

***Aedes aegypti* (L.) and *Aedes polynesiensis* Marks (Diptera: Culicidae) in Moorea, French Polynesia: A Study of Adult Population Structures and Pathogen (*Wuchereria bancrofti* and *Dirofilaria immitis*) Infection Rates to Indicate Regional and Seasonal Epidemiological Risk for Dengue and Filariasis**

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Aedes aegypti (L.) and *Aedes polynesiensis* Marks (Diptera: Culicidae) in Moorea, French Polynesia: A Study of Adult Population Structures and Pathogen (*Wuchereria bancrofti* and *Dirofilaria immitis*) Infection Rates to Indicate Regional and Seasonal Epidemiological Risk for Dengue and Filariasis

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ABSTRACT Populations of *Aedes aegypti* (L.) and *Aedes polynesiensis* (Marks) on Moorea Island, French Polynesia, the local vectors of dengue and filariasis, respectively, were sampled by landing/biting collection at nine localities on the east, north, and west coasts, during the late dry season, early and late wet season (September–May) 2003 and 2004, to investigate epidemiologically important features of the populations and compare them between regions and months. Biting rates of both species tended to increase (but not always significantly) for each species in each region each month from the late dry season to the late wet season, and the north coast region had significantly higher biting rates of *Ae. aegypti*. Insemination rates of *Ae. polynesiensis* females (94.5–98.8%) were consistently greater than those of *Ae. aegypti* (87.5–93.5%) throughout the study, but there was no significant difference in the insemination rates of either species between months and regions. Parity rates were generally highest in north coast samples and lowest in west coast samples for both species and generally increased (albeit not always significantly) by month for each species, with a range of 52.9–88.8% for *Ae. polynesiensis* and 28.6–53.6% for *Ae. aegypti*, although the high gravid rate (15.8–45.9%) of *Ae. aegypti* samples (reflecting its feeding more than once in a gonotrophic cycle) confounded both intraspecific and interspecific comparisons. Filarial infection was rare in *Ae. aegypti*, although both *W. bancrofti* and *D. immitis* were recorded, and infection rates in *Ae. polynesiensis* increased through the study period in each region for both filarias, with up to 4.6% infected and 1.4% infective for *W. bancrofti* and up to 6.3% infected and 2.5% infective for *D. immitis*. For *W. bancrofti*, infection rates were significantly lower on the west coast and also in the dry season, whereas rates for infective stages were significantly greater in the late wet season. For *D. immitis* there was no significant difference in infection rates between regions, but rates were significantly greater in the late wet season. Rainfall in all months sustains populations of both vectors and explains the relatively few significant differences between seasons; however, the wet season may provide for increased vector abundance and longevity, and present a potentially increased risk for transmission. Although the differences shown between regions also were limited in a statistical sense, there were increased risks for the northern and eastern regions, where both locals and tourists are concentrated and where the seaports and airport are located, and these areas should be priority targets for disease surveillance and vector control.

KEY WORDS *Aedes*, parity rates, *Wuchereria bancrofti*, *Dirofilaria immitis*, French Polynesia

ON THE ISLAND OF MOOREA, French Polynesia, *Aedes aegypti* (L.) and *Aedes polynesiensis* (Marks) are the dominant pest mosquitoes and also the local vectors of viral (dengue viruses) and filarial (*Wuchereria bancrofti* and *Dirofilaria immitis*) pathogens, respectively.

Bancroftian filariasis (*W. bancrofti*) is endemic in French Polynesia, and the most important vector is *Ae. polynesiensis* (Rosen 1955). Kessel (1971) noted that

Tahiti had the highest microfilarial rates in the South Pacific region after the Second World War. A control program was instituted in the 1950s, and for many years case treatment and mass drug administration with diethylcarbamazine reduced disease in French Polynesia to <1% in 1980, compared with a prevalence of 30–40% in the 1940s (Burkot et al. 2002), but after mass treatment stopped, the prevalence rose to ≈20% (Lardeux et al. 2002).

Dengue viruses circulate in the Pacific region intermittently, and in French Polynesia they have caused 10 epidemics in the past 60 yr (Deparis et al. 1998, Lardeux et al. 2002). *Ae. aegypti* is generally

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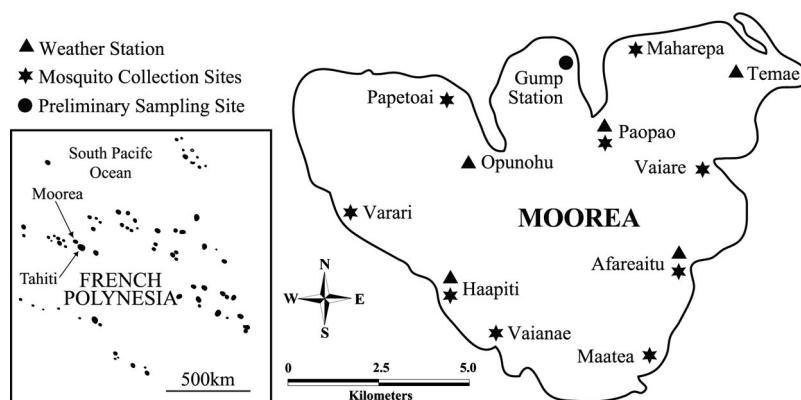


Fig. 1. The island of Moorea, French Polynesia, showing the preliminary study site; the principal mosquito collection sites on the east, north, and west coasts; and the meteorological stations.

thought to be the principal vector of dengue viruses in most urban situations in the Pacific region as elsewhere (Gubler 1988). However, Maguire et al. (1971) proposed that *Ae. polynesiensis* was a vector of dengue viruses in rural areas, and Rosen et al. (1985) showed *Ae. polynesiensis* to be highly susceptible to infection with various dengue viruses, noting that, circumstantially, it must have been responsible for transmission in the South Pacific region.

Because there is no specific vaccine or antiviral chemotherapy against dengue viruses, control of the vectors through source reduction, and other sanitation and environmental management approaches directed at its artificial container habitats in domestic situations, has been integral to disease control. Although filaricides do exist to counter *W. bancrofti*, it is thought that disease management through chemotherapy will not eliminate infection from the Polynesian communities (Esterre et al. 2001), but control of *Ae. polynesiensis* has proven extremely problematic (Lardeux et al. 2002), principally because of its extensive colonization of natural containers such as tree holes, palm fronds, coconuts, and crab holes in peridomestic situations as well as the artificial containers used by *Ae. aegypti* (Lee et al. 1987). An understanding of the relative roles of *Ae. aegypti* and *Ae. polynesiensis* as local vectors is critical to appropriate and effective management of dengue and filariasis on Moorea.

The determinants of the vectorial capacity of mosquitoes are complex (Hardy 1988, Turell 1988). Additionally, variability in competence can exist among populations of the one vector species. Failloux et al. (1995) found different geographic strains of *Ae. polynesiensis* displayed different vectorial competence for *W. bancrofti* in French Polynesia, and Lardeux and Cheffort (2001) described a statistical model for filariasis in French Polynesia that demonstrated an association between ambient temperature and latitude, *Ae. polynesiensis*, and *W. bancrofti*, and the dynamics of transmission in the various island groups. Gubler et al. (1979) showed significant variation in susceptibility to four dengue serotypes among strains of *Ae. aegypti* from Asia, Africa, and the Pacific, and

Vazeille-Falcoz et al. (1999) found geographic differences in oral susceptibility for dengue viruses between east coast and west coast populations of *Ae. aegypti* on Tahiti, indicating the existence of genetically and perhaps ecologically different groups. All these results have implications for the behavioral and physiological characteristics of the vectors that influence epidemiological risk on Moorea.

The principal objective of this investigation was to gain an overview of the seasonal and regional risk of arboviral (dengue) and filarial (*W. bancrofti*) infection for humans (and with *D. immitis* for dogs) being bitten by *Ae. aegypti* and *Ae. polynesiensis* in Moorea. Identification of spatial and temporal differences in epidemiologically important features of the vector population, such as relative density, survivorship, and infection with pathogens, can provide data for modeling the dynamics of such infections.

Materials and Methods

The island of Moorea (17° 30' S latitude, 149° 50' W longitude) is located in French Polynesia, 19 km to the northwest of Tahiti and is ≈132 km² (Fig. 1). It has a resident population of 14,471 people (Census November 2002, Institut Statistique de Polynésie Française), many of whom commute to Tahiti for business and employment (1,493,007 ferry passengers between Tahiti-Moorea in 2003; Source: Port autonome de Papeete). Moorea receives ≈100,000 visitors annually (Moorea Visitors Bureaus 2002).

Moorea has a tropical climate with a wet season (November–April) and a dry season (May–October). Rainfall data for the duration of the study period were gathered from Meteo France weather stations on the north (Opunohu and Paopao, 80 and 100 m above sea level [a.s.l.], respectively), east (Temae and Afareaitu, both 1 m a.s.l.), and west (Haapiti, 2m a.s.l.) coasts of Moorea for the months of the study period in 2003 and 2004 and with long-term data for 1980–1991. Monthly average maximum and minimum temperatures vary little throughout the year; mean temperatures during

the dry season range from 24.5 to 25.9°C and during the wet season from 26.1 to 27.2°C (Meteo France).

Human bait collections were used to sample the host-seeking component of the *Ae. aegypti* and *Ae. polynesiensis* populations on the island. All sampling was undertaken by the same person (R.C.R.) to provide consistency in attraction and technique, with an aspirator while sitting outside houses and other buildings in residential communities of Moorea. Spatial variation was investigated by sampling at nine localities among three regions, the north, east, and west coasts of this triangular-shaped island: Maharepa, Paopao, and Papetoai on the north coast; Maatea, Afareaitu and Vaiare on the east coast; and Vaianae, Haapiti, and Varari on the west coast (Fig. 1). Temporal variation was investigated by sampling during the late dry season in the mid-September and mid-October 2003, during the early wet season during mid-November 2003, and during the late wet season in the last week of April and first week of May 2004.

Preliminary Investigation. To optimize sampling for the vectorial indices of abundance, insemination, parity and infection, morning and afternoon samples of *Ae. aegypti* and *Ae. polynesiensis* were compared in a preliminary investigation. Over 3 d in early September 2003, human bait collections were conducted for 2 h postsunrise (called morning) and for 2 h presunset (called afternoon) at the Gump Station on the north coast (Fig. 1), and the samples were dissected to reveal insemination and ovarian development. The mean percentage of mated, gravid, and parous mosquitoes was compared between the two collection times using one-way analysis of variance (ANOVA).

Principal Investigation. The results of the preliminary investigation determined that collections for the principal investigation of relative abundance, physiological status, and survivorship, and filarial infection, that followed during September, October, and November 2003 and April–May 2004 should be undertaken during the afternoon. Thus, biting collections were undertaken during the 2 h preceding sunset in each of the nine localities over ≈ 2 wk in each of the months, with ad hoc sampling at a number of sites in each locality and with collection times at each site being not time limited in an effort to collect as many specimens as possible. All site collections for each locality in each region were then combined for dissection and presentation on a regional (east, north, and west coast) basis.

Relative abundance was, however, investigated strictly by recording the biting rate (number of females collected per 15-min interval) at the same three selected sites (one per locality mentioned above) in each region on each occasion, following Tidwell et al. (1990) who proposed that several collection sites in any particular area were required to obtain reliable data on adult populations. Collections in each locality occurred on the same day and under similar conditions, but the regional sampling necessarily took place on separate but consecutive days under generally similar conditions, and the mean biting rates for each

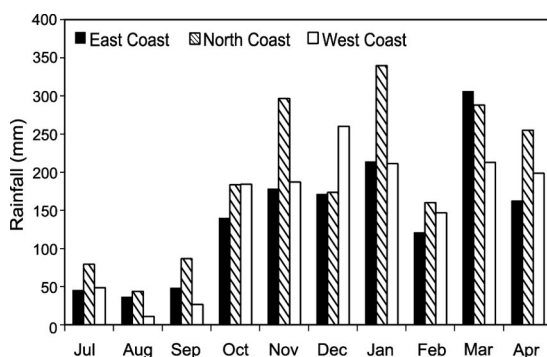


Fig. 2. Total monthly rainfall on the east coast, north coast and west coast of Moorea, French Polynesia, July 2003–April 2004.

species in the three regions over the 3 mo (October–December) were compared using two-way ANOVA.

Physiological status and survivorship were investigated by recording the insemination rate and parous rate in the collection samples. The aspirated mosquitoes were frozen within a few hours of collection so that ovarian development would not proceed, and blood-fed and gravid mosquitoes could be assumed to have been in that state when collected. All females were dissected by the same person (R.C.R.) to provide consistency in technique and interpretation, with the spermathecae being inspected for insemination, and the ovaries being examined for eggs developed to stage III or later to be called gravid (Christophers 1960) or the ovarian tracheoles being examined for extension to be called parous (Detinova 1962). The percentages of mated, gravid, and parous mosquitoes of each species were compared using chi-square analysis for each region across months and for each month across regions.

Filarial infections were investigated in those females determined as being gravid or parous, by dissection for developing filariae in the thoracic musculature (for *W. bancrofti*) and Malpighian tubules (for *D. immitis*), and in the head and other body areas for infective stage filaria that could be identified as either *W. bancrofti* or *D. immitis* as per Iyengar (1957). The mean percentage of infected and infective mosquitoes of each species collected was compared between months and regions by using two-way ANOVA.

Results

During the study period, rainfall increased progressively on all coasts from September to a January peak and gradually decreased toward May (Fig. 2), similar to the long-term pattern (Fig. 3), although the quantity of rain during December and February at the three weather stations was below the long-term average. Data over the 12-yr period from 1980 to 1991 show that the north coast was always the wettest region, but there was little difference between the east and west coast regions (Fig. 3).

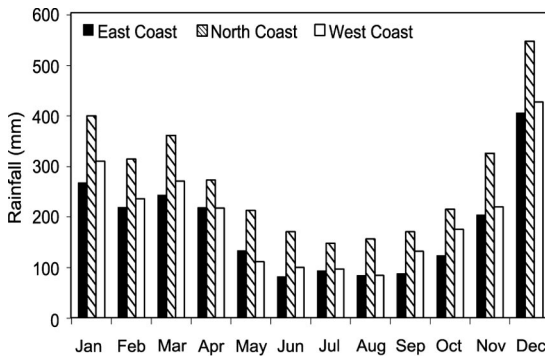


Fig. 3. Average monthly rainfall on the east coast, north coast, and west coast of Moorea, French Polynesia, 1980–1991.

Preliminary Investigation. In the September 2003 comparison of morning and afternoon samples (Table 1), the numbers of each species collected for dissection were dissimilar, reflecting the relatively greater local abundance of *Ae. polynesiensis* in the Gump Station locality. For *Ae. aegypti*, there was a significantly greater proportion of mated ($F_{1,5} = 7.95$; $P = 0.04$) and gravid ($F_{1,5} = 31.06$; $P < 0.01$) mosquitoes collected in the afternoon. For *Ae. polynesiensis*, there was a significantly greater proportion of mated ($F_{1,5} = 12.11$; $P = 0.03$) mosquitoes collected in the afternoon but no significant difference ($F_{1,5} = 1.00$; $P = 0.37$) in the numbers of gravid mosquitoes collected at each time. For both species, there was no significant difference ($F_{1,5} = 2.91$; $P > 0.05$) in the mean proportion of parous mosquitoes collected in the morning or the afternoon. These results indicated that, for both species, the component of the population feeding in the morning was relatively younger and less likely to be inseminated than those attracted to hosts in the afternoon. Therefore, for the principal investigation that followed, only afternoon collections were undertaken.

The Principal Investigation. In total, 341 *Ae. aegypti* and 853 *Ae. polynesiensis* were collected for dissection.

Relative Abundance. In October and November 2003 and April–May 2004, the mean biting rates of the two species in the three regions varied substantially (Fig. 4). Overall, there was a significantly lower biting rate ($F_{1,53} = 21.4$; $P < 0.01$) of *Ae. aegypti* ($10.8 \pm 2.3/15$ min) compared with *Ae. polynesiensis* ($28.7 \pm 3.1/15$ min) reflecting the relative local abundance of each species in each region. There was no significant difference ($F_{2,26} = 0.34$; $P = 0.71$) in mean biting rates

of *Ae. aegypti* between months for each region, but there was a significantly higher ($F_{2,26} = 4.91$; $P = 0.02$) mean biting rate recorded on the north coast (Fig. 4). There was a general increase in the mean biting rate of *Ae. polynesiensis*, but no significant difference between months ($F_{2,26} = 2.58$; $P = 0.10$) or locations ($F_{2,26} = 3.29$; $P = 0.06$) (Fig. 4).

Physiological Status and Survivorship. The overall insemination rate for *Ae. aegypti* was $90.9 \pm 1.8\%$ and for *Ae. polynesiensis* $97.0 \pm 1.6\%$. For *Ae. aegypti*, there was no significant difference in the insemination rate in the three regions in September ($\chi^2 = 0.29$, $P = 0.86$), October ($\chi^2 = 0.56$, $P = 0.76$), November ($\chi^2 = 0.04$, $P = 0.98$), or April ($\chi^2 = 0.09$, $P = 0.95$), and there was no significant difference in the insemination rate between months for the east coast ($\chi^2 = 0.55$, $P = 0.91$), north coast ($\chi^2 = 0.30$, $P = 0.96$), and west coast ($\chi^2 = 0.03$, $P = 0.99$). For *Ae. polynesiensis*, there was no significant difference in the insemination rate in the three regions in September ($\chi^2 = 1.40$, $P = 0.49$), October ($\chi^2 = 0.33$, $P = 0.85$), November ($\chi^2 = 0.80$, $P = 0.67$), or April ($\chi^2 = 2.15$; $P = 0.34$) or between months for the east coast ($\chi^2 = 2.80$, $P = 0.42$), north coast ($\chi^2 = 2.07$, $P = 0.56$), and west coast ($\chi^2 = 1.70$, $P = 0.64$).

There was a general increase by month in the percentage parous for both species, with the overall mean parity rate higher for *Ae. polynesiensis* ($73.6 \pm 10.8\%$) than *Ae. aegypti* ($41.0 \pm 8.4\%$) and generally higher on the east coast and north coast for both species (Fig. 5). For *Ae. aegypti*, there was no significant difference in the parity rate in the three regions in September ($\chi^2 = 1.89$, $P = 0.39$), October ($\chi^2 = 0.57$, $P = 0.75$), November ($\chi^2 = 0.79$, $P = 0.67$), or April ($\chi^2 = 0.23$, $P = 0.89$), and there was no significant difference in the parity rate between months for the east coast ($\chi^2 = 2.12$, $P = 0.55$), north coast ($\chi^2 = 3.08$, $P = 0.38$), and west coast ($\chi^2 = 1.44$, $P = 0.70$). For *Ae. polynesiensis*, there was no significant difference in the parity rate in the three regions in September ($\chi^2 = 2.74$, $P = 0.26$), October ($\chi^2 = 2.62$, $P = 0.27$), November ($\chi^2 = 4.59$, $P = 0.10$), or April ($\chi^2 = 1.96$, $P = 0.38$), but the parity rate was significantly higher in April compared with September, October, and November for the east coast ($\chi^2 = 17.90$, $P < 0.01$), north coast ($\chi^2 = 9.99$, $P = 0.02$), and west coast ($\chi^2 = 8.17$, $P = 0.04$).

Comparison of parity rates between species was confounded by the significantly greater ($F_{1,23} = 234.9$; $P < 0.01$) overall percentage of gravid *Ae. aegypti* ($35.7 \pm 2.3\%$) compared with *Ae. polynesiensis* ($0.6 \pm 0.3\%$) (Fig. 6). There was no significant difference in

Table 1. Percentages of *Ae. aegypti* and *Ae. polynesiensis* populations mated, gravid, and parous collected at human bait in the morning (2 h postsunrise) and afternoon (2 h presunset) over 3 d at Gump Station, Moorea, French Polynesia, September 2003

Species	2 h postsunrise				2 h presunset			
	n	% mated	% gravid ^a	% parous	n	% mated	% gravid	% parous
<i>Ae. aegypti</i>	32	77.9 \pm 3.1	21.8 \pm 2.0	25.5 \pm 4.4	52	90.0 \pm 2.5**	40.0 \pm 2.5**	25.5 \pm 2.7
<i>Ae. polynesiensis</i>	49	86.3 \pm 3.0	0	51.3 \pm 2.0	75	97.5 \pm 1.2**	2.3 \pm 2.3	63.9 \pm 7.1

Means significantly (** $P < 0.01$) greater for one-way ANOVA (arcsine square-root transformation).

^a Gravid defined as specimens that had ovaries in Christophers stage III or later.

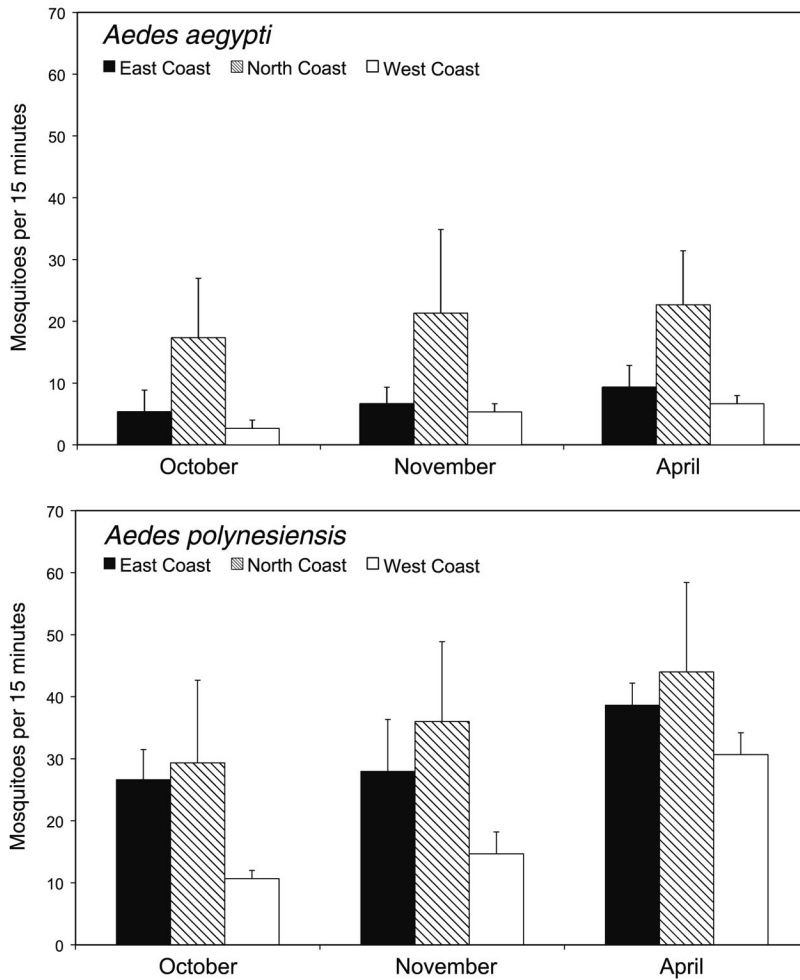


Fig. 4. Mean biting rates (mosquitoes per 15 min) for *Ae. aegypti* (a) and *Ae. polynesiensis* (b) recorded on the east coast, north coast, and west coast of Moorea, French Polynesia, during three sampling periods from October 2003 to April 2004.

the percentage of gravid *Ae. aegypti* collected in the three regions in September ($\chi^2 = 4.79$, $P = 0.09$), October ($\chi^2 = 0.31$, $P = 0.86$), November ($\chi^2 = 1.53$, $P = 0.47$), or April ($\chi^2 = 0.32$, $P = 0.85$), and there was no significant difference in the percentage gravid between months for the east coast ($\chi^2 = 0.79$, $P = 0.85$), north coast ($\chi^2 = 0.47$, $P = 0.92$), and west coast ($\chi^2 = 2.76$, $P = 0.43$). Only a few (five of 853) gravid *Ae. polynesiensis* were recorded. A small number of individuals of both species had a few fully developed eggs in their ovaries; these were taken to be relict eggs from a previous oviposition and the females were classified as parous and not gravid.

Filarial Infections. No dual infections were discovered in either species, and there was a general increase from September to April in the combined regional infection rates (infected and infective) of *Ae. aegypti* and *Ae. polynesiensis* for *W. bancrofti* and *D. immitis* (Fig. 7).

Ae. aegypti only rarely revealed infection with ei-

ther *W. bancrofti* (Table 2) or *D. immitis* (Table 3); only one female with *W. bancrofti* and two with *D. immitis* were found in the 120 collected on the east coast, only one with *D. immitis* from the 130 collected on the north coast, and none of the 91 collected in the west coast region. There was no significant difference in the mean percentage of *W. bancrofti* infected *Ae. aegypti* compared between regions ($F_{2, 11} = 1.00$; $P = 0.42$) or months ($F_{3, 11} = 1.00$; $P = 0.46$), and there was no significant difference in the mean percentage of *D. immitis* infected *Ae. aegypti* when compared between regions ($F_{2, 11} = 1.00$; $P = 0.22$) or months ($F_{3, 11} = 1.00$; $P = 0.12$). No individual *Ae. aegypti* infective for *W. bancrofti* or *D. immitis* was collected.

The filarial infections were principally associated with *Ae. polynesiensis*, with the greatest number of developing larvae and all infective (L3) stages of either filarial species found in that species. Individuals infected and infective with *W. bancrofti* or *D. immitis* were collected. There was a significantly lower ($F_{2, 11}$

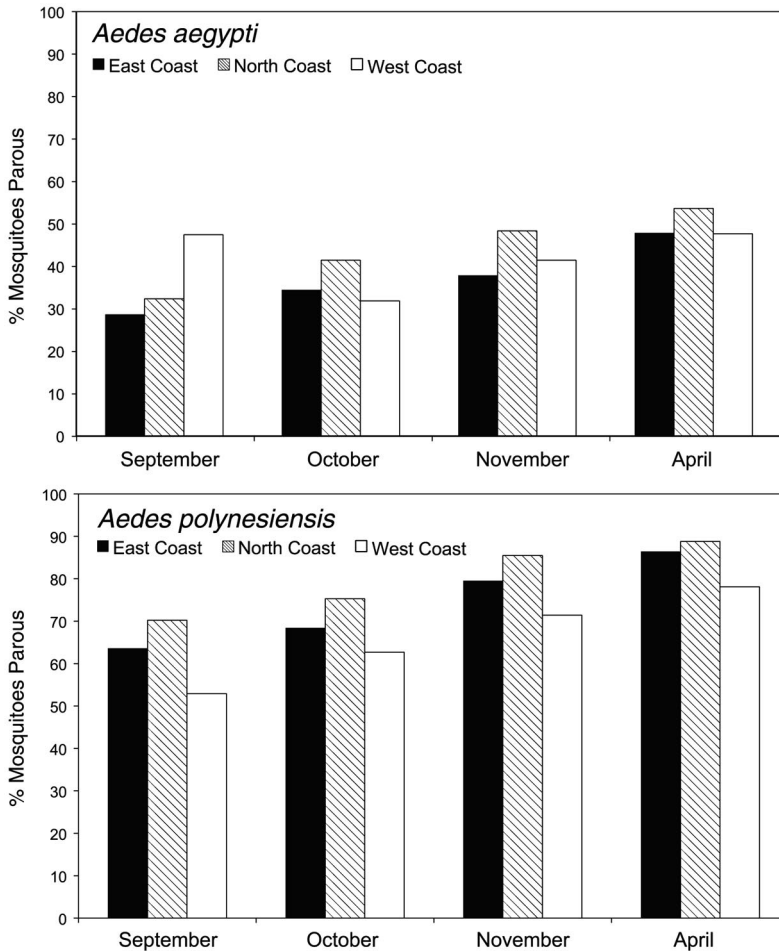


Fig. 5. Percentage parity of *Ae. aegypti* (a) and *Ae. polynesiensis* (b) collected on the east coast, north coast, and west coast of Moorea, French Polynesia, on three occasions between September 2003 and April 2004.

= 12.0; $P < 0.01$) overall percentage of *Ae. polynesiensis* infected with *W. bancrofti* collected on the west coast compared with the east or north coasts, and there was a significantly lower ($F_{3,11} = 19.1$; $P < 0.01$) overall percentage of *Ae. polynesiensis* infected with *W. bancrofti* collected in September compared with the other 3 mo (Table 4). There was no significant difference ($F_{2,11} = 0.6$; $P = 0.60$) in the overall percentage of *Ae. polynesiensis* infective with *W. bancrofti* collected in the three regions, but there was a significantly higher ($F_{3,11} = 6.5$; $P = 0.0$) overall percentage of *Ae. polynesiensis* infective with *W. bancrofti* collected in April compared with the other 3 mo (Table 4).

There was no significant difference in the overall percentage of *Ae. polynesiensis* infected ($F_{2,11} = 1.2$; $P = 0.36$) or infective ($F_{2,11} = 2.9$; $P = 0.13$) with *D. immitis* collected in the three regions, but there was a significantly greater overall percentage of *Ae. polynesiensis* infected ($F_{3,11} = 7.55$; $P = 0.02$) or infective ($F_{3,11} = 9.9$; $P < 0.01$) with *D. immitis* collected in April compared with the other 3 mo (Table 5).

Discussion

Moorea has a tropical climate, with average maximum and minimum temperatures varying little between months. There are wet and dry seasons, but some rain falls in each month. Although the pattern of temporal variation in rainfall is clear, the spatial pattern is less certain, and direct comparison between official records for the three regions is confounded by differences in the elevation of the meteorological stations. Generally, the rainfall during the sampling period was close to long-term averages, although lower than expected rainfall in December and February may have had a short-term influence on the mosquito populations. In March and April, however, rainfall was closer to expected levels and the abundance of the two species was generally greater (although not significantly) than in October and November. Additionally, although sites and locality samples were pooled for regional results, there would have been variability within the regions in microclimatic and other site-related factors that would have influenced the data.

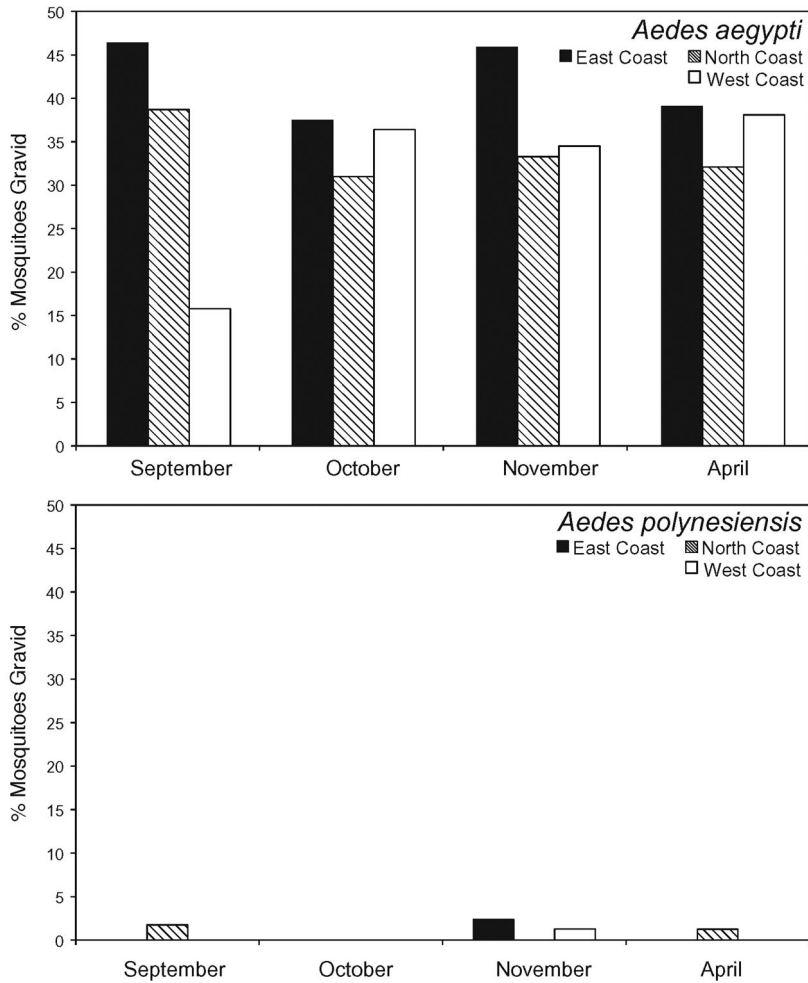


Fig. 6. Percentage gravid of *Ae. aegypti* (a) and *Ae. polynesiensis* collected on the east coast, north coast and west coast of Moorea, French Polynesia, on three occasions between September 2003 and April 2004.

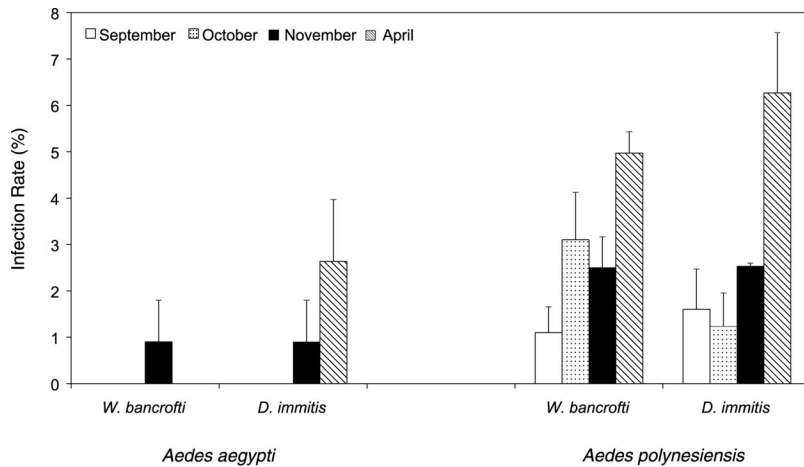


Fig. 7. Infection (infected and infective) rate of *Ae. aegypti* and *Ae. polynesiensis* with filariae (*W. bancrofti* and *D. immitis*) in collections at human bait at all three regions on Moorea, French Polynesia, September 2003 to April 2004.

Table 2. Number dissected (*n*) and infection rate (%) of *Ae. aegypti* with filariae (*W. bancrofti*) in collections at human bait at three regions on Moorea, French Polynesia, September 2003 to April 2004

Mo	East coast			North coast			West coast			Mean		
	<i>n</i>	Infected	Infective	<i>n</i>	Infected	Infective	<i>n</i>	Infected	Infective	<i>n</i>	Infected	Infective
Sept.	28	0	0	31	0	0	19	0	0	26.0	0.0a	0x
Oct.	32	0	0	29	0	0	22	0	0	27.7	0.0a	0x
Nov.	37	2.7	0	42	0	0	29	0	0	36.0	0.9a	0x
April	23	0	0	28	0	0	21	0	0	24.0	0.0a	0x
Mean	30.0	0.7a	0x	32.5	0a	0x	22.8	0a	0x	28.4	0.2 ^a	0 ^b

Means followed by the same letter (% infected; a) (% infective; x) are not significantly different by ANOVA, *P* > 0.05.

^a Mean % infected for all locations and all months, *n* = 341.

^b Mean % infective for all locations and all months, *n* = 341.

Human bait collections were chosen as the sampling procedure because they provided samples of the epidemiologically most important component of the population, the host-seeking females attracted to humans, and both CDC and EVS light traps baited with carbon dioxide and/or octenol were found to be relatively ineffective compared with human bait for collecting large numbers of *Ae. aegypti* and *Ae. polynesiensis* on Moorea (Russell 2004). Overall, *Ae. polynesiensis* was more commonly collected than *Ae. aegypti* in virtually all the study locations in Moorea, reflecting the widespread availability of natural larval habitats (e.g., crab burrows, coconut shells, and palm fronds) for *Ae. polynesiensis* that greatly exceeded the number of artificial containers used by *Ae. aegypti*.

The morning versus afternoon sampling results (Table 1) are generally similar to those found elsewhere for both species. For *Ae. aegypti*, MacDonald (1956) in Malaysia reported the periods of greatest biting activity to be mid-morning and late afternoon, similar to that found by Teesdale (1955) in Kenya. In Trinidad, Chadee (1988) found diurnal peaks at 0600–0700 and 1700–1800 hours with the morning peak being slightly greater, but in a later report described a trimodal pattern of landing with consistent peaks at 0700, 1100, and 1700 hours (Chadee and Martinez 2000), similar to the trimodal pattern reported from Indonesia by Atmosoedjono et al. (1972) and from Tanzania by Corbet and Smith (1974). However, such activity was not obvious in an earlier investigation in Moorea (R.C.R., unpublished data), and this timing was not included in the preliminary investigation. For *Ae. polynesiensis*, Riviere (1988) in Tahiti reported the species was taken at human bait in all hours from

presunrise to postsunset, although numbers were greatest in the hours from mid- to late afternoon.

Ae. aegypti was most abundant in areas of greater urbanization and more container habitats in domestic premises. In each region, there was one locality with consistently more *Ae. aegypti*; on the east coast this was Varari, on the north coast Pao Pao, and on the west coast Haapiti. The biting rates for *Ae. aegypti* in this study (averaging 7.1/h for the east coast, 20.4/h for the north coast, and 4.9/h for the west coast) greatly exceeded those of Riviere (1988) who cited average biting rates of 1.15/h over 39 stations and 1.65/h over 216 stations. The biting rates of *Ae. polynesiensis* in this study, ranging from 18.7 to 36.4/h, also exceeded those (15.62/h over 30 stations and 12.1/h over 216 stations) reported by Riviere (1988) for Moorea. However, the sampling in this current study involved a relatively small number of strategically selected locations and direct comparisons of biting rates are confounded temporally and spatially by different environmental and habitat factors.

The results of the preliminary trials supported the findings of Corbet and Smith (1974) in Tanzania that there was no difference in the diel periodicity of parity in *Ae. aegypti*, although in Moorea the proportion of inseminated and gravid females was greater in afternoon than morning collections, possibly reflecting increased opportunity for mating and an increased urge for feeding during their diurnal activity cycle. For *Ae. polynesiensis*, the lower parity rates recorded in morning samples also were not significant. However, the data on both species were obtained over only 3 d and may not reflect local patterns over various months or throughout the year.

Table 3. Number dissected (*n*) and infection rate (%) of *Ae. aegypti* with filariae (*D. immitis*) in collections at human bait at three regions on Moorea, French Polynesia, September 2003 to April 2004

Mo	East coast			North coast			West coast			Mean		
	<i>n</i>	Infected	Infective	<i>n</i>	Infected	Infective	<i>n</i>	Infected	Infective	<i>n</i>	Infected	Infective
Sept.	28	0	0	31	0	0	19	0	0	26.0	0.0a	0x
Oct.	32	0	0	29	0	0	22	0	0	27.7	0.0a	0x
Nov.	37	2.7	0	42	0	0	29	0	0	36.0	0.9a	0x
April	23	4.3	0	28	3.6	0	21	0	0	24.0	2.7a	0x
Mean	30.0	1.8a	0x	32.5	0.9a	0x	22.8	0a	0x	28.4	0.9 ^a	0 ^b

Means followed by the same letter (% infected; a) (% infective; x) are not significantly different by ANOVA *P* > 0.05.

^a Mean % infected for all locations and all months, *n* = 341.

^b Mean % infective for all locations and all months, *n* = 341.

Table 4. Number dissected (*n*) and infection rate (%) of *Ae. polynesiensis* with filariae (*W. bancrofti*) in collections at human bait at three regions on Moorea, French Polynesia, September 2003 to April 2004

Mo	East coast			North coast			West coast			Mean		
	<i>n</i>	Infected	Infective	<i>n</i>	Infected	Infective	<i>n</i>	Infected	Infective	<i>n</i>	Infected	Infective
Sept.	66	1.5	0	57	1.8	0	34	0	0	52.3	1.1a	0x
Oct.	79	5.1	1.3	81	2.5	0	59	1.7	0	73.0	3.1b	0.4x
Nov.	83	3.6	0	76	2.6	0	77	1.3	0	78.7	2.5b	0x
April	88	5.7	1.1	80	5.1	1.3	73	4.1	1.4	80.3	5.0b	1.3y
Mean	79.0	4.0a	0.6x	73.5	3.0a	0.3x	60.8	1.8b	0.4x	71.1	2.9 ^a	0.4 ^b

Means followed by the same letter (% infected; a, b) (% infective; x, y) are not significantly different by ANOVA, *P* > 0.05.

^a Mean % infected for all locations and all months, *n* = 853.

^b Mean % infective for all locations and all months, *n* = 853.

There was evidence from this Moorea study that successful mating of *Ae. aegypti* females, early in their life and before arrival at a host, was not particularly high. An overall 22.9% of the nulliparous *Ae. aegypti* collected in the afternoon were not inseminated, whereas the figure for *Ae. polynesiensis* was 9.9%. This level of unmated nulliparous females for *Ae. aegypti*, however, is actually lower than those reported for the species from east Africa by Corbet and Smith (1974) and Hartberg (1971) of 39 and 31%, respectively. Compared with the data for *Ae. polynesiensis*, the relatively low insemination rate for *Ae. aegypti* accords with the observation by Teesdale (1955) in Kenya that some females do not mate until after the first bloodmeal. The higher insemination rate for *Ae. polynesiensis* (in both nulliparous and parous females) indicates that mating may take place relatively sooner, perhaps closer to the larval habitat and less near the host blood source. Certainly, relatively more males of *Ae. polynesiensis* were collected at sticky ovitraps on Moorea in a companion study (Russell and Ritchie 2004).

Interpretation of parity data should be based on knowledge of whether the species is autogenous. Although low-level autogeny has been reported in *Ae. polynesiensis* from elsewhere in French Polynesia (Riviere 1983) and from Fiji (Duhrkopf 1980), it is generally accepted that *Ae. polynesiensis* is normally anautogenous (Lee et al. 1987) and, in a separate investigation, no evidence of autogeny was found in Moorea populations (R.C.R., unpublished data). The present results suggest some degree of temporal variability for *Ae. polynesiensis*, with significantly greater parity in April. There is little in the literature on parity rates in populations of *Ae. polynesiensis*, although from

Samoa there are unpublished mentions of a general rate of 40% (Zahar et al. 1980) and that rates may be higher (54.9% cf. 42.6%) in the cool season (June–November) than in the warm season (December–May) (W. A. Samarawickrema, WHO assignment report, Filariasis Research Project, Samoa, 1977–1980; WHO SMA/MPD/001). These data contrast with the present Moorea findings (overall mean 52.9–88.8%), although there is a similar contrast with seasonal abundance of the species in Samoa (Suzuki and Maung 1968) compared with that in Tahiti (Riviere 1988).

Although *Ae. aegypti* is generally considered to be anautogenous, it is well known for taking multiple bloodmeals in a single gonotrophic cycle. Therefore, gravid samples can include some that are truly parous as well as others that have not deposited a batch of eggs and thus are nulliparous but have fed a second time in the gonotrophic cycle. MacDonald (1956) in Malaysia reported that 67% of females collected at human bait had some blood or developed ovaries, 42% were fully fed or gravid, and only 33% were unfed with undeveloped ovaries (but not determined as being parous or nulliparous). More recently, Scott et al. (2000b) estimated that on average *Ae. aegypti* imbibe 0.76 and 0.63 bloodmeals per day in Thailand and Puerto Rico, respectively. There are no reports of *Ae. polynesiensis* feeding more than once per gonotrophic cycle, but a few gravid females (0.6%) were taken in these Moorea collections.

The parity rates for *Ae. aegypti* in this study (28.6–53.6%) need to be considered with the concomitant gravid rates (15.8–45.9%), because a few to many of the gravid females may have been parous. This confounds direct comparisons with *Ae. polynesiensis* in

Table 5. Number dissected (*n*) and infection rate (%) of *Ae. polynesiensis* with filariae (*D. immitis*) in collections at human bait at three regions on Moorea, French Polynesia, September 2003 to April 2004

Month	East coast			North coast			West coast			Mean		
	<i>n</i>	Infected	Infective	<i>n</i>	Infected	Infective	<i>n</i>	Infected	Infective	<i>n</i>	Infected	Infective
Sept.	66	3.0	0	57	1.8	0	34	0	0	52.3	1.6a	0x
Oct.	79	2.5	0	81	1.2	0	59	0	0	73.0	1.2a	0x
Nov.	83	2.4	0	76	2.6	1.3	77	2.6	0	78.7	2.5a	0.4x
April	88	4.5	1.1	80	8.8	2.5	73	5.5	1.4	80.3	6.3b	1.7y
Mean	79.0	3.1a	0.3x	73.5	3.6a	1.0x	60.8	2.0a	0.4x	71.1	2.9 ^a	0.5 ^b

Means followed by the same letter (% infected; a, b) (% infective; x, y) are not significantly different by ANOVA, *P* > 0.05.

^a Mean % infected for all locations and all months, *n* = 853

^b Mean % infective for all locations and all months, *n* = 853

this study and with *Ae. aegypti* in other investigations. Observed parity of *Ae. aegypti* populations will be dependent on locality and environmental conditions as well as collection and dissection methodologies. The parity results for *Ae. aegypti* in the current study may have been influenced by the collections being undertaken outdoors, particularly if a greater proportion of the populations rest indoors before feeding, but this prospect requires further investigation. Average parity rates reported for *Ae. aegypti* have varied from 28.4% in Tanzania (Corbet and Smith 1974) to 37% in Thailand (Gould et al. 1970) to 44% in the United States (Hoeck et al. 2003). Reported gravid rates have also varied, with only 8.3% (of 290) in Tanzania (Corbet and Smith 1974), 31.9% (of 116) in Malaya (MacDonald 1956), and 42.6% in Kenya (Tropis and Hausermann 1986). Recently, from a study in the United States, Hoeck et al. (2003) reported 24% of their *Ae. aegypti* had yolk, indicating prior bloodmeals (i.e., were gravid) and 17% had blood in their gut, indicating 41% were attempting a second (at least) bloodmeal in their present cycle.

Although other studies reporting parous and gravid rates for *Ae. aegypti* are not readily comparable with the present results because they used different collection techniques, they do present evidence for variability associated with location and season—a central consideration in this investigation. For example, in Thailand, Scott et al. (2000a) found gravid females made up 56% of resting collections in houses, whereas parous females made up 19%, and the highest percentage parous (24%) occurred in the dry season compared with 17% parous in the wet season. In Puerto Rico, they found gravid females made up 69% of resting collections, whereas parous females made up 32%, and there was a higher proportion of parous females in the hot season (38%) compared with the cool season (28%), although there were significant differences in parity rates between sites (71 and 58%) and months (0–83%).

The regional filarial infection rates revealed in this study underestimate those in some localities and overestimate others, because the samples were an accumulation of specimens from a number of sites in each region. However, they indicate the risk of transmission of *W. bancrofti* by *Ae. polynesiensis* was greatest in the east and north coast, and least in the west coast region. Unfortunately, there are no data on regional prevalence of human or dog filarial infection for Moorea with which to compare these regional vector data. It was of interest that one individual of *Ae. aegypti* showed a developing (L1) infection with *W. bancrofti* in the thorax musculature, and three individuals revealed L2 stages of *D. immitis* in the Malpighian tubules, with three of the mosquitoes from the east coast region and one from the north coast. Rosen (1955) has reported field infection of *Ae. aegypti* with larvae of *W. bancrofti* in French Polynesia, but with only first stage larvae, and, overall, it is unlikely to be a vector of concern (Lee et al. 1987).

There are no previous mosquito filarial infection data published for Moorea, but for Tahiti, Bonnet et al.

(1956) reported *W. bancrofti* infection rates in *Ae. polynesiensis* were at least 13% in some areas of transmission and 7% of specimens showed infective stage larvae, and Galliard (1964) reported infection and infective rates in *Ae. polynesiensis* had fallen from 13.0 and 8.0% to 2.6 and 0.8%, respectively, over 5 yr of the diethylcarbamazine drug program. More recently in Tahiti, Riviere (1988) found an average of 0.85% *Ae. polynesiensis* were infected with *W. bancrofti* and 2.5% with *D. immitis* at a site on the north coast, whereas an average of 4.57% *Ae. polynesiensis* were infected with *W. bancrofti* and 0.86% with *D. immitis* at a site on the west coast, and infections were found in all months but were much more common in the wetter months. The present results from Moorea accord with these Tahiti seasonal patterns.

The overall prevalence of infections with *D. immitis* in this present Moorea study was generally lower than with *W. bancrofti*. Given the reputedly high prevalence of *D. immitis* infection in dogs on the island, the present results may be associated with collections biased toward mosquitoes with a preference for human bloodmeals. However, this difference in infection rates has been reported also for Samoa, where Samarawickrema et al. (1992) reported *D. immitis* infection rates up to 0.92% and infective rates up to 0.29% in *Ae. polynesiensis*, but they noted that the rates were significantly lower than those for *W. bancrofti* (1.45 and 0.47%, respectively) (Samarawickrema et al. 1987). It could be that *D. immitis* has alternative local vectors; in Fiji, Symes (1960) considered *Culex quinquefasciatus* Say could be important because he found wild-caught specimens with infective stages and he produced mature infections experimentally. *Cx. quinquefasciatus* was relatively common and widespread during the study period on Moorea (Russell 2004), but Rosen (1954) found no evidence of field involvement of this species in transmission of *D. immitis* in Tahiti, and his experimental infections were of a low order compared with *Ae. polynesiensis*. Overall, the data on *Ae. polynesiensis* gathered in this current study indicate that the risk of infection of humans or dogs with filaria is greater for communities in eastern and northern Moorea, and it increases toward and through the wetter months, but the absence of human or dog infection data, with respect to seasonal incidence and regional prevalence, does not allow for correlations with the mosquito data.

There are implications in these present data for transmission of dengue on Moorea, which has a history of outbreaks (Deparis et al. 1998). Overall, the data on *Ae. aegypti* indicate that the risk of infection with dengue viruses is marginally greater for communities on the eastern and northern side of the island and tends to increase toward and through the wetter months, although there are no strong temporal or spatial trends. Unfortunately, the absence of human case data, with respect to seasonal incidence and regional prevalence of dengue transmission, does not allow for correlations with the mosquito data.

The rainfall that occurs in all months in Moorea can sustain populations of both vector species and can

explain the relatively few significant differences between seasons shown in this study. However, the conditions of increased rainfall and higher humidity in the wet season can provide for increased abundance and greater longevity of adults, and present a potentially increased risk for transmission of local filarial parasites and introduced dengue viruses. Although the differences shown between regions also were limited in a statistical sense, there seem to be increased risks for the northern and eastern regions. The eastern side (where the airport and ferry terminals are situated) and the northern side (where passenger ships unload tourists and many hotels are situated) of Moorea are where the majority of the local human population resides and where dengue viruses are likely to enter with infected humans arriving by air or water. Similarly, whereas filarial parasites may be endemic in all regions of the island, overall prevalence of filarial infection may be more associated with the eastern and northern regions because of greater vector abundance and longevity as well as the greater human and dog population densities.

Whatever importance the Moorea findings mentioned above may have in the local epidemiology of the pathogens transmitted by the two species, the variations in vector competences and pathogen susceptibilities reported by Gubler et al. (1979) and Vazeille-Falcoz et al. (1999), and the differences between the findings of the current study in Moorea and the data published on the same species from Tahiti and Samoa, are interesting and should be taken into account when considering vector issues in other Pacific areas. Such differences are likely to complicate the construction and implementation of generalized models (Hales et al. 1999) for vector-borne disease transmission in the Pacific and indicate a need for more detailed ecological work on the vectors in the various island groups.

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