of other investigators than in Pai Lom. We designed our study to be conducted with gravid females during the dry season when oviposition trap efficiency should have been optimal.

We assessed mosquito movement in Lao Bao and Mae Kasa from 2000 to 2001 over a protracted recapture period (24 days), which should have allowed marked mosquitoes maximum opportunity to move. The only factor that impacted dispersal distances in that series of experiments was the village in which mosquitoes were released. That effect may have been due to differences in the layout of houses and distances between houses in the respective villages. Lao Bao (where mean dispersal was 28–93 meters) is a smaller village than Mae Kasa, in which houses are spatially clustered with footpaths between houses. In Mae Kasa, where we detected a maximum dispersal distance of 566 meters and the mean ranged from 75 to 199 meters, houses were located farther apart along one main paved road with fewer foot paths between them. Other studies have similarly cited the effect of

TABLE 6
Recapture rates for *Aedes aegypti* released indoors in Thailand from January to July 2002 in the villages of Lao Bao and Pai Lom

			% Recaptured of total recaptures by location (total number recaptured by location)				
Location	Date	Overall recapture rate (no.)	Release house (no.)	Adjacent house (no.)	1 house removed (no.)	2 houses removed (no.)	> 2 houses removed (no.)
Lao Bao	January 2002	7% (80)	59% (47)	25% (20)	16% (13)	0% (0)	0% (0)
Lao Bao	July 2002	12% (55)	82% (45)	4% (2)	5% (3)	5% (3)	4% (2)
Pai Lom	January 2002	9% (92)	70% (64)	15% (14)	7% (6)	5% (5)	3% (3)
Pai Lom	July 2002	15% (40)	75% (30)	3% (1)	0% (0)	5% (2)	17% (7)

TABLE 7
Recapture rates for *Aedes aegypti* released indoors in Pai Lom, Thailand to assess dispersal, January–July 2001

			% Recaptured of total recaptures by location (total number recaptured by location)				
Location	Date	Overall recapture rate (no.)	Release house (no.)	Adjacent house (no.)	1 house removed (no.)	2 houses removed (no.)	> 2 houses removed (no.)
Pai Lom	January 2001	22% (46)	47% (22)	30% (14)	9% (4)	7% (3)	7% (3)
Pai Lom	July 2001	7% (13)	38% (5)	31% (4)	23% (3)	0% (0)	8% (1)

house distribution and pattern on *Ae. aegypti* dispersal. In a study conducted in China, Tsuda and others reported less dispersal of released *Ae. aegypti* in areas where the houses were clustered closer together than when they were farther apart.[32]

Releases in Lao Bao and Pai Lom (2001–2002) provided an ideal situation for assessing inter-village movement between rural communities. Pai Lom is more similar to Lao Bao than Mae Kasa in layout and the two villages are approximately 300 meters apart. During the course of our experiments in the Mae Sot area, we detected inter-village movement only four times in 834 mosquitoes recaptured (0.5%) and 7,511 marked mosquitoes released, indicating that this range of movement is unusual for flying adult female *Ae. aegypti*. During 2002, recaptures in Lao Bao and Pai Lom were conducted over a short period of time (two days after release) and provide an indication of movement in the initial days after release or emergence. Overall, mosquitoes recaptured during this shorter interval were recovered within 50 meters of the release house, whereas those recaptured over the more protracted period (2000–2001) were collected within 100 meters of their release site. During our 2000 experiments in Lao Bao and Mae Kasa, mosquitoes dispersed greater distances during the rainy compared with the dry season. This indicated that greater dispersal occurs initially during the rainy season, but may even out over several days, as was detected during the 2000–2001 experiments. Despite the differences in the recapture interval, no age-dependent dispersal was detected in either series of experiments. Some investigators have reported greater dispersal among teneral or very young female *Ae. aegypti*.[11] In our experiments from 2002, 1–2-day-old mosquitoes released in January and July dispersed an average of 56 meters, a distance that was not significantly different among a variety of age groups that we released and recaptured.

In a series of 21 mark-release-recapture studies conducted over a 10-year period, we did not detect dispersal of *Ae. aegypti* far from its release site. Our data were derived from replicated releases in several villages, seasons, and geographic locations using different collection procedures. Although maximum flight range has been emphasized by researchers in the past, we chose to focus on the mean dispersal distance, which we consider a more epidemiologically meaningful population parameter than the maximum distance moved by relatively few mosquitoes. The mean dispersal distances detected in our study ranged from 28 to 199 meters depending on the site, village, and country. Although, most mosquitoes did not move from their release houses, the majority of those that did move were recaptured within 100 meters of their release site. Even though in several of our experiments we could have caught mosquitoes that moved thousands of meters, we did not detect the kind of long distance dispersal reported by investigators who assayed for rubidium in *Ae. aegypti* eggs.[21,22] Our data indicate that in rural habitats with abundant human hosts and oviposition sites, *Ae. aegypti* do not disperse far from their development site in and around homes and tend to be spatially clustered at the household level. Interestingly, the same conclusion was made using a different approach, spatial statistics, to analyze data on different measures of *Ae. aegypti* density in Iquitos, Peru.[33]

Our results lead to at least three predictions for different dengue prevention strategies. First, female *Ae. aegypti* may spend their lifetime in or around the houses where they emerged as adults, which is consistent with the feasibility of killing infected mosquitoes by applying localized, intensive vector control around areas of clinically apparent human dengue infection. Second, our data also support the idea that people rather than mosquitoes rapidly move dengue virus within and among communities.[34,35] By itself, therefore, localized insecticide application around a dengue patient's home or community is not likely to prevent the spread of dengue infections. By the time a clinical human infection is detected the resident infected mosquito may have bitten another person who transported the virus beyond the house or community where the mosquito resides. Third, our results highlight the challenges that genetic and autocidal control programs[36] will face. Inoculative releases[37] of modified mosquitoes over relatively short distances (< 100 meters) will be essential to ensure comprehensive introductions, mating with wild type conspecifics, and sweeps of transgenes through populations.

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REFERENCES

1. Kuno G, 1997. Factors influencing the transmission of dengue viruses. Gubler DJ, Kuno G, eds. *Dengue and Dengue Hemorrhagic Fever*. New York: CAB International, 61–88.
2. Service MW, 1997. Mosquito (Diptera: Culicidae) dispersal: the long and short of it. *J Med Entomol 34:* 579–588.
3. Service M, 1993. Mark-recapture techniques and adult dispersal. *Mosquito Ecology: Field Sampling Methods*. New York: Chapman and Hall, 652–751.
4. Scott TW, Takken W, Knols BJG, Boëte C, 2002. The ecology of genetically modified mosquitoes. *Science 298:* 117–119.
5. Gubler DJ, 1997. Dengue and dengue hemorrhagic fever: its history and resurgence as a global public health problem. Gubler DJ, Kuno G eds. *Dengue and Dengue Hemorrhagic Fever*. Wallingford, United Kingdom: CAB International, 1–22.
6. Gubler DJ, Kuno G, eds. *Dengue and Dengue Hemorrhagic Fever*. Wallingford, United Kingdom: CAB International.
7. Burgher JC, Taylor M, 1949. Radiophosphorus and radiostrontium in mosquitoes. Preliminary report. *Science 110:* 146–147.
8. Morland HB, Hayes RO, 1958. Urban dispersal and activity of *Aedes aegypti. Mosq News 18:* 137–144.
9. Trpis M, 1971. *Seasonal Variation in the Adult Populations of Aedes aegypti in the Dar es Salaam Area Tanzania*. Geneva: World Health Organization. WHO/VBC 71.
10. Hervy JP, 1977. Experience de marquage-lacher-recapture portant sur *Aedes aegypti* Linne, en zone de savane soudanienne ouest Africaine. II. Relastions entre habitat, morphologie et comportement. *Cah ORSTOM Entomol Med Parasitol 15:* 365–372.
11. Sheppard PM, Macdonald WW, Tonn RJ, Grab B, 1969. The dynamics of an adult population of *Aedes aegypti* in relation to dengue haemorrhagic fever in Bangkok. *J Anim Ecol 38:* 661–702.
12. Trpis M, Hausermann W, 1975. Demonstration of differential domesticity of *Aedes aegypti* (L.) (Diptera, Culicidae) in Africa by mark-release-recapture. *Bull Entomol Res 65:* 199–208.
13. Trpis M, Hausermann W, 1978. Genetics of house-entering behaviour in east African populations of *Aedes aegypti* (L.) (Diptera: Culicidae) and its relevance to speciation. *Bull Entomol Res 68:* 521–532.
14. Trpis M, Hausermann W, 1986. Dispersal and other population parameters of *Aedes aegypti* in an African village and their possible significance in epidemiology of vector-borne diseases. *Am J Trop Med Hyg 35:* 1263–1279.
15. Trpis M, Hausermann W, Craig GB, 1995. Estimates of population size, dispersal, and longevity of domestic *Aedes aegypti* (Diptera: Culicidae) by mark-release-recapture in the village of Shauri Moyo in eastern Kenya. *J Med Entomol 32:* 27–33.
16. Muir L, Kay BH, 1998. *Aedes aegypti* survival and dispersal estimated by mark-release-recapture in northern Australia. *Am J Trop Med Hyg 58:* 277–282.
17. Edman JD, Scott TW, Costero A, Morrison AC, Harrington LC, Clark GG, 1998. *Aedes aegypti* (Diptera: Culicidae) movement influenced by availability of oviposition sites. *J Med Entomol 35:* 578–583.
18. Harrington LC, Bounaccorsi JP, Edman JD, Costero A, Kittayapong P, Clark GG, Scott TW, 2001. Analysis of survival of young and old *Ae. aegypti* (Diptera: Culicidae) from Puerto Rico and Thailand. *J Med Entomol 38:* 537–547.
19. Bond HA, Craig GB, Fay RW, 1970. Field mating and movement of *Aedes aegypti. Mosq News 30:* 394–402.
20. Hausermann W, Fay RW, Hacker CS, 1971. Dispersal of genetically marked female *Aedes aegypti* in Mississippi. *Mosq News 31:* 37–51.
21. Reiter P, Amador MA, Anderson RA, Clark GG, 1995. Short report: Dispersal of *Aedes aegypti* in an urban area after blood feeding as demonstrated by rubidium-marked eggs. *Am J Trop Med Hyg 52:* 177–179.
22. Honorio NA, da Costa SW, Leite PJ, Goncalves JM, Lounibos LP, de Lourenco RO, 2003. Dispersal of *Ae. aegypti* and *Ae. albopictus* (Diptera: Culicidae) in an urban endemic dengue area in the State of Rio de Janeiro, Brazil. *Mem Inst Oswaldo Cruz 98:* 191–198.
23. Day JF, Edman JD, Scott TW, 1994. Reproductive fitness and survivorship of *Aedes aegypti* (Diptera: Culicidae) maintained on blood, with field observations from Thailand. *J Med Entomol 31:* 611–617.
24. Buonaccorsi J, Harrington LC, Edman JD, 2003. Estimation and comparison of mosquito survival rates with release-capture-removal data. *J Med Entomol 40:* 6–17.
25. Nimmannitya S, Halstead SB, Cohen SN, 1969. Dengue and Chikungunya virus infection in man in Thailand, 1962-1964. I. Observations on hospitalized patients with haemorrhagic fever. *Am J Trop Med Hyg 18:* 954–971.
26. Ordonez-Gonzalez JG, Mercado-Hernandez HR, Flores-Suarez AE, Fernandez-Salas I, 2001. The use of sticky ovitraps to estimate dispersal of *Aedes aegypti* in northeastern Mexico. *J Am Mosq Control Assoc 17:* 93–97.
27. Gerade BB, Lee SH, Scott TW, Edman JD, Harrington LC, Kitthawee S, Jones JW, Clark JM, 2004. Field validation of *Aedes aegypti* (Diptera: Culicidae) age estimation by analysis of cuticular hydrocarbons. *J Med Entomol 41:* 231–238.
28. Macdonald WW, Sebastian A, Maung Tun M, 1968. A mark-release-recapture experiment with *Culex pipiens fatigans* in the village of Okpo, Burma. *Ann Trop Med Parasitol 62:* 200–209.
29. Sheppard PM, MacDonald WW, Tonn RJ, Grab B, 1969. The dynamics of an adult population of *Aedes aegypti* in relation to dengue haemorrhagic fever in Bangkok. *J Anim Ecol 38:* 661–702.
30. Sinsko MJ, Craig GB, 1979. Dynamics of an isolated population of *Aedes triseriatus* (Diptera: Culicidae). *J Med Entomol 15:* 89–98.
31. Ritchie SA, Long S, Smith G, Pyke A, Knox TB, 2004. Entomological investigations in a focus of dengue transmission in Cairns, Queensland, Australia, by using the sticky ovitraps. *J Med Entomol 41:* 1–4.
32. Tsuda Y, Takagi M, Wang S, Wang Z, Tang L, 2001. Movement of *Aedes aegypti* (Diptera: Culicidae) released in a small isolated village on Hainan Island, China. *J Med Entomol 38:* 93–98.
33. Getis A, Morrison AC, Gray K, Scott TW, 2003. Characteristics of the spatial pattern of the dengue vector, *Aedes aegypti*, in Iquitos, Peru. *Am J Trop Med Hyg 69:* 494–505.
34. Morrison AC, Getis A, Santiago M, Rigau-Perez JG, Reiter P,

1998. Exploratory space-time analysis of reported dengue cases during an outbreak in Florida, Puerto Rico, 1991–1992. *Am J Trop Med Hyg 58:* 287–298.

35. De Benedictis JE, Chow-Schaffer E, Costero A, Clark GG, Edman JD, Scott TW, 2003. Identification of the people from whom engorged *Aedes aegypti* took blood meals in Florida, Puerto Rico using polymerase chain reaction–based DNA profiling. *Am J Trop Med Hyg 68:* 437–446.

36. Weidhaas DE, Focks DA, 2000. Management of arthropod-borne diseases by vector control. Eldridge BF, Edman JD, eds. *Medical Entomology: A Textbook on Public Health and Veterinary Problems Caused by Arthropods*. Boston: Kluwer Academic Publishers, 539–563.

37. van Driesche, RG, Bellows TS, 1996. Kind of biological control targets, agents and methods. *Biological Control*. New York: Chapman and Hall, 21–34.