Vectors of *Wuchereria bancrofti* in the Sepik Provinces of Papua New Guinea

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Abstract

The vectors of *Wuchereria bancrofti* were investigated in two areas of the Sepik Provinces of Papua New Guinea. At the village of Yauatong, indoor-resting *Anopheles punctulatus* had an infection rate of 47·3% and an infective rate of 3·4%. No infections occurred in 382 *Culex annulirostris* obtained in night-landing catches. At the village of Yankok only *An. koliensis* contained infective larvae but *An. punctulatus* and *Cx quinquefasciatus* were infected. Probit values of the cumulative percentages of filariae-positive mosquitoes plotted against the logarithm of the corresponding filaria count are illustrated.

Introduction

Bancroftian filariasis is known to occur in coastal areas of Papua New Guinea and on several offshore islands (BACKHOUSE & HEYDON, 1950; BEARUP & LAWRENCE, 1950; DESOWITZ *et al.*, 1966; KNIGHT *et al.*, 1979). Studies on the vectors now span more than five decades. Since BACKHOUSE (1934) first described the development of *Wuchereria bancrofti* in *Anopheles farauti* and *An. punctulatus* the role of these species in filariasis transmission in New Guinea and the Solomon Islands has been confirmed by several other authors (HOPLA, 1946; TOFFALETI & KING, 1947; SCHLOSSER, 1949; DE ROOK, 1957, 1959; BYRD & ST. AMANT, 1959; PETERS, 1963). A third member of the *An. punctulatus* group, *An. punctulatus* group, *An. koliensis* has also been found naturally infected (TOFFALETI & KING, 1947; PERRY, 1950).

BACKHOUSE & HEYDON (1950) regarded the members of the *punctulatus* group as the principal vectors of filariasis in those areas of Melanesia in which they occur. However, there are areas in Irian Jaya in which there is no malaria because of the virtual absence of *Anopheles* species, but filariasis is hyperendemic (VAN DIJK, 1958, 1959; DE ROOK, 1957b; DE ROOK & VAN DIJK, 1959). Studies in these areas revealed that culicine species such as *Culex annulirostris, Cx bitaeniorhynchus, Cx quinquefasciatus* (= *Cx pipiens fatigans*) and *Mansonia uniformis* were naturally infected. In addition *Ma. papuensis, Cx squamosus* and *Aedes kochi* have been experimentally infected (BACKHOUSE & HEYDON, 1950; VAN DIJK, 1958, 1959, 1961; DE ROOK 1957b, 1959; DE ROOK & VAN DIJK, 1959). It is probable that the vector on Pam Island, Irian Jaya was wrongly identified as *Ae. kochi* by DE ROOK (1957b) and that he was dealing with *Ae* "Marks sp. No. 117" (LEE *et al.*, 1982).

Knowledge of the vectors in the eastern half of New Guinea is limited as very few studies have been undertaken in that area. This paper presents the results of preliminary investigations to determine the vector/vectors in two areas in north-eastern Papua New Guinea.

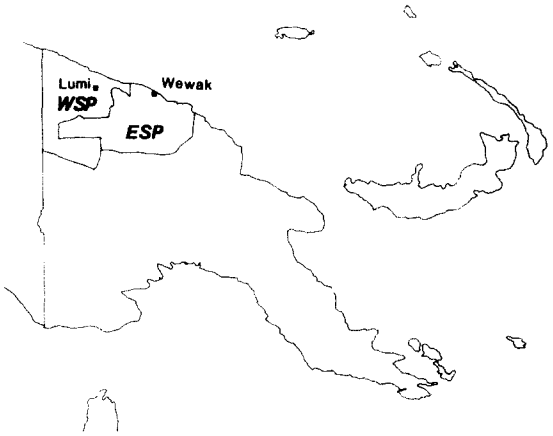
Materials and Methods

Study areas

Both study areas are situated on the southern foothills of the Torricelli Mountains. The natural vegetation is rainforest but this has been cleared in many areas for cultivation. Rainfall is approximately 1,600 mm per annum with most rain occurring from November to March; however rain falls throughout the year. The inhabitants are subsistence farmers cultivating mainly taro, sago, coconuts, bananas and green leaf vegetables. Houses are constructed of bush timber and the roofs are of thatch. No systematic mosquito control has been carried out in either area.

The study areas, situated close to the Wewak-Lumi road (Map 1) are:

1. Yauatong, East Sepik Province, which is about 15 km from the government station of Dreikikier. Most mosquitoes were collected in a hamlet of five houses situated close to the river "Wara Rok Rok". Some neighbouring houses, within 0·5 km were also searched.



Map 1. Map of Papua New Guinea showing the East Sepik Province (ESP) and the West Sepik Province (WSP).

2. Two hamlets near Anguganak, (Centre of the Christian Mission to Many Lands) West Sepik Province. One hamlet, Wansu, is adjacent to the Mission and within a few metres of the River Opan and consists of 12 houses. The second hamlet, Mutuk, is on the other side of the river about one km upstream and consists of over 20 houses. Both hamlets belong to the village of Yankok.

Collection and dissection of mosquitoes

At Yauatong, mosquito collections were made between 17th and 31st March 1983. Most mosquitoes were obtained by daytime searches for specimens resting inside houses. However, miniature CDC light-traps were operated inside

houses on nine occasions and seven early night-landing catches, using human bait situated outside houses, were carried out from dusk to 2100 or 2130 hours. The light traps were set up at dusk and the specimens collected the next day.

Collections in the Anguganak region were made from 7th to 20th April 1983. Heavy rain maintained the river Opan at a very high level throughout the duration of the survey and prevented access to Mutuk until 19th April, so initial collections were confined to Wansu. As in Yauatong, most specimens were obtained by indoor-resting catches. CDC light traps were operated on 10 occasions. As three early night-landing catches at Wansu yielded only four mosquitoes, they were discontinued. Only one night-landing catch was conducted at Mutuk.

After capture, the mosquitoes were identified and then each species was preserved separately in 70% alcohol for transporting to Sydney, where they were stained in Mayer's acid haemalum as described by NELSON (1958). The mosquitoes were dissected under a dissecting microscope, with the head, thorax and abdomen being examined separately using a compound microscope at × 125. A sample of 647 *An. punctulatus* from indoor resting catches at Yauatong was dissected. Attempts were made to dissect all other specimens. No attempt was made to examine the gut contents for ingested microfilariae.

The identification of *Cx annulirostris* and *Cx quinquefasciatus* was confirmed by Dr E. N. Marks, formerly of the Queensland Institute of Medical Research, Brisbane.

Scoring of filariae

Young, small worms were measured by a measuring eyepiece or from *camera lucida* drawings; older, larger worms were drawn and measured. Not all worms could be measured, usually because they had been cut during the mosquito dissection. When there were many worms only a sample, representing all sizes, was measured. Specific identification of the infective larvae was made according to the criteria of NELSON (1959).

Presentation of results

The same parameters that are used to characterize filarial infections in human populations (SASA, 1967; WHO, 1967) are used for the filarial infections in mosquitoes in this study. Thus the mosquitoes containing from 1 to 10 filariae are classified as digital groups; mosquitoes are grouped into class intervals of 10 for infections from 11 to 100 filariae and into class intervals of 100 from 101 to 1000. Results are presented for the total number of filariae in the mosquitoes. In addition, for the indoor-resting sample of *An. punctulatus* at Yauatong, the numbers of pre-sausage-stage larvae, of sausage-stage larvae, stage 2 and stage 3 larvae are also presented. The probit values of the cumulative percentages of filariae-positive mosquitoes are plotted against the logarithm of the corresponding filaria count. Regression lines are calculated by the method of least squares and the median larval density for each line is calculated from the regression equation $y = a + b \log x$ where y is the probit of the cumulative frequency at a density x of filaria, and a and b are the regression coefficients which determine the position and slope of the line. The regression parameters a and b and the correlation co-efficient r are also given.

Results

Yauatong

Almost all the mosquitoes caught resting indoors had fed the night before, whereas those in the light traps were mostly unfed. Some specimens in the light trap collections were dead and dehydrated, and after fixing and staining, could not be dissected satisfactorily.

The indoor-resting catches at Yauatong yielded *An. punctulatus* almost exclusively, with over 1,000 specimens of this species, but only three *An. koliensis*. The light traps captured 49 *Ae. nocturnus*, 19 *An. punctulatus* and 14 *Cx annulirostris*. Night-landing catches yielded 382 *Cx annulirostris* and 30 *An. punctulatus*.

Yauatong—Indoor-resting sample

Only *An punctulatus* was infected (47·3%; 306/647) and this species also contained infective larvae (3·4%; 22/647). All infective larvae agreed with the description of *W. bancrofti* as given by NELSON (1959).

The youngest filarial larvae closely resembled the pre-sausage-stage as described by IYENGAR (1957), and according to his description of the rate of development, these worms had been ingested the night before capture. Measurements of sausage-stage larvae revealed that they belonged to two groups with clearly differentiated sizes, i.e., those shorter than 180μ and those longer than 180μ. In lowland areas of Papua New Guinea, the gonotrophic cycle in *An. punctulatus* is completed in 48 hours (PETERS & STANDFAST, 1960) and only one blood meal is required for the first and each subsequent batch of eggs (VAN DEN ASSEM, 1959; BRYAN, 1973). Therefore the filariae in mosquitoes caught resting indoors during the day belong to the following age groups 0·5, 2·5, 4·5, 6·5, 8·5, 10·5 and 12·5 days. The smaller of the sausage-stage larvae are considered to be 2·5 days old and the larger 4·5 days old. 14 mosquitoes contained two broods of sausage-stage worms of disparate sizes and these infections are regarded as super-infections.

The second-stage larvae were much more difficult to assign to age groups as the ranges of sizes in individual mosquitoes were often wide, usually with no sharp discontinuities. However, in nine cases there were such marked differences in sizes amongst the second-stage larvae within one mosquito that they were considered to be of different ages (e.g., one mosquito contained worms of the following lengths: 356μ, 390μ, 730μ and 830μ). Over-all, superinfections occurred in 109 specimens of *An. punctulatus* (Table I) and one infective mosquito contained six broods of worms ingested with each of six successive blood meals. The number of superinfections followed a Poisson distribution; the categories of five and more superinfections were summed before performing the Standard Goodness of Fit Test.

The regression lines of the probit values of the cumulative percentages of filariae-positive mosquitoes plotted against the logarithm of the corresponding filaria count are shown in Figs. 1 and 2 and the descriptive parameters summarized in Table II

The median larval density was 7·33 for all stages of larvae; 5·78 for pre-sausage stages; 4·87 for sausage stages; 3·44 for second-stage larvae and 1·33 for third-stage larvae. The highest number of pre-sausage-stage worms was 286, of sausage-stage 168, of second-stage larvae 70 and infective larvae 13. The heaviest infection of 317 worms included both pre-sausage and sausage-stage worms.

Stage-specific mean densities varied from 21·03 for all stages (including superinfections), to 18·99 for pre-sausage stages to 15·80 for sausage stages to 8·85 for second-stage larvae to 3·32 for infective larvae.

Yauatong—Night-landing catches

Although only a small number of *An. punctulatus* (30) was caught at night, eight (26·7%) were infected

Table I—Superinfections in *An. punctulatus* from indoor-resting samples at Yauatong

No. of infections	Observed No.	Expected* %	Expected* No.
0	341	49·81	322·24
1	197	34·76	224·62
2	81	12·17	78·29
3	22	2·81	18·19
4	5	0·49	3·17
5	0	0·068	0·44
6	1	0·008	0·05
7+	0	0·001	0·0065

Total No. of infections 647

Mean 0·6971
Variance 0·8059
S.D. 0·8977

* On the basis of a Poisson distribution of mean 0·6971
Standard Goodness of Fit Test $\chi^2_4 = 6{\cdot}9473$ $(0{\cdot}10<p<0{\cdot}25)$

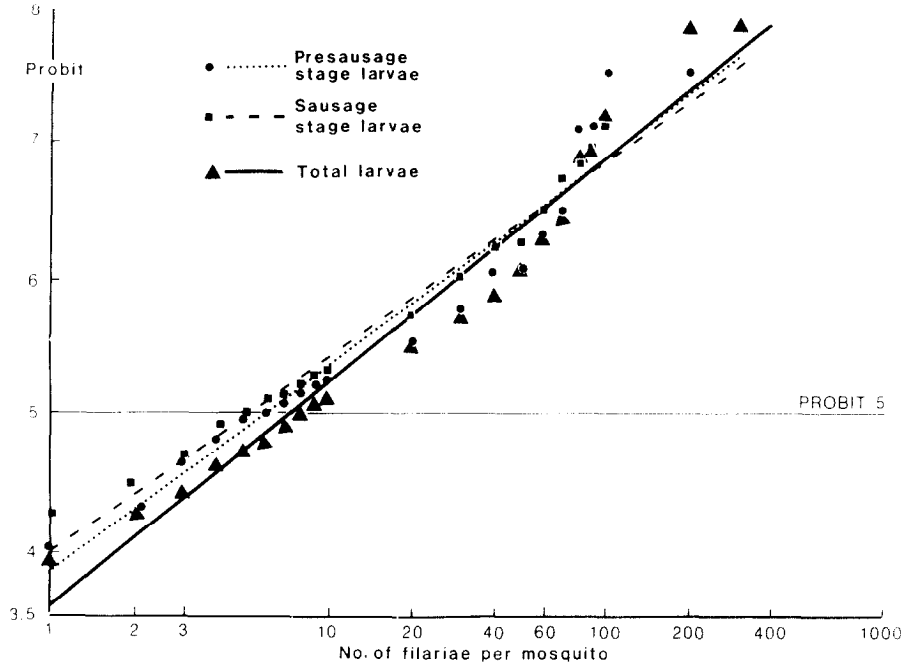


Fig. 1. Regression lines of the cumulative percentage of filaria positive *An. punctulatus* at Yauatong against filaria density on a log-probit scale; infections with total number of filariae, presausage stage larvae and sausage stage larvae are illustrated separately.

and two (6·7%) contained infective larvae. All 382 *Cx annulirostris* were without filariae.

Yauatong—Light trap catches

Only small numbers of mosquitoes were caught and only one of nine *An. punctulatus* was infected and all 46 *Ae. nocturnus* were without filariae.

Yankok—Indoor-resting sample

The domestic mosquito population at Yankok differed markedly from that at Yauatong and there were also marked differences between the two hamlets. At Wansu, the predominant mosquito in indoor-resting samples was *An. koliensis*, comprising 61·9% of the total catch, with *An. punctulatus* accounting for 32% and *Cx quinquefasciatus* 6·2%. In contrast, at Mutuk, *Cx quinquefasciatus* comprised 61·3% of the catch while only 3·4% were *An. koliensis*. Although *An. punctulatus* was relatively less common at Mutuk (25·4%) than at Wansu (31·4%), more were caught at Mutuk where mosquitoes were more abundant. Only nine specimens of *An. farauti* s.l. were collected, all at Wansu.

Filarial infections occurred in the indoor-resting samples of *An. punctulatus* (5·8% at Wansu, 3·5% at Mutuk), *An. koliensis* (14% at Wansu, 5·9% at

Mutuk) and *Cx quinquefasciatus* (23·3% at Wansu, 10·8% at Mutuk) (Table III). However only *An. koliensis* contained infective larvae (0·67%). Infection rates were higher in the Wansu than the Mutuk samples but the differences are not significant ($p>0·5$ χ^2_1 test) and *An. punctulatus* was the only species for which more than 50 specimens were obtained from each hamlet. For this species the results from the two hamlets have been summed before determining the median larval density.

The probit values of the cumulative percentages of filariae-positive mosquitoes plotted against the logar-

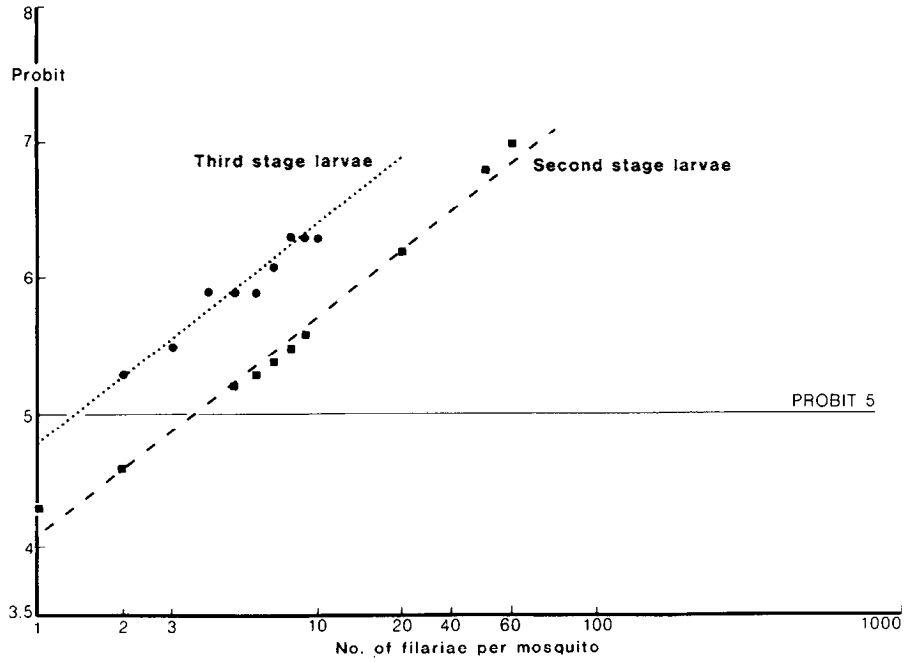


Fig. 2. Regression lines of the cumulative percentages of filaria positive *An. punctulatus* at Yauatong against filaria density on a log-probit scale; infections with second and third stage larvae are illustrated separately.

Table II—Descriptive parameters of filarial infections in *An. punctulatus* at Yauatong

Parasite stage	Percentage infected	Larval median density	Regression parameters a	b	r
All	47·30	7·33	3·55	1·68	·9816
Pre-sausage	28·13	5·78	3·81	1·56	·9701
Sausage	20·56	4·87	4·00	1·46	·9909
L2	14·65	3·44	4·13	1·63	·9946
L3	3·4	1·33	4·81	1·58	·9855

Table III—Filarial infections in mosquitoes from indoor-resting catches at Yankok

Species	No. dissected	No. infected	No. infective
An. punctulatus			
Mutuk	256	9(3·5%)	0
Wansu	155	9(5·8%)	0
An. koliensis			
Mutuk	34	2(5·9%)	0
Wansu	300	42(14%)	2(0·67%)
Cx quinquefascaitus			
Mutuk	618	67(10·8%)	0
Wansu	30	7(23·3%)	0
An. farauti			
Wansu	9	0	0

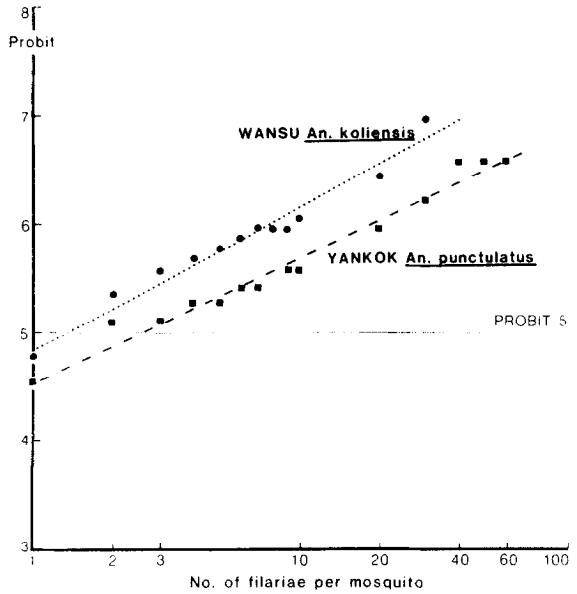


Fig. 3. Regression lines of the cumulative percentages of filaria positive *An. koliensis* at Wansu and *An. punctulatus* at Yankok, against filaria density on a log-probit scale.

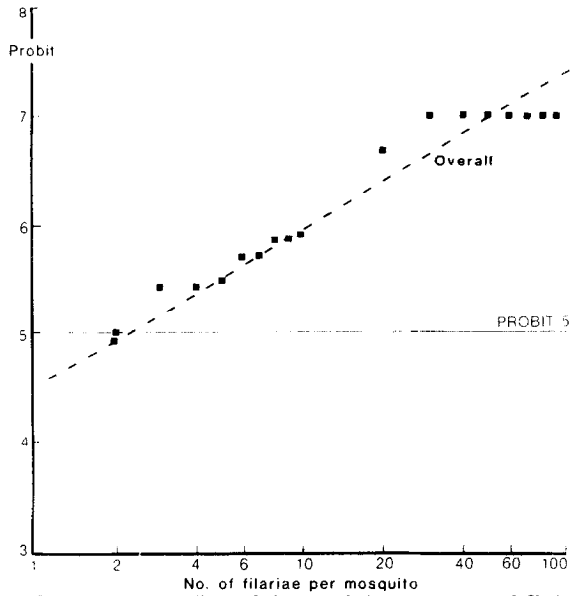


Fig. 4. Regression lines of the cumulative percentages of filaria positive *Cx quinquefasciatus* at Mutuk against filaria density on a log-probit scale.

ithm of the corresponding filaria count are shown in Fig. 3 for *An. punctulatus* and for *An. koliensis* and in Fig. 4 to *Cx quinquefasciatus*. The descriptive parameters are summarized in Table IV.

The 18 infected *An. punctulatus* contained 411 filariae, the maximum number in one mosquito being 62. The median larval density was 2·41. At Wansu, 42 infected *An. koliensis* contained 205 worms with a maximum infection of 23. Most of the infections were with one or two worms and the median larval density was 1·30. In *An. punctulatus* the mean numbers of larvae were 7·9 for pre-sausage stages, 17·2 for sausage stages and 3·8 for second stages. In *An. koliensis* the means were pre-sausage stage, 4·88; sausage stages, 3·22; second-stage larvae, 5·35 and one for infective larvae. At Mutuk, 67 infected *Cx quinquefasciatus* contained 438 worms with a maximum infection of 98. Considering all stages of larvae, the median larval density was 2·09. The mean numbers of larvae were 6·72 for pre-sausage stages, 2·93 for sausage stages and two for second-stage larvae.

Considering the total Yankok sample of *An. punctulatus*, 4·4% were infected and 1·2% contained larvae which were second-stage or older. In *An. koliensis* 16·3% were infected and 4·98% contained larvae of the second or third stage. In contrast, although 10·8% of *Cx quinquefasciatus* at Mutuk were infected only two (0·36%) contained filarial worms more mature than the first stage.

Yankok—Night-landing catches

None of the six *An. koliensis* or the 29 *Cx quinquefasciatus* obtained in the night-landing catches was infected.

Yankok—Light trap catches

The infection rates in the light trap samples were 1·8% (1/56) in *An. punctulatus* and 4·3% (2/47) in *An. koliensis* and 0% (0/30) in *Cx quinquefasciatus*.

Discussion

Yauatong—An. punctulatus

Yauatong was first drawn to the attention of filariasis investigators when medical personnel in hospitals noticed a high prevalence of filarial disease in people from the Dreikikier area. Discussions with the local people indicated that the disease is very focal and a high prevalence of elephantiasis is restricted to a few hamlets. The focality of the disease first suggested that the vectors were not members of the *An. punctulatus* group. These species must be present throughout the area, as malaria, of which they are the primary vectors, is a major health problem in both Yauatong and surrounding areas. Also IYENGAR

Table IV—Descriptive parameters of filarial infections (all parasite stages) in mosquitoes at Yankok

	Place	% infected	Larval median density	Regression parameters a	b	r
An. punctulatus	Wansu + Mutuk	4·38	2·41	4·56	1·15	·9870
An. koliensis	Wansu	14·00	1·30	4·85	1·31	·9828
Cx quinque fasciatus	Mutuk	10·80	2·09	4·54	1·44	·9815

(1965) suggested that in New Guinea there is very little elephantiasis in areas where filariasis is *Anopheles*-borne. This was thought to be due to the relatively low densities of *Anopheles* compared to culicine mosquitoes. Studies so far carried out in New Guinea reveal relatively low densities of anophelines, e.g., at Maprik, the average, per house, per day, over one year was 24·4 *An. punctulatus* , 3·15 *An. farauti* and 3·12 *An. koliensis* (PETERS & STANDFAST, 1960). The number of bites per human per night was approximately 65 for *An. farauti* in the D'Entrecasteaux Islands (SPENCER, 1965). The biting rate of over 500 per man per night for *An. farauti* on Han Island was noteworthy because it was much higher than that usually encountered (SWEENEY, 1968). However, the density of culicine mosquitoes attacking man is rarely quantified in earlier work in New Guinea. Usually there are inexact statements such as "the density was very high" (IYENGAR, 1965). Although there are some areas of *Anopheles*-borne filariasis with high elephantiasis rates in New Guinea, e.g., some coastal villages in the north of Vogelkop, it is "conjectured that...the primary anopheline vectors are supported by culicine vectors" (IYENGAR, 1975). It is possible that further vectors may be found at Yauatong but the high infective rate in *An. punctulatus* indicates that this species alone is able to maintain a very high rate of transmission.

Even when malaria and *W. bancrofti* have the same vectors, in highly endemic malarious areas, the endemicity of malaria is not a reliable guide to the endemicity of filariasis; the vectorial capacities of the vectors may greatly exceed the critical level necessary to maintain malaria at holo-endemic levels. However, the prevalence and mean larval density of filariasis may be a good indicator of the stability of holo-endemic malaria.

Most of the previous studies in New Guinea have been carried out in areas with low densities of *An. punctulatus*, or only small numbers of this species have been dissected, e.g., three of 36 were infected at Jayapura (= Hollandia, = Djajapura) (TOFFALETI & KING, 1947) and none of five at Rabaul (BACKHOUSE & HEYDON, 1950). At Maprik, in the only other study involving substantial numbers of *An. punctulatus*, 3·8% of 546 were infected (PETERS, 1963); no details of the infectivity rate are given. The infection rates in *An. punctulatus* at Dreikikier were high compared to those found in *Anopheles* in other parts of the world, except for the bizarre results of KARTMAN (1946) in which up to 49% of *An. gambiae* were infected; however filariae in the gut were inclined in these results. The highest infection rates in samples of over 100 *An. gambiae* in Tanga, Tanzania were 6·8% infected and 1·6% infective (MCMAHON *et al.*, 1981). Infective rates in *An. funestus* have varied from 0·46% in Muheza, Tanzania (KRAFSUR & GARRETT-JONES, 1977) to 0·99% at Jaribuni, Kenya (WIJERS & KIILU, 1977) to 1·4% at Muheza (WHITE, 1971). However, the infection rates at Dreikikier were of the same order of magnitude as the rates recorded in some other studies in the Western Pacific area; in the Solomon Islands, 50·9% of 655 *An. farauti* were infected (BYRD & ST. AMANT, 1959) and 41·1% of 467 *An. farauti* on Pam Island were infected and 6·6% contained infective larvae (DE ROOK, 1957a). However, de Rook held his mosquitoes for at least two days before dissection thus increasing the percentage of mosquitoes with infective larvae.

By presenting the results using the regression and mean larval density parameters, comparisons with future studies should be easier; it is recommended that this format be used in future to overcome some of the problems of lack of uniformity in data presentation.

The high infection rate in this present study, in the indoor-resting samples, is partly attributable to the very large number of infections with pre-sausage-stage larvae which would only be encountered in mosquitoes which had fed the previous night. However, 30·9% were infected with worms that were 2·5 days or older. Such a high infection rate is only possible in highly susceptible mosquitoes which are very anthropophilic, relatively long lived and feeding on a human population with a high prevalence-rate of microfilaraemia of suitable density.

The very large number of larvae in some mosquitoes is somewhat surprising in the light of experimental results with the closely related *An. farauti* No. 1 and *Brugia pahangi*; up to 95% of ingested microfilariae were destroyed by the pharyngeal and cibarial armatures (MCGREEVY *et al.*, 1978). The armatures of *An. punctulatus* are very similar to that of *An. farauti* No. 1 as depicted by MCGREEVY *et al.* (1978), (Bryan, unpublished).

In the indoor-resting samples there were marked declines in the mean number of larvae and in the median larval density as the infections aged. Such a situation would occur if, during the life of the oldest mosquito captured during this study, there had been: (i) marked increases in the numbers and availability of infected hosts, and/or (ii) increases in the mean microfilariae density of the population on which the sampled mosquitoes were feeding, and/or (iii) mortality of some filarial larvae in the more heavily infected mosquitoes, and/or (iv) differential survival of heavily and lightly infected mosquitoes. (Changes in the recruitment rate into the mosquito population or in the degree of anthropophily would have influenced the relative number of mature and immature infections, but not the mean number of larvae per infected mosquito as the filariae matured).

Although it is not known who was present in the study area immediately before the commencement of this study, the occupants of the houses did not alter during the sampling period and the use of mosquito nets did not alter over the same period. Although the microfilaraemia of infected hosts does vary over short periods of time (HAIRSTON & JACHOWSKI, 1968; WILSON & RAMACHANDRAN, 1971), a sudden increase in the mean microfilaraemia of the population on which the mosquitoes were feeding seems an unlikely explanation for this phenomenon. No larvae which had died in a living mosquito were seen, so mortality of some larvae within mosquitoes was of little or no importance.

The most likely explanation for the dramatic reduction in the parasite load as the infections aged is that there was selective mortality of the more heavily infected mosquitoes.

Increased mortality and reduced flying capability of mosquitoes, heavily infected with filariae developing in the thoracic muscles, have been well documented for laboratory infections (KERSHAW *et al.*, 1953;

TOWNSON, 1970, 1971). However, increased mortality occurs immediately after the infective blood meal or when the larvae are well developed, i.e., stage 3 larvae. To the author's knowledge, this is the first time that date supporting the hypothesis of increased mortality due to heavy infestation with young larvae has been recorded in a natural mosquito population.

The age of filarial infections in mosquitoes has been used to estimate the natural mortality of populations of *Ae. kocki*)[*sic*], see p. 123) and *An. farauti* in Irian Jaya (VAN DIJK, 1966), *Cx quinquefasciatus* and *An. peditaeniatus* in India (LAURENCE, 1963) *Cx quinquefasciatus* in Sri Lanka (SAMARAWICKREMA, 1967) and *An. funestus* in Tanzania (KRAFSUR & GARRETT-JONES, 1977). In all these studies, the presence of filarial larvae in the mosquitoes did not influence the daily rate of survival of their hosts. In the Yauatong *An. punctulatus* indoor-resting sample, this age grading technique was invalid, as the filariae were contributing to mortality.

The Poisson distribution of superinfections clearly indicates that the presence of an infection did not inhibit the establishment of young infections. Super infections in *An. funestus* in Tanzania also had a Poisson distribution (KRAFSUR & GARRETT-JONES, 1977).

Because so few specimens were collected in the light-traps and in the night-landing catches, no meaningful comparisons can be made between the different capture techniques. However, infected specimens are likely to be under-represented in the light-trap samples; the more heavily infected specimens are more likely to have died and thus to have become unsuitable for dissection.

Endophagic but exophilic species which feed late at night and are not attracted to light would not have been adequately sampled during this survey. The sampling was also limited in time, and species which were relatively scarce during the rains, but more abundant at other times, could have been missed during this survey. However, although there is a possibility that a vector could have escaped detection, *An. punctulatus* is certainly a vector of major importance at Yauatong.

Yauatong—Cx annulirostris

Altogether, 391 *Cx annulirostris* were examined without detecting any filarial infections. However, larvae, believed to be *W. bancrofti*, including infective stages, have been recorded in this mosquito in Irian Jaya at Inanwatan (DE ROOK, 1959) and at Pam Island (DE ROOK, 1959); at Inanwatan, the infection rate of 25% was similar to that in *An. farauti*. It has been suggested that the taxon *Cx. annulirostris* embraces two biological entities (DE ROOK, 1959); in areas where it is an "efficient" vector its larvae occur in brownish peaty water, never in association with *An. punctulatus*; the "poor" vector spends its larval stages in clean water, often in association with *An. punctulatus*. Whether the larvae at Yauatong were in the habitat of the "good" or "poor" vector is unknown as the limited number of larval searches failed to reveal any larvae of this species. There are also disparities in the behaviour of the adults; at Inanwantan most of the mosquitoes captured inside houses were *Cx annulirostris*. In the present investigation, in spite of capturing over 1,000 *An. punctulatus* resting indoors, not one *Cx annulirostris* was found in houses. However, night-landing catches indicated that it was prevalent at the time of this survey. Considering the high infection rates in *An. punctulatus*, the results of this investigation support the hypothesis that in the study area *Cx annulirostris* is not a vector. Its exophilic behaviour conforms to that of the "poor" vector of previous studies.

Yankok—An. punctulatus

The infection rates at Yankok (5·8% & 3·5%) were considerably lower than that at Yauatong (47·3%). The median larval density was also much lower at Yankok (2·41) than at Yauatong (7·33). These results presumably reflect a lower prevalence rate and density of microfilaraemia in the human population at Yankok compared to Yauatong. A lower infection rate would also occur if the Yankok mosquito populations were less anthropophilic than *An. punctulatus* at Dreikikier. However, this is unlikely as alternative hosts were uncommon in both areas.

Yankok—An. koliensis

There is very little information available on infection rates in *An. koliensis;* although no infections were detected in 286 specimens at Maprik (PETERS, 1963), at Gaudalcanal 4·84% of 351 specimens were infected and 0·28% were infective (BYRD & ST. AMANT, 1959). In three villages in the Nimboran region of Irian Jaya, three years after the beginning of a residual spraying campaign for malaria control, but six months after the previous spray round, 7·5% of 133 *An. koliensis* were infected (IYENGAR *et al.*, 1959). As no surveys had been conducted before the commencement of spraying, the significance of this result is not clear. The infection rate of 14% at Wansu was higher than that of other anopheline vectors such as *An. funestus* and *An. gambiae* in Kenya and Tanzania (see above in discussion of *An. punctulatus*). However an infective rate of 0·67% was similar to that seen in many other anophelines.

That *An. koliensis* is very susceptible to infection with *W. bancrofti* in this area is supported by the high percentage of infections which were well developed; 18 of the 42 infected specimens at Wansu contained either second or third-stage larvae. It is therefore somewhat surprising that the infective rate was only 0·67%.

Yankok-Cx quinquefasciatus

The importance assigned to *Cx quinquefasciatus* in filariasis transmission in New Guinea has been controversial (DE ROOK, 1957a; DE ROOK & VAN DIJK, 1959; MCMILLAN, 1960). This is partly a result of the contradictory results of experimental infections. Higher infection reates have been obtained in the western half of the island (VAN DIJK, 1965) than in the eastern half (BACKHOUSE & HEYDON 1950; MCMILLAN, 1960). However, even in such areas as Inanwantan (western New Guinea) where *Cx quinquefasciatus* was a good laboratory host, infection rates in natural populations were much higher in *An. farauti* than in *Cx quinquefasciatus* (see DE ROOK, 1959). Although in 1959 DE ROOK & VAN DIJK (1959) felt that *Cx quinquefasciatus* should not be regarded as a harmless species, particularly in urban areas, six

years later VAN DIJK (1965) considered it doubtful that this species could maintain endemic filariasis in the absence of other vectors. Similarly, IYENGAR (1965) regards this species as of little importance in filariasis transmission in New Guinea.

In previous studies in areas where *Cx quinquefasciatus* occurred sympatrically with members of the *An. punctulatus* complex, the infection rate in the former was lower than in the latter. This was not the case at Mutuk where the infection rate in *Cx quinquefasciatus* exceeded that of *An. punctulatus* (Table III). About one third of the infections in *An. punctualus* and *An. koliensis* were of second or third-stage worms. In contrast, although 10·8% of *Cx quinquefasciatus* were infected at Mutuk, only two (0·36%) contained worms more mature than the first stage. This very low infection rate with older worms could have resulted from a number of causes:

(i) Infected mosquitoes being killed by filarial larvae before the larvae reached the second stage. This is unlikely as the number of worms per infected mosquitoes was small; in only three cases did the number of filariae exceed 20, and 80% of infections were of less than 10 filariae. However, some mosquito mortality might have occurred as a result of infection as the mean number of larvae per infected mosquito decreased from 6·72 for pre-sausage stages to 2·93 for sausage-stage larvae, but the median larval density decreased only slightly from 2·13 to 1·92.

(ii) *Cx quinquefasciatus* is refractory to infection and this refractoriness operates on the post-sausage stages. However, no encapsulated filariae or ones which were thought to have died in a living mosquito were seen.

(iii) The development of filariae in *Cx quinquefasciatus* was protracted. This has already been observed in some experimental infections, although retarded development noted at Maprik may have been due to low ambient temperatures (MCMILLAN, 1960).

(iv) The population of *Cx quinquefasciatus* was increasing at the time of the study and therefore was composed largely of young individuals. This is unlikely as the wet season was well advanced and breeding sites would have been established for some time before the start of this study.

(v) The population of *Cx quinquefasciatus* was naturally short-lived, so few survived long enough to sustain development of filariae beyond the first stage. Studies at Jayapura indicated that *Cx quinquefasciatus* in that locality had a very low natural survival rate (VAN DIJK, 1965) and this may also apply to the Yankok population.

Higher infective rates in anophelines compared with *Cx quinquefasciatus* have also been recorded in Africa; the infective rates in *Cx quinquefasciatus* were inferior to those of *An. funestus* and *An. gambiae* s.l. in Tanzania (WHITE, 1971; MCMAHON *et al.*, 1981) and Kenya (NELSON *et al.*, 1962; WIJERS & KIILU, 1977).

The results reported here highlight the complexity of filariasis transmission in New Guinea with different species acting as the major vectors in areas which are in close proximity to each other. Therefore great care must be taken before results obtained in one area are extrapolated to other areas.

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