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Article *in* Journal of Medical Entomology · September 2012

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J Med Entomol. 2012 September ; 49(5): 971–980.

Estimation of Population Size and Dispersal of *Aedes polynesiensis* on Toamaro *motu*, French Polynesia

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Abstract

Mark-release-recapture methods were used to compare *Aedes polynesiensis* Marks adult numbers and dispersal between dry and wet seasons in a closed population on a small island (*motu*) in French Polynesia. Females were more than three times more common during wet (December 2008) than dry (May 2007) season samplings although high numbers of vectors were collected during both seasons. Lincoln–Petersen estimates for *Ae. polynesiensis* females on the *motu* were 6,055 per hectare for the dry season and 18,860 per hectare for the wet season. Marked females dispersed rapidly to all parts of the *motu* and survived until recaptures on days 1–5 after release. Males were not adequately sampled using human sentinels or Biogent Sentinel traps.

Keywords

mosquito vector population; mark-release-recapture; Lincoln-Petersen Index; French Polynesia

Aedes polynesiensis Marks (Diptera: Culicidae) is the primary vector of *Wuchereria bancrofti* (Cobbold) and *Dirofilaria immitis* (Spirurida: Onchocercidae), the causative agents of human lymphatic filariasis and dog heartworm, respectively (Rosen 1955, Laigret et al. 1965, Russell et al. 2005a), and a secondary vector of dengue virus in French Polynesia (Rosen et al. 1954, Maguire et al. 1971). This highly anthropophilic, exophilic species is diurnal with peak periods of host-seeking during early morning and late afternoon hours (Russell et al. 2005a). Control of the vector is complicated by its use of dispersed and varied habitats for larval development; these habitats include phytotelmata and deciduous plant matter (especially rat-chewed coconuts), rock pools, artificial containers, and burrows of the land crab *Cardisoma carnifex* Herbst (Decapoda: Gecarcinidae) (Lardeux et al. 2002). Novel technologies are currently under development for the integrated control of this vector, and the numerous and discrete islands of French Polynesia provide isolated populations of *Ae. polynesiensis* for experimental trials (Brelsfoard and Dobson 2011, 2012; Mercer et al. 2012).

Mark-release-recapture (MRR) techniques depend upon releasing a known number of indelibly marked individuals (*M*) that subsequently disperse into a study population (Krebs 1999). The population is then sampled and the number of recaptured (i.e., previously marked and released) individuals (*R*) is determined as a proportion of the total captured (*C*); the estimation assumes that recaptured individuals in a sample are in the same proportion as marked individuals relative to the total population at time of release (*N*). Populations under

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study may be closed (i.e., with negligible migration, recruitment, or death) or open; closure of a population tends to be time sensitive (Krebs 1999).

MRR techniques have been broadly applied to mosquito populations (Service 1993). Recent applications have monitored dispersal patterns of *Aedes albopictus* (Skuse) associated with Chikungunya virus transmission in Rome, Italy (Marini et al. 2010) and *Aedes aegypti* (L.) for dengue transmission in Rio de Janeiro, Brazil (Maciel-de-Freitas et al., 2010) and Queens-land, Australia (Russell et al. 2005b, Johnson et al. 2012). In anticipation of preliminary field trials of novel control methods, the population size and movement patterns of *Ae. polynesiensis* were monitored during the annual dry (May–October) and wet (November–April) seasons on a small reef-formed island (*motu*) along the western shoreline of Raiatea, Society Archipelago.

Materials and Methods

Study Site and Climate

MRR studies were performed on Toamaro, an uninhabited, privately owned *motu* formed on the reef ≈0.5 km off the western shoreline of Raiatea. Toamaro has an area of ≈4 ha; the island's greatest width is 0.1 km and its long axis (0.5 km) is oriented NE to SW. The *motu* has a nearly complete (70–95%) canopy of native vegetation with well-developed herbaceous and shrub layers, is minimally manipulated, and houses two semipermanent structures that are visited infrequently. A transect was laid down along the length of the *motu* with 21 locations at 25 m intervals (Fig. 1).

Dry Season Sampling

On 4 May 2007 (at the beginning of the annual dry season), wild *Ae. polynesiensis* adults attracted to sentinels walking the length of the *motu* were collected between 830 and 1300 hours. One collector used a 12-volt battery powered backpack aspirator (J. W. Hock Company, Gainesville, FL) to aspirate mosquitoes from a sentinel; every 5 min, adults were mouth aspirated into labeled containers and provided with 10% sucrose solution on cotton. To minimize effects because of humans, the researchers subsequently departed the *motu;* all sorting and identification of captured adults were done on the Raiatea shoreline, a distance >500 m across an open lagoon. In total, 1,600 *Ae. polynesiensis* adults were captured during 830–1300 hours; of these, 1,597 (99.8%) were females. Adults were identified to species, sexed and counted. Adults were transferred to a quart-sized container (i.e., an "ice cream" coated cardboard tub topped with bridal veil mesh) in which they were lightly dusted with fluorescent powder (DayGlo Color Corporation, Cleveland, OH). The container holding marked *Ae. polynesiensis* adults was placed in a pan of water (to exclude ants) centrally on Toamaro (275 m along the transect, 16° 51′0.5″ S; 151° 29′18.4″ W; Fig. 1). The mesh was removed and researchers departed from the *motu.* After 24 h, dead individuals were counted to determine the number of marked individuals released to the *motu;* none of the three males initially captured survived marking and release. Females (1,508) that flew out of the cage on day 0 represented the number of individuals marked initially (M_1).

Two researchers collected host-seeking mosquitoes at 3-min stops along transects during the morning peak of adult activity on the following 5 d (i.e., 5–9 May) between 800–1000 hours; as often as possible, the same researchers carried out the collections to minimize bias. The backpack aspirator was again used to aspirate mosquitoes from a sentinel. Adults were transferred to labeled vials to indicate where they had been captured. On day 1, adults were collected along five nearly parallel transects near the release point set up perpendicular to the long axis of the *motu;* because marked individuals were found at collection sites most distant from the release point, subsequent sampling (days 2–5) was done along the transect

running the length of the *motu*. Sampling was done in alternating directions each day of the survey to avoid systematic errors. All captured mosquitoes were held for individual microscopic inspection using UV light to visualize the fluorescent powder. Wing lengths were subsequently measured using ImageJ software (National Institutes of Health) on preserved specimens. Therefore, the number of marked individuals (M_{i+1} in Table 1) available for recapture was decreased each day by the number of marked females trapped (R_i) and removed from the population.

Wet Season Sampling

Sampling was repeated during December 2008 to correspond with the period of seasonally high rainfall. Unbaited Biogent Sentinel (BiogentsAG, Regensburg, Germany) traps were used for more uniform and simultaneous collections. The protocol was further altered by using F_1 progeny of free-flying Toamaro adults with the aim of increasing the opportunity for male population analysis. Eggs were allowed to hatch under vacuum and larvae were reared at low density with lyophilized bovine liver powder (MP Biomedicals USA, Solon, OH) added ad libitum. Males and females were separated by pupal size and visual inspection after adult emergence; adults were provided with 10% sucrose solution exchanged daily. On 11 December 2008, counted adults (2–3 d posteclosion) were dusted with pink (females) or yellow (males) DayGlo powder and held overnight. Control individuals (25 each of marked and unmarked females and males) were held to monitor survival. A prerelease sample of free flying adults was taken on Toamaro to establish background insemination and parity rates. On 12 December, marked adults were allowed to disperse (in the absence of researchers) from an open cage at the same release point. Numbers of females (526) and males (644) initially released were determined by counting dead and injured individuals in the cage.

Adults were captured in 11 BG traps at fixed sites across the *motu* (Fig. 1) between 600–800 hours on five mornings after initial release (13–17 December). Captured individuals were kept cool (4°C) and held for microscopic inspection for presence of fluorescent markings. Sex and species were determined for each individual. Insemination and parity rates were determined on females (10 randomly selected females/trap × 11 traps/d = 110 females/d) from the prerelease sample and adults captured 1–5 d after release. Insemination and parity rates were determined by dissection of spermathecae (Lea 1968) and ovarial skeins (Service 1993), respectively.

Calculation Methods

The Lincoln–Petersen Index can be used to estimate N for a closed population at the time of release: N = marked × total captured/recaptured = MC/R (equation 1). Formulae proposed by G. A. F. Seber $N = [(M + 1)(C + 1)]/(R + 1) - 1$ (equation 2) and N. T. J. Bailey $N = [M(C + 1)]/(R + 1)$ (equation 3) were also used to minimize bias (Krebs 1999).

Meteorological data were generously provided by Meteo France. The Bora Bora Airport weather station (16° 26′42″ S 151° 45′06″ W) lies 53 km NNW of the release point on Toamaro (Fig. 1). Hourly readings of precipitation, temperature, barometric pressure, wind velocity, and direction were used to compare weather conditions for 30-d periods before and during recapture efforts associated with the dry and wet season experiments. Because wind direction is a circular measurement (i.e., values range from 0 to 360° rather than increasing linearly, confounding representations of northerly winds), daily means were calculated based upon hourly deviations from the first daily measurement. Although Polynesian islands experience micro-climatic differences (especially rainfall events, which are a related to cloud size), weather conditions are more similar between archipelago islands separated by ocean (without vertical relief) than corresponding land masses separated by equivalent

distances (unpublished data). Weather conditions were comparable between the Bora Bora Airport data set used and data generated by a stand-alone weather station installed between seasonal surveys on a neighboring *motu* (Mercer et al. 2012).

The average distance flown by recaptured adults (mean [distance between trap and release point × number of marked individuals]) was determined for each day after release. Wind speed and direction were also correlated with numbers and distances moved by recaptured adults. All statistical tests were performed using JMP Software (version 8, SAS Institute, Inc., Cary, NC).

Results

Dry Season Sampling

Of the females that were aspirated and marked for release, 94.4% successfully left their cage and naturally dispersed on day 0. In total, 1,884 *Ae. polynesiensis* adults were captured during the following 5 d of collection. Of these, 135 had been marked, representing a recapture rate of 8.95%. Only five male *Ae. polynesiensis* (0.265% of total adults) were captured (all unmarked; no marked males were released). The initial Lincoln–Petersen population estimate was 10,130.7 (95% CI = 5,800 – 18,850) *Ae. polynesiensis* females. During the 5 d of recapture, N_i estimates ranged from ≈10,000 to ≈36,000 individuals with a mean of 24,584 (13,071–36,096) females. The estimates differed by ≈3.5× and increased daily as marked individuals were recaptured less frequently; by comparison, the numbers of females (C_i) captured differed by ≈2.3× (Table 1). The *Ae. polynesiensis* density (based upon the mean) was, therefore, 6,055 females per hectare. The mean wing length for females was 2.483 ± 0.1624 mm (N = 100). The five (unmarked) males captured had mean wing lengths of 2.055 ± 0.0677 mm. Mean female wing lengths did not differ among the 5 d of capture (analysis of variance [ANOVA] $F_{4,95} = 1.12$, $P = 0.352$) or among trapping sites ($F_{7,92} = 1.86$; $P = 0.085$).

Marked females were recaptured on each day with the exception of day 4. Most marked females were recaptured on the first day during the dry season collection. Among the 135 recaptured females, the mean distance flown (i.e., distance of recapture from release point) was >160 m (Table 2). The number of marked females captured per day was not significantly correlated with wind direction at the start of collection (Pearson's $r = 0.18$, $P > 0.05$), mean wind direction during the previous 24 h ($r = 0.66$), wind velocity ($r = 0.71$) or mean wind velocity during the previous 24 h ($r = 0.49$). Although positive, the correlation between mean distance flown and wind velocity ($r = 0.87$) was not significant. Nonetheless, marked females dispersed to all parts of the *motu* (Fig. 2). Within the first 24 h after release, seven marked females (out of 78 recaptured on day 1) were collected >230 m from their release point.

Wet Season Sampling

In total, 1,310 wild adults were captured in BG traps during the presurvey collection on the day before release of marked adults. Trap catches consisted of 1,271 females and 39 males; females represented 97.0% of total. Most of the laboratory reared Toamaro F_1 progeny survived initial handling and marking; 96.7% of females and 86.3% of males departed the cage to disperse onto the *motu.* Although 187 unmarked males (1.74% of total adults) were captured in BG traps during six sampling periods (i.e., 39 captured on the day before release and 148 after release), none of the 644 marked males was recaptured. During the 5 d of recapture, 9,622 *Ae. polynesiensis* adults were captured in BG traps, 9,435 (98.1%) of which were females. Nine *Ae. aegypti* females were also captured. During the six trapping dates (i.e., 1 d prerelease plus 5 d postrelease), the proportion *Ae. polynesiensis* females in traps

did not differ significantly (χ^2 = 0.988; df = 3; P > 0.05). Among females captured postrelease, 120 individuals (1.32%) had been previously marked for a recapture rate of 22.8%. The relative percentages of marked females differed among days after release (χ^2 = 90.5; df = 3; P < 0.0001). The majority of females were recaptured 2 and 3 d after release but marked females were represented in trap catches on each day; females were recaptured in all 11 traps.

Survival was high among caged control individuals. Among 100 individuals held in cages with sucrose solution, 77 survived during the 5 d when recapture was carried out; equal numbers of DayGlo marked and unmarked males and females survived (χ^2 = 2.77; df = 2; P = 0.25). The initial Lincoln–Petersen *Ae. polynesiensis* female estimate for Toamaro during December 2008 was 128,607 (64,777.5–215,534.8). Population estimates varied widely (≈7×) by date of recapture whereas daily samples varied by ≈1.4×. The mean Lincoln–Petersen wet season population estimate was 73,664 (27,258–120,071) females and female density was 18,860 individuals per hectare. As during the dry season, no estimate is possible for males.

Marked female *Ae. polynesiensis* again dispersed rapidly and reached all parts of Toamaro during December 2008 (Table 2). By the second day, marked females had reached all collection stations (Fig. 2). Marked females were still captured at both ends of the *motu* on the final day of trapping. Days 2 and 3 corresponded to the greatest numbers of recaptured females and the greatest cumulative distance flown by marked individuals (Table 2). In contrast, the greatest mean distance flown by marked females was on the day after release (i.e., eight females moved a mean distance of 45 m within a day of release). Numbers of females recaptured did not correlate significantly with wind speed (r = −0.32) or wind direction (r = −0.36) at the time of collection. Correlations between total distance traveled by marked females for a given day and wind direction during trapping (r = −0.57), during the previous 24 h (r = −0.22), wind speed during trapping (r = −0.57) and wind speed during the previous 24 h (r = −0.64) were also not significant. Although stronger than the analogous correlations during the dry season, these coefficients were negative. The correlations between Lincoln–Petersen estimates for a given day and wind direction during trapping (r = 0.13), during the previous 24 h (r = 0.29), wind speed during trapping (r = 0.15) and wind speed during the previous 24 h (r = 0.33) were not significant.

Overall insemination and parity rates were 97.7 and 79.4%, respectively (Table 3); the frequencies of insemination (χ^2 = 0.721; P > 0.05) and parity (χ^2 = 0.120; df = 3; P > 0.05) did not differ by date of collection. Interestingly, the lowest capture, insemination (88%), and parity (66%) rates were among females collected before the release date.

Weather conditions that differed between the dry and wet season collections included wind direction, total rainfall, barometric pressure, and relative humidity. The prevailing wind direction associated with the dry season collection was ESE (perpendicular with the eastern shoreline) while that associated with the wet season was NE (approximately parallel with the long axis of the *motu*). During the 30 d period preceding the trials, total precipitation during the dry season was ≈54% of total rainfall during the same period of the wet season (Table 4). However, because of heavy precipitation on the day of adult release (4 May 2007), mean daily rainfall (between release of marked adults and final collection) did not differ between dry and wet seasons (Kruskal–Wallis χ^2 = 0.163; df = 1; P = 0.686). High variability in rainfall patterns, including heavy rainfall during the dry season, is typical of the Society Archipelago (Mercer et al. 2012). Mean temperatures (χ^2 = 0.231; df = 1; P = 0.631) and mean wind speeds (Student t = −1.86; df = 6.41 for unequal variances; P = 0.115) did not differ significantly between the seasons. Mean barometric pressure (t = 4.26; df = 7.5 for unequal variances; P = 0.0032) was higher during the wet season while mean relative

humidity ($t = -2.89$; df = 9.93 for unequal variances; $P = 0.016$) was lower during the wet season.

Discussion

Population estimates based upon MRR assume that marking does not affect survival or mobility of individuals and that all members of the population are equally likely to be sampled. Dusting did not appear to be detrimental to female *Ae. polynesiensis* in view of relatively high initial flight out of the cage, survival of controls, and rapid dispersal across the *motu.* Marked females were also recaptured from all cardinal directions relative to their release site, suggesting good mixing with the *motu* population during both seasons. Surprisingly, dispersal of marked females appeared to be independent of prevailing wind. Similar observations were made for *Ae. aegypti* in Brazil (Maciel-de-Freitas et al. 2010) and for *Ochlerotatus triseriatus* Say in New England (Ellis 2008). During the dry season, some marked *Ae. polynesiensis* females dispersed into the prevailing wind whereas females dispersed across the prevailing wind during the wet season.

Lincoln–Petersen estimates further assume that the population is closed. High survival of marked and unmarked control individuals during the days of collection suggests high survival in the field. Additionally, high insemination and parity rates are consistent with low recruitment into this island population during the study periods. While the distance of the *motu* from other sources of mosquitoes likely prevented immigration, putative rates of emigration, adult emergence, and death became more important factors, especially toward the end of the dry season sampling when numbers of recaptured females decreased.

The Lincoln–Petersen estimation method does not typically consider repeated captures. Additional methods and estimates have been developed for repeated samplings from a population. These were not appropriate for *Ae. polynesiensis* because they require release of repeatedly recaptured individuals into the population after application of distinguishable markings (e.g., dusting with colors in a sequential order that establish a capture “history” for each individual). Because of the logistics involved with sampling the population, we chose to conduct repeated collections. The daily recaptures were considered as separate trials with the number of marked individuals reduced each day by the number captured during previous days. The confounding effects of mortality of marked individuals and recruitment of young, unmarked adults increased with time. Each collection considered separately yielded great variation in population estimates, especially during the wet season. The unitless coefficient of variation (CV = SD/mean) allows for comparison of measures. The coefficient of variation for the wet season (0.72) was nearly twice that for the dry season (0.48). Similarly, Seber and Bailey estimates (that reduce population estimate bias) were much more similar to Lincoln–Petersen estimates during the dry season than during the wet season.

Estimation after repeated sampling can be improved by calculating the mean over repeated estimations (Krebs 1999); a population estimate based upon the mean of repeated samplings is more valid than an estimate based upon totals of mosquitoes captured and recaptured because the numbers of marked individuals (M) changes with each sample. An estimate attributed to C. H. N. Jackson is an improvement over an estimate based upon the mean (Cox 2002). This index yields a weighted estimate of the theoretical number of recaptures at time = 0 based upon multiple recaptures of marked individuals released singularly into a closed population. For the dry season, the Jackson estimate for the number of *Ae. polynesiensis* females on Toamaro was 8,579 (2,150 females per hectare). For the wet season, this estimate was 89,964 *Ae. polynesiensis* females (22,500 females per hectare), a 10-fold increase over the dry season estimate. Greater day-to-day variability in the total numbers of females captured (i.e., C) during the dry season (CV = 0.31) than the wet season

(CV = 0.14) resulted in a Jackson estimate for the dry season that was lower than the corresponding Lincoln–Petersen estimate while the reverse was true for the wet season. The variability in recaptured females (*R,*1.1 vs. 0.92 for dry vs. wet) and percent of total females (0.92 vs. 0.94) were similar for the two seasons.

Both of these population estimates were lower than those determined by Riviere et al. (1985) for *Ae. polynesiensis* populations on atolls of Tuamotu Archipelago with access to *C. carnifex* burrows for larval developmental (i.e., 50,000–120,000 females per hectare) but considerably greater than their estimate for populations without access to land crab burrows (i.e., <1,000 females per hectare). Female recapture rates for Toamaro (where *C. carnifex* burrows are plentiful) were high for the dry season (8.95%) and higher for the wet season (22.8%); in comparison, recapture rates ranged from 8.8 and 11.2% for two periurban populations of *Ae. aegypti* in Rio de Janeiro (Maciel-de-Freitas et al., 2010) to 3.4% for *Ae. aegypti* in suburban Cairns (Russell et al. 2005b) and 4.3% for an urban population of *Ae. albopictus* in Rome (Marini et al. 2010). We cannot speculate whether Toamaro offers fewer alternative blood sources (or host-mimicking proxy traps) than these other locales or whether *Ae. polynesiensis* responds differently from the aedine species tested in those other studies.

While marking was not a significant source of mortality and marked females reached all parts of the *motu,* only host-seeking females and mature males seeking mates will be collected at sentinels and by BG traps. Therefore, these population estimates apply to mature females at the appropriate stage of their gonotrophic cycle. Estimates based upon host-seeking exclude gravid females and those too young to seek a bloodmeal. Under ideal conditions in the laboratory, newly emerged *Ae. polynesiensis* females do not seek bloodmeals during their first 2 d (unpublished data). Once they secure adequate bloodmeals, they do not respond to host cues for an additional 4 or 5 d while they produce a clutch of eggs. In nature, bloodmeal sources may be unpredictable but ≈80% of wet season Toamaro females caught in BG traps were parous (i.e., ≥1 clutch of eggs already produced); on Moorea (≈125 km southeast of Raiatea but within the Society Archipelago), parity rates for *Ae. polynesiensis* ranged between 52.9– 88.8% for wet and dry seasons (Russell et al. 2005a). We can estimate that between 10% (securing bloodmeal on first day of seeking) and 50% (low success rate at securing bloodmeal, the more likely scenario in view of attack rates in the field) of females will actively seek bloodmeals at any given time. Under these assumptions, the female population estimates for Toamaro should, conservatively, be doubled.

Population estimates are not influenced by the capture method used as long as the method is unbiased in capturing consistent proportions of marked relative to unmarked individuals (i.e., absolute numbers do not matter). Therefore, unless human sentinels and BG traps are differentially attractive to released (and marked) relative to unmarked individuals, population estimates based upon relative recapture rates can be compared for dry and wet seasons. During the dry season, marked adults came from the field population itself; therefore, insemination and parity rates were not determined. Russell et al. (2005a) determined that insemination and parity rates were high for *Ae. polynesiensis* on Moorea during both seasons and greater than comparable values for sympatric *Ae. aegypti.* Although marked adults released during the wet season had been reared under ideal lab conditions and may have been more robust than mosquitoes developing in the field, the similarities in insemination and parity rates for prerelease and postrelease samples suggest that our nulliparous marked individuals did not introduce age or parity bias to that trial relative to the dry season aspiration from sentinels.

Likewise, the dispersal of females was rapid and encompassed the entire *motu* for both seasons. The procedural change to releasing F_1 adults during December 2008 was an attempt to monitor males, and using multiple BG traps extended collection times relative to human sentinel captures and standardized collections. Furthermore, this trapping method was used in developing novel vector control strategies for Toamaro and neighboring *motu* and shoreline populations (Mercer et al. 2012). In that study and consistent with the present findings, significantly more (albeit smaller) *Ae. polynesiensis* females were captured in BG traps during two wet seasons than during two corresponding dry seasons (Mercer et al. 2012).

Marked adults released during the dry season had been collected at human sentinels whereas marked adults released during the wet season were F_1 progeny of wild Toamaro females. Russell et al. (2005a) determined that early morning *Ae. polynesiensis* collections were more likely to include younger females than afternoon collections. For logistic reasons, our collections were limited to the morning peak of adult activity. Marked females during the dry season, all of which had been initially captured while actively host-seeking, may have been more heterogeneous in age but more uniform in host-seeking status than those subsequently used during the wet season. Marked females during the wet season were more uniform in age (and uniformly nulliparous) but were not initially collected for marking based upon a host-seeking commitment (although their release was timed for maximum host-seeking). Whether female age differentially influenced attraction of marked females to human sentinels and BG traps is unknown, but recapture rate was much lower during the dry season. Each of the pathogens vectored by *Ae. polynesiensis* requires an extrinsic incubation period (i.e., for development of the filarial worm or replication of the virus); therefore, older females are more likely to be infective than nulliparous females.

Adult mosquitoes captured on Toamaro were overwhelmingly female *Ae. polynesiensis;* similar species compositions and sex ratios were encountered during the 2-yr study involving Toamaro and three other neighboring but relatively isolated populations (Mercer et al. 2012). The paucity of male capture is in contrast to greater proportions of males in trap catches for other Stegomyia species. Males represented ≈77% of recaptured *Ae. aegypti* using sticky lures during an outdoor MRR study in Pentland, Queensland (Muir and Kay 1998) whereas marked males represented >18% of recaptured adults using BG traps without chemical attractants during an indoor MRR study in Cairns, Queensland (Johnson et al. 2012). Males made up 25 and 53% of wild *Ae. albopictus* captured in two New Jersey counties (Farajollahi et al. 2009); for one of the counties, BG Sentinel traps without lures captured males at >6% of total adults. During a MRR trial in Rome, Marini et al. (2010) recaptured males at a rate >19% of the total *Ae. albopictus* captured using sticky traps.

During the current study, males were rarely collected at human sentinels or in BG traps and never recaptured. This is despite the 1:1 sex ratio for the species under nonlimiting conditions and overproduction of males (that have about half the biomass) from populations facing restrictive conditions (Mercer 1999). Additionally, of 1,026 adults emerging from immatures collected from 49 domestic and natural developmental sites surrounding Raiatea's western lagoon between July to December 2007, 56% were male (data not shown). Adult male mosquitoes are attracted to human odors (Davis 1977) where they may intercept host-seeking females. However, males approach humans at lower rates than females and generally do not alight, resulting in lower capture rates (unpublished data). Schmaedick et al. (2008) demonstrated that BG Sentinel traps were more effective in capturing *Ae. polynesiensis* females than two other commonly used traps; that study was conducted with host odor-baited traps and male capture rates were not reported. In our study, the BG traps were not baited with chemical cues and relied exclusively upon visual cues (i.e., black contrasting with white); presumably, males of this diurnal species are trapped when they

seek females based upon the same visual cues. On Tahiti and Moorea, female *Ae. polynesiensis* outnumbered males 2:1 in unbaited BG traps in 18 trials (J.M. and D.R.M., unpublished data); nonetheless, the bias toward females (>97%) in trap catches and sentinel captures on Toamaro is extreme.

To increase the opportunity for recapturing males, F_1 offspring of field-collected females were used for the wet season estimate. Despite the release of 644 marked males during December 2008, none was subsequently recaptured. Therefore, no estimates on male *Ae. polynesiensis* numbers or dispersal patterns can be made based upon these surveys. Failure to be recaptured was, presumably, not because of high mortality. Both marked and unmarked caged males held as controls survived well during the wet season sampling. The collection period was selected to take advantage of the morning period of activity for females and may not reflect peak male activity on Toamaro. Toamaro males may be less attracted to sentinels or unbaited BG traps than females or males from other populations. Similarly, males were rarely captured on Toamaro using additional methods including aspiration from crab burrows and resting boxes, sweep net sampling, and flight intercept traps (unpublished data). However, the high insemination rate of captured females suggests that there were adequate numbers of males in the population to provide sperm. Males do not directly participate in disease transmission cycles but are important in population dynamics. Males compete with females during larval development and males may outnumber females emerging from resource-limited habitats (Mercer 1999). It is important to develop a more effective means of sampling male *Ae. polynesiensis.*

Dissimilar recapture rates (i.e., 8.95 and 22.8% for dry and wet season, respectively) could have been because of biological (seasonal) or procedural (sources of marked individuals and trapping methods) differences. However, the mean distance moved by marked females was greater during the dry than the wet season. Although wind gusts were stronger during the dry season, it is unlikely that marked females were blown off the *motu* more frequently than unmarked females (thereby reducing their chance for recapture) compared with their counterparts during the wet season. Biting rates and trap catches of *Ae. polynesiensis* females both decline as wind velocity increases (unpublished data).

The recapture rate during the dry season followed the expected pattern with a majority of marked individuals recaptured initially (i.e., they resumed host-seeking immediately) with fewer subsequent recaptures (Table 1). In comparison, the recapture of relatively few marked females during the first collection of the wet season followed by 2 d with high recapture rates resulted in a very broad Lincoln– Petersen 95% CI.

Dispersal differences among mosquito species may influence disease transmission dynamics. However, dispersal for a species is influenced by local conditions such as available resources (including blood sources), wind, vegetation or other cover. *Ae. aegypti,* which is highly endophilic, is generally reported to have limited dispersal, resulting in localized dengue outbreaks. Muir and Kay (1998) reported that *Ae. aegypti* females dispersed a mean distance of 56 m in Pentland, and Russell and coworkers (2005b) reported mean dispersal of 78 m by *Ae. aegypti* in Cairns; both studies were conducted in Queensland, Australia. Multiple cohorts of *Ae. aegypti* dispersed mean distances of 25–114 m throughout two periurban settings in Rio de Janeiro (Maciel-de-Freitas et al., 2010). *Ae. albopictus,* which is more exophilic, is generally reported to disperse greater distances. Marini et al. (2010) report *Ae. albopictus* dispersal of 50–200 m, with mean dispersal of 119 m during their 9 d study; these distances overlap strongly with those published for *Ae. aegypti.* Similarly, Liew and Curtis (2004) found no differences between *Ae. albopictus* and *Ae. aegypti* dispersal across a 320 m transect in Singapore.

Ae. polynesiensis is highly exophilic, but dispersal distances were influenced by the *motu* dimensions. On Toamaro, permanent blood sources include rats, wild birds, and feral chickens and cats; seasonal differences in blood sources because of migratory birds have not been investigated but are likely to be minimal. Mean distances traveled by marked females were greater during the dry than the wet season (150 vs. 18 m), but individuals moved to all parts of the *motu* during both seasons. During the dry season, prevailing wind was perpendicular to the long axis of the *motu* while during the wet season the winds were more parallel with its long dimension; surprisingly, neither wind direction nor wind velocity correlated significantly with adult movement. Therefore, the prevailing wind did not assist mosquito dispersal and may even have limited dispersal during the December 2008 survey. Host-seeking female *Ae. polynesiensis* do not typically leave the vegetational cover of *motus* to secure bloodmeals from humans on the shoreline or in boats (unpublished data); therefore, it is unlikely that females would have actively dispersed across the open lagoon. However, flying individuals caught by wind gusts would have ended up off the *motu.*

Lower population densities during the dry than the wet season could result from fewer individuals emerging from the same number of developmental sites (of reduced quality) or similar numbers of adults emerging from fewer productive developmental sites. During the dry season, some developmental habitats (e.g., rat-chewed coconuts, tree holes, pools, and containers) may persist long enough to allow completion of adult emergence (as a function of unpredictable but heavy rainfall such as occurred 4–5 May 2007). Other developmental sites, particularly crab burrows whose filling is determined by ground water, are less likely to be available during the dry season. As a result, developmental sites are less plentiful and more ephemeral and adults are fewer.

In addition to adult numbers, female size is determined (in part) by larval developmental conditions. Mean wing lengths of dry season females were midrange for adults developing in the field (Mercer 1999). Adults captured during the wet season were improperly stored to allow wing length measurements; nonetheless, this population was monitored during a concurrent study. Mean wing lengths for Toamaro females collected during two dry seasons were significantly greater than wing lengths from females collected during the corresponding wet seasons (Mercer et al. 2012). Numbers of mosquitoes were likely limited by available developmental sites during the dry season, but physical crowding within developmental sites may have been lower whereas per capita resources were greater during the dry season than the wet season in view of larger wing lengths for females (Mercer et al. 2012).

The *Ae. polynesiensis* population of Toamaro remains high during both seasons and swarms of aggressive females attack visitors year round (unpublished data). Although absolute numbers vary dramatically, outcomes of these studies coupled with field observations suggest that uncontrolled *motu Ae. polynesiensis* populations are made up of tens of thousands of females per hectare year-round.

Acknowledgments

We thank Jerome Petit, the Richard B. Gump Biological Research Station, and Meteo France for providing weather data. This research was sponsored by grants from the National Institutes of Health (NIH) (AI)-067434 and the Bill and Melinda Gates Foundation BMGF 44190. This is publication 11-08-088 of the University of Kentucky Agricultural Experiment Station.

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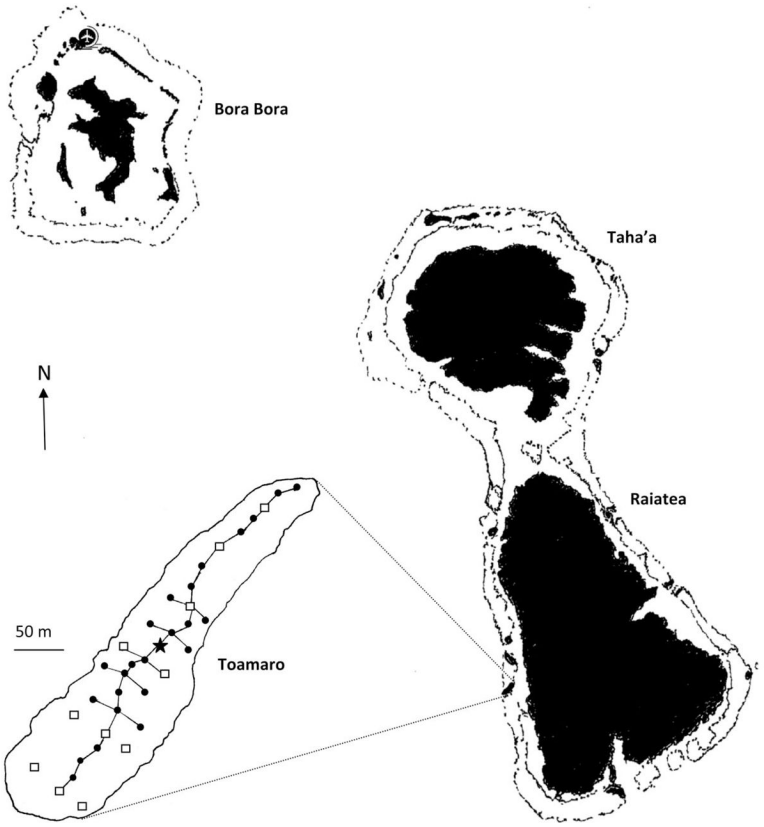

Fig. 1.
Map of Toamaro relative to Raiatea, Taha'a, and Bora Bora (weather data from airport) showing marked mosquito release point (star), transect and BG trap collection sites (squares). Inlaid line represents 50 m.

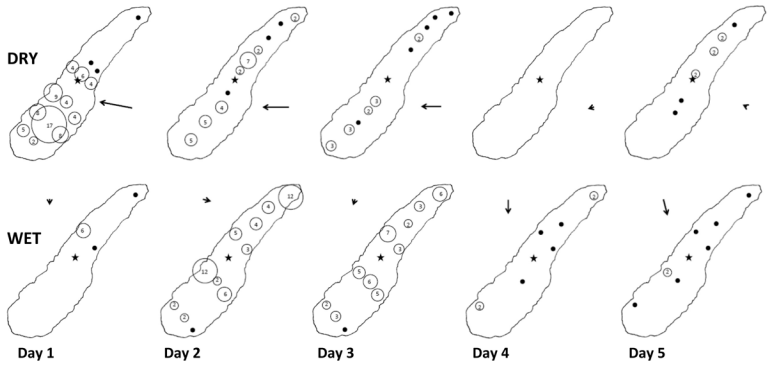

Fig. 2.

Numbers and distributions of recaptured *Aedes polynesiensis* females after release from central location (star) on Toamaro during dry (May 2007) and wet (December 2008) seasons. Filled circles represent single females. Arrows indicate wind direction and relative velocity.

Table 1

Capture rates and pop size estimates of *Aedes polynesiensis* on Toamaro *motu,* Raiatea, French Polynesia after release of marked females during May 2007 and Dec. 2008

Season	Days after release	Marked females[a] (*M*)	Total females captured (*C*)	Recaptured females (*R*)	Percent of total females	Males (all unmarked)	Lincoln–Petersen estimate (equation 1)	Seber estimate (equation 2)	Bailey estimate (equation 3)
Dry	1	1,508	524	78	14.89	2	10,130.7	8,537.3	10,021.5
	2	1,430	421	30	7.13	0	20,067.7	18,094.2	19,466.5
	3	1,400	418	18	4.31	1	32,511.1	29,567.5	30,873.7
	4	1,382	284	0	0.00	0	ND	ND	ND
	5	1,382	232	9	3.88	2	35,624.9	30,978.2	32,200.6
	Mean	NA	375.8	27	6.04	1	24,583.6	21,794.3	23,140.6
Wet	1	526	1,956	8	0.41	9	128,607.00	114,592.2	114,375.8
	2	518	1,854	53	2.86	31	18,120.23	17,827.61	17,794.26
	3	465	1,737	43	2.48	32	18,783.84	18,406.00	18,367.50
	4	422	1,606	8	0.50	38	84,716.50	75,528.00	75,350.44
	5	414	2,282	8	0.35	38	118,093.50	105,270.7	105,018.00
	Mean	NA	1,887.0	24	1.32	29.6	73,664.21	66,324.9	66,181.2

Dry season collections were made using a battery-powered backpack aspirator and wet season collections were made using unbaited BG Sentinel traps.

[a]Marked females = total marked mosquitoes released - recaptured marked mosquitoes for each day.

Table 2

Numbers and distances flown by marked *Aedes polynesiensis* females on Toamaro *motu,* Raiatea, French Polynesia and wind speed and direction during May 2007 and Dec. 2008

Season	Days after release	Recaptured females	Total distance flown (m)	Mean distance flown (m)	Wind direction during trapping (degrees)[a]	Wind direction during previous 24 h (degrees)[a]	Wind speed during trapping (m/s)[a]	Wind speed previous 24 h (m/s)[a]
Dry	1	78	11,985	153.7	110	115	4.1	4.71
	2	30	5420	180.7	100	90	3.1	4.21
	3	18	3640	202.2	90	90	4.1	3.21
	4	0	0	0.0	30	70	1	1.04
	5	9	780	86.7	175	110	1	0.92
	Mean	27	4,365	161.7	NA	NA	2.7	3.45
Wet	1	8	360	45	0	0	0.0	1.04
	2	53	838.64	15.8	20	285	1.2	1.55
	3	43	737.27	17.1	250	35	0.5	1.11
	4	8	137.27	17.2	340	0	2.5	2.33
	5	8	138.18	17.3	350	345	2.2	2.60
	Mean	24	442.272	18.43	NA	NA	1.3	1.71

Dry season collections were made using a battery-powered backpack aspirator and wet season collections were made using unbaited BG Sentinel traps.

[a]Wind data measured at Bora Bora Airport, 53 km NWN of Toamaro.

Table 3

Insemination and parity rates of *Aedes polynesiensis* females captured on Toamaro *motu,* Raiatea, French Polynesia during Dec. 2008

Days after release	Females captured	Dissected	Inseminated (%)	Parity (%)
−1	1,271	110	88.2	66
1	1,956	110	99.1	87
2	1,854	110	100	78
3	1,737	110	100	80
4	1,606	110	100	85
5	2,282	110	99.1	80
Mean	1,788.33	660	97.7	79.4

Females were randomly selected from unbaited BG-Sentinel trap collections.

Table 4

Weather data from Bora Bora Airport, French Polynesia, during dry season (May 2007) and wet season (Dec. 2008) mosquito collections on Toamaro *motu*

Time period	Total rainfall (mm)	Mean daily rainfall (mm/d)	Mean temp (°C)	Mean pressure (hPa)	Mean wind speed (m/s)	Mean relative humidity (%)
Dry: previous 30 d	139.6	4.67	28.00403	1,012.4	4.04	80.24
0		40.2	25.51	1,010.3	4.17	88.04
1		3.6	27.17	1,010.2	4.71	85.13
2		0.2	28.08	1,010.3	4.21	83.38
3		0	28.27	1,009.7	3.21	80.17
4		0.6	27.41	1,009.1	1.04	83.54
5		0	27.46	1,009.9	0.92	81.71
During trial	44.6	8.92	27.29	1,009.9	3.45	84.05
Wet: previous 30 d	257.4	7.4	27.45	1,012.1	2.51	80.62
0		0.2	27.51	1,011.4	1.66	79.63
1		0	27.55	1,011.5	1.04	78.75
2		3.4	28.18	1,011.5	1.55	76.96
3		8.4	27.20	1,010.7	1.11	82.54
4		8	27.19	1,011.6	2.33	81.17
5		0.4	27.83	1,013.4	2.60	74.25
During trial	17.6	3.4	27.56	1,011.7	1.71	78.88