Wuchereria bancrofti (Filariidea: Dipetalonematidae) and Its Vector *Aedes polynesiensis* (Diptera: Culicidae) in a French Polynesian Village

FREDERIC LARDEUX, NGOC LAM NGUYEN,[1] AND JEAN-LOUIS CARTEL[1]

Institut Français de Recherches Scientifiques pour le Développement en Coopération (ORSTOM), B.P. 529, Papeete, Tahiti, French Polynesia

J. Med. Entomol. 32(3): 346–352 (1995)

ABSTRACT In March 1991, a study on *Wuchereria bancrofti* (Cobbold, 1887) infection rates in its vector, *Aedes polynesiensis* Marks, was carried out in a village of French Polynesia. Our data were collected 10 yr after the suspension of human mass chemoprophylaxis and served as a baseline for pending ivermectin treatment scheduled in 1991–1993. In total, 1,789 biting females were collected, of which 1,740 were dissected and 1,183 (68%) were parous. Among these, 106 (8.96%) were infected with *W. bancrofti* and 34 (2.87%) harbored infective L3 larvae. The mean number of larvae per infected mosquito was 2.69, and the mean number of L3 larvae per L3 positive mosquito was 1.44. The *Ae. polynesiensis* biting index was 4.7 bites per 15 min, but varied significantly among habitats. The highest parous biting rates occurred in fields and peridomestic gardens and the lowest was close to houses. The proportion of parous infected and infective mosquitoes was higher in peridomestic habitats (0.25 infective bites per 15 min) than in domestic habitats (0.09) or in fields (0.11).

KEY WORDS *Wuchereria bancrofti, Aedes polynesiensis,* French Polynesia

IN FRENCH POLYNESIA, the subperiodic lymphatic filaria *Wuchereria bancrofti* (Cobbold), is transmitted by the mosquito *Aedes polynesiensis* Marks. This mosquito is also the vector of *Dirofilaria immitis* Leidy, the agent for dog heartworm and is suspected of transmitting dengue virus (Rosen et al. 1954). Even if it was not involved in disease transmission, *Ae. polynesiensis* would still be important as a pest mosquito because of its abundance. Since the 1940s, filariasis control programs have been implemented in the French Polynesian islands, emphasizing the mass administration of diethylcarbamazine (Perolat et al. 1986). As a result, the microfilariae carrier prevalence rate, which was estimated to be ≈30% in 1950, fell to 0.3–0.2% in Tahiti in 1980. Because of logistical constraints, mass chemoprophylaxis was interrupted in 1980, and on some islands, recrudescence of filariasis has been observed.

Before 1960, filaria transmission by mosquitoes was well documented in French Polynesia (Rosen 1955, Bonnet et al. 1956), but since then, no precise entomological description of transmission has been carried out. The purpose of the current article is to describe *W. bancrofti* transmission in Opoa, a small village of French Polynesia, 10 yr after the suspension of chemoprophylaxis and just before the initiation of ivermectin treatment scheduled for 1991–1993 (Cartel et al. 1992a). In early 1991, Cartel et al. (1992b) carried out a human population census of Opoa, mapped the microfilaremia carrier prevalence, and presented preliminary results on mosquito infection rates. Our study extends these results by emphasizing mosquito ecology and habitat characteristics, describing the dynamics of biting vector, and quantifying aspects of Bancroftian filariasis transmission.

[1] Institut Territorial de Recherches Médicales Louis Malardé, B.P. 30, Papeete, Tahiti, French Polynesia.

Materials and Methods

Study Area. The experiment was carried out in the village of Opoa, on Raiatea Island, one of the leeward islands west of Tahiti (Society Archipelago). Raiatea (151° 26′ W, 16° 48′ S) is typical of the high volcanic islands of Polynesia in respect to its tropical flora and fauna and human habitation. Most inhabitants reside in the town of Uturoa, whereas others live in houses grouped in coastal villages scattered along the main road that encircles the island. The village of Opoa, situated ≈30 km from the main town, is one of these coastal villages and at the time of the study (March 1991) 935 inhabitants lived in 148 houses spread over 12 km along the main road. Most houses were surrounded by vegetation that provided harborage for *Ae. polynesiensis.* The village was divided into 21 clusters of houses, based on the average dispersal of *Ae. polynesiensis,* which is ≈100 m (O'Connor 1923, Jachowski 1954). Houses within each cluster were separated from each other by <100 m, whereas the distance between adjacent clusters was >100 m.

Just before the termination of mass chemoprophylaxis in 1980, the microfilaremia prevalence rate was 6.4% among the human population of Opoa (Cartel et al. 1992b). At the beginning of 1991, 122 of 577 venous blood samples were microfilaremia positive (prevalence, 21.4%). These microfilaremia-positive individuals lived in 72 of the 146 houses of the village. The distribution of microfilaremia carriers per household was 1 in 37 houses, 2 in 26 houses, 3 in 5 houses, 4 in 2 houses, and 5 in 2 houses (Cartel et al. 1992b); 18 of the 21 clusters of houses had at least one carrier.

Mosquito Collections. Day-biting *Ae. polynesiensis* were collected for 15 min at each sampling station by one person acting both as bait and collector (Bonnet et al. 1956). Collections were done in the morning from 0630 (dawn) to 1030 hours and from 1500 to 1800 hours (sunset) to include the two peaks of *Ae. polynesiensis* biting activity (O'Connor 1923, Jachowski 1954, Ramalingam 1968, Rakai et al. 1974). Sampling lasted 16 d, and each station was visited on 1–6 occasions. Sampling stations were classified into different mosquito habitat types as domestic (i.e., within 10 m of each house), peridomestic (i.e., gardens or premises between 10–60 m from each house), fields (i.e., plantations and *bush*), and two bus stops which resemble fields from their environmental aspect. Fields and houses surrounded by vegetation were referred to as bush habitat (Ramalingam 1968).

Mosquito Dissections. In Opoa, mosquitoes were killed with chloroform and sorted according to species (generally *Ae. aegypti* or *Ae. polynesiensis*) and sex. The parity of *Ae. polynesiensis* females was determined using the ovarian tracheation method of Detinova (1962). Nulliparous females as well as those impossible to classify according to parity were discarded. Parous females were divided into head, thorax, and abdomen, lacerated with needles in glycerol, and then examined to determine filaria infection.

Identification of Filaria Larvae and Development Stages. In addition to *W. bancrofti, D. immitis,* and an unidentified *Strongyloides*-like species were found in *Ae. polynesiensis.* The identification of filaria larvae was performed using morphological criteria. The *Strongyloides*-like species was separated easily from microfilariae of both *W. bancrofti* and *D. immitis* on the basis of its larger size. Stages of *D. immitis* and *W. bancrofti* were classified into microfilariae (mf), sausage stage (L1), second stage (L2), and third stage (L3), following World Health Organization (WHO 1967) criteria. *D. immitis* was separated from *W. bancrofti* using Nelson (1959). Mosquitoes that harbored at least one L1, L2, or L3 larva were defined as infected, whereas those with only L3 larvae were defined as infective.

Entomological Criteria. Transmission statistics were computed using numbers of parous females and consisted of the number of infective mosquitoes divided by the number of parous females (i.e., a measure of prevalence) and the number of infective larvae per parous female (i.e., a measure of intensity of infection). Other entomological statistics included the biting index (number of females per human per 15 min), the parous biting index (as above, but computed with parous females), the infected biting index (i.e., number of females with at least one filaria larva per human per 15 min), the infective biting index (number of females with at least one L3 larvae per human per 15 min). These statistics were grouped by the name of catcher, date of sampling, time of sampling, house, cluster of houses, and mosquito habitat type (domestic, peridomestic, field, or bus stops).

Statistical Analysis. Usually data were transformed to $\log(x + 1)$ to normalize the distribution and stabilize the variance to fulfill parametric test assumptions. When no adequate transformation was found, nonparametric tests (Kruskal–Wallis) were used. Means were compared using student's *t*-test or analysis of variance. When mean differences were significant, means were classified into homogenous groups using Scheffé's method. Proportions were compared by Pearson's chi-square test with Yates' corrections for small counts in 2 × 2 tables. If an expected value was <5, Fisher exact probability was computed for 2 × 2 tables.

Results

***Aedes polynesiensis* Biting Dynamics.** In total, 247 sites were sampled during 382 mosquito collections resulting in the capture of 1,789 *Ae. polynesiensis* females (Table 1). The overall biting index was 4.68 (SD = 6.82) biting females per human per 15 min. The biting index varied significantly ($F = 15.8$; df = 3, 379; $P < 0.001$) among habitat types, with the greatest number collected at field sites. Therefore, habitat type should be used as a stratifying variable for determining biting indices and planning sampling.

No significant difference was observed in biting indexes among hours of catches ($F = 0.9$; df = 19, 363; $P = 0.57$) or between morning and afternoon catches ($F = 0.71$; df = 1, 381; $P = 0.59$) indicating a uniform biting activity for *Ae. polynesiensis.* There also were no significant differences among the days of capture ($F = 0.91$; df = 15, 367; $P = 0.55$) or among the three collectors ($F = 1.51$; df = 2, 380; $P = 0.22$), according to habitat type stratification (biting index for the three collectors was 2.43 [3.91], 2.78 [4.54], and 3.89 [3.88]).

When a biting index was computed for each of the 21 clusters of houses, no significant differences were observed, except for numbers 4 and 11 situated in a bush environment (Table 2).

Transmission of *W. bancrofti*. Among the 21 clusters of houses, 18 (85%) were positive (i.e., at least one capture with one mosquito infected with *W. bancrofti* larvae) and 14 (66.6%) had at least one infective mosquito. The percentage of positive collections within positive clusters was 18.7% with

Table 1. Entomological statistics stratified into four habitats in Opoa

Category	Habitats								Total	
	Domestic		Peridomestic		Fields		Bus stops			
No. sites	134		82		29		2		247	
No. mosquito collections (1)	265		83		31		3		382	
No. negative catches (%) (2)	90	(33.9)	17	(20.5)	1	(3.2)	0	(0)	108	(28.3)
No. collections with parous females (%) (3)	162	(61.1)	63	(75.9)	28	(90.3)	3	(100)	256	(67.0)
No. collections with infected females (%) (4)	33	(20.4)	29	(46.0)	5	(17.8)	1	(33.0)	68	(26.6)
No. collections with infective females (%) (4)	14	(8.6)	12	(19.1)	3	(10.7)	0	(0)	29	(11.3)
Total no. biting females	996		415		331		47		1,789	
Mean females per host per 15 min (SD)	3.76	(5.29)	5.00	(7.46)	10.68	(11.60)	15.66	(4.04)	4.68	(6.82)
No. mosquito females dissected (5)	964		402		328		46		1,740	
No. parous females (%) (6)	654	(67.8)	300	(74.6)	196	(59.8)	33	(71.7)	1,183	(68.0)
Parous biting index (SD)	2.47	(3.47)	3.61	(5.47)	6.32	(7.19)	11.00	(5.29)	3.10	(4.55)
No. infected females (%) (7)	39	(6.0)	57	(19.0)	9	(4.6)	1	(3.0)	106	(8.9)
No. infective females (% (7)	15	(2.3)	16	(5.3)	3	(1.5)	0	(0)	34	(2.9)
Infected biting index (SD)	0.24	(0.52)	0.90	(1.56)	0.32	(0.82)	0.33	(0.57)	0.41	(0.87)
Infective biting index (SD)	0.09	(0.31)	0.25	(0.57)	0.11	(0.31)	0	(0)	0.13	(0.30)
No. infective heads (%) (7)	7	(1.0)	10	(3.3)	2	(1.0)	0	(0)	19	(1.6)
Mean no. L1 per L1 positive mosquito (SD)	4.20	(3.74)	1.54	(1.00)	1.25	(0.71)	2.00	(0.00)	2.22	(2.35)
Mean no. L2 per L2 positive mosquito (SD)	2.75	(2.05)	2.00	(2.03)	0	(0)	0	(0)	2.28	(2.02)
Mean no. L3 per L3 positive mosquito (SD)	3.78	(3.28)	1.73	(2.07)	2.67	(8.33)	0	(0)	2.72	(2.64)
Mean no. larvae per infected mosquito (SD)	3.67	(3.33)	1.96	(1.78)	1.33	(0.86)	2.00	(0.00)	2.69	(2.52)
No. larvae per parous female	0.22		0.35		0.06		0.06		0.22	
No. L3 larvae per parous female	0.081		0.086		0.041		0		0.073	

Biting index is computed on the basis of the mean number of bites per man per 15 min. (2), Percentage computed with (1) as denominator; (4), percentage computed with (3) as denominator; (6), percentage computed with (5) as denominator; (7), percentage computed with (6) as denominator.

Table 2. Data of infection of the human population and entomological statistics within clusters of houses in Opoa

Cluster, *n*	No. houses	Total no. inhabitants	No. inhabitants aged >15	No. mf positive inhabitants	Mean mf per ml blood	No. mosquito collections	No. infected collections	No. infective collections	No. *Ae. polynesiensis* collected	No. parous females	Parous biting index (SD)	No. infected females	Infected biting index (SD)	No. infective females	Infective biting index (SD)
1	1	10	3	1	160	1	0	0	17	11	11.00* (0.00)	0	0.00 (0.00)	0	0.00 (0.00)
2	11	78	55	10	270	25	6	3	88	57	2.28 (2.54)	7	0.28 (0.54)	3	0.12 (0.33)
3	6	40	29	6	216	17	5	2	71	55	3.23 (4.44)	12	0.70 (1.40)	2	0.12 (0.33)
4	2	15	7	0	1	5	4	4	79	53	10.60* (8.80)	16	3.20* (3.56)	6	1.20* (0.84)
5	6	25	14	1	21	16	1	1	75	54	3.37 (4.81)	5	0.31 (1.25)	1	0.06 (0.25)
6	12	96	59	10	586	46	4	0	95	72	1.59 (2.93)	5	0.11 (0.38)	0	0.00 (0.00)
7	12	87	57	11	906	59	9	4	166	84	1.76 (2.74)	10	0.17 (0.42)	4	0.06 (0.25)
8	4	23	14	0	1	19	5	3	71	41	2.15 (3.37)	7	0.37 (0.76)	4	0.21 (0.53)
9	7	35	25	5	41	12	1	1	53	36	3.00 (1.81)	1	0.08 (0.29)	2	0.17 (0.58)
10	8	42	29	3	255	12	1	0	42	24	2.00 (4.82)	1	0.08 (0.29)	0	0.00 (0.00)
11	6	32	20	6	311	9	3	1	113	65	7.22* (4.55)	4	0.44 (0.72)	1	0.11 (0.33)
12	6	22	20	8	822	10	1	1	41	27	2.70 (2.94)	1	0.10 (0.31)	1	0.10 (0.31)
13	7	26	17	7	1,837	7	0	0	36	20	2.86 (2.48)	0	0.00 (0.00)	0	0.00 (0.00)
14	19	134	87	25	259	24	4	2	78	48	2.00 (2.71)	6	0.25 (0.61)	2	0.08 (0.28)
15	5	39	25	9	381	12	6	0	91	62	5.16 (6.74)	9	0.75 (0.96)	0	0.00 (0.00)
16	5	26	14	3	1,667	12	6	1	68	46	3.83 (2.37)	6	0.50 (0.52)	1	0.08 (0.29)
17	2	11	5	0	1	4	1	1	20	18	4.50 (5.81)	1	0.25 (0.50)	1	0.25 (0.50)
18	12	89	49	8	329	34	3	0	122	96	2.83 (5.96)	3	0.08 (0.28)	0	0.00 (0.00)
19	5	38	24	1	16	7	0	0	10	10	1.43 (0.97)	0	0.00 (0.00)	0	0.00 (0.00)
20	3	29	16	4	112	8	1	1	25	13	1.62 (2.06)	1	0.12 (0.35)	2	0.25 (0.71)
21	9	38	26	4	218	7	1	1	32	29	4.14 (3.18)	1	0.14 (0.38)	1	0.14 (0.38)
Total	148	935	595	122	347	346	62	26	1,393	921	2.46 (3.73)	96		31	

* Indicates that the cluster is significantly different from the others for the statistic computed; mf, microfilameria.

a range of 8–80%. For infective mosquitoes, this rate was 7.8% (range, 6–80%).

Among the 346 mosquito collections done in domestic and peridomestic sites, 62 (17.9%) and 26 (7.5%) contained infected and infective females, respectively.

The overall parous biting index was 3.10 (4.55) parous females per human per 15 min. The parous biting index differed significantly among habitat types ($F = 12.3$; df = 3, 253; $P < 0.001$) with the highest value observed for field collections (Table 1). This index was not statistically different between domestic and peridomestic sites (Scheffé's test). Similar to the biting index, no difference was observed among the three collectors ($F = 1.85$; df = 2, 254; $P = 0.16$), among days of capture ($F = 0.85$; df = 15, 241; $P = 0.62$), or between morning or afternoon ($F = 0.81$; df = 1, 255; $P = 0.37$). Clusters of houses appeared to be similar, with an overall index of 2.46 (3.73) except for the two in a bush environment that were higher (numbers 4 and 11, Table 2).

The prevalence of infected and infective mosquitoes per parous female was computed according to habitat type. Prevalence in peridomestic were significantly higher than in domestic or field habitats (Table 1).

The parous infected and infective biting indices were significantly greatest in peridomestic habitats ($F = 7.97$; df = 3, 252; $P < 0.001$ and $F = 4.06$; df = 3, 252; $P < 0.001$). The proportion of infected collections among parous collections was also higher in peridomestic habitats (33%) than in domestic habitats (20.4%) and in fields (17.8%). Results for infective collections were similar; i.e., 19.1% in peridomestic habitats, 8.6% in domestic habitats, and 10.7% in fields.

The overall mean number of *W. bancrofti* larvae per infected mosquito was 2.69 (SD = 2.52) with a range of 1–15, and the mean number of infective larvae per infective mosquito was 2.72 (2.64) with a range of 1–12 (Table 1). There were no significative differences among locations for each stage, except for a higher load of L1 for mosquitoes captured in domestic habitats. The numbers of larvae (all stages) per parous female were significantly different among the habitat types, with a higher value in peridomestic habitats. However, the numbers of L3 larvae per parous female were not significantly different among habitat types.

Human filarial infection rates in clusters of houses and mosquito transmission dynamics were not significantly correlated when tested using linear models (Table 2).

Discussion

***Aedes polynesiensis* Biting Dynamics.** Our sampling schedule for mosquito collection encompassed the mosquito daily biting cycle, and no differences were observed between morning and afternoon collections. Biting indices may be biased by modifications of mosquito activity caused by environmental factors. Even though these variations were not the purpose of the study, it was important to test whether the collection conditions were stable on average throughout the experiment. For example, *Ae. polynesiensis* may become more active when the day is cloudy (Jachowski 1954). Fortunately, no difference among days of capture or time (morning or afternoon) was observed in our study and, therefore, biting indices in Opoa were compared using stratifying variables such as habitat types.

Populations of *Ae. polynesiensis* living in the coastal plain (as in Opoa) do not exhibit marked seasonal changes in population abundance (Jachowski 1954, Burnett 1960, Rivière 1988). Therefore, even though the duration of our study was short and included only a single village, these biting rates may be representative. In Opoa, the overall biting rate of 4.7 female *Ae. polynesiensis* per human per 15 min is similar to the rate of 5.25 bites observed by Bonnet et al. (1956) in Tahiti during the period 1953–1955. Jachowski & Otto (1952) reported a capture rate of 21 mosquitoes per 15 min in a bush environment, whereas Jachowski (1954) indicated rates of 19.4 and 14.5 for two stations located in the bush, 4.65 in clearings (i.e., peridomestic habitats like gardens) and 2.1 near houses. In Samoa and Tonga, Ramalingam (1968) reported catches ranging from 4.5 to 24.0 *Ae. polynesiensis* per 15 min, depending on the environment (bush, open, or plantation), with catch rates highest in plantations and bush villages. These results are similar to those obtained in Opoa and further indicated that *Ae. polynesiensis* is primarily a bush mosquito. *Ae. polynesiensis* breeds in natural containers (Suzuki & Sone 1978), and generally rests in bushy areas (Rivière et al. 1979). This may explain the lower biting indices close to houses. Moreover, breeding sites may be removed easily by inhabitants. Nevertheless, these values are still lower than those obtained for *Ae. polynesiensis* on atolls of French Polynesia, where rates of >150 mosquitoes per 15 min of catch were reported by Lardeux et al. (1992).

In our study, 71.7% of samples collected at least one mosquito, which was within the range of 16.4–81.2% reported by Bonnet et al. (1956) for several surveys in Tahiti (mean of 46%). In the village, clusters of houses (apart from those in a bush environment) did not differ in terms of biting activity indicating a homogenous distribution of vectors among houses.

Transmission of *W. bancrofti*. Sites with the greatest frequency of filaria transmission differ among authors. O'Connor (1923) indicated that transmission occurred within villages and Byrd et al. (1945) stressed that villages were the hyperendemic foci of infection in Samoa. On the other hand, Jachowski & Otto (1952) in Samoa and McCarthy & Fitzgerald (1956) in western Samoa maintained that transmission occurred mainly in plantations and bush areas along trails and less frequently in the villages themselves. Ramalingam (1968) proved that in Samoan bush villages, most of the transmission occurred within the village and less within the plantations whereas, in open villages different situations exist and transmission can occur in villages or in plantations or equally in both. In our study, the biting index and the parous biting index were higher in plantations and bush environments than around houses. In the contrast, the proportion of infected and infective mosquitoes was higher in domestic and peridomestic habitats than in plantations. Habitats may be ordered from highest to lowest, based on the infected and infective indices: peridomestic, fields (bush and plantation), and domestic habitats. In Opoa, transmission occurred mainly in village gardens, but not close to houses. Plantations also appear to be sites at risk. Opoa may be characterized as a bush village according to Ramalingam's (1968) classification. The probability of transmission is proportional to the number of infective bites and to the number of infective larvae transmitted. Because the number of L3 larvae per infective mosquito is constant within habitat type, the risk of infection is only linked to the number of infective bites, which was greatest in the gardens around the houses.

Southgate (1974) and Samarawickrema et al. (1987) have explained the higher microfilaremia prevalence rates in males than females as being the result of a greater exposure of males who are more often in contact with biting mosquitoes during their daily activities outside houses than females who generally remain indoors. In Opoa, Cartel et al. (1992b) also noticed this microfilaremia prevalence difference. However, the explanation may be not as simple as in the previous studies. In Opoa, not all the males work in plantations, some are fishermen and old and young males usually stay at home. Moreover, females often help in plantations. A sociological study should be carried out to determine the occupational risk factors for infection in relation to work or activity site.

Within each location, the mean number of stage 1–3 larvae per positive mosquito was relatively stable, indicating that if the mosquito does not die, the larval mortality rate was very low (Table 1). The number of larvae per positive mosquito ranged from 1 to 15 in our study. This is in agreement with the theory of parasite yield in filariasis vectors of Pichon (1974a, b) who described a limitation phenomenon in *Ae. polynesiensis* leading to the stoppage of microfilariae when passing through the stomach wall and consequently to a small number of developing larvae per host.

With an a priori proportion of 10% infected parous females, a type I error of 5%, and a precision of 2%, the sample size to compute the proportion of infected females was estimated to be 900 parous females using the formula of Schwartz (1963). This sampling requirement was realized at the village level (1,183 parous females dissected), but not within the clusters of houses where the maximum of collected mosquitoes was 166. Because of these small sample sizes in clusters, predictive parameters related to filarial transmission were impossible to derive. In particular, attempts to correlate the distribution of infected humans with infective mosquitoes failed. Moreover, complex interrelationships between humans and vector ecology may mask (if they exist) the a priori trends tested here. Even the presence or absence of infected individuals and infective mosquitoes was not well correlated. For example, the three clusters found negative according to mosquito infection were positive in terms of microfilameria carriers, one comprising seven infected people with a mean mf density of 1,837. In the same way, 3 clusters among 18 were found to be negative for microfilameria carriers and positive in terms of infected mosquitoes. Clusters were most likely not isolated regarding mosquito dispersal within the village. Moreover, microfilameria carriers did not always stay at the same place but moved for their daily activities and may have infected mosquitoes in other clusters. Moreover, people aged <15 yr (not taken into account in the parasitological survey for ethical reasons) have been infected and influenced our results; i.e., some clusters of houses may have been false negatives. However, at the village level (i.e., when the clusters are pooled), the sample size becomes statistically relevant. Therefore, if data from other villages could be obtained, correlations between mosquito infection and microfilameria prevalence in humans could be investigated.

Filariasis epidemiological situations vary among seasons (Brengues 1975, Sasa 1976). Our results are representative of the end of the rainy season. No data are available on the probable seasonal variations (if they exist) of transmission by *Ae. polynesiensis* in French Polynesia. It will be interesting to compare our results with other samples carried out at different times of the year. A simple model of transmission could be produced then and used in further studies to control the disease.

Acknowledgments

We acknowledge the valuable field assistance of M. Chebret, B. Moutampo, and J. J. Tavaearil for mosquito collections and A. Ung for mosquito dissections. We thank S. Loncke for his helpful suggestions. We would also like to thank the two anonymous referees and D. R. Mercer for their critical review of the manuscript. This study received financial support from the United Nations Development Program/World Bank/World Health Organization Special Programme for Research and Training in Tropical Diseases.

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Received for publication 14 December 1993; accepted 30 December 1994.