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FILARIASIS IN AMERICAN SAMOA

V. BIONOMICS OF THE PRINCIPAL VECTOR, *AEDES POLYNESIENSIS* MARKS [1]

BY

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Throughout its range *Aedes polynesiensis* Marks is a mosquito of great medical importance. Where it coexists with nonperiodic filariasis, this species is either the principal or the sole vector (Bahr, 1912; O'Connor, 1926; Byrd et al., 1945; Jachowski and Otto, 1953). It is also a potential vector of dengue and may be responsible for the sporadic epidemics of this disease on those islands where *Aedes aegypti* is not known to occur (Rosen et al., 1954). Moreover, even if it was not involved in disease transmission, *A. polynesiensis* still would be important as a pest mosquito because of its abundance.

Field data collected in American Samoa from 1948 through 1950 provided information on the distribution, habitat, activity, abundance, and reproduction of *A. polynesiensis*. Supplementary laboratory studies at The Johns Hopkins University produced additional information on survival and feeding of adults and on the development of immature stages of this mosquito. These studies were preliminary to those on *A. polynesiensis* by Wallis (1954) and Ingram (1954) and complement those of Rosen and Rozeboom (1954), Rozeboom and Gilford (1954) and Rosen et al. (1954).

METHODS

Both the surveys and the experimental work involving adult female mosquitoes in the field depended upon standardized collecting techniques. Although many procedures were tried, including a variety of traps baited with animals and human beings, light traps set at dawn and dusk, and nets used to sweep low vegetation wherein the mosquitoes rested, the only successful technique was to capture with aspirators mosquitoes attempting to feed upon the collectors. This method was employed by Byrd et al. (1945) and was adapted to our needs.

Each collection was made at a designated station by 2 of the 5 men in the research unit. On arrival at the station, the collectors spent a minute or two unpacking the equipment and recording the necessary data. Meanwhile mosquitoes began to attack. Then for a period of 10 minutes, the two collectors endeavored to collect all of those mosquitoes attempting to feed upon them. If the number of mosquitoes taken was less than 125 to 150 in the 10-minute period, the collection provided an ac-

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curate index of the biting population; if, however, the number was greater many mosquitoes were lost.

Data recorded for each collection included the names of the collectors, the collecting station, date and time of the survey, the temperature, the wind velocity, the sky condition and precipitation during the survey.

To supplement the field observations, attempts were made to establish a permanent colony of *Aedes polynesiensis* in Samoa but were unsuccessful. In 1950, at the Naval Medical Research Institute, 12 out of more than 300 eggs of this species brought from Samoa were hatched. These eggs had been matured for 4 days, then dried and were 73 days old when hatched. Progeny from these eggs provided the nucleus of the colony at The Johns Hopkins University. About 3,000 more eggs were brought back from Samoa in 1950 to enlarge the colony.

The procedures used to maintain this mosquito in the laboratory were simple. Waxed cardboard cartons lined with a strip of filter paper or paper toweling and partially filled with water were placed in the cages to collect the eggs, which usually were deposited on the wet paper just above the water line. The strips of paper were removed daily and stored for 4 days in tightly covered containers to allow maturation of the eggs. Following this maturation period, they were removed from the container and allowed to dry for 3 days at room temperature. Larvae were hatched by submerging the maturated eggs in white enameled pans containing approximately 2 liters of tap water in which 3 or 4 alfalfa pellets (rabbit chow) had been allowed to dissolve for 24 hours. The larvae fed upon the alfalfa pellets. Additional food was added as needed but care had to be taken to avoid overfeeding for, if excessive food was added, a high larval mortality resulted.

Pupae were removed daily and put into small cups. Emerging adults were collected in lantern globes which fitted over the cups or in wire cages into which cups were placed. Pads of absorbent cotton saturated with a solution of sugar (approximately 5 per cent) were placed upon the tops of the cages as a source of food. Arms of human volunteers were exposed to the mosquitoes daily to provide blood meals.

The most critical problem in colonizing this mosquito was maintenance of a high relative humidity in the cages. Although the laboratory had controlled temperatures of 80 ± 5 F and relative humidities of 70 ± 8 per cent, an unusually high mortality among the adult mosquitoes shortly after emergence continued until the cages were covered with wet cloths.

In studies on the survival of adult females, the frequency of blood meals, and the number of eggs per blood meal laid by *A. polynesiensis,* individual mosquitoes were studied. One female and one male pupa (separated by size) were transferred to a small vial. The emerging adults were trapped in small plastic cylinders placed over the vials. These cylinders, 2 inches high and 1 inch in diameter, formed small cages when covered at the top with cloth screening and at the bottom with a double thickness of filter paper. They were stored upright in a pan lined with wet absorbent cotton. Small pledgets of cotton saturated with sugar solution placed on the tops of the cages provided food. Blood meals from the human arm were offered for 15 minutes daily. The mosquitoes fed readily through the cloth covering of the cages. Any mosquito which had begun to feed during this exposure was allowed to engorge. Eggs were collected

FIGURE 1. Distribution of larval, adult or larval and adult collections of *Aedes polynesiensis* in American Samoa, September, 1948, through April, 1953.

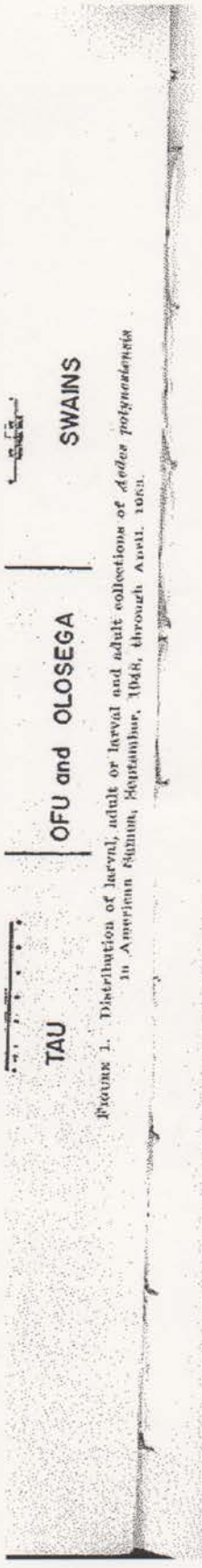

FIGURE 1. Distribution of larval, adult or larval and adult collections of *Aedes polynesiensis* in American Samoa, September, 1948, through April, 1951.

on the moist filter paper which covered the bottoms of the cages. This paper was replaced when eggs were deposited.

Distribution

In their revision of the *scutellaris* group of the genus *Aedes*, Farmer and Bohart (1945) have reported that the range of *A. polynesiensis* combined with that of a closely related species, *A. tongae*, almost exactly coincided with that of endemic nonperiodic filariasis. More precisely, *A. polynesiensis* has been reported from Samoa, Fiji, Wallis Island, Cook Islands, Society Islands, Marquesas Islands, Ellice Islands and the Tuamotu Islands. Thus, except for the Tonga group where *A. tongae* is found, this mosquito occurs throughout the South Pacific area from the Ellice and Fiji Islands on the west to the Tuamotu and Marquesas Islands on the east.

In American Samoa, *A. polynesiensis* was collected on all inhabited islands (figure 1). Wherever the environment affords suitable breeding places and adult resting places, whether at sea level or on the mountain ridges, larval or adult specimens were taken. Although ubiquitous in the geographic sense, their distribution was not uniform.

Bionomics of adults

Directly or indirectly, the habits and behavior of *Aedes polynesiensis* in all stages of its life history have a bearing upon the epidemiology of filariasis. The habits of the adult female mosquitoes will be discussed in detail since they are directly responsible for the transmission of the filariae.

Diurnal activity. All observers agree that *A. polynesiensis* is diurnally active. O'Connor (1923) described this mosquito as being most active at dawn, just before sunset, and during the day if rain is threatening. However, no data have been presented to support these observations. Therefore, a series of collections was made to define more precisely the hours of day when these mosquitoes were active.

In January, 1949, collections of mosquitoes were made at hourly intervals for 24 hours at each of 3 stations in and near the village of Mapasaga on the

TABLE 1

Diurnal fluctuations in the density of Aedes polynesiensis *as determined by 10-minute collections from human bait at hourly intervals at stations in the open, in a house and in the bush at Mapasaga, American Samoa.*

Hour	Number of mosquitoes collected					
	24-hour survey January 10, 11, 1949			19-hour survey November 30, 1949		
	House	Open	Bush	House	Open	Bush
A.M. 1	0	0	0			
2	1	0	0			
3	1	0	1			
4	0	0	1			
5	1	0	4	6	0	22
6	1	4	15	0	3	14
7	2	0	20	5	0	31
8	4	0	21	0	0	22
9	4	0	10	3	0	22
10	10	1	26	2	0	9
11	12	0	13	1	0	4
12	4	0	6	2	0	9
P.M. 1	14	0	3	1	0	13
2	6	1	35	10	0	42
3	17	0	50	2	0	16
4	14	2	33	4	0	49
5	30	0	21	3	0	51
6	27	4	53	0	3	16
7	1	3	23	0	0	2
8	0	0	28	0	0	9
9	0	0	21	0	0	0
10	1	1	12	0	0	0
11	0	0	1	0	0	0
12	0	0	0			
Totals	150	16	397	39	6	331
Per cent of total	27	3	70	10	2	88

island of Tutuila. The stations were located as follows: (1) in the central clearing of the village approximately 25 yards from the nearest house; (2) in a house partially surrounded by vegetation; and (3) along a trail in the banana grove behind the village, approximately 50 yards from the nearest house. Each collection period lasted 10 minutes during which a two-man team captured, by means of aspirators, all mosquitoes attempting to feed on them. The mosquito density is expressed as the number of mosquitoes captured in one third of a man-hour (table 1).

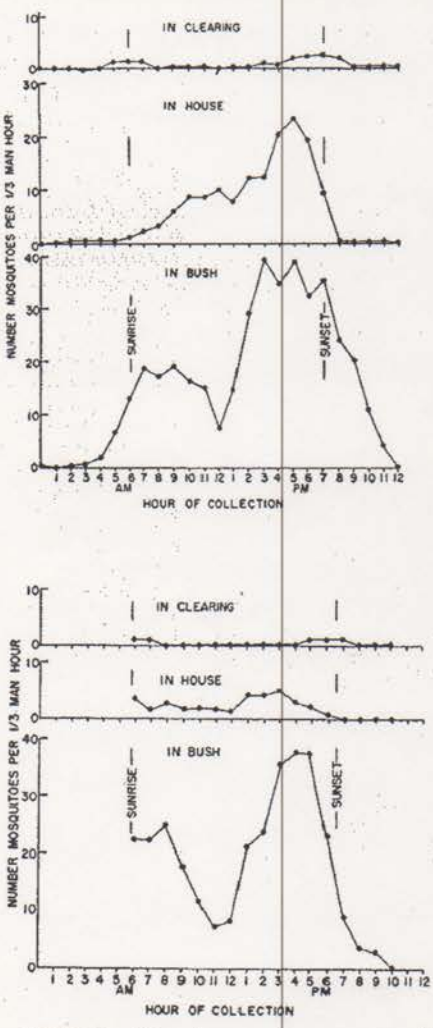

FIGURE 2. Three-hour moving averages of the numbers of female *A. polynesiensis* caught in one third man-hour collections at hourly intervals at the village of Mapasaga. Upper figure, collections on January 10 and 11, 1949; lower figure, collections on November 30, 1949.

In November, 1949, a similar survey was made at the same stations between 3 P.M. and 11 P.M. The collections in the late night were omitted because it was believed that the use of flashlights in the earlier survey had activated mosquitoes which normally would not have attempted to feed at night.

The mosquito densities, as judged by these two surveys plotted as 3-hour moving averages, show rather consistent patterns (figure 2). The few mosquitoes caught in the clearing were taken in the early morning and early evening hours. The two series of collections made in the bush vary only in detail. Both curves are bimodal with the lesser peak occurring in the morning and the greater one in the late afternoon. The numbers of mosquitoes on the latter survey are believed to reflect the destruction of suitable mosquito harborage around the house. Whereas a rank undergrowth was present in January, the area had been cleared and planted in taro in November. However, other unrecognized factors may have been involved.

Comparing the numbers of mosquitoes collected at the 3 stations it becomes obvious that more mosquitoes may be found in the bush at almost any hour of the day than in the village proper. Moreover, there is no evidence of an extensive migration of *A. polynesiensis* into the clearing even in the absence of brilliant sunlight.

Dispersal. The distance that *A. polynesiensis* travels from its breeding or resting place is of great importance to both the epidemiology and control of filariasis. This distance has been identified by a variety of names, but "range of dispersal" used by Eyles and Bishop (1943) seems most appropriate.

The range of dispersal of *A. polynesiensis* is considered to be 100 yards or less. O'Connor (1923) found that this mosquito was fairly abundant on one islet, yet absent from two others located only 20 to 100 yards away. Amos (1947) reported that during the heat of the day, *A. polynesiensis* would venture only rarely as far as 25 yards into a sunlit area, but that on calm evenings it would travel just short of 150 yards. The statements of O'Connor and of Amos are of interest, but they are not supported by data. Both have found how far this mosquito will travel into unfavorable environments, but their statements do not explain the sources of blood meals for infected mosquitoes found some distances from villages. Were these mosquitoes infected locally, or were they infected in the village? Byrd et al. (1945) showed that the rate of infection with *Wuchereria bancrofti* in mosquitoes was greatest in the village and decreased markedly at the periphery of the village. They assumed that all transmission occurred within the village and cited the infection rates as evidence of a flight range of 100 yards or less. Since their basic assumption is open to considerable doubt, more direct evidence of the dispersal of *A. polyensiensis* was needed. To obtain this information two experiments were performed in which *A. polynesiensis* were collected, marked with dye, released, and recaptured.

Adult female *A. polynesiensis* were collected outside of the test area on the days that the experiments began. They were divided into lots and dusted with a mixture of flour and dye in order to mark the specimens. The dyes used were gentian violet, eosin, and methyl green. Gentian violet proved too toxic. The colors were mixed with flour in the proportion of 1 to 25. After dusting, the mosquitoes were released in the experimental area. In tests to determine the efficiency of this method of marking all of 25 mosquitoes dusted with eosin and 24 out of 25 mosquitoes treated with each of the other two dyes showed the stain when dipped into a dye solvent (70 per cent alcohol, 3 parts; glycerin, 1 part; and chloroform, 1 part).

Recovery of stained specimens was made by collecting mosquitoes from human bait by means of hand aspirators. One, 3, 5, 7, 14 and 21 days after the releases collections were made at each capture station for a period of 10 minutes. The mosquitoes that were caught were killed with chloroform fumes in labeled test tubes. In the laboratory, these specimens were spread on a piece of filter paper and a small amount of dye solvent was dropped on each. Marked mosquitoes were immediately recognized by staining of the filter paper by dye washed from them.

These two experiments were performed at the air base at Tafuna, Tutuila, American Samoa. Until World War II, this area had been planted by Samoans in food crops (bananas, papayas and coconuts). During the war, the air base was constructed. By 1950, most of the area, except for roads, airstrip, and small areas around the remaining buildings had reverted to jungle (figure 3). The terrain is flat. The prevailing wind is from the east. One week prior to each release, the experimental area was sprayed by airplane with DDT emulsion at the rate of 0.2 pound of

DDT per acre. This procedure virtually eliminated the indigenous adult *A. polynesiensis* population, but did not affect the immature stages. By the time the experiments began, the adult mosquito population was appearing again. This procedure proved very helpful for it reduced the numbers of unstained mosquitoes in the collections and probably reduced the competition between the introduced and indigenous populations.

On February 13, 1950, 128 mosquitoes stained with gentian violet were released at station 2; 194 stained with eosin at station 4; and 198 stained with methyl green at station 6. Capture stations, all located in the bush, are indicated on the map (figure 3). On March 20, 1950, 235 mosquitoes stained with

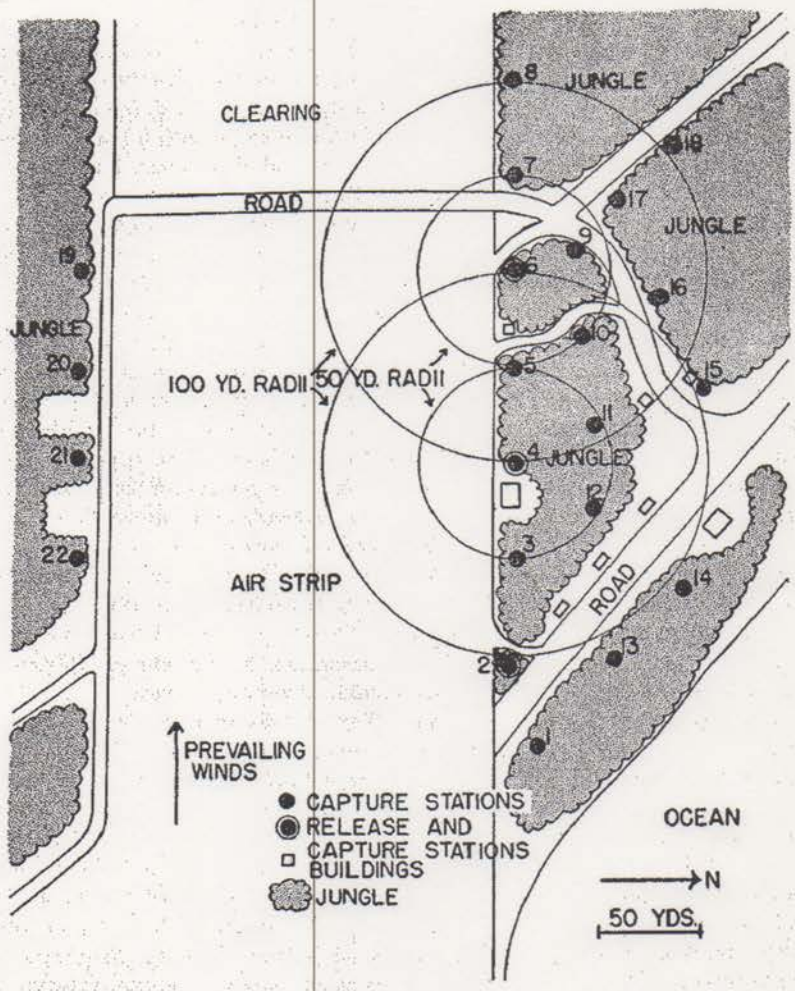

FIGURE 3. Sketch map of the Tafuna area in which dispersal studies of *A. polynesienses* were conducted.

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The numbers of stained specimens recaptured was not great. None of those stained with gentian violet was found again. Of the 429 marked with eosin 29 (6.3 per cent) were recovered, while only 20 (4.5 per cent) of the 244 stained with methyl green were taken (table 2).

The results of these studies are not conclusive and are too few for statistical analysis. Nevertheless, some important information has been derived from them: (1) Nearly 75 per cent of all the mosquitoes recaptured were taken within 5 days at the points of release (table 3); (2) the dispersal that has been observed is apparently slow, because recovery of mosquitoes at stations 50 yards from the points of release were made after 3 to 23 days and at stations 100 yards away after 7 to 14 days; (3) *A. polynesiensis* can travel 100 yards through the jungle, but this apparently approaches its maximum dispersal; (4) clearings, such as the main roads and the airstrip, seem to act as barriers to the movements of this mosquito; and (5) flight seems oriented along the path of the prevailing winds. Taken collectively, these points strongly suggest that the dispersal of *A. polynesiensis* is very limited as the earlier writers have stated.

TABLE 2

Recovery of stained female Aedes polynesiensis *in dispersal studies, at Tafuna, American Samoa*

Collecting station*	Number of mosquitoes recaptured		
	Methyl green	Eosin	Total
2	0	1	1
3	0	1	1
4	2	21	23
5	1	4	5
6	16	2	18
9	1	0	1
Totals	20	29	49

* Locations shown in figure 3.

TABLE 3

Distance traveled by stained Aedes polynesiensis *dispersal studies at Tafuna, American Samoa*

Days after release	Total	Distance from release point (*yards*)			
		0	50	100	>100
1	28	28	0	0	0
3	11	7	4	0	0
5	3	2	1	0	0
7	4	0	0	4	0
14	1	0	0	1	0
21	1	0	1	0	0
23	1	0	1	0	0
	49	37	7	5	0

Abundance and some modifying factors

A vector of filariasis must be present in sufficient numbers to transmit the parasite (Brug, 1929). In Samoa, *Aedes polynesiensis* was by far the most abundant mosquito (Byrd et al., 1945; Jachowski and Otto, 1952). However, more precise information on the abundance of the females of this species was needed to determine the time and place of transmission of the filarial parasite and to define the areas in which mosquito control was to be practiced.

Role of ecological conditions. A. polynesiensis is primarily a bush mosquito (Jachowski and Otto, 1952). The data collected to determine the diurnal variations in the density of this mosquito population clearly indicate that the vector was more abundant throughout the hours of its activity in dense vegetation than in clearings of villages (table 1). To further document this observation, collections which were made at the village of Masausi have been tabulated. Between October, 1948, and April, 1950, 21 mosquito surveys were conducted periodically and in March,

1951, another was made at this village. By March, 1950, four collecting stations had been established which were located as follows: in a house near the center of the village (station A); on the malae (village green) which was partially shaded by coconut trees (station B); in the bush (near the community pigpen) approximately 50 yards from the nearest house (station C); and in a banana grove along the principal trail over the mountain ridge about 200 yards from the village (station D). In summary, the results of these collections again indicate a much greater mosquito density in the bush than in the village proper (table 4). Significant differences in the mean numbers of mosquitoes per survey occur between collections in the village and those in the bush but not between the two village collections or between the two collections in the bush.

All of the available information indicates that the density of the *A. polynesiensis* population is consistently and significantly greater in the undergrowth of the plantations and of forested areas than in the villages.

Seasonal variation. In those islands of the South Pacific wherein recognizable seasons occur, seasonal variations in the density of *A. polynesiensis* have been observed. Thus, Davis (1949) reported that in Raratonga during the

TABLE 4

Number of Aedes polynesiensis *collected in one third of a man-hour at 4 stations in and near Masausi, American Samoa, between October 5, 1948, and May 30, 1950*

Date of collection	(A) House	(B) Clearing	(C) Bush	(D) Bush
Oct. 5, 1948			28	
Nov. 22			22	
Dec. 20			11	
Jan. 24, 1949	2	1	13	
Feb. 25	11	8	17	
Mar. 7	3	0	11	5
Apr. 4	25*	31*	12	14
May 2	5	1	59	14
May 31	1	9	38	30
June 27	0	2	11	31
July 25	0	12	30	19
Aug. 23	0	6	31	14
Sept. 20	1	6	15	38
Oct. 18	1	13	26	20
Nov. 14	0	1	4	19
Dec. 12	0	0	10	25
Jan. 9, 1950	2	0	21	56*
Feb. 6	0	20	9	28
Mar. 6	0	0	15	38
Apr. 13	0	1	8	38
May 30	0	0	17	26
Totals	51	111	408	415
Mean ± SE_x	2.8 ± 1.2	6.2 ± 2.9	19.4 ± 2.6	25.9 ± 3.2
SD	5.0	8.2	12.1	12.3

* Unusually large numbers for this station.

months of April to November, inclusive, the population of this mosquito is appreciably lowered probably because of reduced rainfall, usually occurring as light showers, which limits mosquito breeding. Moreover, during this period, lowered temperatures fluctuate around 65 F. In Fiji, Paine (1943) found that *A. polynesiensis* is most abundant from February to June and only intermittently abundant after rainy periods during the other months. In Samoa, on the other hand, the seasons are not marked (Jachowski and Otto, 1953). Temperature fluctuations are small. Rainfall does show some seasonal variation, but these changes are more generally in intensity rather than in frequency of rainfall. Consequently, one would not expect any appreciable variation in mosquito density except during unusually prolonged dry periods.

The results of the surveys at Masausi do not suggest definite seasonal variations in the density of *A. polynesiensis* (figure 4). The variations beyond those of random sampling, which do occur may be explained on the basis of weather conditions at the time of each survey.

Variations due to weather. When the numbers of mosquitoes collected per survey are separated into frequency distributions according to the prevailing wind and sky conditions at the time of the collections, variations in these distributions appear which suggest that weather conditions may influence mosquito activity (table 5). Thus, in 36 collections made within the village of Masausi, more than 6 mosquitoes were collected on 8 occasions and on each the same general weather conditions prevailed, i.e., wind velocity of less than 5 knots and cloudy skies. Under these conditions the mean number of mosquitoes collected per survey was 7.5;

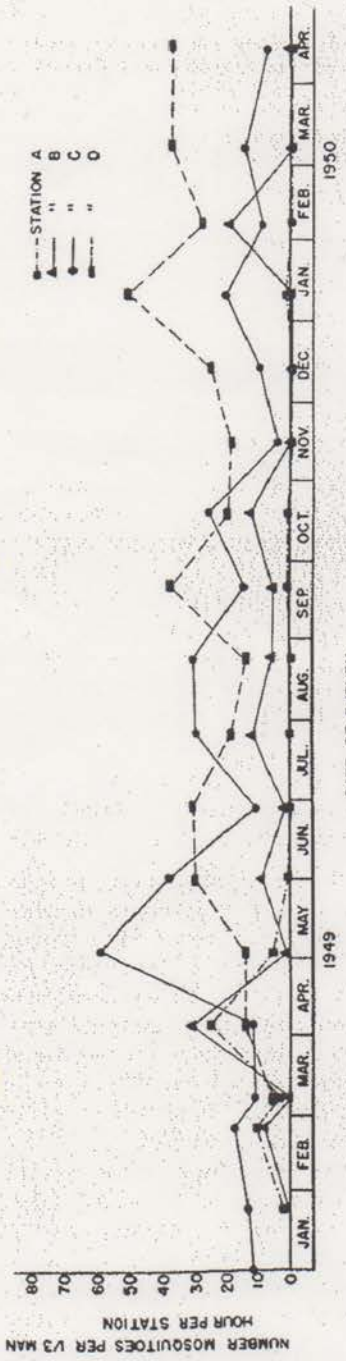

FIGURE 4. The number of female *A. polynesiensis* caught at collecting stations in and near the village of Masausi during surveys made from January, 1949, to April, 1950.

TABLE 5

Frequency distributions of the numbers of female Aedes polynesiensis *collected in 10-minute surveys under various weather conditions at Masausi, American Samoa, October, 1948, to March, 1951*

Number of mosquitoes per survey	Wind < 5 knots			Wind > 5 knots	Total
	Clear	Cloudy	Rain		
A. Collections in the village					
0	2	5	2	6	15
1– 9	4	7	1	2	14
10–19	0	3	0	0	3
20–29	0	2	0	0	2
30–39	0	1	0	0	1
Total no. of collections	6	18	3	8	35
Total no. of mosquitoes	15	136	3	8	162
Mean no. of mosquitoes	2.1	7.5	1.0	1.0	4.5
B. Collections in the bush					
0	0	0	0	0	0
1– 9	1	2	0	2	5
10–19	3	8	2	1	14
20–29	3	4	0	1	8
30–39	1	5	0	2	8
40–49	0	0	0	0	0
50–59	2	0	0	0	2
Total no. of collections	10	19	2	6	37
Total no. of mosquitoes	276	403	27	118	824
Mean no. of mosquitoes	27.6	21.2	13.5	16.3	22.5

under all other circumstances the mean was 1.4. Similar comparisons of collections made in the bush fail to suggest any role of weather in determining the mosquito density. Under conditions which apparently favor mosquito activity in the village, the mean number of mosquitoes collected on 19 surveys in the bush was 21.2. In all other types of weather the mean was 23.4.

The apparent effects of the weather on mosquito activity in cleared areas, on one hand, and the apparent lack of influence in uncleared areas, on the other, may be logically explained. In a clearing, the full force of the weather is felt by the mosquito population. Bright sun, strong winds, and rain act directly upon the mosquitoes. On the other hand, these forces are modified by the dense vegetation in the bush which screens direct sunlight and rainfall and diminishes the force of the wind. When, for example, the wind is lashing the tops of coconut trees, conditions may be almost calm at ground level. During such conditions, repeated observations indicate that the mosquitoes will land and probe on the collector's legs. In calm air they land on almost any part of the body, but seem to prefer the exposed portions of the head, neck and arms. In downpours of rain, the large leaves of such trees as bananas

and breadfruit afford protection from the rain drops for both man and mosquitoes and the activity of the latter is not markedly affected.

Survival of female A. polynesiensis. No data are available on the longevity of female *A. polynesiensis* either in the laboratory or in nature. Since the mosquito must survive long enough to permit development of the filarial larvae (a period of 12 to 20 days in Samoa), this information is epidemiologically essential.

In two laboratory experiments single female mosquitoes were isolated in 50 small plastic cages (see methods). In the first experiment they were offered blood meals daily; in the second, twice weekly. Another difference in the tests was that in the first, males were not replaced when they died, while in the second, they were.

Under these artificial conditions, the mean length of life for 50 adult females was 22.1 ± 1.2 days in the first test and 20.8 ± 1.7 days in the second. The difference between these means (1.3 ± 2.1 days) was not significant. When the results of the two tests were combined, the mean period of survival was 21.2 ± 1.0 days. As reflected by the difference in the standard error of the means, the patterns of the survival data were different in the two experiments (table 6). Maximum survival in the first test was 36 days and in the second, 56 days. These studies were continued by Ingram (1954) who has completed extensive studies under more rigidly controlled laboratory conditions.

Resting places. Davis (1949) in the Cook Islands and Paine (1943) in Fiji agree that during periods of inactivity, *A. polynesiensis* rests on low-growing trees and shrubs and normally do not remain in houses. O'Connor found them resting in dry tree holes and behind partially detached bark on dry coconut husks.

TABLE 6

Survival periods of female A. polynesiensis *in the laboratory*

Number of weeks	Number surviving		
	First test	Second test	Combined results
1	46	46	92
2	44	30	74
3	31	21	52
4	6	9	15
5	1	5	6
6	0	4	4
7	0	3	3
8	0	0	0
Total no. of mosquitoes	50	51	101

In Samoa, *A. polynesiensis* were *never* observed resting in native or in European houses. In a village in which large numbers of this species were taken, 3 houses were fumigated with an aerosol of pyrethrum and DDT. Many insects fell on sheets spread on the floors, but no *A. polynesiensis* were found.

Resting mosquitoes frequently could be located in two types of environments. The first was on the undersides of leaves of bushes sheltering breeding containers; the other was in the crevasses of stone walls built to confine pigs.

Blood meals

Apparently, *Aedes polynesiensis* requires a blood meal for oviposition. In 4 years of laboratory colonization, no autogeny has been observed. Although both O'Connor (1923) and Bahr (1912) found this species on "uninhabited" islands, they undoubtedly were referring to the absence of a human population. Small animals and birds could have provided the necessary source of blood.

Host preferences. Man appears to be the preferred host for these mosquitoes. Attempts in Samoa to collect feeding mosquitoes from pigs, dogs, horses and chickens were uniformly unsuccessful although they have been observed feeding on some of these animals. Buxton (1928) reported them feeding on a horse and I observed them feeding on pigs. However, if more than one host is present, the choice is man. They must feed on dogs, for specimens have been taken in nature which harbored all stages of the dog heartworm, *Dirofilaria immitis*. In the laboratory some *A. polynesiensis* will engorge on small animals and chickens placed in the cage, but many, obviously hungry, will attack the hand as it removes the animal from the cage.

Nature of the bite. Aedes polynesiensis approaches man quietly, seldom "buzzing." After landing on exposed skin, it moves very little, usually probes only once and settles down to a complete blood meal. The bites usually are painless and produce very little reaction. After feeding has begun, this mosquito is tenacious. It hangs on to a hand, for example, even if shaken violently. The mosquito can be touched and even lifted entirely off its legs without interrupting a blood meal.

If undisturbed, the engorged mosquito will withdraw its proboscis and rest on the skin for a minute or more. Then it flies directly to a dark, humid place to rest. In the field they rested in stone walls or in vegetation: in the laboratory they moved to the darkest corners of the cages.

Time of feeding. As shown in the experiments to determine the diurnal activity, the numbers of *A. polynesiensis* seeking blood meals was greatest in the late afternoon (3 to 6 P.M.) and in the early morning (6 to 9 A.M.), with the afternoon peak approximately twice that of the morning one (figure 2).

Size of the blood meal. To determine the size of the blood meals, 50 female *A. polynesiensis* were anesthetized with carbon dioxide and weighed. They were then permitted to take a full blood meal from a human arm after which they were again anesthetized and reweighed. The difference in their weights before and after feeding is considered the weight of the blood meal. These mosquitoes, all 6 days old and without previous blood meals, were handled in groups of 10. The entire procedure took approximately 45 minutes for each group.

The sizes of the blood meals varied from 1.3 to 2.8 milligrams with the mean 2.1 ± 0.4 milligrams. The time required by these specimens to engorge extended from 2 minutes and 30 seconds to 3 minutes and 45 seconds. The mean was 3 minutes and 10 seconds, with a standard deviation of 23 seconds. No apparent correlation exists between the size of the blood meal and the time to acquire it. In 3 minutes and 45 seconds one mosquito obtained 1.7 milligrams of blood, while in 3 minutes and 35 seconds another ingested 2.8 milligrams.

Similarly, no correlation appears between the weight of the mosquito and that of the blood meal. An index value of the weight of the blood meal divided by the original weight of the mosquito varied from 0.8 to 2.3. The mean value was 1.3 ± 0.5. Thus, most of the mosquitoes took at least their own weight in blood.

Frequency of blood meals. In this laboratory experiment 50 female mosquitoes were used. Each was isolated with a male in a small plastic cage. Blood meals were offered daily.

Four females died before taking a blood meal, while one lived to take 5.

TABLE 7

Mean ages of female A. polynesiensis *at times of blood meals in laboratory*

Blood meal number	Number of mosquitoes	Age at blood meal (*days*)	
		Mean ± S.E.	S.D.
I	46	3.3 ± 0.0*	0.8
II	41	11.4 ± 0.8	5.1
III	24	17.0 ± 1.0	5.0
IV	12	22.6 ± 1.2	4.3
V	1	(22)	

*S.E. = 0.012.

The ages of the mosquitoes, at the time the blood meals were taken, were not uniform; consequently the standard deviations are large (table 7). Nevertheless, some pattern emerges. The mean ages at the time of the first, second, third and fourth blood meals were approximately 3, 11, 17 and 23 days respectively. As a part of this study, the survival of these mosquitoes was also recorded. The mean was 22.8 ± 1.2 days. These results have already been discussed, but are of interest here because only 24 of the mosquitoes had lived long enough to take a third blood meal. In terms of transmission potential this means that less than half of the mosquitoes in this study had survived long enough to transmit filariasis even if all had become infected with the first blood meal.

Another measurement of interest is the interval between blood meals required by the individual mosquitoes. These intervals are fairly uniform, the means being 7.3, 7.3 and 7.6 days between blood meals I-II, II-III and III-IV respectively (table 8). Again the results suggest that only a minority of the female *A. polynesiensis* would take a sufficient number of blood meals in their life times to transmit the filarial parasite.

Reproduction

Sexual behavior. As described by O'Connor (1923), male *Aedes polynesiensis* were frequently observed in Samoa resting on and swarming around the breeding containers. The sexes paired on the wing and copulation was completed when the female landed with the male inverted beneath her. In areas of extensive breeding, the males frequently attempted copulation while the females were taking blood meals. When the females attacked a person in numbers, the males swarmed around him.

In cages in the laboratory, males usually rested on or near the receptacles for collecting eggs. They apparently were excited as the females swarmed to take blood meals for, as in the field, copulation was attempted then.

Number of eggs per female. In preliminary studies, female *A. polynesiensis* which had taken blood meals were transferred in groups of 100 from the stock cage to lantern globes. Eggs resulting from this blood meal were collected on sheets of moist filter paper in Petri dishes which covered the bottom of the globes. Seven days after the blood meals the papers were removed and the eggs were counted. From 5 such tests the mean number of eggs per female per blood meal was 54.8 (table 9).

These results are crude, however, since the ages of the mosquitoes were

TABLE 8

Intervals between blood meals in the laboratory

Blood meals	Number of mosquitoes	Interval (*days*)	
		Mean ± S.E.	S.D.
I– II	41	7.3 ± 0.8	4.8
II–III	24	7.3 ± 0.8	3.8
III–IV	22	7.6 ± 0.5	1.7
IV– V	1	(2)	

TABLE 9

Numbers of eggs laid by A. polynesiensis *in groups of 100 after a blood meal in the laboratory*

Number of mosquitoes	Number of eggs	Mean number of eggs per blood meal
100	4,617	46.2
100	5,892	58.9
100	5,329	53.3
100	5,174	51.7
100	6,385	63.9
500	27,397	54.8

not known precisely. Therefore, in a second series of tests, 100 females isolated individually were given their first blood meals and the number of eggs from each was recorded. The mean number of eggs per female in this series was 57.4 and the extremes were 21 and 97 (table 10). Thus in these two series of experiments *A. polynesiensis* laid approximately 55 eggs per blood meal.

Breeding sites. Eggs of *A. polynesiensis* are laid singly on the sides of containers just above the water line. Cracks and niches in the container seem to be preferred to smooth surfaces.

Usual sites for oviposition were small water containers, both natural and artificial, in well shaded areas. Larvae have been found in artificial containers made of wood, metal, glass, china, and rubber and in such natural containers as clam shells, tree holes, fallen leaves and coconut shells. On two occasions larvae were found in tremendous numbers in large, shaded pools in lava rock. By far the most common breeding site was the coconut shell (table 11).

Larval and pupal development

Each day for a period of 30 days, approximately 100 eggs were hatched in a pan containing 1 liter of water in which 3 or 4 alfalfa pellets (rabbit chow) had been dissolved overnight. These eggs were a week old, having been maturated for 4 days and dried for 3 days. No record was kept of the development of the various larval instars. Pupae were removed daily and sepa-

TABLE 10

Number of eggs laid by individual A. polynesiensis *after the first blood meal in the laboratory*

No. eggs per female	Frequency				
	Test no.				Total
	1	2	3	4	
30	1	2	0	0	3
30–39	3	1	3	2	9
40–49	3	4	5	3	15
50–59	12	9	7	9	37
60–69	5	1	7	4	17
70–79	0	3	3	3	9
80–89	0	4	0	2	6
90	1	1	0	2	4
Total no. of mosq.	25	25	25	25	100
Total no. of eggs	1,360	1,466	1,362	1,551	5,739
Mean no. of eggs per female	54.4	58.6	54.5	62.0	57.4

TABLE 11

Sources of larval collections of Aedes polynesiensis *in American Samoa*

Breeding source	Number of collections		
Ground waters	2		
rock pools		2	
Natural containers	1,873		
concavity in stone		1	
clam shells		6	
tree holes		36	
coconut			5
breadfruit			21
others			10
fallen leaves		41	
coconut			15
breadfruit			18
bananas			5
others			3
coconut shells and husks		1,789	
Artificial containers	884		
metal		663	
cans			646
drums and barrels			6
truck bodies			3
airplane fusilages			8
wood		21	
log drums			15
canoes			6
other		200	
glassware			14
china			4
tires			182
Total number of larval collections	2,759		

rated according to the date that the eggs were hatched, the date of pupation, and, on the basis of size, by sex. The resulting adults were removed daily and the numbers of each sex recorded.

In this experiment the mean interval from eclosion to pupation was 6.9 days and from eclosion to emergence was 9.0 days for the males and 9.4 days for the females (table 12). The difference in the mean periods of development for the two sexes (0.4 ± 0.058 days) is significant. Apparently this difference is due primarily to the longer pupal period of the females since they required a mean of 2.4 days while the males completed that stage of development in 2.1 days. Again the difference between the sexes (0.14 ± 0.02 days) is significant.

SUMMARY

1. *Aedes polynesiensis* was successfully colonized at The Johns Hopkins University School of Hygiene and Public Health in June, 1950, from eggs brought from American Samoa.

2. Although this mosquito is diurnally active, two peaks of activity were observed: a greater one in the afternoon and a lesser one in the early morning.

3. This mosquito was found to be much more abundant in well shaded areas than in clearings and showed little inclination to migrate from its favored habitat.

4. The range of dispersal, even in the bush, was limited (approximately 100 yards).

5. The abundance of adult female *A. polynesiensis* is reduced by unfavorable weather in those areas where strong sunlight, wind and rain can act directly upon the mosquitoes. In sheltered areas weather does not seem to affect the mosquito population.

6. In Samoa, no evidence of seasonal variation in the *A. polynesiensis* population was observed.

7. Resting mosquitoes were not found in houses or other man-made shelters, but were observed in low vegetation and in crevasses of stone walls.

8. In the laboratory, the mean survival of adult females was 21.2 days at 80 F and high relative humidity.

9. *A. polynesiensis* apparently cannot reproduce autogenously.

10. Man is the preferred host, but these mosquitoes will feed upon dogs,

TABLE 12

Time (in days) from eclosion to pupation and to emergence of A. polynesiensis in the laboratory

Days after hatch	Pupation		Adult emergence			
			Male		Female	
	Number	Per cent of total	Number	Per cent of total	Number	Per cent of total
1	0		0		0	
2	0		0		0	
3	26	1.5	0		0	
4	741	41.5	0		0	
5	676	37.8	0		0	
6	163	9.2	1	0.1	0	
7	106	5.9	15	1.8	2	0.2
8	40	2.2	364	43.1	125	15.2
9	20	1.1	270	32.0	414	50.3
10	6	0.3	100	11.9	167	20.3
11	4	0.2	42	5.0	81	9.8
12	2	0.1	37	4.4	18	2.2
13	2	0.1	11	1.3	11	1.3
14	0		2	0.2	2	0.2
15	0		1	0.1	3	0.4
16	0		1	0.1	0	
17	0		0		1	0.1
18	0		0		0	
19	0		0		0	
20	0		0		0	
Totals	1,786	99.9	844	100.0	824	100.0

horses and pigs in nature and upon a variety of animals in the laboratory.

11. The blood meal weighs approximately 1.8 milligrams, and averages 1.3 times the weight of the mosquito. The mean age at the time of the first blood meal was 3.3 days and successive meals were taken at intervals of about 1 week thereafter. The biting mosquito was quiet, persistent and relatively painless.

12. Mating occurred in flight but copulation did not seem to be completed until the female landed with the male inverted beneath her.

13. Breeding sites were small collections of water in both natural and artificial containers. Coconut shells were preferred. The containers were usually hidden by dense undergrowth.

14. Eggs were laid in cracks and crevasses just above the water line. The mean number per female was approximately 55 per blood meal.

15. In the laboratory at 80 F larval development required 6.9 days. The mean interval from eclosion to emergence was 9.0 days for males and 9.4 days for females.

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