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OBSERVATIONS ON THE EPIDEMIOLOGY OF HUMAN FILARIASIS IN FRENCH OCEANIA^{1, 2}

By

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It has long been recognized that endemic elephantiasis is especially prevalent in many Polynesian archipelagoes, including the Society Islands in French Oceania (Lesson, 1829; Bennett, 1831). More recently, the importance of other clinical manifestations of filariasis (*Wuchereria bancrofti*) in these areas was emphasized by the experience of the Armed Forces of the United States during World War II (Wartman, 1947).

Previously published studies have dealt with the prevalence, clinical manifestations, and treatment of filariasis in French Oceania (Galliard et al., 1949; Beye et al., 1952; Beye et al., 1953). The investigations herein reported, which were carried out in French Oceania from September, 1950, to August, 1952, were concerned primarily with the following aspects of the epidemiology of *W. bancrofti*: (1) The role of each of the local species of mosquitoes in the transmission of the infection; (2) The quantitative characteristics of the sources of mosquito infection; (3)

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The minimum blood density of microfilariae necessary to infect a significant proportion of vector mosquitoes; (4) The quantitative characteristics of infections produced in vector mosquitoes by various infective blood densities of microfilariae; (5) The effect of the filarial infection on the longevity of vector mosquitoes.

The last three topics enumerated have recently acquired increased significance as a result of the discovery of a relatively safe and orally administrable drug, Hetaoran (1-diethylcarbamyl-4-methylpiperazine) which is capable of eliminating, or greatly reducing the numbers of, microfilariae in the peripheral blood (Santiago-Stevenson et al., 1947 and subsequent publications by other authors).

W. bancrofti does not multiply in its invertebrate hosts. Consequently, the number of mature larvae which can be transmitted by a mosquito is dependent upon the number of microfilariae ingested at the time of the infective blood meal. On the other hand, heavy infections with filarial larvae are thought to be injurious to mosquitoes (Bahr, 1912; Menon and Rimamurti, 1941). Thus, although fewer microfilariae are available to mosquitoes as a result of the treatment of an infected population with Hetaoran, it is possible that the drug might cause certain individuals, who previously had been unimportant sources of infection because of the lethal effect on mosquitoes of their high parasitemia, to become more dangerous sources of infection.

METHODS

Mosquitoes to be dissected were lightly anesthetized and identified as to species. After removal of legs and wings, the head, thorax, and abdomen were separated in a drop of saline on a slide under a dissecting microscope. Each part was then placed in a separate drop of saline on the same slide, the malpighian tubules and midgut were withdrawn intact from the abdomen, and all tissues were carefully teased apart.

Unless otherwise noted, the mosquitoes used in the laboratory experiments were reared from larvae and pupae collected on Tahiti. Adult specimens were kept in muslin and bobbinet cages (12 inches x 12 inches x 12 inches) which were supported by a wooden frame. The cages were kept in a quiet darkened room in which the weekly mean dry bulb temperature fluctuated between 83.7 and 75.0 F. A high relative humidity was maintained by placing wet burlap sacks over the wooden cage frames. The mosquitoes were fed only sugar water except for the experimental blood meal. Under these conditions the larvae of *Wuchereria bancrofti* completed their development in good mosquito hosts approximately 13 days after the infective blood meal.

All blood samples were obtained by drawing up 20 ml of blood in a clean dry pipette from a small wound made on a finger with a pointed scalpel blade. The tip of the pipette was wiped clean of excess blood, and the sample was then expelled in the form of a thick film about 15 millimeters in diameter on a clean slide. The smear was allowed to dry, laked with water, fixed with absolute methyl alcohol, and stained with Giemsa stain.

The entire area of each blood film was examined with a compound microscope equipped with a mechanical stage and an ocular disc on which two horizontal parallel lines had been ruled. The ocular disc assisted in the systematic examination of the slide by sharply delineating the upper and lower borders of each field. If microfilariae were present, they were counted with the aid of a hand tabulator.

FINDINGS

Aedes pseudoscutellaris was stated to be the principal vector of *Wuchereria bancrofti* in the Society Islands by Galliard et al. (1949) and Beye et al. (1952). However, neither group of investigators reported the experimental infection of this species nor did they present data on the role of any other local species of mosquitoes as vectors, despite the fact that the latter authors recorded the presence of *Aedes tongae* Edwards, a species closely related to *A. pseudoscutellaris* and one which is thought to be the principal vector of *W. bancrofti* in the Tonga Islands (Farner and Bohart, 1945). Moreover, subsequent to the completion of the studies in the Society Islands cited above, Marks (1951) showed that mosquitoes from Polynesia previously identified as *A. pseudoscutellaris* belonged in reality to two sibling species, true *A. pseudoscutellaris* (Theobald) and a theretofore undescribed species which she named *Aedes polynesiensis*.

It was apparent at the beginning of the present studies that further taxonomic study of the mosquito fauna of French Oceania, especially with respect to the *scutellaris* group of *Aedes* (to which the 3 species mentioned above belong), was of fundamental importance to the other investigations which were

blood film was made microscope field stage and two horizontal lines ruled. The systematic drawings by sharply defined borders of filariae were made with the aid

was stated to be *Wuchereria* in Islands by Beye et al. A group of individuals experimental nor did they any other local factors, despite hours recorded *iae* Edwards, *A. pseudoscutellaris* thought to be *W. bancrofti* later and subsequently to studies in the above, Marksquitoes from identified as *A. pseudoscutellaris* theretofore she named

beginning of further taxonomic fauna of with respect to *Aedes* (to be mentioned above importance which were

to be undertaken. The significance of such information was accentuated by the report of Manson-Bahr and Muggleton (1952) from the Fiji Islands that *Aedes horrescens* Edwards, a species in which the females are indistinguishable from those of both *A. pseudoscutellaris* and *A. polynesiensis*, is not a suitable host for *W. bancrofti*.

A taxonomic study of the *scutellaris* group of *Aedes* in French Oceania was carried out and has been reported in detail elsewhere (Rosen and Rozeboom, 1954; Stone and Rosen, 1953). In summary, only one species of this complex, *A. polynesiensis*, was found in the area. Moreover, it was discovered that the larvae of this species when found in certain types of environment had morphologic characteristics which previously had been considered distinctive of *A. horrescens*.

The complete list of mosquitoes which were found in French Oceania is as follows: *Aedes polynesiensis* Marks, *Aedes aegypti* (Linn.), *Aedes edgari* Stone and Rosen, *Culex quinquefasciatus* Say, *Culex annulirostris* Skuse, *Culex atriceps* Edwards, *Culex marquesensis* Stone and Rosen, *Culex* sp.

The exact taxonomic position of *Culex* sp. is currently under study. The larvae of this species were usually found in brackish water and both the larvae and the adults are similar to those of the brackish-water species *Culex litoralis* Bohart and *Culex sitiens* Wiedemann. Both of the latter species have been reported to occur in the Society Islands (Beye et al., 1952) but the type of material on which these identifications were based is not given. By the use of the presently available keys, the larvae of *Culex* sp. would be identified as *C. litoralis* and the fe-

males of *Culex* sp. would be identified as *C. sitiens*.

The mosquito species of French Oceania vary greatly in relative abundance depending on the locality and season. In general, *A. polynesiensis* is the most abundant species, but none of the others, with the exception of *A. edgari*, is uncommon.

All the species, with the exception of *C. marquesensis*, have been observed to feed on man in nature but their relative anthropophilism is unknown. *A. polynesiensis* feeds almost exclusively during the day, *A. aegypti* feeds either day or night, and the other species feed at night. *A. polynesiensis* is especially aggressive and when feeding on a human subject is reluctant to stop short of repletion.

Dissection of field-caught mosquitoes

Dissections were performed of field-caught mosquitoes from 3 study areas where control procedures had never been undertaken, two on the island of Tahiti (Papara and Vairao) in the Society Islands and one on the island of Makatea in the Tuamotu Islands.

All the mosquito species known from French Oceania except *C. marquesensis* occur on Tahiti. Only *A. polynesiensis*, *A. aegypti*, *C. quinquefasciatus*, and *C. annulirostris* occur on Makatea.

Specimens for dissection were collected within 40 yards of human habitations. The various species were captured as follows: *A. polynesiensis* while attempting to feed on persons used as bait; *C. quinquefasciatus* and *A. aegypti* primarily in their resting places in houses; and the other species while attempting to feed on animal bait (man, dog, or pig). Most of the latter group were caught before they began to feed. No mosquitoes were collected from hosts

TABLE 1
The prevalence of *W. bancrofti* in field-caught mosquitoes from Tahiti and Makatea, French Oceania

Mosquito species	Number dissected	Mosquitoes with <i>W. bancrofti</i>	
		Number	Per cent
<i>A. polynesiensis</i>	2,390	233	9.7
<i>C. quinquefasciatus</i>	1,061	126	11.9
<i>C. annulirostris</i>	446	0	
<i>C. atriceps</i>	81	1	1.2
<i>A. aegypti</i>	80	16	20.0
<i>C. sp.</i>	58	1	1.7
<i>A. edgari</i>	47	0	

which had detectable microfilariae in their peripheral blood. All field-caught mosquitoes were dissected within 48 hours of the time of collection.

In collecting mosquitoes for dissection an attempt was made to sample systematically the areas studied rather than to try to collect in localities having known carriers of microfilariae. Collections were made throughout the year

but chiefly during the warmer months.

Since the dog heartworm, *Dirofilaria immitis*, is very prevalent in French Oceania it was necessary to distinguish the larvae of *W. bancrofti* from those of this filaria as well as from other nematodes parasitizing mosquitoes. The criteria by which these distinctions were made, as well as other data on *D. immitis* in French Oceania, are presented elsewhere (Rosen, 1954).

Preliminary inspection of the data available from the dissection of field-caught mosquitoes revealed no indication of seasonal or geographical differences and hence the results are grouped in this presentation (tables 1 and 2). It is seen (table 1) that only 3 species, *A. polynesiensis*, *A. aegypti*, and *C. quinquefasciatus*, commonly harbored *W. bancrofti*. However, it will be noted (table 2) that advanced-stage larvae were commonly found only in *A. polynesiensis*. First-stage larvae were found in the single infected *C. atriceps* and

TABLE 2
The stage of development of *W. bancrofti* in field-caught mosquitoes of 3 species from Tahiti and Makatea, French Oceania

Stage of development	Mosquito species					
	<i>A. polynesiensis</i>		<i>C. quinquefasciatus</i>			
	No. of mosquitoes* having indicated type of larvae	Per cent of total no. of mosquitoes with <i>W. bancrofti</i>	No. of mosquitoes* having indicated type of larvae	Per cent of total no. of mosquitoes with <i>W. bancrofti</i>	No. of mosquitoes* having indicated type of larvae	Per cent of total no. of mosquitoes with <i>W. bancrofti</i>
Microfilariae and first stage larvae	121	51.9	67†	95.7	16†	100.0
Second-stage larvae	69	29.6	2	2.9	0	0
Third-stage larvae	43	18.5	1‡	1.4	0	0
Totals	233	100.0	70	100.0	16	100.0

* Mosquitoes having more than one type of larvae are tabulated according to the most advanced larvae which they contained.

† Most of the mosquitoes in these groups had only undeveloped microfilariae.

‡ This mosquito had a single dead degenerated third stage larva.

the warmer months. The worm, *Dirofilaria*, is prevalent in French Oceania and necessary to distinguish *W. bancrofti* from those as well as from other species of mosquitoes. The distinctions were based on data on *D. bancrofti* in French Oceania, are presented (1954).

tion of the data from dissection of field-caught mosquitoes revealed no indication of geographical differences. Results are grouped (tables 1 and 2). At only 3 species, *A. aegypti*, and *C. triticeps* and *C. quinquefasciatus* harbor *W. bancrofti*. It will be noted that only 3 species, *A. aegypti*, and *C. triticeps* and *C. quinquefasciatus* harbor *W. bancrofti*. In addition, the discovery of an individual on Tahiti with a periodic infection of *W. bancrofti* acquired on Martinique (French West Indies) made possible the testing of several of the local mosquito species for susceptibility to infection with this type of *W. bancrofti*.

third-stage larvae were found in the single infected *Culex* sp.

Infection of mosquitoes in the laboratory

To complement the data derived from the dissection of field-caught mosquitoes, a series of laboratory experiments was undertaken in which each of the 7 mosquito species known to occur on Tahiti was tested for its ability to serve as a host for the local nonperiodic strains of *W. bancrofti*.

In addition, the discovery of an individual on Tahiti with a periodic infection of *W. bancrofti* acquired on Martinique (French West Indies) made possible the testing of several of the local mosquito species for susceptibility to infection with this type of *W. bancrofti*.

The subject with the periodic infection was a Negro male, approximately 30 years of age, who had lived only on Martinique before coming directly to Tahiti. At the time that the following experiments were begun he had been on Tahiti for 1 year. At this time his mean number of microfilariae per 20 cu. mm. of blood was 1.5 at noon and 107.0 at 11:00 P.M. One year later, when all the experiments had been completed, his mean number of microfilariae per 20 cu. mm. was 1.5 at noon and 52.5 at 8:00 P.M. Mosquitoes were fed on this subject only at those times when his mean number of microfilariae was above 35 per 20 cu. mm. and most were fed when the mean number of microfilariae was near 100 per 20 cu. mm.

Aedes polynesiensis. In a large series of experiments *A. polynesiensis* was found to be a very efficient host in the laboratory for Tahitian strains of *W. bancrofti*. These experiments are de-

scribed in detail elsewhere in this paper. (see table 11).

Two lots of *A. polynesiensis* were fed on the subject with periodic *W. bancrofti*. It was found that the development of this form of *W. bancrofti* in *A. polynesiensis* was clearly different from that of Tahitian nonperiodic strains. The maturation of larvae of the periodic strain required 16 days of incubation as compared with 13 days necessary for the maturation of Tahitian strains in the same mosquito species held in the laboratory at the same time. Moreover, though 68 of 78 mosquitoes (87.2 per cent) of one lot dissected between 16 and 20 days after feeding harbored third-stage larvae (3 terminal papillae), most of these larvae were abnormal in morphology. The most commonly observed abnormality was a reduction in length (but normal width). Many larvae were only one-half the length of comparable larvae of Tahitian strains of *W. bancrofti* in *A. polynesiensis*. Only 31 of the mosquitoes (39.7 per cent) in this lot had any third-stage larvae which appeared normal. The average number of all third-stage larvae per mosquito was 5.0 and the average number of apparently normal third-stage larvae per mosquito was 1.0 (i.e. 80 per cent of the third-stage larvae were abnormal). The development of larvae in the second, smaller lot of *A. polynesiensis* fed on the same subject on another occasion was essentially the same as that described above. Subsequent to these two experiments it was demonstrated that the vast majority of microfilariae of this periodic strain were capable of undergoing normal development in *C. quinquefasciatus* (see below).

Culex quinquefasciatus. *C. quinquefasciatus* is an important vector of periodic *W. bancrofti* in many areas and

3 species

A. aegypti

of mosquitos having third type larvae	Per cent of total no. of mosquitoes with <i>W. bancrofti</i>
16†	100.0
0	0
0	0
16	100.0

o the most advanced

i.e.

TABLE 3
The susceptibility of C. quinquefasciatus to infection with Tahitian strains of W. bancrofti

Experiment no.	Average no. of microfilariae in 20 cu. mm. of donor's blood at time of mosquito feeding	No. of mosquitoes dissected 13 or more days after feeding	No. of mosquitoes with third-stage larvae	Percentage of mosquitoes with third-stage larvae	Average no. of third-stage larvae per infected mosquito	Range: no. of third-stage larvae per infected mosquito
1	2.0	10	2	20.0	1.0	1
2	2.3	32	0	0.0		
3	5.8	179	4	2.2	1.0	1
4	7.4	161	0	0.0		
5	30.6	46	5	10.9	1.6	1-3
6	34.8	48	13	27.1	1.3	1-2
7	38.1	59	18	30.5	2.8	1-7
8	40.7	143	27	18.9	1.4	1-5
9	105.9	88	29	33.0	3.0	1-30*
10	150.6	98	15	15.3	1.8	1-5
11	160.3	17	2	11.8	1.5	1-2
12	161.4	180	46	25.6	2.5	1-8
13	244.5	12	2	16.7	1.0	1
14	270.8	23	3	13.0	1.0	1
15	274.6	10	3	30.0	3.3	1-5
16	294.5	17	3	17.6	1.3	1-2
17	488.5	11	3	27.3	4.3	3-6

* The next highest number of larvae in a mosquito in this experiment was 7.

was the species suspected as the vector of *W. bancrofti* in Polynesia (Theobald, 1910) before the discovery of the importance of the *scutellaris* group of *Aedes*.

Data on the susceptibility of *C. quinquefasciatus* to infection with Tahitian strains of *W. bancrofti* are presented in table 3. Ten different donors were used in these 17 experiments. Four of the donors (Roo, exp. 3; Doris, exp. 5, 6, 7, 8; Joseph, exp. 10, 11; Taumu, exp. 12) were also used in experiments with *A. polynesiensis* (see table 1). In all proportion of the mosquitoes in some of the experiments summarized in table 3 were dissected a week or more after the larvae had matured. However, there were no significant difference in the percentage of specimens infected or in the average number of larvae per infected mosquito between these mosquitoes and those of the same lots which

were dissected just after the larvae had matured.

Some of the third-stage larvae encountered in these experiments were shorter than were third-stage larvae of the same strains of *W. bancrofti* in *A. polynesiensis*. In some instances degenerate larvae in various stages of development were found. These are not included in table 3.

It will be noted that in comparison with *A. polynesiensis* (see table 11) *C. quinquefasciatus* was a poor host for these nonperiodic strains of *W. bancrofti* whether judged by the percentage of mosquitoes with third-stage larvae or by the average number of third-stage larvae per infected mosquito. Since the percentage of mosquitoes infected and the average number of third-stage larvae per infected mosquito did not increase with the higher blood densities

of microfilariae it would appear that it is a characteristic of individual mosquitoes rather than of individual microfilariae which determines whether or not complete development of these strains of *W. bancrofti* will take place in *C. quinquefasciatus*.

Five lots of *C. quinquefasciatus* were fed on the subject with periodic *W. bancrofti*. A total of 158 specimens in these lots was dissected 13 or more days after feeding and 147 (93.0 per cent) harbored normal third-stage larvae. The mean number of normal third-stage larvae per infected mosquito was 12.2 and the range in the number of normal third-stage larvae per mosquito was from 1 to 52. It is apparent that *C. quinquefasciatus* is much more susceptible to infection with this periodic strain of *W. bancrofti* than it is to infection with Tahitian nonperiodic strains.

It was demonstrated that the relative insusceptibility of *C. quinquefasciatus* to Tahitian strains of *W. bancrofti* was not the result of a decreased intake of microfilariae. Ten specimens dissected within 24 hours after feeding on a donor with a Tahitian strain of *W. bancrofti*

and an average of 40.7 microfilariae per 20 cu. mm. (exp. 8, table 3) had an average of 7.4 microfilariae per mosquito. Ten specimens dissected within 24 hours after feeding on the subject with periodic *W. bancrofti* when the average number of microfilariae per 20 cu. mm. was 88.0 had an average of 14.4 microfilariae per mosquito.

In one experiment a single lot of *C. quinquefasciatus* was randomly divided into two cages. One cage of mosquitoes was fed on the subject with the periodic infection and the other was fed on a subject with a Tahitian strain of *W. bancrofti* and a similar blood density of microfilariae. The mosquitoes which fed on the donor with the periodic infection became heavily infected with third-stage larvae whereas the mosquitoes which fed on the donor with the Tahitian strain were only lightly infected with third-stage larvae.

Other mosquito species. Data on the susceptibility of the other mosquito species on Tahiti to infection with Polynesian strains of *W. bancrofti* are given in table 4. Each species was fed on from 3 to 5 different donors, each of

TABLE 4
The susceptibility of 5 species of mosquitoes to infection
with Polynesian strains of *W. bancrofti*

Mosquito species	Days after feeding dissected					
	1.5 to 12.5			13.5 to 20.5		
	No. of mos-quitoes dissected	Mosquitoes with first-stäge or older larvae		No. of mos-quitoes dissected	Mosquitoes with second- or third-stäge larvae	
		Number	Per cent		Number	Per cent
<i>A. edgari</i>	55	39	70.9	95	78*	82.1
<i>C. atriceps</i>	53	25	47.2	9	4*	44.4
<i>C. sp.</i>	31	13	41.9	24	3*	12.5
<i>A. aegypti</i>	79	32	40.5	30	0	0
<i>C. annulirostris</i>	56	12	21.4	73	0	0

* Third-stage larvae were found in one or more specimens.

TABLE 5
The prevalence of individuals with microfilariae* among the inhabitants of Papara and Vairao, Tahiti and of Makatea by age group and sex

Age group	Males			Females		
	Number examined	No. with microfilariae	Percentage with microfilariae	Number examined	No. with microfilariae	Percentage with microfilariae
0-4	156	8	5.1	150	12	8.0
5-9	209	25	12.0	183	26	14.2
10-14	153	40	26.1	118	29	24.6
15-19	163	54	33.1	135	35	25.9
20-24	172	79	45.9	117	41	35.0
25-29	128	60	46.9	94	25	26.6
30-34	96	50	52.1	81	32	39.5
35-39	111	56	50.5	73	29	39.7
40-44	68	38	55.9	67	27	40.3
45-49	74	41	55.4	44	19	43.2
50-54	55	30	54.5	26	13	50.0
55-59	30	13	43.3	16	9	56.3
60+	38	18	47.4	23	8	34.8
Totals	1,453	512	35.2	1,127	305	27.1

* As measured by the examination of a single 20-cu. mm. sample of capillary blood.

which had a blood density of microfilariae high enough to infect 90 per cent or more of *A. polynesiensis* (see table 11). Most of these subjects were actually used in experiments with *A. polynesiensis*. All of the donors were from Tahiti except 3 from Makatea who were used in the experiments with *A. aegypti*. The specimens of *A. aegypti* employed were also from Makatea. The *A. edgari* and *A. aegypti* used in the experiments summarized in table 4 were all reared in the laboratory. Most of the specimens of the other 3 species were captured after feeding to repletion on the donor in nature. This was necessary because laboratory-reared specimens could not be induced to feed in adequate numbers. All larvae referred to in table 4 were definitely identified as *W. bancrofti*. It will be noted that *A. edgari*, *C. atriceps*, and *Culex* sp. were able to carry at least some larvae to maturity. Of these 3 species, only

A. edgari appeared to be a relatively efficient host when judged by the number of larvae which matured. However, these larvae required 4 to 5 days longer for their maturation in this mosquito than they did under similar conditions in *A. polynesiensis*.

A. edgari and *C. annulirostris* were also fed on subjects with periodic *W. bancrofti*. Of 15 *A. edgari* which were dissected 15 or more days after feeding, 11 (73.3 per cent) had third-stage larvae. The length of time necessary for the maturation of these larvae was similar to that required for the maturation of Tahitian strains of *W. bancrofti* in the same species (see above).

Of 25 *C. annulirostris* fed on the subject with periodic *W. bancrofti*, none was found to have third-stage larvae when dissected 16 days after feeding. One specimen did contain a single late second-stage larva. Specimens of *C.*

quinquefasciatus fed at the same time became heavily infected with third stage larvae.

Human reservoir of infection

The inhabitants of the areas from which mosquitoes were collected for dissection were examined to determine the relative frequency with which various blood densities of microfilariae occurred in an untreated population. A single 20-cu. mm. sample of capillary blood was obtained during the day from each of 2,580 persons (almost the entire population of the 3 study areas).

The prevalence by age group and sex of individuals with one or more microfilariae per 20 cu. mm. of blood is given in table 5. It will be noted that the prevalence of persons with microfilariae increases with age until early adulthood, after which it remains more or less constant. The prevalence is higher among males than among females except below the age of 15 years and, perhaps, above the age of 50 years.

Only 21.7 per cent of 46 persons with elephantiasis were found to have micro-

filariae. This is a significantly lower percentage than that observed for the age groups which they represent.

Approximately 80 per cent of the households (about 300) in two of the study areas (Vairao and Papara) had one or more members with microfilariae. Household data were not available for Makatea.

The blood densities of microfilariae which were found varied from 1 to 1,296 microfilariae per 20 cu. mm. of blood. The frequency with which individuals with various densities of microfilariae were encountered is indicated, by sex, in table 6. It is seen that the great majority of individuals with microfilariae had blood densities which fell in the lower part of the wide range noted above. In general, males had higher densities than did females.

Because of the combination of the extremely skewed distribution and the wide range of values encountered, it is difficult to portray adequately the density of microfilariae by age group by means of the usual descriptive terms such as the mean and the median. The

TABLE 6
A frequency distribution, by sex, of the number of individuals from Papara and Vairao, Tahiti, and from Makatea with various blood densities of microfilariae

Microfilariae per 20 cu.mm. of blood	Males		Females	
	No. with indicated density of microfilariae	Per cent of total no. with microfilariae	No. with indicated density of microfilariae	Per cent of total no. with microfilariae
1-5	34	16.7	66	22.1
6-10	41	8.2	39	13.0
11-20	52	10.4	39	13.0
21-30	34	6.8	15	5.0
31-40	27	5.4	17	5.7
41-50	21	4.2	17	5.7
51-75	52	10.4	30	10.0
76-100	24	4.8	21	7.0
101-200	87	17.3	36	12.0
201-400	53	10.6	13	4.3
400+	28	5.6	5	1.7

TABLE 7

The mean number of microfilariae per 20 cu. mm. of blood, by age group and sex,
for individuals with microfilariae from Papara and Vairao, Tahiti
and from Makatea

Age group (years)	Males		Females	
	No. of individuals with microfilariae in indicated age group	Mean no. of micro- filariae for individuals with microfilariae in indicated age group	No. of individuals with microfilariae in indicated age group	Mean no. of micro- filariae for individuals with microfilariae in indicated age group
0-14	73	42.3	65	30.7
15-24	130	112.0	74	61.3
25-34	106	120.2	57	53.8
35-44	94	127.3	54	63.9
45-54	68	106.0	32	98.2
55 +	31	111.9	17	125.7

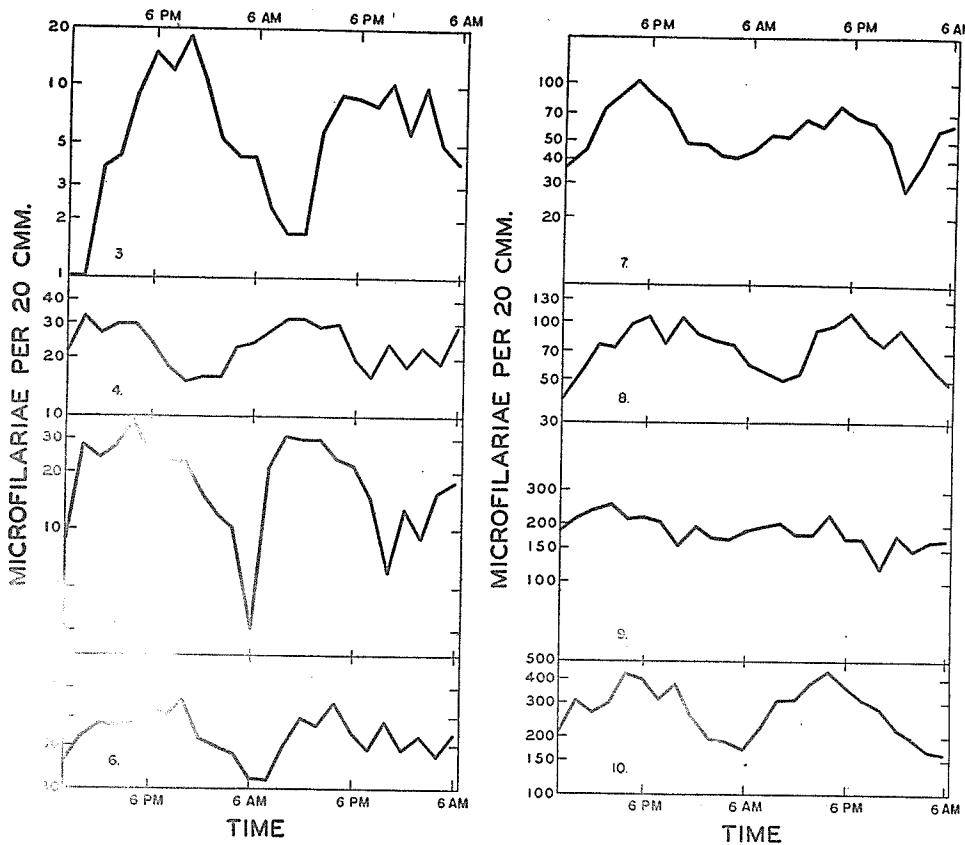


FIGURE 1. The proportionate variation (vertical scale is logarithmic) over a 48-hour period in the density of microfilariae in the peripheral blood of 8 individuals with *W. bancrofti* (see table 8).

TABLE 8
The variation over a 48-hour period in the density of microfilariae in the peripheral blood of 10 individuals with *W. bancrofti*

Time of examination	Microfilariae per 20 cu. mm. of blood*									
	1	2	3	4	5	6	7	8	9	10
First 24 hours	First 24 hours	Second 24 hours	First 24 hours	Second 24 hours	First 24 hours	Second 24 hours	First 24 hours	Second 24 hours	First 24 hours	Second 24 hours
8:00-9:00 A.M.	0.0	0.8	1.0	1.0	2.3	22	28	19	21	42
10:00-11:00 A.M.	1.1	1.0	0.3	2.3	1.0	1.7	33	32	31	57
12:00-1:00 P.M.	1.7	1.0	2.7	1.7	3.7	27	32	24	71	73
2:00-3:00 P.M.	2.3	1.0	1.7	1.7	4.3	6.0	30	29	28	65
4:00-5:00 P.M.	1.3	0.8	1.0	1.0	9.0	9.0	30	30	37	85
6:00-7:00 P.M.	1.3	0.7	0.7	2.3	14.7	8.7	24	20	24	77
8:00-9:00 P.M.	1.0	1.7	0.7	1.0	12.0	8.0	18	16	23	15
10:00-11:00 P.M.	1.0	0.8	0.3	1.0	18.3	10.7	15	24	23	6
12:00-1:00 A.M.	1.0	1.3	1.3	2.0	10.7	5.7	16	18	16	55
2:00-3:00 A.M.	0.3	0.0	0.7	0.3	5.3	10.3	16	23	12	9
4:00-5:00 A.M.	0.3	1.3	1.0	0.0	4.3	5.0	23	19	10	16
6:00-7:00 A.M.	0.3	1.0	1.3	0.3	4.3	4.0	24	29	3	18

* Three successive 20-cu. mm. blood samples were taken from each subject at 2-hour intervals. The mean of each set of 3 observations is given in this table.

relatively small number of individuals in each group also precludes the effective use of frequency distributions. With these reservations in mind the data in table 7 are presented as a rough indication of the density of microfilariae by age group. It is seen that the mean number of microfilariae for individuals with microfilariae in a given age group roughly parallels the prevalence of individuals with microfilariae in the same age group (see table 5). Adults had higher densities than did children, and males between the ages of 15 and 45 years had higher densities than did females in the same age groups.

It has recently been reported (Eyles et al., 1947; Edgar et al., 1952) that the blood density of microfilariae in persons with Polynesian strains of *W. bancrofti*, theretofore considered nonperiodic, actually undergoes a fluctuation over a 24-hour period. To obtain additional data on the magnitude of this fluctuation and its consequent influence on the infection of mosquito vectors, 10 individuals from Polynesia with various average densities of microfilariae were chosen for detailed study. All the subjects were active during the day and slept, as much as was possible under the circumstances, during the night. Three blood samples were taken from each individual every 2 hours for 48 hours.

The results of this study are presented in table 8 and figure 1. It is seen that in most of the subjects the blood density of microfilariae exhibited a rhythmic fluctuation with a peak density in the late afternoon or early evening. The magnitude of this fluctuation was roughly the same proportionately for the various average densities studied.

In one of the study areas, Papara, it was possible to compare the data for

261 persons examined in the survey herein reported with the results of an examination conducted 3 years previously (these latter data were kindly supplied by Dr. H. K. Beye and his collaborators). No control measures were undertaken in this area during this 3-year period. It was found (table 9) that the majority of individuals had blood densities of microfilariae which remained remarkably constant for this period of time, especially in view of the variation in values of blood samples obtained from the same individual in a short period of time (see table 12) and of the fluctuation in the density of microfilariae during a single day (table 8).

Quantitative aspects of the infection of Aedes polynesiensis with Tahitian strains of Wuchereria bancrofti

Naturally infected A. polynesiensis. Data on the magnitude of natural infections with *W. bancrofti* in individual specimens of *A. polynesiensis* were obtained from the dissection of the field-caught mosquitoes previously referred to in tables 1 and 2. *A. polynesiensis* is a species of mosquito especially well suited for this type of investigation since it can be easily captured while attempting to feed on man. When specimens are obtained in this way there can be no doubt as to their ability to seek out a blood meal and feed. If mosquitoes are captured while resting, not only is there doubt concerning the ability of infected specimens to seek out another blood meal, but also one might be more apt to capture heavily infected specimens if they were adversely affected by their parasites.

It is seen from the available data (table 10) that the magnitude of infections in mosquitoes harboring either

TABLE 9
The density of microfilariae in the peripheral blood of 261 individuals residing in an endemic area of W. bancrofti (Papara, Tahiti) before and after a 3-year interval

Number of microfilariae per 20 cu. mm. of blood							
Before*	After*	Before	After	Before	After	Before	After
0	1	3	23	35	67	104	68
0	1	7	0	36	27	115	10
0	3	7	0	36	47	121	111
0	9	7	10	37	11	124	214
0	10	8	0	46	25	129	501
0	14	8	8	49	5	135	10
0	15	8	30	48	102	144	111
0	15	8	38	53	0	145	147
0	17	9	0	56	0	152	144
0	21	10	3	56	27	170	534
0	45	10	9	58	0	179	133
0	96	10	15	59	1	184	232
0	98	12	0	62	223	215	192
0	105	15	14	71	1	227	365
1	0	18	0	74	9	235	144
1	0	20	0	79	59	236	345
1	0	22	1	79	70	252	447
1	0	23	9	83	35	261	121
1	31	27	95	84	0	334	189
2	0	29	77	85	59	462	613
2	80	30	24	87	96	503	602
3	0	33	102	94	87	566	190
3	0	35	12	99	171	594	174

* No microfilariae were found in the blood of 169 individuals at either examination. Each pair of observations in this table represents an individual who had microfilariae on at least one of these two examinations.

first- or second-stage larvae is about the same. However, mosquitoes with third-stage larvae definitely had fewer larvae per specimen than did mosquitoes with first-stage larvae.

Experimental infection of A. polynesiensis. When it became apparent that *A. polynesiensis* was an important vector of *W. bancrofti* in French Oceania a series of laboratory experiments was undertaken with this mosquito which were designed to obtain information on the quantitative aspects of infections with *W. bancrofti* referred to in the introduction to this paper.

All *A. polynesiensis* used in these experiments, unless otherwise noted, were allowed to feed on the hand and forearm of the donor. Engorged specimens were transferred to a clean cage after the completion of the feeding period. Some of the mosquitoes which died before the maturation of the filarial larvae were dissected in order to observe the characteristics of early infections. Insofar as was possible, all mosquitoes dying after the appearance of third-stage larvae in any of the specimens in the lot were dissected.

The development of the local strains of *W. bancrofti* in *A. polynesiensis* con-

TABLE 10
*The number of larvae of *W. bancrofti* and their stage of development
in naturally infected *A. polynesiensis**

Number of larvae	Mosquitoes with* first-stage larvae		Mosquitoes with* second-stage larvae		Mosquitoes with* third-stage larvae	
	No. of mosquitoes with indicated no. of larvae	Percentage of total no. of mosquitoes with larvae	No. of mosquitoes with indicated no. of larvae	Percentage of total no. of mosquitoes with larvae	No. of mosquitoes with indicated no. of larvae	Percentage of total no. of mosquitoes with larvae
1-4	65	53.7	38	55.1	32	74.4
5-9	26	21.5	16	23.2	8	18.6
10-19	20	16.5	14	20.3	2	4.7
20 +	10	8.3	1	1.4	1	2.3
Totals	121	100.0	69	100.0	43	100.0
Mean no. of larvae per infected mosquito	6.7		5.8		4.6	
Median no. of larvae for infected mosquitoes	4		4		2	

* In the relatively few mosquitoes harboring larvae of more than one stage, only the larvae of the most advanced stage are included in the table.

formed with the accepted descriptions with the exception of one point. It is generally stated that complete maturation of the larvae of *W. bancrofti* takes place in the thoracic musculature of the mosquito and that the larvae subsequently migrate to other parts of the mosquito. Several investigators (Yamada, 1927; Pratt and Newton, 1946) have indicated that the mature larvae migrate to the abdominal hemocoele before migrating to the head and proboscis. In the experiments herein reported it was also observed that larvae migrated to the abdominal hemocoele before going to the head and proboscis. However, some of the larvae found in the abdominal hemocoele were not completely mature, although they were third-stage larvae as indicated by their terminal papillae. These larvae were somewhat shorter and thicker than

were fully mature larvae. Apparently final maturation of at least some of the larvae took place in the abdominal hemocoele and not in the thoracic musculature.

The data on the experiments with *A. polynesiensis* and Tahitian strains of *W. bancrofti* are summarized in table 11. All larvae therein referred to are third-stage larvae except for a few late second-stage larvae which occurred in heavily infected specimens which also contained third-stage larvae. Presumably, the "crowding effect" prevented the maturation of all the larvae simultaneously. It will be noted that mosquitoes became infected after feeding on comparatively low blood densities of microfilariae. The percentage of mosquitoes infected and the number of larvae per mosquito increased with the increase in the blood density of micro-

ment

Mosquitoes with* third-stage larvae	
of mosquitos with stated no. larvae	Percentage of total no. of mosquitoes with larvae
32	74.4
8	18.6
2	4.7
1	2.3
3	100.0
4.6	
2	

e, only the larvae of

ae. Apparently at least some of n the abdominal he thoracic mus-

periments with *A.* itian strains of larvalized in table referred to are t for a few late ich occurred in tens which also arvae. Presum- "fect" prevented he larvae simul- noted that mos- d after feeding blood densities of entage of mos- the number of reased with the ensity of micro-

TABLE 11
The susceptibility of *A. polynesiensis* to infection with *Takifitan* strains of *W. bancrofti*

Average number of microfilariae in 20 cu. mm. of donor's blood at the time of mosquito feeding	Number of mosquitoes dissected 13 or more days after feeding	Percentage of mosquitoes with larvae*	Average number of larvae per mosquito	Range: number of larvae per infected mosquito	Number of mosquitoes with indicated number of larvae											
					0	1	2	3	4	5	6	7	8	9	10 to 14	
0.4	38	5.3	.05	1.0	1	36	2									
0.6	69	11.6	.1	1.0	1	61	8									
2.1	36	55.6	.8	1.5	1-3	16	13	5	2							
3.1	70	64.3	1.3	2.0	1-6	25	20	14	5	2	3	1				
3.3	49	49.0	1.1	2.3	1-6	25	9	7	3	2	2	1				
3.5	67	47.9	.8	1.6	1-4	50	29	10	4	3						
4.8	13	38.5	.8	2.0	1-3	8	2	1	2							
5.1	18	50.0	1.1	2.1	1-5	9	4	3	1	1						
11.4	17	76.5	2.1	2.8	1-7	4	4	4	1	1	2					
11.5	138	68.1	2.1	3.1	1-14	44	30	20	14	10	5	9	1	1	1	3
12.8	66	83.3	3.5	4.1	1-11	11	8	9	6	11	2	1	4	3	2	
27.0	66	86.4	3.5	4.0	1-14	9	12	12	4	2	3	3	4	5		
28.4	33	97.0	6.1	6.3	1-21	1	2	4	4	1	6	1	2	4	5	
31.9	67	82.1	4.5	5.5	1-12	12	5	8	7	6	7	2	4	3	2	11
31.9	28	96.4	5.6	5.8	1-15	1	3	2	5	1	2	1	2	4	2	
38.0	76	89.5	4.6	5.1	1-18	8	11	10	11	5	5	9	1	3	2	10
52.1	26	88.5	5.1	5.7	1-14	3	3	2	3	3	1	2	1	3	1	4
97.4	43	97.7	12.7	13.0	1-42	1	5	3	1	1	3	1	4	1	9	5
167.0	74	94.6	13.4	14.2	1-53	4	2	3	2	1	6	1	5	3	6	15
195.6	22	95.5	18.8	19.7	4-44	1				1	1	1	1	3	2	4
208.0	36	97.2	16.7	17.2	2-41	1				1	1	3	2	1	3	7
533.9	25	100.0	16.4	16.4	3-33	1				1	1	2	3	6	5	2
555.1	54	100.0	21.7	21.7	2-60	1				1	1	2	1	11	12	8
																13

* All were third-stage larvae except for a few late second-stage larvae in heavily infected mosquitoes which also contained third-stage larvae.

filariae. At the lower blood densities of microfilariae the ratio between the mean number of microfilariae in the 20 cu. mm. of the donor's blood and the mean number of larvae per mosquito was approximately 5 to 1. As the blood density of microfilariae increased, this ratio also increased so that in the experiments with the highest blood densities of microfilariae the ratio was more than 25 to 1. Apparently some of the numerous microfilariae ingested by mosquitoes fed on donors with high blood densities of microfilariae failed to complete their development because of the

"crowding effect." It will be noted that there was a wide range in the number of larvae in individual mosquitoes of the same lot.

To determine if mosquitoes feeding on other parts of the body became infected to the same extent as did those feeding on the hand and forearm, a single lot of mosquitoes was divided into two cages. Both groups of mosquitoes were fed simultaneously on the same donor, one cage on his hand and forearm, and the other on the center of his back. This experiment is represented in table 11 by the data for the

TABLE 12
Some characteristics of the donors used in experiments with A. polynesiensis (see table 11)

Average number of microfilariae in 20 cu.mm. of blood at the time of mosquito feeding	The no. of microfilariae per 20 cu.mm. of blood in individual samples of blood taken at the time of mosquito feeding*	Name of donor	Age	Sex	Previous treatment with Hетразан†
0.4	0, 1, 0, 0, 1, 1, 0, 0	Vahine	35	F	Two courses
0.6	1, 1, 0, 1, 0, 1, 1, 0	Tuira	29	F	One course
2.1	5, 2, 3, 1, 2, 1, 1, 2	Roo	16	M	Two courses
3.1	0, 3, 4, 4, 2, 3, 3, 6	Andre	15	M	None
3.3	2, 3, 2, 7, 2, 4	Roo			
3.5	7, 1, 3, 7, 4, 4, 2, 0	Fifi	32	F	One course
4.8	6, 5, 3, 2, 3, 7, 4, 8	Tihoni	44	F	Two courses
5.1	1, 8, 7, 0, 5, 7, 5, 8	Fine	19	F	One course
11.4	14, 15, 13, 11, 14, 9, 7, 8	Tautu	28	M	Two courses
11.5	6, 9, 13, 15, 15, 18, 8, 8	Marere	65	M	Partial course
12.8	11, 11, 16, 12, 13, 14, 12, 13	Daniel	15	M	None
27.0	28, 26	Jacque	12	M	None
28.4	32, 29, 34, 28, 17, 27, 31, 29	Doris	13	F	None
31.9	25, 32, 33, 26, 42, 25, 39, 33	Vahipi	18	M	None
38.0	32, 32, 39, 47, 46, 17, 42, 39	Vahipi			
52.1	3, 11, 10, 10, 10, 10, 10, 41	Doris			
97.4	65, 84, 100, 56, 33, 114, 154, 151	Joseph	16	M	Partial course
167.0	174, 171, 138, 201, 174, 213, 216	Taumu	47	M	None
195.6	123, 121, 127, 232, 114, 167, 221, 234	Tom	17	M	None
208.0	166, 306, 219, 244, 160, 279, 192, 98	Taumu			
533.0	357, 643, 510, 483, 654, 446, 486, 692	Timi	25	M	None
555.1	502, 273, 436, 582, 479, 612, 609, 511	Timi			

* Samples are listed in the order in which they were taken. In most instances 4 samples were taken just before the mosquitoes began feeding and 4 were taken after an interval of 1 hour when the mosquito feeding was discontinued.

† A course of Hетразан consisted of 2 milligrams of the drug per kilogram of body weight given 3 times a day for 7 days.

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two lots of mosquitoes fed on a donor with 31.9 microfilariae per 20 cu. mm. The infection rate of 82.1 per cent was obtained for specimens feeding on the hand and forearm and the rate of 96.4 per cent was obtained for those feeding on the back.

The lot of mosquitoes which was fed on the donor with 52.1 microfilariae per 20 cu. mm. was reared from hairy larvae which until recently had been considered distinctive of *A. horrescoens* (see Rosen and Rozeboom, 1954). It will be noted that the local *W. bancrofti* developed as readily in these mosquitoes as it did in mosquitoes reared from ordinary nonhairy larvae.

Some characteristics of the various donors used in the experiments summarized in table 11 are given in table 12. A comparison of these two tables shows that no evidence was found that the infectivity of microfilariae for *A. polynesiensis* was influenced by the donor's age, sex, or previous treatment with Hetrazan.

Longevity of infected A. polynesiensis. Data on the longevity of the mosquitoes used in the experiments cited in table 11 are presented in table 13. Considerable difficulty was encountered in keeping *A. polynesiensis* alive for long periods of time in the field laboratory in French Oceania. It was obvious that at least part of the difficulty was unrelated to the infection of this species with *W. bancrofti*. Other workers in the South Pacific have had similar experiences (Bahr, 1912; O'Connor, 1923; Edgar, 1950; Jachowski, 1951; Manson-Bahr and Muggleton, 1952). The observations in table 13 demonstrate that there was no recognizable deleterious effect of heavy infection with *W. bancrofti* on the longevity of *A. polynesiensis* for at least

TABLE 13
The survival of *A. polynesiensis* after feeding
on donors with Tahitian strains
of *W. bancrofti*

Average no. of microfilariae in 20 cu. mm. of donor's blood at the time of mos- quito feeding	Number of mos- quitoes fed	Percentage of mosquitoes surviving		
		6.5 days	9.5 days	12.5 days
0.0	46	100	52	41
0.0	131	91	81	50
0.4	88	86	66	46
0.6	207	99	76	33
2.1	57	97	97	77
3.1	81	99	91	86
3.3	175	70	35	30
3.5	144	98	85	47
4.8	176	15	11	7
5.1	192	94	53	10
11.4	151	83	35	16
11.5	159	98	98	88
12.8	126	96	95	95
27.0	128	88	82	52
28.4	145	90	72	32
31.9	79	100	96	86
31.9	60	100	93	47
38.0	125	98	67	62
52.1	46	96	83	59
97.4	131	84	51	51
167.0	110	96	78	74
195.6	94	96	78	23
208.0	165	90	54	22
533.9	177	91	67	14
555.1	207	94	77	29

the first week after the infective blood meal. It also appears from these data that there was no extensive mortality due to parasitism up to 9.5 days after feeding.

The data available for the evaluation of the effect of parasitism with *W. bancrofti* on *A. polynesiensis* after 9.5 days of incubation are, in general, unsatisfactory. However, there are a few observations which indicate that the longevity of this mosquito species was adversely affected near the end of the period required for the maturation of the filarial larvae (table 14). It will be noted that in each of the experiments

cited in table 14, those mosquitoes dying near the time of maturity of the larvae (approximately 13 days after feeding) had, on the average, a greater number of larvae than did those dying later. There are two possible causes for this phenomenon. The mosquitoes in each lot with the heaviest infections might have succumbed first because of their infection, or the mosquitoes might be losing mature larvae from the proboscis or other regions. It has been demonstrated that mosquitoes do lose mature larvae in the laboratory without taking a blood meal (Pratt and Newton, 1946). In three of the experiments referred to in table 14 it is not possible to evaluate the relative importance of these two possible causes. However, in the experiment in which mosquitoes fed on a donor with 167.0 microfilariae per 20 cu. mm. it appears that a distinct

tion can be made. At 13 days after feeding, 8 mosquitoes were selected at random from the cage and were killed and dissected. These mosquitoes contained fewer larvae on the average than did mosquitoes dying just before and just after this time, but they contained approximately the same number of larvae on the average as did all mosquitoes dying afterwards. It would seem that in this instance the more heavily infected mosquitoes died before those with lighter infections.

DISCUSSION

Mosquito vectors

Aedes polynesiensis. It has been shown by both field and laboratory data that *A. polynesiensis* is a major vector of *Wuchereria bancrofti* in those areas of French Oceania where the present studies were carried out. As far as can be determined this is the only species of the *A. scutellaris* complex which occurs in these study areas or in other localities in French Oceania from which mosquitoes have been studied (Rosen and Rozeboom, 1954). Correspondence with Dr. Alan Stone has established that no specimens of *Aedes tongae* from French Oceania exist in the collection of the United States National Museum and that the report of this species from the area by Beye et al. (1952) was apparently a misidentification.

The data herein reported show that *A. polynesiensis* is a poorer host for a periodic strain of *W. bancrofti* from the West Indies than it is for Tahitian nonperiodic strains. Bahr (1912) reported that *Aedes pseudoscutellaris* was just as efficient a host for a periodic strain of *W. bancrofti* from the Solomon Islands as it was for the Fijian nonperiodic strains. However, few mosquitoes were fed on the subject

TABLE 14
The average number of larvae in *A. polynesiensis* dying at various times after feeding on subjects with Tahitian strains of *W. bancrofti*

Average no. of microfilariae in 20 cu.mm. of donor's blood at the time of mosquito feeding	No. of days after feeding which dissected mosquitoes survived	No. of mosquitoes dissected at indicated time after feeding	Average no. of larvae per mosquito
555.1	12.5 to 13	25	26.0
	13.5 to 14	23	19.9
	14.5 to 15	6	12.7
195.6	12.5	10	22.3
	13.5 to 15	12	15.8
	9.5 to 13	8	25.3
167.0	13*	8*	12.9
	13.5	13	24.2
	14.5	22	14.6
	15.5	1	8.0
	16 to 19	14	4.4
97.4	13.5 to 15.5	22	18.2
	18 to 24	21	6.9

* These mosquitoes were selected at random from mosquitoes in the lot and were then killed and dissected.

13 days after were selected at and were killed mosquitoes con- n the average ing just before , but they con- e same number age as did all ards. It would ance the more oes died before tions.

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It has been laboratory data a major vector i in those areas ere the present . As far as can he only species nplex which occurs or in other ania from which studied (Rosen Correspondence has established des tongae from n the collection ational Museum his species from (1952) was ap- ation.

orted show that orer host for a bancrofti from is for Tahitian Bahr (1912) re- seudoscutellaris a host for a bancrofti from ; it was for the ains. However, d on the subject

with the periodic strain and no details of the results were given. Furthermore, 3 species of the *scutellaris* complex, any one of which would have been identified as *A. pseudoscutellaris* at that time, are now known to occur in the Fiji Islands.

Culex quinquefasciatus. An assessment of the importance of *C. quinquefasciatus* as a vector of *W. bancrofti* in Polynesia is of great interest to persons concerned with the control of filariasis since this mosquito is abundant in many parts of the endemic area. Control procedures directed against mosquitoes of the *A. scutellaris* complex are often ineffective for the control of *C. quinquefasciatus*.

The data which have been available on the experimental infection of *C. quinquefasciatus* with Polynesian strains of *W. bancrofti* are difficult to evaluate because of the lack in many instances of information on the numbers of the mosquitoes used, the interval at which mosquitoes were dissected after the experimental blood meal, the number of donors used, and the blood density of microfilariae of the donors.

Bahr (1912), in the Fiji Islands, found one third-stage larva in 15 mosquitoes dissected after 13 days of incubation. Byrd et al. (1945) found one third-stage larva in 22 specimens dissected after 15 days of incubation. Manson-Bahr and Muggleton (1952) found 3 mosquitoes with third-stage larvae out of a total less than 13 specimens dissected 9 or more days after feeding. Hu (1952), using donors infected in Polynesia and *C. quinquefasciatus* from the Hawaiian Islands, concluded that this mosquito "could act as a suitable intermediate host" but he gave no details of his experiments.

On the other hand, O'Connor (1923)

in the Samoa Islands, and McKenzie (1925) and Davis (1949) in the Cook Islands found no development in *C. quinquefasciatus* beyond the first larval stage. They did not give the number of mosquitoes examined.

In the present studies, in which more than 1,100 *C. quinquefasciatus* fed on 10 different donors with various blood densities of microfilariae were dissected after an interval adequate for the maturation of the larvae, a small percentage of the specimens was found suitable for the maturation of Tahitian strains of *W. bancrofti*. However, the number of third-stage larvae per infected mosquito was small and some of them appeared abnormally short.

In view of the limited nature of the experimental evidence available from areas other than Tahiti it is not possible to determine if *C. quinquefasciatus* differs significantly in its ability to serve as a host of *W. bancrofti* in various parts of Polynesia. It is apparent, however, that the results obtained by workers in Polynesia are different from those obtained with *C. quinquefasciatus* in many parts of the world where this mosquito is a major vector of periodic strains of *W. bancrofti*. Theoretically this difference might be due to differences in strains of the mosquito or it might be due to differences in strains of the parasite.

Newton et al. (1945) found that *Phosphora confinis* from different localities (Puerto Rico and the United States) differed markedly in their susceptibility to the same strain of periodic *W. bancrofti*. Similarly, Kartman (1953) reported that different strains of *A. aegypti* differed in their susceptibility to the same strain of *Dirofilaria immitis*. Eyles and Most (1947), using a donor infected in Polynesia and

mosquitoes from the United States, showed that *Culex pipiens* Linn., a species closely related to *C. quinquefasciatus*, was an excellent host for this nonperiodic strain of *W. bancrofti*. They also found that while one strain of *C. quinquefasciatus* was not a very good host, another lot of mosquitoes which they initially assumed to be *C. quinquefasciatus* was as susceptible as *C. pipiens*. However, the second lot of mosquitoes was later found to have come from an area where both *C. pipiens* and *C. quinquefasciatus* occur and there was doubt as to its true identity.

In support of the argument for differing strains of *W. bancrofti*, Mainson-Bahr and Muggleton (1952) state that *C. quinquefasciatus* from the Fiji Islands was an optimum host for a periodic strain of *W. bancrofti* from Ocean Island. However, the data which they present are not adequate to demonstrate that their results in this instance were significantly different from those which they obtained with Fijian nonperiodic strains of *W. bancrofti*.

The experimental data herein reported seem to indicate clearly that Tahitian strains of *W. bancrofti* are different from at least one periodic strain of *W. bancrofti* in their ability to complete their development in *C. quinquefasciatus*.

The finding that *C. quinquefasciatus* is a relatively inefficient host for Tahitian strains of *W. bancrofti* in the laboratory does not eliminate the possibility that this mosquito might serve as a vector of the parasite in nature. The only series of dissections of a significant number of field-caught specimens of this species in Polynesia which has been reported is that of Byrd et al. (1945) from the Samoa Islands. These workers found that *C. quinquefasciatus*

frequently harbored microfilariae of *W. bancrofti* but the later stages of the parasite were very uncommon. Similar results were obtained in the investigations herein reported. In areas where a high prevalence of infection in human beings is maintained by *A. polynesiensis* it is likely that *C. quinquefasciatus* occasionally transmits a few larvae (which may or may not be capable of further development). However, the crucial question would seem to be whether or not *C. quinquefasciatus* could propagate the infection in the absence of other vectors. This is of special importance in regard to such areas as the Hawaiian Islands where *C. quinquefasciatus* is present but where mosquitoes of the *A. scutellaris* group do not occur.

In view of the data which have been presented, it is the author's opinion that *C. quinquefasciatus* cannot propagate Polynesian strains of *W. bancrofti* in the absence of more efficient vectors. However, direct evidence on this subject is not available and it is unlikely that such data will be available until complete control of other vectors is obtained in some part of Polynesia.

Aedes aegypti. Although *A. aegypti* is common in many endemic areas of *W. bancrofti* throughout the world it has never been incriminated as a vector of this parasite. However, both periodic and Polynesian strains of *W. bancrofti* will mature in the laboratory in a very small percentage of certain strains of *A. aegypti*. Eyles and Most (1947) obtained third-stage larvae of a Polynesian strain of *W. bancrofti* in 3.3 per cent of 90 specimens of an insectary strain of *A. aegypti* in the United States, and Pester (1952) found third-stage larvae of a Fijian strain of *W. bancrofti* in 8.0 per cent

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of 25 specimens of a West African strain of *A. aegypti*. On the other hand, Bahr (1912) and Manson-Bahr and Muggleton (1952), in the Fiji Islands, found no advanced larvae in 28 and 31 local specimens of *A. aegypti*, respectively, which had fed on local strains of *W. bancrofti*. Similarly, in the present studies no development beyond the first larval stage was observed in 104 specimens of *A. aegypti* which were dissected 10.5 days or more after feeding on 1 of 3 donors with blood densities of microfilariae high enough to ensure that practically all the mosquitoes would ingest some microfilariae.

It is not possible to determine from the data cited above if the maturation of Polynesian strains of *W. bancrofti* in certain strains of *A. aegypti* and not in others is due to true strain differences in the mosquito or is the result of chance. Kartman (1953) was able to produce susceptible and refractory strains of *A. aegypti* with respect to infection with *D. immitis* by selective breeding. He was unable to do so with *Culex* mosquitoes.

In regard to findings in *A. aegypti* captured in nature, Byrd et al. (1945) found no *W. bancrofti* in 141 specimens from the Samoa Islands. In the studies herein reported no larvae more developed than first stage were found in the 80 mosquitoes dissected.

The rarity with which Polynesian strains of *W. bancrofti* complete their development in *A. aegypti* would appear to eliminate consideration of this mosquito as a vector of the parasite in Polynesia.

Culex annulirostris. This species is abundant in many endemic areas of *W. bancrofti* in the Australasian Region and the eastern part of the Oriental Region. Complete development

of periodic *W. bancrofti* in the laboratory has been reported by Cabrera and Tubangui (1951) in an unspecified number of laboratory-reared specimens of *C. annulirostris* in the Philippine Islands, and by Brug (1938) in 1 of 3 wild-caught specimens in Indonesia. On the other hand, Walker (1924) found only a single second-stage larva in 9 *C. annulirostris* exposed to periodic *W. bancrofti* in Australia and in the present studies only one second-stage larva was found in 25 specimens exposed to a periodic strain from the West Indies.

Previous investigators (Bahr, 1912; O'Connor, 1923; Byrd et al., 1945; and Davis, 1949) were unable to obtain complete development of Polynesian strains of *W. bancrofti* in *C. annulirostris*. In the present studies no advanced larvae were found in mosquitoes which were exposed to 5 different donors with Tahitian strains of *W. bancrofti*. In addition, no *W. bancrofti* were found in 446 wild-caught mosquitoes, but a high prevalence of infection with *D. immitis* was observed (Rosen, 1954).

Other species. Although *Aedes edgari* is a relatively efficient host of Tahitian strains of *W. bancrofti* in the laboratory, data on its distribution and abundance in nature indicate that it is not an important vector of this parasite. It is of interest that this mosquito is closely related to *Aedes vigilax* (Skuse) which is suspected (Kerrest, 1952) to be a vector of nonperiodic *W. bancrofti* on New Caledonia. Mosquitoes of the *A. scutellaris* group do not occur on New Caledonia. *A. vigilax* has been found to be a "rather poor host" of periodic *W. bancrofti* in Australia (Heydon, 1931). Like *A. edgari* it required a longer period for the maturation of larvae than did more efficient hosts used as controls.

Neither *C. atriceps* nor *Culex* sp. appear to be of importance as vectors of *W. bancrofti* in French Oceania because of their inefficiency as hosts in the laboratory. *C. sitiens*, which is related to *Culex* sp., has been found to be a poor host of a periodic strain of *W. bancrofti* in Australia (Heydon, 1931).

Sources of mosquito infection

The data in this report on the prevalence of individuals with microfilariae in their peripheral blood and on the magnitude of their parasitemia have been presented as an indication of the sources of infection available to mosquitoes in the study areas. An extensive discussion of these data in relation to the actual prevalence or intensity of infection with adult worms is beyond the scope of this presentation. However, it has long been recognized that many individuals harboring living adult worms do not have microfilariae in their peripheral blood (Manson, 1883). Moreover, it is as yet uncertain what relation exists within a community between the prevalence of individuals with microfilariae in their peripheral blood and the prevalence of infection with *W. bancrofti* or the prevalence of clinical disease due to this parasite. Similarly, it is not known what relationship exists between the blood density of microfilariae in an individual and the magnitude of his infection with adult worms. Recent experimental work on animal filariasis has indicated that the foregoing relationships are not simple. Thus, Bertram (1952) working with *Litomosoides carinii*, a filaria of the cotton rat, has shown that the number of microfilariae in an animal's blood is an unsuitable measure of its burden of adult worms. He

found that superinfected animals (with large numbers of adult worms) had lower blood densities of microfilariae than did animals with simple infections (with few adult worms). Moreover, the duration of parasitemia was shorter for the superinfected animals than it was for the animals with simple infections.

Although a rhythmic fluctuation in the blood density of microfilariae over a 24-hour period was observed in most of the 10 subjects studied, the magnitude of this fluctuation was very small in comparison with that of other human filariae for which periodicity has been described. Consequently, it is the author's opinion that the term "diurnal periodicity" suggested as descriptive of Polynesian strains of *W. bancrofti* (Eyles et al., 1947; Edgar et al., 1952) is inappropriate. It is of interest that the high and low points of the fluctuation in density of microfilariae observed in the present study were, in general, similar to those of fluctuations of human body temperature (Best and Taylor, 1950).

Quantitative aspects of filarial infections in mosquitoes

Although the use of Hetrazan as a public health measure against *Wuchereria bancrofti* has had as its goal the reduction of the number of circulating microfilariae to a level not infective for mosquito vectors, there have been relatively few data available on the magnitude of the parasitemia necessary to infect mosquitoes. Similarly, there has been very little information available on the effect of heavy parasitism with *W. bancrofti* on the longevity of mosquitoes.

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mosquitoes failed to imbibe microfilariae from an individual with 9 microfilariae per 20 cu. mm. of blood (the species of mosquito was not given), whereas lots of *Aedes pseudoscutellaris* feeding on individuals with densities of 89 microfilariae and 275 microfilariae per 20 cu. mm. nearly all died before the larvae had completed their development. He stated that mosquitoes of the same species nearly all survived the length of time necessary for complete development of the larvae when fed on individuals with "small numbers" of microfilariae, and concluded that "an individual with a moderate infection may be a greater danger to the community than one with a large infection." More recently the same author (Manson-Bahr, 1952), on the basis of additional work carried out in the Fiji Islands, concluded that 4 microfilariae per 20 cu. mm. is a subinfective density for *A. pseudoscutellaris*.

Hicks (1932), utilizing West African strains of *W. bancrofti*, failed to obtain infections in *Anopheles gambiae* with densities of microfilariae lower than 20 per 20 cu. mm., but found that densities as high as 200 to 300 per cu. mm. did not increase the mortality rate among several species of *Anopheles*.

Hu (1937), employing Chinese strains of *W. bancrofti*, was able to obtain infections in *C. pipiens* with a density of 7 microfilariae per 20 cu. mm. In regard to survival he concluded (Hu, 1939) that "the mosquitoes in the infected lots which were able to survive longest were generally those that were either negative to the infection or those that were harboring few of the filarial larvae."

Basu and Rao (1939), using Indian strains of *W. bancrofti*, stated that a minimum of 12 microfilariae per .2 cc.

(this is probably an error and should be 20 cu. mm.) was found infective for *C. quinquefasciatus*.

Menon and Ramamurti (1941), also using Indian strains of *W. bancrofti* and *C. quinquefasciatus*, reported that "patients with a very heavy microfilarial rate were found unsuitable, since a good percentage of the fed mosquitoes died in the first few days due to the severity of the infection."

In contrast to the concept of detectable but subinfective blood densities of microfilariae, a few investigators have indicated that mosquitoes are able to imbibe a greater number of microfilariae than can be found in an equal quantity of blood obtained by other means. It has even been suggested that one might be able to use mosquitoes to detect very low blood densities of microfilariae that were undetectable by other methods of examination (Highby, 1946).

Manson (1883) was the first to report that mosquitoes ingested a greater number of microfilariae than could be found in the same quantity of blood in the peripheral circulation. Ashburn and Craig (1907) stated that *C. quinquefasciatus* fed on Philippine Island strains of *W. bancrofti* took up to 40 to 50 times as many microfilariae as there were in an equal quantity of blood obtained by a pin prick. O'Connor and Beatty (1937) found that while *C. quinquefasciatus* fed on West Indian strains of *W. bancrofti* ingested a greater number of microfilariae than there were in an equivalent amount of peripheral blood, *A. aegypti* did not do so.

In disagreement with the observations cited above, Bahr (1912) reported that the number of microfilariae imbibed by *A. pseudoscutellaris* was not in excess of the number in a corresponding

amount of the circulating blood, and Smith (1951) stated that the number of microfilariae taken up by *C. quinquefasciatus* fed on East African strains of *W. bancrofti* was about the same as that in an equivalent volume of peripheral blood.

In the present experiments it was demonstrated that a significant proportion of *A. polynesiensis* became infected after feeding on individuals with blood densities of microfilariae well below those referred to above. In fact, it appears that any density of microfilariae likely to be detected on the examination of a single 20-cu. mm. sample of capillary blood is infective for this mosquito species.

No direct investigation was made of the claim that mosquitoes ingest more microfilariae than can be found in an equal amount of blood obtained by other means. However, there was little to suggest that such a phenomenon occurs to a significant extent with *A. polynesiensis*. Although the data presented in table 11 refer to mature or nearly mature larvae, evidence from dissections performed on other specimens at shorter intervals after the infective blood meal indicate that practically all microfilariae ingested by *A. polynesiensis* fed on low blood densities of microfilariae complete their development. It will be noted that mosquitoes fed on low blood densities of microfilariae had, on an average, about the same number of larvae as there were microfilariae in about 4 cu. mm. of the donor's blood. No measurements were made of the amount of blood ingested by *A. polynesiensis*, but from data given by Bahr (1912) for *A. pseudoscutellaris* and from data available for related mosquito species (Bates, 1949) it appears that most specimens ingest somewhat less than 4 cu. mm. of

blood. This small discrepancy may be the result of the mosquitoes feeding on the smaller blood vessels which have a higher concentration of microfilariae than do the larger vessels (Gordon and Lumsden, 1939). Blood from vessels of various sizes would be obtained by a finger prick.

A. polynesiensis was not observed to expel blood while in the process of taking a blood meal, but it did expel drops of clear serum-like fluid. Thus, it would appear that the loss of microfilariae in expelled blood which has been observed in *Anopheles* (Reid, 1953) and *C. quinquefasciatus* (O'Connor and Beatty, 1937) does not occur with *A. polynesiensis*. Reid (1953) found no microfilariae in the serum-like fluid expelled by *Mansonooides* while feeding on blood containing microfilariae.

The observations of Gordon and Lumsden (1939) that adjacent capillaries often have widely varying concentrations of microfilariae and that mosquitoes may feed in several different ways, afford an explanation for the extensive variation in the number of larvae found in individual mosquitoes fed on the same donor at the same time in the present experiments. Kartman (1953) observed that mosquitoes fed on a dog with microfilariae of *Dirofilaria immitis* showed wide individual variations in the number of ingested microfilariae whereas mosquitoes fed on microfilariae suspended in blood in vitro showed significantly less individual variation.

On the basis of experiments carried out in the Fiji Islands, Manson-Bahr (1952) reported that the microfilariae which persist in the peripheral blood after the treatment of the host with Hetrazan are so modified by the drug that they are not capable of normal

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data in tables 11 and 12 this was not
found to be the case in the present
experiments.

Basu and Rao (1939) stated that the
infectivity of the microfilariae of *W.*
bancrofti is related to the age of the
individual used as a donor. No evi-
dence of such a relationship was found
in the present studies.

Although it has been the impression
of several authors (see above) that
heavy infections with *W. bancrofti* ad-
versely affect the longevity of mos-
quitoes, adequately controlled observa-
tions on this subject have not been
available. In regard to the time after
the infective blood that this adverse
effect is manifested, Bahr (1912) re-
ported that *A. pseudoscutellaris* died
mainly from 6 to 10 days after feeding
and that "the last few days, that is
when the filaria has entered the pro-
boscis, appears to be the critical time
for the mosquito." On the other hand,
Menon and Ramamurti (1941) stated
that *C. quinquefasciatus* died primar-
ily in the first few days after feeding
on donors with high blood densities of
microfilariae.

In the experiments herein reported
practically no mortality was observed
for the first week among *A. polynesiensis*
which had fed on high blood den-
sities of microfilariae. These observa-
tions are in sharp contrast to data
obtained with the same mosquito species
when fed on high blood densities of
microfilariae of *D. immitis* (Rosen,
1954). With the latter parasite it was
found that the adverse effect of the
larvae was manifested in the first few
days after feeding. The difference in
the effect of these two filariae may be
the result of the difference in their site
of development in the mosquito. It

would seem that damage to the mal-
pighian tubules, where *D. immitis* de-
velops, would more seriously affect the
survival of the mosquito, especially in
the first few days after a blood meal,
than would similar damage by the
larvae of *W. bancrofti* in the thoracic
musculature.

In contrast to the experience of
Menon and Ramamurti (1941) cited
above, essentially no immediate mortal-
ity attributable to filarial infections was
observed in the present experiments
among *C. quinquefasciatus* fed on high
densities of microfilariae of periodic *W.*
bancrofti (100 microfilariae per 20 cu.
mm.) or nonperiodic *W. bancrofti*
(densities up to 500 microfilariae per
20 cu. mm.). However, evidence was
obtained that heavy infections with *W.*
bancrofti do adversely affect *C. quinque-*
fasciatus later in the course of infection.
In one experiment 13 mosquitoes chosen
at random and killed 16 days after
feeding on the subject with periodic
W. bancrofti had an average of 11.5
third-stage larvae per mosquito, whereas
11 mosquitoes which were found mori-
bund or unable to fly in the same cage
16 to 18 days after feeding had an
average of 34.5 third-stage larvae per
mosquito. Similar observations were
made for *A. polynesiensis* (see table
14). From these data it appears that
the adverse effect of heavy infections
with *W. bancrofti* on mosquitoes is
most clearly manifested, at least in the
laboratory, near the end of, and after,
the period of time necessary for the
maturation of the filarial larvae.

It can be anticipated that different
species, and especially different genera,
of mosquitoes will vary in their sus-
ceptibility to the adverse effects of
filarial infections. Although conclusive
data are lacking, *A. polynesiensis* seemed
more affected than did *Culex quinque-*

fasciatus by the same number of larvae. *A. polynesiensis* is the smaller of the two species and in addition is a species adapted to surviving adverse climatic conditions in the egg while *C. quinquefasciatus* survives adverse climatic conditions as an adult.

There are multiple factors to be considered in attempting to determine the blood density of microfilariae which would result in the successful transmission of the largest number of larvae by a given mosquito population.

It has been noted that although the number of third-stage larvae per infected mosquito increases with an increase in the density of microfilariae in the donor's blood, it does not do so proportionally for the higher densities of microfilariae. Presumably this is the result of the "crowding effect" which limits the number of larvae which can mature in a single mosquito. Not all of the larvae in heavily infected mosquitoes matured simultaneously. It is not known whether or not all of the advanced larvae eventually complete their development; and if they do, whether or not they are equal in vigor to the larvae which develop in less heavily infected mosquitoes.

It appears that heavy infections with *W. bancrofti* do adversely affect the longevity of mosquitoes in the laboratory. It is not known to what extent filarial infections influence various physiological functions of mosquitoes (egg-laying, ability to seek out a blood meal, etc.), especially under natural conditions.

Mature larvae can escape from an infected mosquito, even though the mosquito does not take a blood meal (Pratt and Newton, 1946), and hence are lost for purposes of transmission. In the experiments herein reported it seemed that a higher percentage of larvae es-

caped from heavily infected mosquitoes than was the case for lightly infected specimens.

In studies on *A. polynesiensis* infected with mature larvae of *D. immitis* it was observed that many mature larvae did not escape from mosquitoes when they took a single uninterrupted blood meal on a dog (Rosen, unpublished data). Presumably this would also occur with mosquitoes infected with *W. bancrofti*. It would seem that a higher proportion of larvae could escape from lightly infected mosquitoes than from heavily infected specimens, but no evidence on this point is available.

It has been observed that dead larvae can be recovered from the surface of the skin around the wound made by mosquitoes infected with *W. bancrofti* (Menon and Ramamurti, 1941). Apparently larvae normally enter man only by way of the wound made by the mosquito's proboscis (Yokogawa, 1939; Menon and Ramamurti, 1941). It is not known whether the number of larvae of *W. bancrofti* which succeed in escaping from a mosquito at the time of feeding influences the percentage which succeed in entering the host. However, it is not unlikely that a higher percentage of a small number of larvae would succeed in penetrating than would be the case for a large number.

In view of the factors outlined above it would not seem possible at the present state of knowledge to predict the blood densities of microfilariae that are the most dangerous from the point of view of transmission. In general, it appears that these factors tend to equalize the number of larvae which would be successfully transmitted by a given mosquito population which fed on individuals with various blood densities of microfilariae.

SUMMARY

On the basis of dissections of both field-caught and experimentally infected mosquitoes of 7 species which were present in study areas on the islands of Tahiti (Society Islands) and Makatea (Tuamotu Islands) it is concluded that *Aedes polynesiensis* is a major vector of *Wuchereria bancrofti* in French Oceania. Although complete development of local strains of *W. bancrofti* was observed in 4 other species, *Culex quinquefasciatus*, *Culex atriceps*, *Culex* sp., and *Aedes edgari*, it is concluded that these mosquitoes are not important vectors, either because of their inefficiency as hosts of the parasite (in the case of the 3 *Culex* species) or because of a limited distribution and abundance (*A. edgari*).

The availability of an individual with a periodic infection of *W. bancrofti* acquired in the West Indies made possible a comparison of the susceptibility of several local species of mosquitoes to infection with both periodic and non-periodic forms of *W. bancrofti*. *A. polynesiensis* was found to be a poorer host for the periodic strain than it was for the local nonperiodic strains. *C. quinquefasciatus* was an excellent host for the periodic strain but a poor host for nonperiodic strains. Neither the periodic nor nonperiodic strains of *W. bancrofti* were observed to complete their development in *Culex annulirostris*.

Data on the prevalence of individuals with microfilariae (and on the magnitude of their parasitemias) among a population of 2,580 persons living in the study areas are presented as an indication of the sources of infection available to mosquitoes. It is concluded that these data probably are not an accurate indication either of the prevalence or

of the intensity of infection with adult *W. bancrofti*.

A rhythmic fluctuation in the blood density of microfilariae over a 24-hour period was observed in subjects with Polynesian strains of *W. bancrofti*. However, the magnitude of this fluctuation was very small in comparison with that of other human filariae for which periodicity has been described.

From a study of the infectivity of various blood densities of microfilariae it is concluded that any density of microfilariae likely to be detected on the examination of a single 20-cu. mm. sample of capillary blood is infective for *A. polynesiensis*. It was found that microfilariae in the blood of persons who had been treated previously with Hetrazan developed as readily in *A. polynesiensis* as did the microfilariae of untreated individuals.

Observations on the effect of infection with *W. bancrofti* on the longevity of mosquitoes in the laboratory indicated that *A. polynesiensis* and *C. quinquefasciatus* were adversely affected by large numbers of maturing larvae.

From a consideration of the mechanism of transmission it appears that there are factors which tend to equalize the importance of individuals with various blood densities of microfilariae as sources of infection. It is suggested that, in view of the present absence of precise knowledge on certain factors which are discussed, the percentage of the population with 1 or more microfilariae per 20 cu. mm. of blood be used for comparative purposes in evaluating the effect of Hetrazan on transmission in areas where *A. polynesiensis* is a vector.

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