The epidemiology of filarial transmission in Samoa and Tonga*

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For nearly forty years following the classical studies of Bahr (1912) in Fiji, *Aedes* (*Stegomyia*) *pseudoscutellaris* (Theobald, 1910), a day-biting mosquito, was considered to be the sole vector of sub-periodic *Wuchereria bancrofti* in the South Pacific Islands. Marks (1951) clearly demonstrated that two species have been confused as *Aedes pseudoscutellaris* in all previous epidemiological studies in Fiji and indicated that the proven vector in most Polynesian areas was probably the new species, which she named *Aedes polynesiensis*. Later, Symes (1955, 1960*a*, 1960*b*) demonstrated that both *A. pseudoscutellaris* and *A. polynesiensis* were efficient transmitters and that a third species, the night-biting *Aedes* (*Finlaya*) *fijiensis* Marks, 1947, of the *kochi* group, was an equally efficient vector. This work was confirmed by Burnett (1960). Rosen (1955) and Symes (1955, 1960*a*, 1960*b*) showed that *Culex fatigans*, the classical vector of nocturnally periodic *W. bancrofti*, could also transmit sub-periodic *W. bancrofti* to a limited extent in the Society Islands and in Fiji. Iyengar (1955) demonstrated that in New Caledonia sub-periodic *W. bancrofti* was transmitted by *A.* (*Ochlerotatus*) *vigilax* (Skuse, 1850), a species that bites at all times of the day and night but with a peak of activity about sunset. Belkin (1961, 1962) pointed out the need for a re-examination of the potential vectors, particularly in those areas where one or more members of the *scutellaris* group and the *kochi* group have been reported.

As filariasis control programmes were about to be organized in American Samoa and in Western Samoa in 1963, it was considered desirable to re-examine the potential vectors in both areas. Earlier, epidemiological studies on filariasis in Samoa had been made before Symes's work in Fiji incriminated *A. fijiensis*, a member of the *kochi* group, and before Marks (1957) had described another member of the *scutellaris* group, *A. upolensis*, from Western Samoa. Belkin (1962) showed that, in Samoa, the *kochi* group was represented by at least two species, one of which he suspected might be a vector comparable to *A. fijiensis* in Fiji. No epidemiological studies had ever been made in Tonga and *A.* (*S.*) *tongae* Edwards, 1926 was considered to be the vector on circumstantial evidence.

The present study was therefore undertaken in Samoa and Tonga with the following primary objectives: (*i*) to determine the vectors and to study their bionomics (vector studies); (*ii*) to determine the important places or sites of transmission of filariasis (transmission studies); and (*iii*) to make studies on the periodicity of microfilaraemia (periodicity studies). In addition, incidental observations were made on *Dirofilaria immitis* (Leidy, 1856) in dogs and in mosquitoes.

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The mosquito fauna of both island groups was poorly known. This aspect was studied at length and is reported elsewhere (Ramalingam and Belkin, 1965; Ramalingam, 1965).

The basic data and material for this study were obtained in the field during the period January 28th–July 28th, 1963. Of this period, approximately a month and a half (May 16th–June 30th, 1963) was spent in Tonga, the rest of the time being distributed between American Samoa and Western Samoa.

GEOGRAPHY AND CLIMATE

Samoa. The islands of Samoa (see map) lie in the South Pacific between about latitude 11° and 15°S., and longitude 168° and 173°W., and extend, in general, from north-west to south-east. The islands are situated 400–500 miles north-east of Fiji. The group consists of eight islands, six of volcanic origin and two coral. The four westernmost islands comprising Western Samoa are, from west to east, Savaii, Apolima, Manono and Upolu, and the remaining islands comprising American Samoa are, from west to east, Swains, Tutuila, the Manua group and Rose, the two major subgroups being separated by a distance of 40 miles. Savaii, the largest island of Western Samoa, is about 45 miles long and 25 miles wide, with an area of 703 square miles and a maximum elevation of 6,096 feet. Apolima and Manono are small but inhabited islands situated in the straits, about 8 miles wide, separating Savaii and Upolu. Upolu is about 45 miles long and 10 miles wide, with an area of 430 square miles and a maximum elevation of 3,607 feet. Apia, the capital and principal port of Western Samoa, is situated on the mid-northern side of Upolu. Swains, a coral atoll, lies 200–350 miles north of the other islands of Samoa. Tutuila, the largest island of American Samoa, is 25 miles long and 2–6 miles wide, with an area of 52 square miles and a maximum elevation of 2,141 feet. The only town and harbour of American Samoa, popularly known as Pago Pago, is a complex of six villages, one of which actually is Pago Pago.

Of the three major islands of Samoa, Tutuila is the oldest and Savaii the youngest. The islands have a central ridge of mountains running across them from east to west. Streams are plentiful.

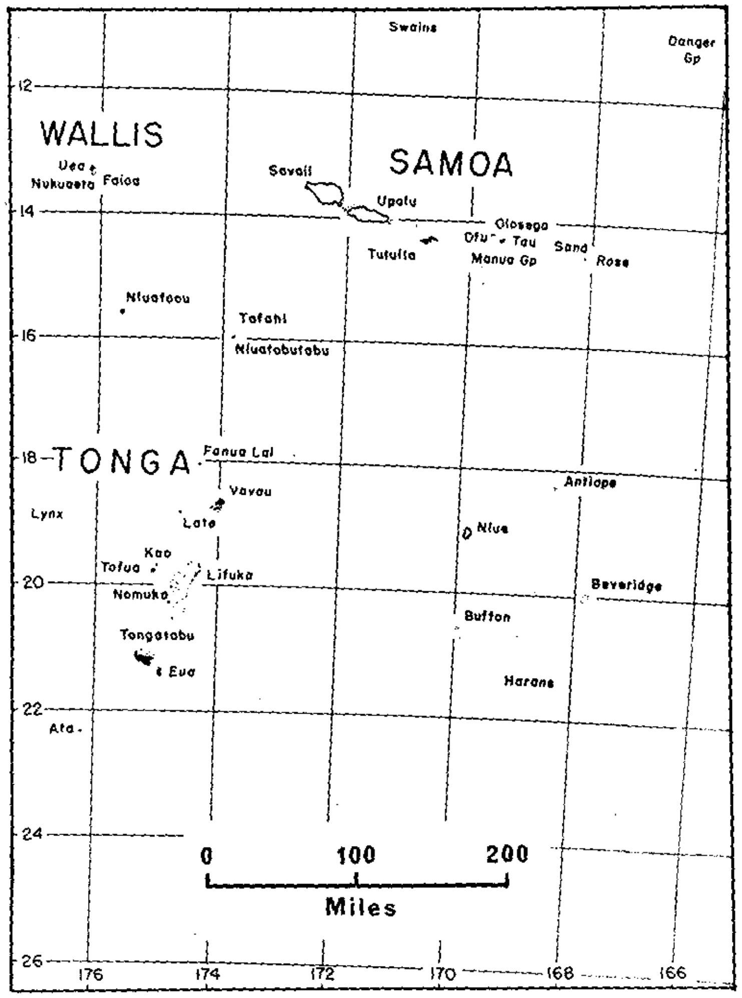
Rainfall in Samoa averages between 115 and 200 inches per year, being generally much higher on the south side of the islands than on the north. The highest rainfall occurs between December and March (14–18 inches per month). During the other months rainfall averages about 6·5 inches. Yearly temperatures range between 70° and 90°F.

Tonga. The islands of the Kingdom of Tonga (see map) lie between latitude 15° and 23° 30′S., and longitude 173° and 177°W. There are about 150 islands in the Kingdom, of which only 36 are inhabited, and the total land area is only 269 square miles. Three main groups of islands are recognized from north to south, the Vavau, Haapai and Tongatabu groups. The southernmost group takes its name from the largest island in the Kingdom, Tongatabu, on which is located Nuku'alofa, the capital of Tonga. Tongatabu has an area of slightly less than 100 square miles and is a flat, slightly elevated coral island.

Tonga has a very mild climate that is not typically tropical. Annual rainfall is seasonal and varies from 82 inches in Vavau to 63 inches in Tongatabu (Kennedy, 1959). The rainy season lasts from January to June. During the dry season rainfall averages about 1–2 inches per month. In Tongatabu the average maximum temperature is 90° F. and the average minimum 51° F.

METHODS

Mosquito collections. Mosquito collections were made on human bait, a boy stripped to the waist. Each collection lasted exactly 10 minutes, the collector attempting to capture every specimen that alighted on the motionless bait. Every 10-minute collection at a specific location constituted a 'station'. Mosquitoes collected at each station were placed in a large test-tube wrapped in a damp towel.



MAP showing the Samoa-Tonga area (adapted from Belkin 1962).

Dissection. Over 3,100 mosquitoes were dissected and examined during this study. As far as possible the mosquitoes were dissected a few hours after collection, but on several occasions they were kept refrigerated overnight. The mosquitoes were killed with chloroform, identified, and all the pertinent data were noted on a special form. If there were 10 or less mosquitoes of a species in a station, all were dissected, but if more than 10 of a species were present only 10 of that species were selected at random for dissection. The wings and legs were removed and the mosquito divided into three parts, head, thorax and abdomen. Each part was placed separately in a drop of normal saline, dissected and carefully examined. The dissections were usually made by an assistant from the local Health Department. All identifications and examinations of the dissected material were done by the author.

Criteria for the identification of filaria larvae. In addition to *W. bancrofti* (Cobbold, 1877), only *D. immitis* (Leidy, 1856) was found in the mosquitoes. The following criteria were used to separate the two species at their various stages.

Throughout the survey, mosquitoes harbouring only microfilariae were considered to be negative as the microfilariae may have been derived from a blood-meal on the bait.

In the first stage (sausage) and second stage, the site of development was the sole criterion, *W. bancrofti* occurring in the muscles of the thorax and *D. immitis* in the Malpighian tubules of the abdomen.

The third stage larva of *W. bancrofti* was distinguished by the presence of three and sometimes four anal papillae instead of only one as found in *D. immitis*, and by a greater length, about 1,600μ instead of 1,000μ.

For every infected mosquito, the species of parasite, the number of larvae, their developmental stage and location were noted on the record form.

Experimental infections. The conventional method of obtaining experimental infections was used with *A.* (*S.*) *tabu* Ramalingam and Belkin, 1965. Adult females 3–7 days old, reared from the immature stages collected in the field, were given a single blood-meal on microfilaria carriers. They were then held in the laboratory on daily feedings of sucrose until dissection.

With the *kochi* group, it was not possible to obtain vigorous females from field-collected immature stages for feeding on microfilaria carriers. Experimental data were obtained for this series from wild females, which were allowed to engorge fully in a native house (fale) on microfilaria carriers and were afterwards held in the laboratory on a diet of sucrose before dissection.

Transmission studies. The techniques described by Bonnet *et al.* (1956) were used for the collection of mosquitoes and for evaluating the transmission of filariasis. For the day collections, 12–30 stations were selected in each village in such a manner as to sample the village as evenly as possible. The stations were never more than 25 yards away from a human habitation and were always in the shade. In the plantations, the stations were at least 30 yards apart. All night collections were made within houses (fales).

VECTOR STUDIES

In the current study, in addition to *A. polynesiensis*, three other mosquitoes were definitely incriminated for the first time as efficient vectors of subperiodic *W. bancrofti*; *A.* (*F.*) *samoanus* (Grünberg, 1913) and *A. upolensis* Marks, 1957 in Samoa and *A. tabu* Ramalingam and Belkin, 1965 in Tonga. A fourth species, *A.* (*F.*) *tutuilae* Ramalingam and Belkin, 1965 may also be a vector in Samoa. In preliminary reports on the present study (Ramalingam and Belkin, 1964) *A. tabu* was reported as *A. tongae*, and *A. tutuilae* was reported as *Aedes* (*Finlaya*) South Pacific sp. no. 25 (UCLA collection).

Dissections of small numbers of the following species were all negative for filaria infection: *C.* (*Culex*) *pipiens fatigans* Wiedermann, 1828; *C. annulirostris* Skuse, 1889; *A.* (*F.*) *oceanicus* Belkin, 1962; *A.* (*S.*) *aegypti* (Linnaeus, 1762); and *A.* (*Aedimorphus*) *nocturnus* (Theobald, 1903).

Table I summarizes the results of all the dissections of mosquitoes made in Samoa and in Tonga during the present study, including the experimental infections. The results are discussed and interpreted below separately for every important species of proven or potential vector. The biology of the mosquitoes is also given.

TABLE I

Showing the natural and experimental infections of mosquitoes with *Wuchereria bancrofti* in Samoa and Tonga

Locality and species	No. dissected	Mosquitoes positive All stages of larvae		Mosquitoes positive Stage III larvae	
		No.	Per cent.	No.	Per cent.
American Samoa					
A. (*S.*) *polynesiensis* ...	1,274	66	5·2	13	1·0
A. (*S.*) *upolensis*	48	3	6·3	1	2·1
A. (*F.*) *samoanus*	371	20	5·4	7	1·9
A. (*F.*) *oceanicus* ...	76	0	0	0	0
A. (*F.*) *tutuilae*	2	1		1	
C. (*C.*) *p. fatigans*	18	0	0	0	0
C. (*C.*) *annulirostris* ...	3	0	0	0	0
A. (*F.*) *samoanus**	10	10	100	10	100
A. (*F.*) *tutuilae**	1	1		1	
Western Samoa					
A. (*S.*) *polynesiensis* ...	407	34	8·4	12	2·4
A. (*S.*) *upolensis*	59	7	11·9	1	1·7
A. (*F.*) *samoanus*	380	17	4·5	1	0·3
A. (*F.*) *oceanicus*	60	0	0	0	0
A. (*Aedim.*) *nocturnus* ...	2	0	0	0	0
C. (*C.*) *p. fatigans*	51	0	0	0	0
C. (*C.*) *annulirostris* ...	8	0	0	0	0
Tonga					
A. (*S.*) *tabu*	274	16	5·8	1	0·4
A. (*S.*) *aegypti*	19	0	0	0	0
A. (*F.*) *oceanicus*	13	0	0	0	0
A. (*Aedim.*) *nocturnus* ...	3	0	0	0	0
C. (*C.*) *p. fatigans*	76	0	0	0	0
C. (*C.*) *annulirostris* ...	1	0	0	0	0
A. (*S.*) *tabu*†	12	8	66·7	6	50

*Experimental infections with wild adults.
†Experimental infections with reared adults.

Aedes (*Stegomyia*) *polynesiensis* Marks, 1951

Vector capacity. Of 1,681 *A. polynesiensis* dissected from Samoa, 100 (5·95 per cent.) were positive for all stages of larvae of *W. bancrofti* and 25 (1·5 per cent.) for the third stage. The figures represent natural infections of *A. polynesiensis* and show that in general the mosquito is an efficient vector of *W. bancrofti* in Samoa. This confirms the findings of earlier workers (O'Connor, 1923; Byrd *et al.*, 1945; Jachowski and Otto 1952, 1953;

Iyengar 1954), who found *A. polynesiensis* to be the only important vector of sub-periodic *W. bancrofti* in Samoa on the basis of both experimental and natural infections.

Distribution and Bionomics. A. polynesiensis has a wide distribution in the South Pacific. It occurs in the following groups of islands: Fiji, Samoa, Horne, Wallis, Ellice, Tokelau, Cook, Austral, Marquesas, Tuamotu, Pitcairn and Society Islands.

Since *A. polynesiensis* is the principal vector of sub-periodic *W. bancrofti* over a wide area of the South Pacific, it has attracted much notice. Several workers have studied its bionomics, notably O'Connor (1923), Buxton and Hopkins (1927), Jachowski (1954) and Bonnet and Chapman (1958). The more significant aspects of the bionomics of this mosquito, from past work and from the present findings, are summarized below.

A. polynesiensis shows great plasticity in the selection of its breeding places. In the present survey of American Samoa and Western Samoa, the mosquito was collected from tree-holes, rock-holes, coconut shells, artificial containers (large and small), leaf axils of pandanus, banana stumps and leaves, crab-holes, ground pools (very small), and cacao pods. The breeding of *A. polynesiensis* in the leaf axil of pandanus appears to be a new record.

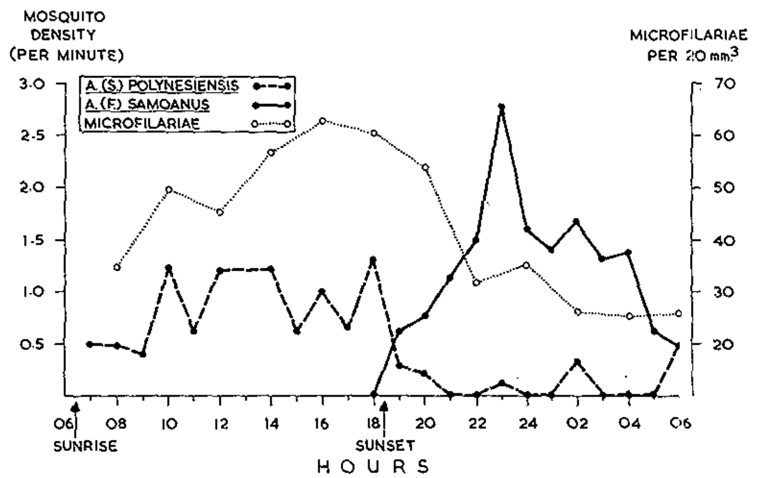


FIG. 1. Showing the biting activity of *A.* (*S.*) *polynesiensis* in bushes at the edge of Asau and the mean biting activity of *A.* (*F.*) *samoanus* from a set of catches in a house in Asau and two sets of catches from two houses in Aoloau, American Samoa. The microfilaria periodicity is represented from an average of 10 microfilaria carriers from American Samoa (see Table III).

Although the biting activity of *A. polynesiensis* is largely diurnal, some females bite at night, both indoors and in the bush. Jachowski (1954) reported *A. polynesiensis* as being diurnally active with two peaks of activity, a lesser one in the morning, and a greater one in the afternoon. In Aoloau and Asau in American Samoa studies were made on the biting activities of the mosquito. Fig. 1 shows the diel biting-cycle of *A. polynesiensis* in bushes at the edge of Asau. The biting activity corresponds in general with Jachowski's findings except for higher catches between 12.00 and 14.00 hours, which may be due to the presence of clouds on an otherwise clear and sunny day. It is known (Jachowski, 1954) that the mosquito becomes more active when the day is cloudy.

The 'range of dispersal' of the species is fortunately not very great. From mark and release experiments, Jachowski considered it to be 100 yards or less.

Although females of *A. polynesiensis* enter houses in order to feed, they do not rest there except on rare occasions. In spite of careful scrutiny, no adults were obtained resting indoors. In Western Samoa a knock-down spray was applied in two houses and the dead insects were collected on white sheets that had been spread on the floor, but no *A. polynesiensis* were obtained. O'Connor found that the natural resting places were dry holes in trees, the undersides of partially detached bark on dead or dying trees, leaves, dry coconut husks, and similar locations that are sheltered from the wind.

Man is considered to be the main host of *A. polynesiensis* although the species has been found to feed on pigs, horses and dogs, and in nature it probably feeds also on birds. According to Jachowski (1954), *A. polynesiensis* cannot produce viable eggs without a blood meal. The mean weight of a blood meal was 1·8 mgm. and averaged 1·3 times the body-weight (Jachowski, 1954).

Swarming of males occurs around the breeding containers and has been noted to take place also around the head of collectors in the bush. Copulation begins on the wing and is completed when the female lands with the male inverted beneath her.

Aedes (*Stegomyia*) *upolensis* Marks, 1957

Vector capacity. As *A. upolensis* was described recently, nothing was known about its relation to *W. bancrofti*. Of 107 wild-caught specimens from Samoa, 10 (9·1 per cent.) were positive for all stages of larvae, and two (1·8 per cent.) for third-stage larvae, which strongly suggests that it is a vector of sub-periodic *W. bancrofti* in Samoa. No experimental infections were made because of the failure to find immature stages in sufficient numbers for rearing. *A. upolensis* could play an important role in transmission in interior villages and in coastal villages and plantations that are closely surrounded by bush.

Distribution and bionomics. *A. upolensis* is restricted to the Samoan islands. The immature stages were obtained in only two collections, both at the edge of the rain forest. One of the breeding sites was a deep, longitudinal depression in a fallen tree trunk in Tutuila, the other in a fern-tree stump in the type locality, Afiamalu, Upolu.

The species can be described as a truly forest or bush mosquito. The adults were obtained on several occasions, but always in dense bush. They occur in some villages where the virgin forest borders the village. They feed readily on man, and eggs were obtained from several females. Like *A. polynesiensis*, this species bites by day, but because it is not abundant no opportunity arose to make detailed observations on biting habits, resting places or even breeding sites.

Aedes (*Stegomyia*) *tabu* Ramalingam and Belkin, 1965

Vector capacity. In Tonga the vector of *W. bancrofti* had never been established although it was suspected that '*Aedes tongae*', the only member of the *scutellaris* group previously reported from Tonga, was involved. During the present studies on Tongatabu 274 *A. tabu* that had been collected on human bait were dissected and examined for infections of *W. bancrofti*. Of these, 16 (5·8 per cent.) were positive for all stages of larvae, and one (0·4 per cent.) was positive for third stage larvae. A small series of experimental infections was also made in Tongatabu. Adult females of *A. tabu*, 3–7 days old, which had emerged from immature stages collected in the field, were allowed to feed on microfilaria carriers, one with a count of 11 and the other with 19 per 20 c.mm. They were then held in the laboratory on daily feedings of sucrose. Of the 12 surviving mosquitoes, three were dissected on the 14th day, four on the 15th and five on the 16th. As Table I shows, eight (66·7 per cent) of the 12 mosquitoes were positive for all stages of larvae and six (50 per cent.) for the third stage. The data strongly suggest that *A. tabu* is a vector on Tongatabu. The temperature and relative humidity on Tongatabu at the time of the survey were low when compared to Samoa and the Society Islands. This difference might account for the lower rate of infection with third-stage larvae in *A. tabu* than in *A. polynesiensis*.

Systematics, distribution and bionomics. The presence of two distinct species of the *scutellaris* group of *Aedes* (*Stegomyia*) in the Tonga islands, was only recently established (Ramalingam and Belkin, 1965). In the past, both species had been reported as *A. tongae* by numerous investigators. The first of the two species, *A. tongae*, is known only from the Haapai and Vavau groups. The second species, *A. tabu*, occurs in the Tongatabu group and also in the Haapai group. The latter is the species that has been most commonly collected since it occurs on the principal island of Tongatabu. The two species have so far not been recorded outside the Tonga islands.

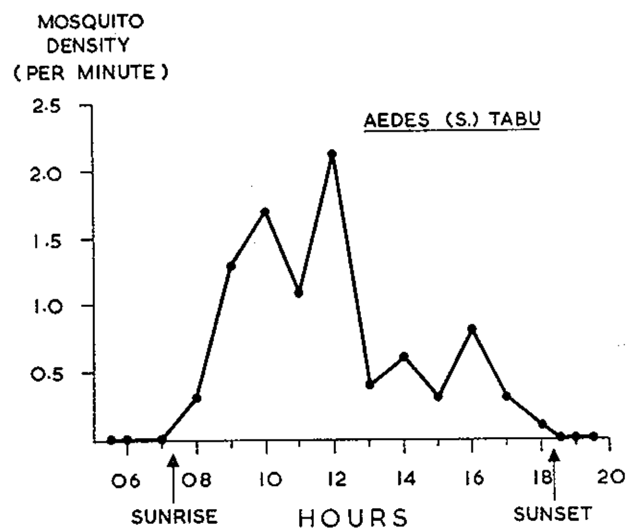


FIG. 2. Showing the biting activity of *A.* (*S.*) *tabu* from 05.30 to 19.30 hours.

The breeding places of *A. tabu* are tree holes, artificial containers, coconut shells and spathes, and leaf axils of taro. The mean number of eggs laid per female in a sample of seven was 47·6 and the range 22–66. In Samoa the mean number of eggs laid by *A. polynesiensis* was approximately 55 per blood-meal (Jachowski, 1954).

A. tabu is primarily a bush mosquito, most abundant in plantations but also occurring in shady areas in villages. Fig. 2 illustrates its biting activity. The peak of activity was reached between 10.00 and 12.00 hours, with no biting before sunrise or after sunset. Several collections of mosquitoes were made at night in villages in Tongatabu but not a single specimen of *A. tabu* was taken. It may be concluded that *A. tabu* is strictly a diurnal and crepuscular species. *A. tabu* was not found resting within several houses which were examined during the day. In Tongatabu three houses were sealed and a knock-down spray was used, but no specimens of *A. tabu* were obtained. Adults of *A. tabu* were observed on several occasions resting in tree holes and in other sheltered places on trees. Females were obtained from sweeps made in grass and bushes.

Aedes (*Finlaya*) *samoanus* (Grunberg, 1913)

Vector capacity. O'Connor (1923) examined 73 '*Finlaya kochi*' from Western Samoa and obtained a first-stage filaria larva with 'arrested development' in one mosquito. He subsequently tried experimental infections and obtained the same type of 'arrested development'. Byrd and and St. Amant (1959) dissected 251 *A.* '*samoanus*' in American Samoa and reported all to be negative. Iyengar (1954) dissected seven *A.* '*samoanus*' from Western Samoa and found 'arrested development' in two mosquitoes. In 1962 Belkin differentiated between the pale and dark form of adults, restricting *A. samoanus* to the pale form and describing the dark form as a new species, *A. oceanicus*. Belkin (1961, 1962) suspected that in the past *A. oceanicus* and *A. samoanus* had probably been confused in epidemiological studies, and he showed the need to re-examine the vector status of the two species.

During the present survey 751 *A. samoanus* collected from villages were examined for natural infections; of these, 37 (4·9 per cent.) were positive for all stages of larvae, and eight (1·1 per cent.) for third-stage larvae. Experimental infections with *A. samoanus* presented a problem as it was not possible to obtain vigorous females for infection from field-collected immature stages. Experimental data were obtained for this series from wild females which were allowed to engorge fully on microfilaria carriers with counts of 7 and 11 per 20 c. mm., and which were afterwards held in the laboratory on a diet of sucrose. Of the 10 surviving mosquitoes, four were dissected on the 10th day and six on the 11th. All 10 mosquitoes contained third-stage larvae. Most of the larvae were in the thorax but in one mosquito there were three larvae in the head.

There can be little doubt that *A. samoanus* is a highly efficient vector. It is abundant in the interior villages and in some coastal villages closely surrounded by bush. In these villages it may be even more important than *A. polynesiensis* as a vector. This aspect will be further discussed in the section on transmission studies.

Distribution and bionomics. So far this species has only been recorded from the islands of Samoa. In American Samoa the immature stages were found commonly in the leaf axils of *Freycinetia* sp., a forest creeper belonging to the family Pandanaceae. This is a new record for *A. samoanus*, as the immature stages had not been previously described. In numerous collections made in the axils of taro (*Colocasia*) and pandanus in American Samoa, *A. samoanus* was never recovered, and it was found only once in the leaf axil of the giant taro ('ta'amu', *Alocasia indica*). In Western Samoa heavy breeding of *A. samoanus* occurred in the leaf axils of *Freycinetia* sp. as well as in pandanus. The adults are nocturnal in habit, becoming active after sunset and reaching a peak of activity at 23.00 hours (fig. 1). They are primarily outdoor resters and only a few were collected resting indoors during the day. In American Samoa the mosquito is exceedingly abundant in the interior villages and in those coastal villages that are closely surrounded by native forest. In Western Samoa, because of breeding in the leaf axils of pandanus, *A. samoanus* is abundant in all villages and especially so in the interior.

Aedes (*Finlaya*) *tutuilae* Ramalingam and Belkin, 1965

Vector capacity. A third member of the *kochi* group, *A. tutuilae*, may also be a vector. This species is the same as *Aedes* (*Finlaya*) South Pacific sp. no. 25 (UCLA collection) of Ramalingam and Belkin (1964). One specimen collected in nature contained third-stage larvae. In the experimental infection series with the *kochi* group, one female survived for 10 days and two third-stage larvae were found in the thorax. Additional studies with this mosquito will have to be made before it can be definitely incriminated as a vector. As it was never found in high densities in nature, its role as a vector is probably insignificant.

Distribution and bionomics. A. tutuilae is so far reported only from the Samoa islands. It breeds almost exclusively in the leaf axils of pandanus, from sea level to elevations of 1,500 feet. No definite information is available at present regarding the bionomics of the adults; they are probably nocturnally active as in the case of *A. samoanus*.

Culex (*Culex*) *pipiens fatigans* Wiedermann, 1828

Vector capacity. The mosquito is a major vector of nocturnally periodic *W. bancrofti* in many areas of the world. In the South Pacific there are conflicting reports regarding the importance of *C. p. fatigans* in the transmission of sub-periodic *W. bancrofti*. In Western Samoa, O'Connor dissected 25 adult females for natural infections and found them all negative. He also infected a few specimens in the laboratory and obtained 'arrested development' of the first stage larvae. Byrd *et al.* (1945) dissected 1,063 wild-caught *C. p. fatigans* in American Samoa and obtained an infection rate of 7·4 per cent., but most of the larvae were early stages and none were infective. In the experimental studies with the species only one mosquito contained infective larvae. Rosen (1955), in Tahiti, fed a large number of *C. p. fatigans* on microfilaria carriers and found infective larvae in a small percentage (15·6 per cent.). His natural infection studies likewise showed a low percentage of infection with third-stage larvae of sub-periodic *W. bancrofti*. He was of the opinion that *C. p. fatigans* could not propagate Polynesian strains of *W. bancrofti* in the absence of more efficient vectors. Symes (1955, 1960*a*) dissected nearly 2,000 females for natural infections and found 3·6 per cent. positive for all stages of larvae and 0·9 per cent. for third-stage larvae. Experimental infection rates were high (45 per cent.).

In the present study only 145 *C. p. fatigans* from Samoa and Tonga were dissected (18 from American Samoa, 51 from Western Samoa, and 76 from Tonga) and none was found infected. It appears, therefore, that in Samoa and Tonga *C. p. fatigans* is not a significant vector at the present time.

Distribution and bionomics. C. p. fatigans is present on the islands of Upolu and Tutuila in Samoa and on Tongatabu in Tonga. It is widely distributed elsewhere in the South Pacific and throughout the tropical, sub-tropical and warm temperature regions of the world. It is still found in greatest density around the ports and on the densely populated islands.

Most of the breeding occurs in polluted pools, drains, artificial containers and only rarely in tree holes and coconut shells. *C. p. fatigans* is a nocturnally active species that bites readily within houses and rests indoors during the day.

TRANSMISSION STUDIES

There has been a great deal of controversy over the sites where the greatest amount of transmission of filariasis occurs in Samoa. From O'Connor's work (1923), it can be inferred that transmission occurred in the villages. Byrd *et al.* (1945) and Iyengar (1959) stressed the villages as the hyperendemic foci of infection. Jachowski and Otto (1952, 1953), on the other hand, maintained that transmission of sub-periodic *W. bancrofti* occurred mainly in a 'wild ecological niche'. They found the transmission potential (mosquito density × proportion of mosquitoes infected) to be much higher in the plantations and in the bush along the trails to the plantations than in the villages themselves. They divided the villages into two types: (*i*) large *open villages* in which the houses are set out in clearings; and (*ii*) *bush villages* which are in, or are very close to, the undergrowth and native forest. They considered that the high microfilaria rates in the bush villages did not represent true domestic transmission but an 'extension of man's home into the mosquito habitat'. Jachowski and Otto noted that up to the age of puberty there was little difference in the microfilaria rate between the sexes, but from then onwards the rate increased with a significantly greater percentage in men than in women. They explained this difference as being due to the differences in habits of the Samoans. The women remained in the vicinity of the villages while the men worked in the plantations and were subject to greater exposure. McCarthy and Fitzgerald (1956), working in Western Samoa, were also of the opinion that most of the transmission occurred in the plantations, along paths leading to the waterpoints, and in similar situations.

In order to investigate the nature of transmission in Samoa, 11 villages and the town of Apia were selected for intensive mosquito surveys. The studies were made during the day in the villages and their neighbouring plantations, and at night in the villages only. On Upolu, Solosolo was the only open coastal village. The other two villages, Aleisa and Manunu, were bush villages. On Savaii, Asau is a semi-bush village on the coast and Aopo a bush village in the interior. On Tutuila, American Samoa, three of the villages studied, Amanavi, Amouli, and Malaeloa, could be classified as open villages and three, Aoa, Asau and Aoloau, as bush villages. The first four villages had been selected in July 1962 by Dr. J. F. Kessel and his staff for pilot studies to evaluate the drug diethylcarbamazine in the control of filariasis. In the present survey, mosquito surveys were made in these villages after drug treatment had begun. The data from the four villages thus represent post-treatment data and are not used for comparison with the other villages. Instead, pre-treatment data for the villages obtained by Dr. Kessel and his team are used.

In order to evaluate transmission, it is essential to have an index or yard-stick to measure the extent of transmission in different kinds of villages and to determine the relative importance of different vectors. The '*transmission potential*' (mosquito density × percentage of mosquitoes infected) of Jachowski and Otto (1953), did not reflect in any way the microfilaria density in the human population. The importance of the microfilaria density was stressed by Bonnet *et al.* (1956) who found that, in Tahiti, the number of developing larvae per infected mosquito is reduced markedly when the microfilaria density in the human population drops. This information was incorporated by these investigators in a '*potential transmission index*' which was obtained by multiplying the mosquito density by the average number of larvae per dissected mosquito and multiplying the resultant figure by 250 to produce a large number for easier comparison. This index was used in the present study. Potential transmission indices are prepared for each species separately and for all species combined, for each of the representative areas selected for the study of transmission (Table

TABLE II

Showing the potential transmission index of *Aedes* (*S.*) *polynesiensis*, *Aedes* (*S.*) *upolensis*, and *Aedes* (*F.*) *samoanus* in various villages in American and Western Samoa

Locality	Mosquito density*			Infection rate†			Filaria density‡			Transmission index§			Total in village
	A. polynesiensis	*A. upolensis*	*A. sam. oanus*	*A. polynesiensis*	*A. upolensis*	*A. samoanus*	*A. polynesiensis*	*A. upolensis*	*A. samoanus*	*A. polynesiensis*	*A. upolensis*	*A. samoanus*	
American Samoa—Tutuila													
Aoloau July 1963 BV	0·3	0·01	1·0	12·5		5·9	1·0		0·5	79		116·5	195·5
Asau Mar. 1963 BV	1·2	0·1	3·0	15·6	8·1	3·5	0·7	0·7	0·1	202·5	18·4	87·6	308·5
Aoa July 1962 BV	0·7			17·3			1·1			200·8		not done	200·8
P	0·3			18·2			0·2			12·6			
Amouli July 1962 OV	0·3			12·8			0·5			40·8			40·8
P	1·5			0			0			0			
Amanave July 1962 OV	0·5			10·3			0·4			51·0			51·0
P	0·8			8·8			0·2			36·5			
Malaeloa July 1962 OV	1·0			10·4			0·3			80·8			80·8
P	1·6			3·4			0·4			141·3			
Western Samoa—Upolu													
Alesia April 1963 BV	0·8	0·2	0·7	9·4	10·0	9·3	0·8	0·2	0·2	162·3	6·9	39·6	208·7
Manunu April 1963 BV	0·4	0·1	0·5	12·9	6·7	4·1	0·6	4·0	0·1	55·2	89·5	16·7	161·4
P	0·7	0·1		8·6			0·6			105			
Solosolo April 1963 OV	0·2		0·3	2·8		6·7	0·1		0·1	5·2		8·3	13·5
P	2·1	0·2		10·8	27·3		0·2	0·4		115	15·3		
Apia Town April 1963	2·4		0	5·5		0	0·2			121·5		0	121·5
Savaii													
Aopo April 1963 BV	0·4	0·02	9·1	6·8	33·3	0	0·2	0·4	0	13·5	2·1	0	15·6
Asau April 1963 BV	0·1	0	2·0	0		5·5			0·3	0		151·7	151·7

* Average number of mosquitoes per minute.
† Percentage dissected mosquitoes containing larvae.
‡ Average number of larvae per dissected mosquito.
§ Mosquito density × filaria density × 250.
P = Plantation. BV = Bush village OV = Open village.

II). The indices are used to evaluate the degree of transmission and the relative importance of the various vectors in different situations, and they are discussed in the following sections.

Transmission in Open Villages versus Bush Villages

American Samoa. Considering the villages alone, it can be seen from Table II that transmission in the bush villages was much higher than in the open villages. The high rates in these villages were associated with transmission by both *A. polynesiensis* and *A. samoanus*, and in certain cases by *A. upolensis* also. For example, in Aoloau the transmission index of *A. samoanus* (116·5) was much higher than that of *A. polynesiensis* (79). The addition of a night-biting vector in the bush villages increases the transmission and the microfilaria rate in these villages. Furthermore, because both the sexes are equally exposed to a night-biting mosquito, the microfilaria rates in the sexes are about the same. This is well illustrated in Aoloau where the microfilaria rate was 25 per cent. for females, 21·9 per cent. for males, and 23·5 per cent. for both males and females, (J. F. Kessel, *personal communication*; Ciferri *et al.*, *personal communication*). As a contrast the microfilaria rates for the villages in the open were 14·7 per cent. in females, 21·0 per cent. in males, and 17·9 per cent. for both males and females (Jachowski and Otto, 1955).

In the open villages *A. polynesiensis* played the major role in filariasis transmission. This was particularly true on Tutuila where *A. samoanus* breeds almost exclusively in the leaf axils of the creeping plant, *Freycinetia* sp., which occurs only in native bush and jungle. *Aedes samoanus* played an important part in transmission in the two bush villages studied, one of which was situated on the northern side of the island and the other in the interior. This was probably the case also in the other bush villages in Tutuila.

Western Samoa. As in American Samoa, transmission in the bush villages of Western Samoa was much higher than in the open villages. Table II shows that this was generally true except in the village of Aopo. This exception will be explained later. The epidemiology of filariasis in Western Samoa was slightly different from that of Tutuila. *Aedes samoanus* in Upolu and Savaii breeds abundantly in the leaf axils of pandanus besides those of *Freycinetia*. As pandanus was commonly grown in nearly every village, *A. samoanus* played a role in transmission in the open villages as well as in the bush villages. For instance, in the village of Solosolo the density of *A. samoanus* was slightly higher than that of *A. polynesiensis*. In Asau and especially in Aopo, on Savaii, the density of *A. samoanus* was exceedingly high. In fact, in one of the stations indoors, in the village of Aopo, 237 *A. samoanus* were collected within a period of 10 minutes (20.00–20.10 hours). These two villages were notorious among the inhabitants of Western Samoa for their high mosquito densities. A total of 110 *A. samoanus* was dissected from Aopo but they were all negative. It is suspected that the greater proportion of the *A. samoanus* were freshly emerged and were taking blood for the first time. This could be the reason for the apparent lack of transmission in Aopo. Asau, which was more like a bush village than an open village, showed a very low density of *A. polynesiensis*, and *A. samoanus* played the major role in filariasis transmission.

Transmission in Villages versus Plantations

Samoa. From the previous section it is clear that in the bush villages most of the transmission occurred in the village itself and there was a high rate of transmission during both the day and the night. Some transmission did occur in the plantations as well. It is in the open villages that the old question arises, 'where does transmission occur, in the village or in the plantation?'. From the evidence collected during this study it is clear that the amount of transmission in the two areas varied a great deal from village to village. For example, in Amouli all transmission (index = 40·8) probably occurred in the village. In Amanave the transmission index was slightly higher in the village (51·0) than in the plantation (36·5). In Malaeloa it was much higher in the plantation (141·3) than in the village (80·8). This was also true in Solosolo, Upolu (130·3 in the plantation compared with 13·5 in the village). Transmission was probably not restricted either to bush and plantations (Jachowski and Otto, 1952) or to the village alone (Iyengar, 1954). Transmission did occur in both places and the relative proportion depended on the particular ecological situation at the time.

Mention must also be made of the important socio-economic changes that have occurred in American Samoa since the time that Jachowski carried out his investigations (1948–1950). Much construction and development has taken place on Tutuila; roads have been extended and a number of Western-type buildings, including schools, offices and apartment houses have been built. The men no longer spend a good part of the day in plantations, but most of the able-bodied ones now work for the Government or in industry, many in the urban area. They work mostly in the bay area (Pago Pago), or on roads, construction sites and so on during the day and return to their villages at night. During weekends they may work in the plantations which are now being worked for the most part by the women and the older men. They buy the part of their food that they cannot produce, even importing taro into Tutuila from the Manua group of islands and from Western Samoa. A garbage pick-up scheme has been functioning for several years for the villages on the southern side of Tutuila. The changes must necessarily affect the transmission of filariasis in Tutuila either directly or indirectly.

Similar changes are taking place, but much more slowly, in Western Samoa where an agricultural economy still prevails. Most of the exports from Western Samoa are agricultural products, e.g., copra, bananas, cacao, and vanilla. This socio-economic structure requires most of the men to work in the plantations following traditional practice.

Tonga. On Tongatabu, intensive mosquito surveys were made in two villages and in the town of Nuku'alofa. One of the villages (Hofoa) is situated on the coast and the other (Matahau) in the interior. Both villages were similar, i.e., the houses were situated on both sides of the road. The area around the houses was only partly cleared and often the bush was not far from the houses. The vector situation was simple as *A. tabu* was the only vector on Tongatabu. The transmission indices of *A. tabu* in the two villages were Hofoa—village 67·5, plantation 43·7; Matahau— village 97·5, plantation 87·0.

This situation recalls the open villages in Tutuila. Transmission occurred in both the village and the plantation. Day and night surveys in Nuku'alofa revealed no transmission in the town where *C. p. fatigans* and *A. aegypti* were the predominant mosquitoes.

PERIODICITY STUDIES

A striking difference between the sub-periodic form of *W. bancrofti* from the South Pacific islands (Polynesia, Fiji, New Caledonia and Loyalty Islands), and the nocturnally periodic form of this species which occurs elsewhere, is that the number of microfilariae in the peripheral blood of the human host in the sub-periodic form is high throughout the day, whereas in the nocturnally periodic form it is high only during the evening, night and early morning hours and is practically nil during the day. In the earlier work on the South Pacific *W. bancrofti*, the term non-periodic or aperiodic was applied to this indigenous form (see Kessel, 1960 for review). It was later shown by Eyles *et al.* (1947), Edgar *et al.* (1952), Rosen (1955) and Iyengar (1955) that there was a definite fluctuation in the number of circulating microfilariae during the day. Because the density of microfilariae in the peripheral blood was higher in the afternoon (16.00–18.00 hours), the World Health Organization (1962) suggested that a more appropriate term to apply to this form would be 'diurnally subperiodic'. This is commonly designated as 'sub-periodic', although 'diurnally sub-periodic' differentiates it from the 'nocturnally sub-periodic' form of *Brugia malayi*, which is found in Pahang, Malaysia. Presumably, periodicity has been developed as an adaptation of the parasite to transmission by a nocturnal vector (Hawking and Thurston, 1951*a*, 1951*b*).

Buxton and Hopkins (1927) explained the development of the South Pacific sub-periodic form from the nocturnally periodic form as an adaptation to day-feeding mosquitoes after infected human populations entered an area without suitable nocturnal vectors. Although, as pointed out by Belkin (1961), this explanation is no longer tenable because

TABLE III

Showing the microfilaria periodicity (*Wuchereria bancrofti*) in peripheral blood in ten individuals from two villages in American Samoa

Time of examination	Aoloau*						Amanave†			
	1	2	3	4	5	6	A	B	C	D
08·00 hr. ...	0	0·6	2·8	3·7	14·3	‡	25·5	250·3	3·5	0·5
10·00 hr. ...	0	2·0	2·0	2·3	26·3	46·3	44·5	366	3·0	0·5
12.00 hr. ...	0	0	1·7	17·7	23·7	43·7	36·5	316	12	2
14.00 hr. ...	0·3	0·3	3·3	16·3	35·5	101·3	36·5	363	10·5	0·7
16·00 hr. ...	1·0	0·3	0·7	26·7	36·0	105·7	45·5	402	8	1
18.00 hr. ...	0·3	1·3	0·7	36·0	‡	115·0	36·5	373	10·5	0·5
20.00 hr. ...	0·3	1·7	0·3	15·3	20·0	63·3	30·5	398	9	0
22.00 hr. ...	0	0·7	0·7	5·7	28·7	49·0	11·5	208	11	0
24.00 hr. ...	0	1·3	0	5·3	34·0	27·0	7·5	272	2·5	0·5
02.00 hr. ...	0	1·3	0·3	8·7	15·0	32·3	14·0	181	9·5	0
04.00 hr. ...	0	0	0·7	8·7	13·0	‡	12·0	178·5	5·5	1
06.00 hr. ...	0	1·0	1·3	6·0	‡	34·4	23	172	5	0

* No. of microfilariae in 20 c. mm. blood (average of 3 samples).
† No. of microfilariae in 20 c. mm. blood (average of 2 samples).
‡ Smears washed off the slide.

nocturnal vectors are known for the sub-periodic form, the idea persists that there must be a correspondence in the sub-periodic form between the peak of periodicity of the parasite and the peak of activity of the vector. On a percentage basis, Mattingly (1962) compared the density of microfilariae in the human host, averaged from data of Eyles *et al.* (1947), Rosen (1955) and Iyengar (1955), with the activity of *A. polynesiensis* from charts given by Jachowski (1954) in 4-hour periods throughout the day. Mattingley concluded that the diel rhythm of the microfilariae matches the diel activity peak of the principal vector.

He also showed in a similar manner that the periodicity of different strains of *Brugia malayi* in Malaya corresponds with the biting activity habits of various species of *Mansonia* (*Mansonioides*) which transmit them.

As both nocturnal and diurnal vectors were present in American Samoa, it was of interest to determine and to compare the microfilarial periodicity in inhabitants of a bush village (Aoloau) where the night-biting *A. samoanus* played a significant part in transmission, with that of inhabitants of an open coastal village (Amanave), where the day-biting *A. polynesiensis* was the only vector. In Aoloau, three blood smears of 20 c. mm. each were made every two hours for a 24-hour period from each of six known microfilaria carriers of low, medium and high density. In Amanave only two smears of 20 c. mm. each were taken from four similar microfilaria carriers. Table III shows the microfilaria density in each individual throughout the 24-hour period, and fig. 3 represents the data graphically for nine of the carriers. The periodicity was similar in carriers from the two villages and it was essentially the same as reported by previous workers (Rosen 1955; Iyengar 1955).

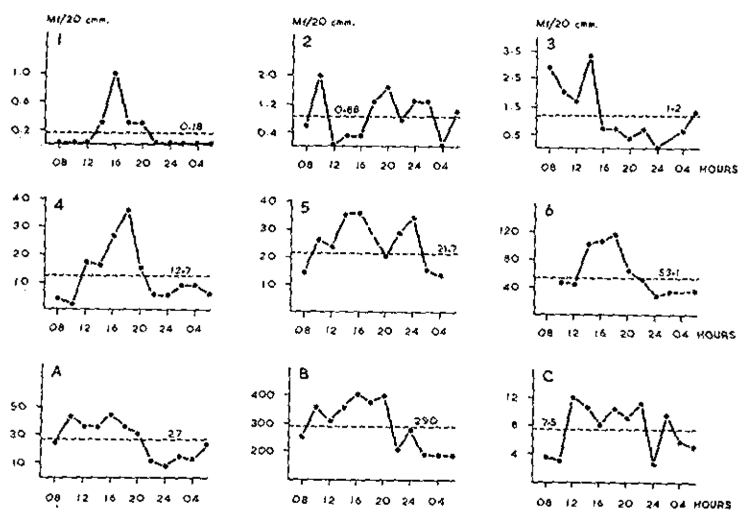


FIG. 3. Showing the microfilaria density in peripheral blood in nine individuals from two villages in American Samoa (data from Table III).

It appears, therefore, that in Tutuila there was no shift in microfilaria density to correspond to the period of maximum activity of the predominant vectors in different ecological situations. However, as the microfilaria density remained high until 22.00 or 24.00 hours, and *A. samoanus* becomes active soon after sunset and reaches the peak of activity around 23.00 hours (see fig. 1), there was ample opportunity for both *A. samoanus* and *A. polynesiensis* to become infected.

DIROFILARIA IMMITIS

O'Connor (1923), in Western Samoa, examined the blood of the following animals for microfilariae: dogs, fowls, wild rats, wild birds, pigs, sheep, cows, horses, donkeys and flying foxes (*Pteropus kerandrenii*). He found microfilariae of *D. immitis* in dogs and a single microfilaria resembling *Microfilaria equisanguinis* in a horse. He also obtained, on two occasions, adults of *D. immitis* from the heart of dogs. Dickson *et al.* (1943) found that approximately three out of four dogs harboured adult *D. immitis* and approximately one out of four dogs showed an enormous number of parasites. Jachowski and Otto (1953) examined the blood of 19 dogs, 7 pigs, 3 insectivorous bats, 51 rats, 50 chickens, 4 frigate birds, 3 other wild birds and 50 lizards. They found microfilariae of *D. immitis* in 12 out of 19 dogs and mentioned that this species was able to develop in *A. polynesiensis* (reported as *A. pseudoscutellaris*). Rosen (1954) working in French Polynesia found developing stages of *D. immitis* in *A. polynesiensis*, *A. edgari*, *C. p. fatigans* and *C. annulirostris*. The infective stages were found only in *A. polynesiensis* and *C. annulirostris*.

TABLE IV

Showing the natural infections of mosquitoes with *Dirofilaria immitis* in Samoa and Tonga

Species	Locality	No. dissected	Mosquitoes positive All stages of larvae		Mosquitoes positive Stage III larvae	
			No.	Per cent.	No.	Per cent.
A. (S.) polynesiensis	W. Samoa	407	7	1·7	2	0·5
	A. Samoa	1,090	7	0·6	4	0·4
A. (F.) samoanus	W. Samoa	380	2	0·5	0	0
	A. Samoa	372	3	0·8	2	0·5
A. (S.) upolensis	W. Samoa	60	0	0	0	0
	A. Samoa	48	0	0	0	0
A. (F.) oceanicus	W. Samoa	60	0	0	0	0
	A. Samoa	72	0	0	0	0
	Tonga	13	0	0	0	0
A. (F.) tutuilae	A. Samoa	1	0	0	0	0
C. (C.) annulirostris	W. Samoa	8	0	0	0	0
	A. Samoa	2	0	0	0	0
	Tonga	1	0	0	0	0
C. (C.) p. fatigans	W. Samoa	51	0	0	0	0
	A. Samoa	17	0	0	0	0
	Tonga	76	0	0	0	0
A. (Aedim.) nocturnus	W. Samoa	2	0	0	0	0
	Tonga	3	0	0	0	0
A. (S.) tabu	Tonga	274	0	0	0	0
A. (S.) aegypti	Tonga	19	0	0	0	0

During the studies on the vectors of bancroftian filariasis in Samoa, incidental observations were made on the dog filaria. Two 20 c. mm. blood smears were made between 18.00 and 19.00 hours from each of 10 dogs. Five of the dogs harboured microfilariae of *D. immitis*, with 57, 96, 334, 880 and 983 microfilariae per 20 c. mm. respectively.

Table IV shows the natural infections of mosquitoes with *D. immitis* in Samoa and

Tonga. Undeveloped microfilariae are not included in the table. In Samoa, only two species of mosquito, *A. polynesiensis* and *A. samoanus*, were found with the developing stages of *D. immitis*, including the infective stage. In Tonga, none of the mosquitoes caught in the present study harboured the dog heart worm, and dogs were not examined for microfilariae of *D. immitis*.

SUMMARY

1. In more than 3,000 dissections of naturally and experimentally infected mosquitoes three new vectors of the sub-periodic form of *Wuchereria bancrofti* were established, the night-biting *Aedes* (*Finlaya*) *samoanus*, and the day-biting *A.* (*Stegomyia*) *upolensis* and *A.* (*S.*) *tabu*; in addition the night-biting *A.* (*F.*) *tutuilae* may be a vector, but the number of infected mosquitoes was too small for definite incrimination. The importance of the previously proven vector, *A.* (*S.*) *polynesiensis*, was also confirmed.

2. The potential transmission index was determined for different situations and for each vector species to compare and evaluate the sites of transmission and the relative importance of the different vectors. It is concluded that the site of transmission and the vector species are determined, to a large extent, by the particular ecological situation and by socio-economic factors.

3. In the open villages in American Samoa, transmission is entirely by *A. polynesiensis*; it is moderately high inside the villages and varies in the associated plantations. In and around the bush villages, however, transmission is much higher and occurs primarily inside the villages. In the bush villages, *A. samoanus* and to a lesser extent *A. upolensis*, in addition to *A. polynesiensis*, are responsible for transmission.

4. In Western Samoa, as in Tutuila, American Samoa, transmission in the bush villages is effected by *A. polynesiensis*, *A. samoanus* and *A. upolensis* and is much higher than in the open villages. The pattern of transmission in Western Samoa is slightly different from that on Tutuila, as *A. samoanus* breeds abundantly in the leaf axils of both *Pandanus* and *Freycinetia* in the former, whereas on Tutuila *A. samoanus* breeds only in *Freycinetia*. Hence in the open villages in Western Samoa, *A. samoanus* plays a role in transmission as well as *A. polynesiensis*.

5. In Tongatabu, Tonga, transmission is accomplished solely by *A. tabu* and is somewhat similar to the open villages in Tutuila. Transmission occurs both in the village and in the plantation and is slightly higher in the village.

6. Studies in American Samoa on the periodicity of microfilariae in the human hosts throughout the diel cycle showed that the periodicity is the same whether the principal vector is the nocturnally active *A. samoanus* or the diurnally active *A. polynesiensis*.

7. In American Samoa, microfilariae of *Dirofilaria immitis* were found in five out of 10 dogs and developmental stages and the stage III infective larvae were noted in *A. polynesiensis* and *A. samoanus*.

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