Monitoring Temporal Abundance and Spatial Distribution of *Aedes polynesiensis* Using BG-Sentinel Traps in Neighboring Habitats on Raiatea, Society Archipelago, French Polynesia

DAVID R. MERCER,[1,2] HERVE BOSSIN,[3] MICHEL CHEONG SANG,[3] LINDA O'CONNOR,[1] AND STEPHEN L. DOBSON[1]

ABSTRACT   Adult numbers and sizes of mosquitoes were monitored for 2 yr in neighboring habitats on the western coast of Raiatea (Society Archipelago) in anticipation of testing new vector control technologies. *Aedes polynesiensis* Marks females comprised the overwhelming majority ($\approx$99%) of the three species of mosquitoes captured in Biogent Sentinel traps placed at fixed sites on three small satellite islands (*motu*) of the western lagoon and on the shoreline of Raiatea. *Aedes polynesiensis* males, *Aedes aegypti* (L.), and *Culex quinquefasciatus* Say rarely were collected. Numbers of *Ae. polynesiensis* females per collection differed among trapping dates and locations, with the majority of females captured on two *motus*, Horea and Toamaro. Shoreline and Horea females had significantly longer mean wing lengths than females from Tiano and Toamaro. Thus, wing lengths were influenced more by local developmental conditions than overall numbers of adults. Significantly more females were captured during the wet season than the dry season. Nonetheless, at least on the two highly productive *motus*, dry-season females had larger wing lengths than their wet season counterparts. Local weather patterns predicted about half the variation in mosquito numbers. Differences in vector abundance observed when comparing neighboring *motus* are likely because of differences in human activity and mosquito suppression.

KEY WORDS   *Aedes polynesiensis* population dynamic, filariasis vector, trap sampling, seasonality, adult size variation

Aedes polynesiensis Marks (Diptera: Culicidae) is the primary vector of *Wuchereria bancrofti* (Cobbold) (Spirurida: Onchocercidae), the causative agent of human lymphatic filariasis (Rosen 1955, Laigret et al. 1965), and a secondary vector of dengue in French Polynesia (Rosen et al. 1954, Maguire et al. 1971). Host seeking mostly is diurnal and outdoors, with peaks of activity at dawn and dusk (Russell 2004). *Aedes polynesiensis* uses a variety of natural and artificial containers for development, complicating vector control (Lardeux et al. 2002). Like many container-breeding mosquitoes, cohorts of *Ae. polynesiensis* respond to overcrowding and resource limitation during larval development through reduced survival, skewed sex ratios, and smaller size at emergence and delayed emergence, especially for females (Mercer 1999, Mercer et al. 2005).

Despite prolonged mass administration of prophylactic drugs (MDA) against *W. bancrofti*, lymphatic filariasis persists in French Polynesia (Esterre et al. 2001, Plichart et al. 2006). It has been hypothesized that the biology of *Ae. polynesiensis* contributes to the failure of MDA in these archipelagoes despite success elsewhere (Burkot et al. 2002, Lardeux et al. 2002, Pichon 2002). *Aedes polynesiensis* females are more efficient at transmission (which requires development of the parasite but is nonpropagative in the vector) as the number of ingested microfilariae decreases (as occurs during MDA) (Rosen 1955, Pichon et al. 1974, Failloux et al. 1995, Stolk et al. 2004). The coupling of MDA with effective vector control may be required to upset disease transmission (Burkot et al. 2002, Pichon 2002, Brelsfoard et al. 2008, Brelsfoard et al. 2009).

The small islands of the archipelago lend themselves to studies of vector biology on replicated sites. Raiatea is the largest of the Leeward Islands in French Polynesia and serves as the regional administrative and public health center for the western Society Archipelago. Like many "high islands" of the South Pacific, the lagoon of Raiatea contains several small satellite islands (*motus*) associated with the surrounding coral reef. Natural dispersal of *Ae. polynesiensis* is augmented across short and long distances by commercial trade; therefore, genetic differences are influenced by human transport in addition to mosquito flight distances, weather patterns, and natural barriers (Failloux et al. 1997). There is sufficient genetic exchange

[1] Department of Entomology, University of Kentucky, Lexington, KY.
[2] Corresponding author, e-mail: randy.mercer@gmail.com.
[3] Laboratoire d'Entomologie et de Parasitologie Médicale, Institute Louis Malardé, Tahiti, Polynésie Française.

between Raiatea and its surrounding *motus* to maintain genetic homogeneity (Shiu et al. 1997).

In addition to *Ae. polynesiensis*, nine mosquito species are reported from the Society Archipelago (Belkin 1962, Huang 1977, Russell 2004, Brunes and Boussès 2009). Although *Culex quinquefasciatus* Say is common on numerous islands of French Polynesia and shares many developmental habitats with *Ae. polynesiensis*, the species is not an important vector of the subperiodic form of *W. bancrofti* found in French Polynesia (Iyengar 1965, Lardeux et al. 2002). The peridomestic species *Aedes aegypti* (L.), the primary vector of dengue in French Polynesia, is common in urban areas and villages of French Polynesia but less common in more rural settings where *Ae. polynesiensis* predominates. *Culex annulirostris* Skuse serves as a vector of encephalitis viruses elsewhere (Kay et al. 1984) and nocturnal periodic filariasis in New Guinea (Belkin 1962) but is not competent for the subperiodic form found in the eastern archipelagoes of the South Pacific (Lee et al. 1989). Most of the other mosquito species are rare endemics with limited distributions and unknown vector status. Although it is imperative to monitor unintended changes in nontarget species (including disease vectors) during control efforts, these species were not of primary interest in the current study.

We implemented a surveillance program for *Ae. polynesiensis* in Raiatea in anticipation of testing new vector-control technologies to augment MDA against filariasis in French Polynesia. We studied natural variation in mosquito numbers and sizes across time on four neighboring locations. The climate of Raiatea is subtropical oceanic with distinct hot, humid (December-February) and cooler, dry (March–November) seasons (Meyer 1996). Thus, we monitored adult numbers and size and local weather conditions of Raiatea during a 2-yr trapping study.

Methods

Study Sites. Three small neighboring *motus* and an adjacent shoreline location along the western coast of Raiatea (Tehurui and Vaiaau villages in the associated commune of Tumaraa) were the focus of this study (Fig. 1). Horea is the smallest of the *motus* surveyed (area = 1.41 ha; perimeter = 443 m; area/perimeter = 31.8, estimates using ArcView 9.2, ESRI Corp., Redlands, CA). This circular *motu* is held publicly, but hosted up to 20 temporary structures during the study and is semipermanently inhabited by area residents for fishing and holidays during which insecticides and wood smoke are used for mosquito control. The vegetation is typical of Polynesian islands with 60–80% canopy cover. An herbaceous layer is present for most of the *motu.* Mosquito developmental sites include artificial containers (e.g., appliances, buckets, cans, glass bottles, plastic and polystyrene containers, tires); coconuts; spathes; phytotelmata (tree holes, plant axils, and stumps); and burrows of the land crab *Cardisoma carnifex* Herbst (Decapoda: Gecarcinidae). Permanent blood sources include dogs, rats (although the
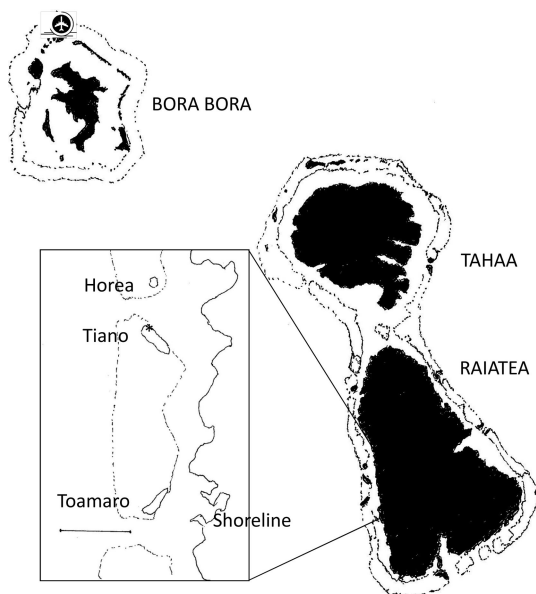

Fig. 1. Location of study sites (inset) relative to Raiatea and airport weather station, Society Archipelago, French Polynesia. Bar in inset represents 1 km.

relative paucity of rat-chewed coconuts suggests low densities), chickens, and other birds and humans.

Tiano is owned privately with three permanent structures. This elongate *motu* is the largest of the three included in the survey (area = 6.34 ha, perimeter = 1,169 m) and presents the greatest area relative to shoreline (area/perimeter = 54.2). The island is managed extensively against mosquitoes (source reduction and pesticides) with open (<20% cover) canopy centrally and denser (80–90%) natural canopy around the edge, particularly at the apices. The central portion of Tiano consists mostly of coconut palms (metal banded, to exclude rats). Putative mosquito developmental sites are limited to cryptic tree holes, crab burrows, and a temporary pool with stagnant freshwater adjacent to the dwellings. Blood sources include rats, humans, dogs, and birds.

Toamaro also is owned privately and has two structures used infrequently. The elongate *motu* is intermediate in size relative to the others (area = 4.06 ha, perimeter = 1,052 m, area/perimeter = 38.6), but has a more complete canopy of native vegetation (70–95%) and greater stratification with well-developed herbaceous and shrub layers. The island is managed occasionally with vegetation clearing, insecticide application, and burning during collection of coconuts to produce copra oil. Mosquito developmental sites are plentiful and include artificial containers, coconuts, phytotelmata, and numerous crab burrows. Blood sources include rats, birds, and occasionally dogs, cats, and humans. Closest linear distances from *motu* to shoreline for Horea, Tiano, and Toamaro were 700, 600, and 526 m, respectively, as estimated using Google Earth (Version 5.0, Google Inc., Mountain View, CA).

Adult Trapping. Trapping of adult mosquitoes was initiated on 17 August 2007. Biogent Sentinel (BiogentsAG, Regensburg, Germany) traps were hung from trees with openings at a height of 0.8 m at three fixed sites on each of the three *motus;* adjacent sites were spaced 50–175 m. Traps were placed at the apices and centers of the elongate *motus* (Tiano and Toamaro) and as far apart as possible on circular Horea; traps were placed amid habitat that was representative of vegetational coverage and putative larval developmental sites (including *C. carnifex* burrows) for each of the *motus.*

The traps were powered by rechargeable 12-V sealed gel-cell batteries. To ensure uniformity of capture, trap opening air velocities were confirmed to be >3 m/s by using a handheld anemometer (La Crosse Technology, Ltd., LA Crosse, WI) at the beginning and ending of each trapping period; spare batteries were available for replacement if velocities were too low. The orders of *motu* visitation and trap placements, as well as the trap numbers and batteries, were randomly assigned to reduce systematic error. Trapping was done during 20-min intervals; all trapping was completed during the morning peak of host-seeking activity reported for *Ae. polynesiensis.* Trapping was repeated at 14-d intervals (with the exception of two dates missed during October 2007 and January 2008) until 13 August 2009.

Adults also were captured in two (beginning 1 February 2008) and then three (22 May 2009) fixed shoreline sites along the western lagoon coast of Raiatea facing Toamaro. These representative sites include the roadside adjacent to the coast, under an open-sided garage, and within a seasonally flooded mudflat bordered with dense vegetation and a high density of crab burrows, respectively at 10-, 75-, and 170-m inland. Cover is sparse (10–40%) and consists of native, ornamental, and cultivated vegetation at the sites nearer the coast, whereas the native vegetation is dense (80–90%) at the inland site. Because of logistic constraints, the *motus* were visited sequentially in a randomly determined order, whereas those on the shoreline were visited first or last on any given trapping day.

Adult Size. Captured mosquitoes were identified, sex determined, and counted for each collection period. Wing lengths were measured for a subset of captured *Ae. polynesiensis* (N $\geq$ 10 per trap when available) by location and collection date by using a stereomicroscope fitted with a micrometer scale. Mean *Ae. polynesiensis* female numbers were compared among dates, locations, sites, trap numbers, and order of collection by using Wilcoxon rank sums and location, season, and their interaction by using the multiple regression model in JMP 9.0.1 software (SAS Institute, Cary, NC).

Weather Data. A stand-alone HOBO weather station (H21-SYS-A, Onset Computer Corporation, Pocasset, MA) was installed on 26 July 2007 in a clearing toward the northwestern apex of Tiano (16° 49′44.85″ S, 159° 29′21.4″ W); not only was this site central for the three *motus*, it offered the best security

Table 1. Total mosquitoes captured in BG-Sentinel traps on three Raiatea *motu* (17 August 2007–13 August 2009)

Species and sex	Total	Mean (SE)[a]	Max[a]	% total
Ap female	13,713	29.682 (2.479)	428	98.90
Ap male	125	0.271 (0.035)	7	0.90
Ae female	11	0.024 (0.007)	1	0.08
Ae male	14	0.030 (0.008)	1	0.10
Cx female	0	0	0	0.00
Cx male	2	0.004 (0.003)	1	0.01
Total	13,865	30.011 (1.396)	431	100.00

Ap, Aedes polynesiensis; Ae, Aedes aegypti; Cx, Culex quinquefasciatus.
[a] Per trap per collection.

for the weather station because of the private status of Tiano. Probes for rainfall, barometric pressure, solar radiation, wind speed, wind gust speed, wind direction, air temperature, relative humidity, and subsurface soil temperature (-50 cm) collected data at 10-min intervals. An Onset HOBO U-Shuttle (U-DT-1, Onset Computer Corporation, Pocasset, MA) was used to download data during mosquito trapping on Tiano. Linear distances were estimated from the weather station to the center of Horea (0.8 km), Toamaro (2.2 km), and the Raiatea shoreline (2.8 km) (Google Earth 5.0).

Weather data were analyzed using HOBOware Pro Software Version 2.7.3 (Onset Computer Corporation, Pocasset, MA). Maxima, minima, means, and standard deviations were estimated for the 10-min logger intervals for each variable across the entire sampling period. In addition, the "Filter Series" of HOBO software was used to generate the maximum, minimum, and average (and total for rainfall) values for each measurement during biweekly intervals. Spearman rank correlations were run on all pair-wise means for weather data and for total mosquitoes collected concurrently. Because mosquito collections were not always concordant with the 14-d intervals upon which weather data were analyzed, mosquito collection periods were matched to the nearest preceding biweekly weather period.

Results

Adult Trapping. During 2 yr of collections, 13,865 adult mosquitoes in total were captured in BG-Sentinel traps on the three *motus* during the 51 collection periods (i.e., 153 samples). Three species were captured (*Ae. polynesiensis, Ae. aegypti*, and *Cx. quinquefasciatus*), with *Ae. polynesiensis* females making up 98.9% of the total (Table 1). By comparison, male *Ae. polynesiensis* were rare (125 individuals), representing 0.90% of trapped individuals. *Aedes aegypti* and *Cx. quinquefasciatus* were rarer still; males slightly outnumbered females for *Ae. aegypti* and both *Cx. quinquefasciatus* individuals captured were males. An *Ae. aegypti* female was captured for the first time on Tiano more than a year after initiation of collections (5 January 2009). Therefore, all three species were recovered from Tiano and Toamaro, whereas no *Cx. quinquefasciatus* was captured on Horea.

Table 2. Mosquitoes collected in BG-Sentinel traps on three Raiatea *motus* (17 August 2007–13 August 2009) and adjacent shoreline (1 February 2008–13 August 2009)

Location	Ap females	Ap males	Ae females	Ae males	Cx males	Total
Toamaro	54.6 (5.3)a	0.418 (0.07)a	0.039 (0.02)a	0.046 (0.02)a	0.007 (0.01)a	55.08 (5.36)a
Horea	31.6 (4.3)b	0.288 (0.07)ab	0.026 (0.01)a	0.026 (0.01)a	0	31.91 (4.35)b
Tiano	3.49 (3.6)c	0.111 (0.04)b	0.007 (0.01)a	0.020 (0.01)a	0.007 (0.01)a	3.63 (0.51)c
Shoreline	5.30 (4.6)c	0.227 (0.11)ab	0.062 (0.04)a	0.268 (0.13)a	0.010 (0.01)a	5.87 (0.89)c

Numbers shown represent mean (SE) mosquitoes per trap per 20-min sampling period. Means followed by different letters within a column are significantly different by Tukey's HSD on ranks.

Ap, Aedes polynesiensis; Ae, Aedes aegypti; Cx, Culex quinquefasciatus.

An additional 569 adults were captured during 33 collection periods (i.e., 97 samples) at the Raiatea shoreline sites. All three species were captured, although the duration of collection period was shorter (Table 2). *Aedes polynesiensis* females again represented the majority of mosquitoes captured at the shoreline, although their proportion (88.8%) was lower relative to *Ae. aegypti* males (4.5%), *Ae. polynesiensis* males (3.8%), *Ae. aegypti* females (1.0%), and *Cx. quinquefasciatus* males (0.2%). As on the *motus*, no female *Cx. quinquefasciatus* was trapped during these morning collections.

Numbers of *Ae. polynesiensis* females correlated significantly with *Ae. polynesiensis* males (Spearman's rank correlation $\rho = 0.432$, $N = 187$, $P < 0.0001$) and *Ae. aegypti* females ($\rho = 0.148$, $N = 187$, $P = 0.045$) among the trap collections from the same date. All three species were captured in the same trap only once (17 July 2008 on the shoreline).

Because *Ae. polynesiensis* females comprised ≈99% of adults captured overall, subsequent comparisons will focus on this species, although statistical outcomes for total mosquitoes were identical. Numbers of *Ae. polynesiensis* captured per trap per collection period were not normally distributed (Shapiro–Wilk's $W = 0.559$, $P < 0.0001$). Mean numbers of females differed by date of collection (Wilcoxon rank sum $\chi^2 = 119.7$, df = 50, $P < 0.0001$). Relative peaks of total adult collections occurred between March and June 2008 and December 2008 and April 2009 (Fig. 2), but trap catches were not significantly correlated for similar dates between years (Pearson's correlation coefficient $r = -0.0053$, $P > 0.05$). The strength of the correlation was improved little by shifting time frames by 1 or 2 wk to account for any time lag between rainfall and adult emergence (data not shown). Among the four trapping locations, mosquito numbers were significantly correlated for corresponding collection dates between years only for Tiano (Pearson's $r = 0.431$, $N = 25$, $P = 0.031$).

Average numbers of *Ae. polynesiensis* females captured per collection date (across locations and traps) were highly variable but equivalent (Student's $t = -0.088$, $P = 0.93$) during the first (mean ± SD = 267.92 ± 273.78) and second (260.0 ± 201.0) years (Fig. 2). Trap catches on a given date (across both years) were significantly correlated for Toamaro × Horea ($\rho = 0.356$, $N = 51$, $P = 0.010$); Toamaro × Tiano

($\rho = 0.508$, $N = 51$, $P = 0.0001$); and Tiano × shoreline ($\rho = 0.549$, $N = 33$, $P = 0.001$).

Collections also differed by location ($\chi^2 = 168.1$, df = 3, $P < 0.0001$) with significantly more *Ae. polynesiensis* females and males captured on Toamaro than on Tiano or the shoreline (Table 2). Mean numbers of *Ae. polynesiensis* captured on Horea were high in magnitude, similar to Toamaro, but with sufficient variability to be not significantly different from numbers on Tiano (Fig. 3). Although initiated later, trapping on the Raiatea shoreline yielded similar numbers between Tiano and the shoreline (Fig. 3). Within a location, site order ($\chi^2 = 0.330$, df = 3, $P < 0.85$) and specific Biogent trap used ($\chi^2 = 1.88$, df = 2, $P < 0.39$) did not influence mean numbers of female *Ae. polynesiensis* captured. However, numbers of female *Ae. polynesiensis* captured among trapping sites at a location were not uniform ($\chi^2 = 8.27$, df = 2, $P < 0.016$). In addition, fewer females were captured at the fourth collection location than the three visited earlier the same day ($\chi^2 = 26.3$, df = 3, $P < 0.0001$).

Adult Size. *Aedes polynesiensis* female wing lengths were not normally distributed ($N = 695$, $W = 0.994$, $P = 0.004$). Female *Ae. polynesiensis* from the shoreline (mean [SE] = 2.466 [0.014] mm) and Horea (2.428 [0.010] mm) had wing lengths that were equivalent (by Steel–Dwass method, $q = 2.569$) but significantly larger than their counterparts from Tiano (2.345 [0.008] mm) and Toamaro (2.374 [0.011] mm), which were equivalent. Mean female *Ae. polynesiensis* wing lengths also differed by date of collection for Horea (Wilcoxon's $\chi^2 = 66.416$, df = 13, $P < 0.0001$) and Toamaro $\chi^2 = 125.33$, df = 14, $P < 0.0001$) but not Tiano ($\chi^2 = 4.403$, df = 8, $P = 0.819$ or the shoreline ($\chi^2 = 5.962$, df = 6, $P = 0.432$). The correlation between numbers of *Ae. polynesiensis* females captured and their mean wing lengths was not significant ($\rho = -0.454$, $N = 17$, $P = 0.109$, $P = 0.675$).

Sizes of *Ae. polynesiensis* females emerging from the densest populations were analyzed further for seasonal trends. Wing lengths of females collected on Horea and Toamaro during the wet (December–March) and dry (April–November) seasons were not normally distributed ($N = 629$, $W = 0.991$, $P = 0.0006$). There was a significant within the model effect ($F = 15.04$; $P = 0.0001$). Overall, mean female wing lengths were significantly longer in the dry season (2.43 [0.011] mm) than in the rainy season (2.35 [0.014]
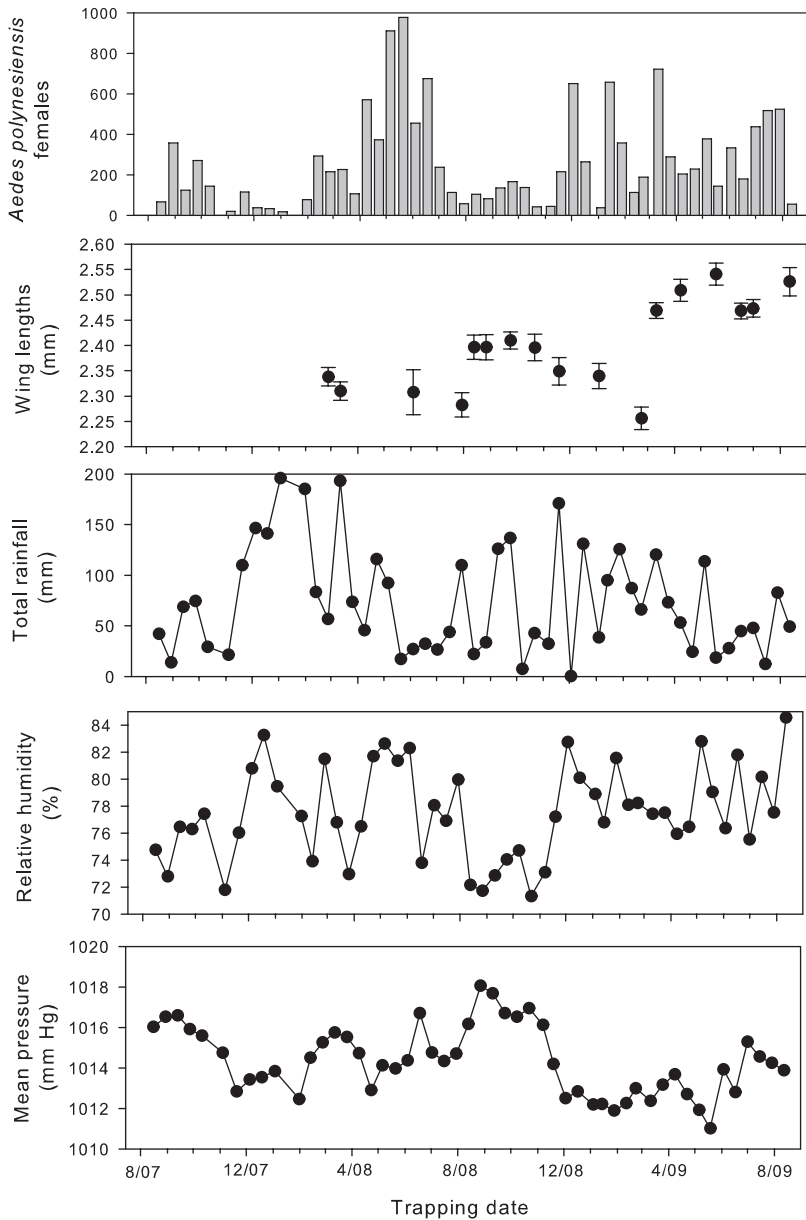
Fig. 2. (A) Total *Ae. polynesiensis* females collected in BG-Sentinel traps on three Raiatea *motus*, (B) *Ae. polynesiensis* mean (SE) female wing lengths captured per date, (C) Total rainfall, (D) Mean relative humidity, and (E) Mean barometric pressure for each sample period.

mm) (LS Means Student's $t = -5.56$, $p = 0.0001$). There were no significant differences between Horea and Toamaro during the wet or the dry seasons (LS Means Tukey HSD $Q = 2.58$, $p = 0.054$ and $p = 0.66$, respectively, Fig. 4).

Weather Data. Typical of the tropical oceanic climate of French Polynesia, weather conditions on Raiatea were variable during the period of study. However, some conditions fluctuated more than others. The weather station on Tiano recorded nine weather variables at 10-min intervals ($N = 92,839$

records); unitless coefficients of variation (SD/mean) allow for comparisons among variables (Table 3). Rainfall showed the greatest variability (CV = 8.72) with frequent high rainfall (>14 mm during 10-min intervals). During the sampling period, 3.62 m of rainfall was recorded by the weather station. Solar radiation also was variable; however, the instrument recorded during both day and night. The mean maximum solar radiation (which excludes nighttime measurements included in Table 3) was 1,174.8 W/m². Wind speed (and gust speed) at 3 m above the ground
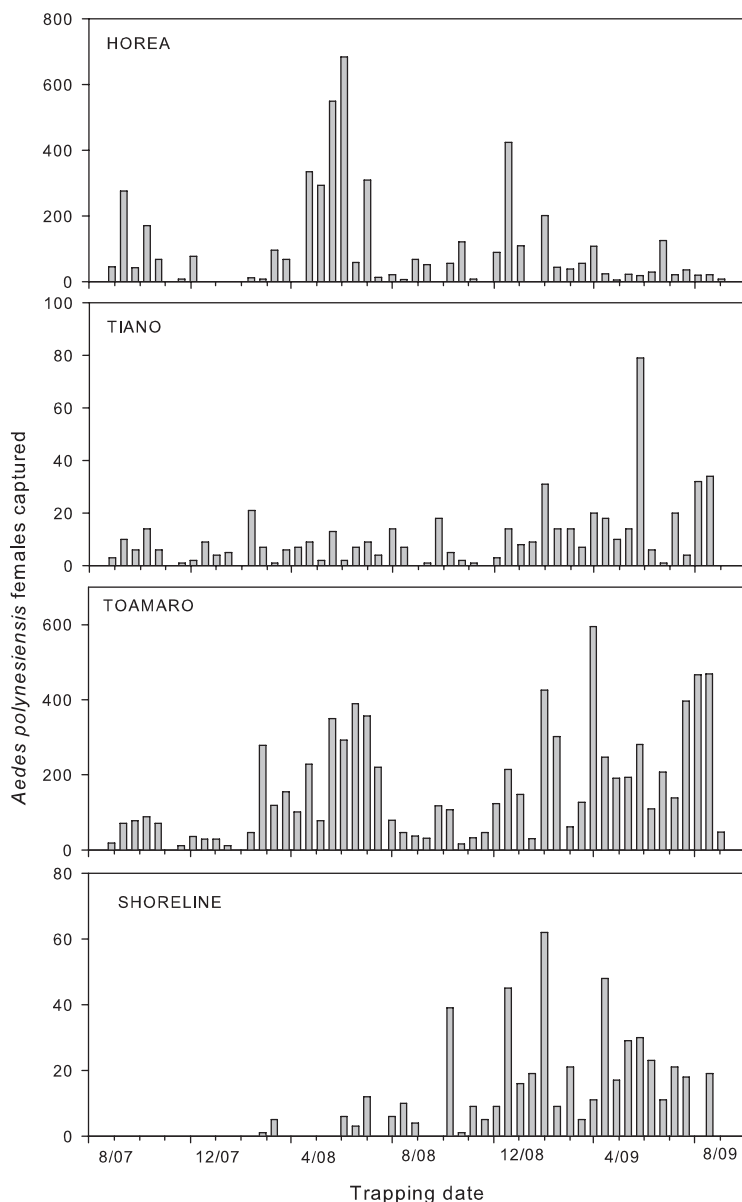
Fig. 3. Total *Ae. polynesiensis* females captured per date on three Raiatea *motus* and adjacent shoreline.

also were variable, with likely consequences upon mosquito movement nearer the ground. The prevailing wind direction (125.66ø) corresponds to ESE subtropical trade winds. Although wind direction shifted to all quarters of the compass, it delivered air masses relatively consistent in air temperature and barometric pressure.

Trap catches during biweekly collections correlated poorly with weather variables measured during the previous fortnight (Fig. 2). Only mean maximum barometric pressure was consistent in being significantly correlated with mean numbers of *Ae. polynesiensis* females captured on Toamaro ($\rho = -0.327$, $P = 0.026$), Tiano ($\rho = -0.342$, $P = 0.020$), and the shoreline ($\rho =$

0.467, $P = 0.011$), but not Horea ($\rho = 0.009$, $P = 0.953$). Maximum solar radiation ($\rho = -0.398$, $P = 0.006$) and minimum air temperature ($\rho = 0.328$, $P = 0.026$) were significantly correlated with Toamaro trap catches, whereas maximum rain ($\rho = 0.414$, $P = 0.026$) and minimum soil temperatures ($\rho = 0.373$, $P = 0.046$) on Tiano were significantly correlated with shoreline *Ae. polynesiensis* female numbers.

The weather station failed to record data during two periods of the study: 6 June-4 July 2008 and 20 November 2008–1 February 2009. Therefore, air temperature, relative humidity, wind gust speed, and wind direction measurements generously were provided by Meteo France from data collected at the Bora Bora
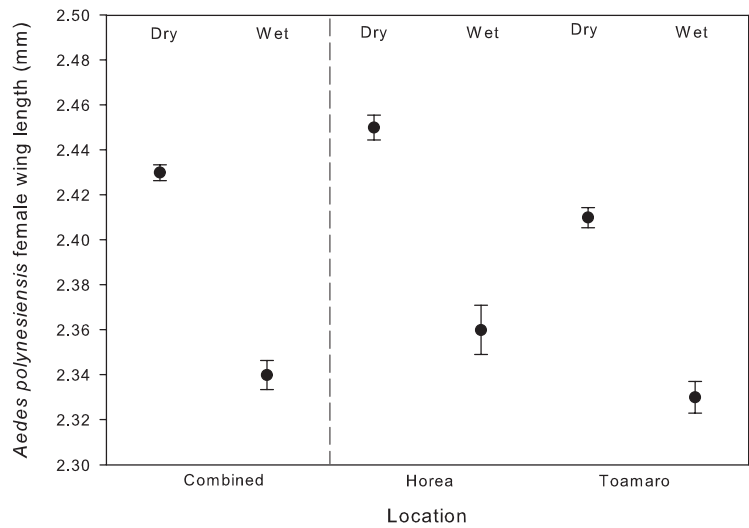
Fig. 4. *Ae. polynesiensis* mean (SE) female wing lengths collected on Horea and Toamaro during the dry (April–November) and the wet (December-March) seasons (combined and individually).

Airport (Fig. 1), 51 km NW of Tiano (Google Earth 5.0). Daily values from the Bora Bora Airport and Tiano correlated significantly for 68 overlapping days when both data sets were available (analysis not shown); therefore, the proxy data were used to fill gaps in weather measurements from Tiano.

For each of nine weather variables, mean, maximum and minimum values from 10-min measurements were calculated across 14-d intervals that corresponded with the frequency of mosquito sampling periods. These data were used in multiple regression analyses to explain the amount of variation in mosquito capture rates during the sampling period. The multiple regression model with all weather variables explained 66.5% of the variation in numbers of TOTAL MOSQUITOES captured for all locations, but represented a model that was not significant ($F_{24, 21} = 1.741$, $P = 0.102$). Only MAX PRESSURE (maximum atmospheric pressure) and MAX RH (maximum relative humidity) during the corresponding fortnightly period were significant factors in the model. Therefore, a forward stepwise regression was performed and MAX SOLAR, MEAN SOLAR, MAX AIR (temperature), MAX RH and MIN RH produced a significant model ($R^2 = 0.430$; $F_{5,40} = 6.04$; $P = 0.0003$). Because Toamaro *motu*

is the least managed of the *motus*, mosquito numbers may be determined more strongly by weather conditions. The forward stepwise regression analysis with MAX PRES, MIN PRES, MAX SOLAR, MEAN SOLAR, MAX WIND, MAX AIR, MAX RH, and MIN RH produced a significant model ($F_{8,37} = 5.03$, $P = 0.00003$) that explained 52.1% of the variation in TOTAL MOSQUITOES captured on Toamaro.

Discussion

Despite the proximity of the four locations, there were dramatic differences in vector numbers sampled, including differences among the *motu Ae. polynesiensis* populations. Typically, *motus* have a coral base and are adjacent to channels cut by streams descending from steep valleys of the main island's volcanic core (or its remnant on "low islands"). The three *motus* were selected because they are similar distances from the shoreline and share a portion of the lagoon. As a result, they have similar substrates and are exposed to similar ocean effects, weather patterns, and natural colonization rates. Contrarily, they represent the range of human use for *motus*, allowing for testing of

Table 3. Weather conditions on Tiano *motu* July 2007–August 2009 from data collected at 10-min intervals

Weather variable	Mean	SD	CV	Max	Min.
Rain (mm)	0.039	0.340	8.72	14.6	0
Air temperature (°C)	27.517	2.349	0.085	48.007	20.246
RH (%)	77.297	8.772	0.113	95.8	45.9
Pressure (mbar)	1,014.61	2.211	0.002	1,021.55	1,006.85
Solar radiation (W/m²)	167.22	286.22	1.71	1,276.9	0.6
Wind speed (m/s)	0.851	0.965	1.13	9.09	0
Gust speed (m/s)	2.357	2.110	0.895	15.59	0
Wind direction (ø)	125.66	88.542	0.705	355.2	0
Soil temperature (°C)	26.575	2.179	0.082	34.255	20.555

SD, standard deviation; CV, coefficient of variation; RH, relative humidity.

control strategies against discrete mosquito populations subject to different human interventions.

All three *motus* host *C. carnifex* populations; the numerous, cryptic burrows of these land crabs represent important sources of *Ae. polynesiensis* mosquitoes that currently escape vector control efforts (Lardeux et al. 2002). Likewise, the cryptic nature of treeholes and other phytotelmata in native and ornamental vegetation make these developmental sites difficult to eliminate. Otherwise, developmental sites among the three *motus* are influenced heavily by the degree of human intervention. Although coconut palms are present on all three *motus*, their decaying fruits do not provide equivalent developmental opportunities for the three mosquito populations. On Tiano, coconut trees are banded to deny treetop access to rats while the fruits are on the trees and fallen coconuts are regularly collected and discarded. Trees are not banded on the other two *motus*, but fallen coconuts are collected more frequently on Horea than on Toamaro. None of the *motus* was occupied permanently; however, humans were encountered more frequently on Horea than on Toamaro. During the survey, the number of temporary dwellings on Horea increased and people were present on 14 survey dates (compared with one date on Toamaro). Although people and their domestic animals represent additional blood sources for mosquitoes and their refuse provides artificial containers for immatures, increased human activities (burning, clearing of vegetation, insecticide, and repellant application) during the second year likely had a greater impact on Horea than on Toamaro.

Toamaro is the least managed of the three *motus.* Other people besides researchers were encountered only once, and there was a single burning record for Toamaro during the 2 yr of the study. *Aedes polynesiensis* biting rates typically reach hundreds per hour everywhere on the *motu* except in presence of a steady breeze on the exposed windward shore (D.R.M., unpublished data). Interestingly, weather data better explained mosquito abundance on Toamaro than on the other *motu* or the shoreline. The Raiatea shoreline does not have an isolated mosquito population and was not intended for trial of new technology. Thus, it was not included in the preliminary sampling scheme. Similar to the *motus*, the three shoreline sample sites are <2 m above sea level. But these sample sites are adjacent to forested volcanic ridges, intervening riparian valleys, the road circling the island, and permanently occupied dwellings; therefore, the shoreline is much more heterogeneous and influenced by surrounding contiguous habitats. The shoreline was ultimately included in the sampling scheme for comparison purposes, particularly to identify any disparities in mosquito numbers relative to the *motu* populations. It is interesting that Tiano, the most managed of the *motus*, had mosquito numbers similar to the shoreline.

There was high variability in BG-Sentinel trap catches with only weak seasonal trends in mosquito numbers consistent between the 2 yr of collection. In addition, there was little consistency by date in size or

numbers between years, with only Tiano's numbers correlated between years. However, there were overwhelming numbers of female *Ae. polynesiensis* captured at all locations and during both years of the study. Mosquitoes were collected during the morning peak of host seeking to maximize capture of *Ae. polynesiensis* females.

Although they differ in size and human activities, Horea and Toamaro were similar in producing high mosquito numbers. Peaks in mosquito numbers overlapped between Horea and Toamaro during the first year (although their magnitudes differed). This likely reflects similarities in developmental sites, bloodmeal sources, and vegetational cover. However, mean female *Ae. polynesiensis* were larger overall from Horea than Toamaro and temporal trapping patterns differed for these two *motus* during the second year of collection (Fig. 3). Horea's mosquito population did not reach equally high numbers March–August 2009. By comparison, numbers of mosquitoes trapped on Tiano were low (<35 in three traps) for all but one of the 51 dates. Extensive chemical control and source reduction on Tiano have reduced but not eliminated mosquito production on this *motu;* such sustained effort is impractical for vector control over larger temporal and spatial scales in French Polynesia. Equivalent wing lengths for Tiano mosquitoes with those from Toamaro (the most productive *motu*) suggest that conditions within developmental sites were similar even though fewer sites were available. Presumably, the low numbers of adults captured on Tiano are consistent with little immigration of mosquitoes from neighboring *motus* or the main island. The shoreline sites on Raiatea yielded relatively few mosquitoes but marginally greater species homogeneity than the *motus*.

Although there were no significant differences among collections as a function of the trap used, trap catches on the *motus* were not spatially uniform. On average, significantly more *Ae. polynesiensis* females were captured at the most central *motu* site. Exposure in the flight paths and distances from putative developmental sites presumably differed across the terrain. Whatever the cause, these data indicate heterogeneity in adult numbers, even across these small isolated habitats.

Trap collections depend upon the presence and activity of mosquitoes and may not reflect absolute numbers, host seeking, or putative disease transmission (Southwood and Henderson 2000). Because no carbon dioxide or artificial attractants were used, male *Ae. polynesiensis* (which intercept host-seeking females, unpublished data) were not adequately sampled by the protocol described here. If not because of a trapping bias, the paucity of male *Ae. polynesiensis* on these Raiatea *motus* would deserve additional attention. Departures from the expected 1:1 sex ratio for *Ae. polynesiensis* because of competition tend to favor males rather than reduce their production (Mercer 1999, Mercer et al. 2005). Trap catches also reflected very low numbers of *Cx. quinquefasciatus.* Individuals of this nocturnal species, which is the principal vector

of periodic *W. bancrofti* in most of the world, were not captured on Horea (despite the presence of developmental sites) and were captured infrequently on Toamaro and the shoreline. Low trap catches of *Cx. quinquefasciatus* and of all mosquitoes at the fourth location sampled per collection day likely reflect non-optimal collection times and trapping methods. Nonetheless, it will be important to monitor other vector species as *Ae. polynesiensis* populations are targeted. Vector control should not augment vector status of other species nor negatively impact beneficial or "neutral" species in the target area.

One promising control strategy involves the mass release of incompatible male *Ae. polynesiensis* hosting a strain of maternally inherited *Wolbachia pipientis* Hertig & Wolbach (Alphaproteobacteria: Rickettsiales). *Wolbachia* are obligate endosymbionts that manipulate the reproduction of their hosts. In mosquitoes, *Wolbachia* cause cytoplasmic incompatibility (CI) when uninfected females mate with infected males (unidirectional CI) or infected females are inseminated by males carrying an incompatible strain (bidirectional CI). An incompatible strain of *Ae. polynesiensis* was developed through interspecific hybridization; mass release of infected males eliminated populations of wild-type *Ae. polynesiensis* in cage studies (Brelsfoard et al. 2008). Irradiation techniques have been developed specifically to target females infected with this strain that might escape mechanical sorting (Brelsfoard et al. 2009).

Because size of female mosquitoes tends to be related to fitness, vector control must consider both numbers and sizes of females in the target population. A control strategy that produces fewer but more robust females may fail at lowering disease transmission rates. There was high natural variability in *Ae. polynesiensis* female size throughout the study period. The mean sizes of female *Ae. polynesiensis* collected from Horea and Toamaro populations during the dry season were significantly greater than those collected during the rainy season, suggesting females are more robust during the dry season on these productive *motus.* However, shoreline females were, on average, larger than females captured on the *motus,* implying that the large populations on the *motus* develop under intense intraspecific competition. Reducing the numbers of adult mosquitoes is likely to ameliorate larval crowding, resulting in higher survival rates and larger, more fecund adults. A control strategy timed to coincide with the sparsest target population may encounter females larger than average.

A large number of *Ae. polynesiensis* was removed from the population of Toamaro in December 2008 for a separate study (data not shown). Although the removal of adults was timed to avoid biweekly collections, we were curious to measure potential impacts upon scheduled Biogent Sentinel trapping. Despite the extra collections, large numbers of *Ae. polynesiensis* were captured on Toamaro during December 2008-March 2009 (with no apparent effect on wing length); by contrast, there was no peak in numbers of mosquitoes captured on Horea between January and March

2009. At least during the short term, mosquito populations on *motus* appear to be resilient. Control strategies must be sustained, perhaps corresponding to the development of several natural cohorts. In addition, in view of high natural variability (between collections, between seasons, and among habitats), it is imperative to monitor *Ae. polynesiensis* female numbers for a sustained period after release of incompatible males.

In view of the variation in mosquito population patterns among the *motus,* it is inappropriate to generalize our results to additional *motus* influenced by different natural and anthropogenic effects. Nonetheless, we successfully monitored temporal and spatial patterns of mosquito numbers and investigated the effects of weather upon mosquito abundance for *motus* that would serve as targets for development of vector control technologies.

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