Trans. R. ent. Soc. Lond. **127** (3), pp. 277–292, 6 figs. 1975

Changes in the feeding behaviour of a malaria vector, *Anopheles farauti* Lav., following use of DDT as a residual spray in houses in the British Solomon Islands Protectorate

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SUMMARY

1. To investigate the failure of DDT to interrupt malaria transmission in parts of the British Solomon Islands Protectorate, regular all-night man-biting catches of malaria vectors were made before and after DDT house spraying on San Cristobal Island.
2. Changes were observed in the man-biting behaviour of *Anopheles farauti*. There was a reduction in the degree of entry into houses and a shifting of the times of peak biting. Whereas before spraying the indoor and outdoor biting cycles differed, after spraying there was no difference although both the indoor and outdoor cycles had altered.
3. DDT was found to have a deterrent effect on *An.farauti* but this effect decreased with time.
4. DDT also appears to eliminate a dominant indoor feeding fraction of the *farauti* population. Following this there can be an increase in an outdoor feeding fraction which can be responsible for a resumption of malaria transmission.
5. Biting cycles obtained before spraying are also shown for *An.koliensis* and *An.punctulatus*.

INTRODUCTION

The British Solomon Islands Protectorate (BSIP) comprises a scattered archipelago of mountainous islands and low-lying coral atolls stretching some 1450 km in a south-easterly direction between latitudes 5° S and 12° 30′ S and longitudes 155° 30′ E and 170° 15′ E (fig. 1). The total land area is approximately 29 500 km^2. The six major islands, Choiseul, New Georgia, Santa Isabel, Guadalcanal, Malaita and San Cristobal, are characterised by precipitous, thickly forested mountain ranges, intersected by deep narrow valleys. The coasts are frequently surrounded by extensive coral reefs and lagoons and there are extensive mangrove swamps in many areas. Guadalcanal is unique in having a large area of flat grassy plain on the north-central side of the island.

The total population in 1970 was almost 161 000 with an overall density of 5·7 persons/km^2 (varying on the large islands from 11·50/km^2 on Malaita to 3·15/km^2 on San Cristobal).

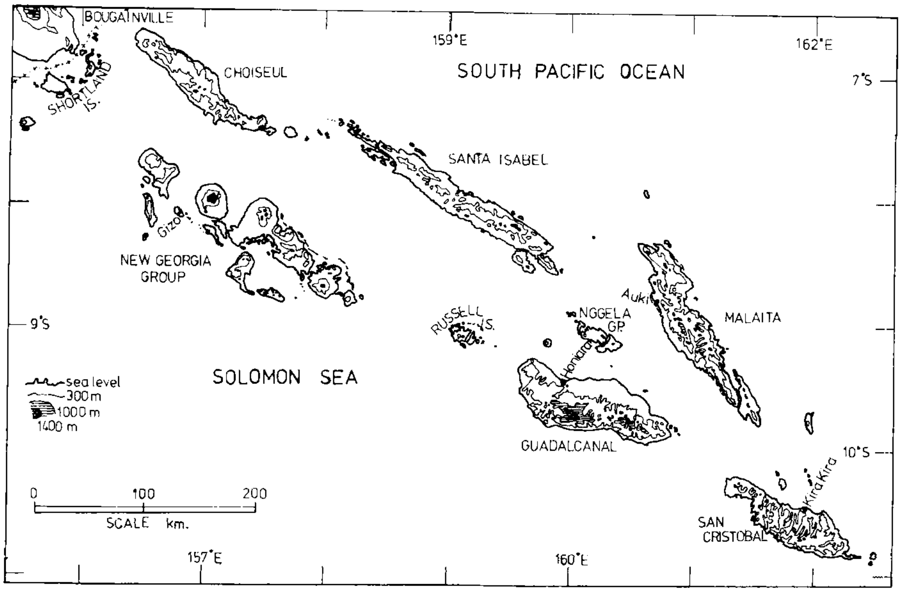

Fig. 1. The principal islands of the British Solomon Islands Protectorate.

The climate is equatorial but modified by the surrounding ocean. The annual mean temperature is around 27°C at Honiara, the capital on Guadalcanal. The annual rainfall averages 3000 to 3600 mm but in some areas may be as much as 7600 mm. There are rarely long periods without rain and this in combination with the relatively high temperature and humidity gives conditions which are usually very favourable for the development and longevity of anopheline mosquitoes. As an almost inevitable consequence malaria is extremely prevalent and stable. *Plasmodium falciparum* demonstrates its usual virulence but the local strain of *P.vivax* is unusual in having an exceptionally high relapse rate and a refractory response to drug treatment. Macgregor (1968) gave a fairly comprehensive historical account of malaria in the South-west Pacific and summarised the early work of the BSIP Malaria Eradication Pilot Project, 1961–64.

BACKGROUND INFORMATION

The operations of the BSIP Malaria Eradication Pilot Project began in October 1961 with the first spraying operations starting on Guadalcanal in October 1962. Relatively limited pre-spraying entomological studies were made from October 1962 to April 1963. These confirmed the status of the malaria vectors *Anopheles* (*Cellia*) *farauti* Lav., *An.punctulatus* Don. and *An.koliensis* Owen. All three species were found to be susceptible to DDT and habitually to rest on the indoor walls of houses after a blood meal.

DDT spraying operations in the BSIP were, and still are, aimed at spraying all human habitations at a rate of 2·0 g of technical DDT/m^2 on all inside walls and ceilings, outside verandahs and eaves, on the underfloor areas of houses built on stilts, and on any other surface on which a blood-fed female anopheline might rest. Spraying operations were repeated at six-monthly intervals.

In epidemiological terms the early operations appeared successful and Macgregor (1968) concluded that, in the Project Area as a whole, complete interruption of malaria transmission had been achieved.

The early entomological results showed that *An.koliensis* and *An.punctulatus* virtually disappeared after two applications of DDT. However, in certain areas, notably on northern Guadalcanal, the density of *An.farauti* remained quite high, particularly in outdoor man-biting situations. Macgregor (1968) noted that there was no obvious resurgence of malaria in the Lunga area of north Guadalcanal although the area did provide the only sporozoite-positive specimen of *An.farauti* found in 6319 individuals dissected after spraying. He also noted that *An.farauti* adapted to a more exophilic habit while showing an increased preference for human blood but he stated that "This alteration in the habits of the principal vector anopheline, though not of immediate significance, was probably the most serious potential problem delineated during the course of the Pilot Project".

A different opinion was expressed in the Eleventh Quarterly Report of the Pilot Project for April–June 1964 and in the Pilot Project Final Report in December 1964 where anonymous authors clearly considered the transmission of malaria on north Guadalcanal, especially along the coastal strip east of Honiara, had probably not been interrupted. An Independent Assessment Team (Kranendonk and Ray, WHO unpublished report) who visited the BSIP in December 1968 to January 1969 commented that there was an increase in the number of indigenous cases on Guadalcanal and Savo and that there was need for an urgent review of the entire spray programme in the area. Slooff (1972) noted very high densities of *farauti* could often be recorded on north Guadalcanal, despite the DDT spraying, and the difficulty of controlling residual malaria transmission, but gave no reasons for the unsatisfactory response to DDT house spraying.

The Pilot Project was restricted to Guadalcanal, Savo and the New Georgia Group and the continuing high levels of malaria on north Guadalcanal were in part due to the importation of cases from Malaita and the Nggela Group. In late 1972 and early 1973 there were epidemics of *P.falciparum* on north Guadalcanal but by this time Malaita (the major source of migrant labourers) had been sprayed for over two years and there malaria levels had dropped most satisfactorily.

One of these epidemics, in the Lunga area east of Honiara, was investigated and the results illustrate the problem.

OBSERVATIONS AND RESULTS

Entomological studies at Burn's Creek, Lunga, Guadalcanal, during the P.falciparum *epidemic of January–February* 1973

In a small group of houses, known as Burn's Creek, there were three *P.falciparum* cases during January and February 1973. The cases, a father and two of his children, were living in the same house. This house was principally of timber and palm-leaf thatch construction with the centre of the roof being corrugated galvanised iron. The most recent DDT spraying round was 10.xi.1972. The following studies were made on *An.farauti*:

(i) A DDT susceptibility test, using the standard WHO Method (Annex 1a of *WHO Expert Committee on Insecticides. Seventeenth report: Insecticide resistance* *and vector control*. Geneva, 1970, WHO Technical Report Series, No. 443): The LC_{50} was around 0·9% DDT and the LC_{100} was 4·0% DDT; thus the *farauti* population was still susceptible to DDT (Davidson & Zahar, 1973). Before spraying in 1962 the LC_{50} was 0·45% DDT and the LC_{100} was 4·0% DDT (Macgregor, 1968).

(ii) Bioassay: exposure of blood-fed *farauti* females, collected biting outdoors, to the sprayed wall using WHO pattern plastic cones (two batches of 15 mosquitoes exposed for 30 min and one batch of 15 mosquitoes exposed for 15 min) led to total mortality.

(iii) Egress traps fitted to both windows of the house caught, in two nights, only four *farauti* females and only one of these was dead when the traps were emptied.

(iv) Observation of the overnight survival of *farauti* females, individually collected in glass vials, indicated a survival rate of between 91·7 and 95·2% for blood-fed females but only 30·8% for unfed females. Maintenance of the survivors of the susceptibility tests, all previously blood-fed and mainly from the control, showed a similar high survival rate with 24 out of 33 specimens still alive after five days.

(v) Comparison of indoor and outdoor-biting showed similar high densities, e.g. indoors, between 18.30 and 20.00 hours on 5th March, 85 *farauti* were collected using a simple aspirator while outdoors two men using glass vials and aiming to capture blood-fed females caught 95 *farauti*.

The failure of the egress traps to collect *farauti* is not surprising since Sweeney (1968) commented that on one occasion in the Carteret Islands he collected 1967 *farauti* man-biting but his window trap caught only 12 specimens. Sweeney also noted a mortality of 41·5% of unfed adults in 24 h but only 1·6% for fed adults. The failure to trap the *farauti* females suggests that the vectors leave from the house immediately after feeding. If the vectors were still in the house at dawn then one might expect them to be attracted to the light coming through the windows. Numerous houseflies and several *Culex annulirostris* were caught in this way.

Long-term entomological studies on San Cristobal Island, June 1971 *to April* 1973

The brief outline of the entomological information gathered during the Pilot Project serves to underline the paucity of information from the BSIP on the vector species, *An. farauti*. To a certain extent this was due to reliance on the findings of US armed forces entomologists based in the South-west Pacific in 1942–45 (Macgregor, 1968 : 54–7). These findings, unfortunately, were nearly all the result of work undertaken after the extremely urgent task of malaria control had been embarked on and insecticide pressure had already been exerted.

Between 1964 and 1970 routine collections were made before spraying on Choiseul, Santa Isabel, Nggela and Malaita, but these were on a half-night basis, 18.30 to 23.30 hours, and usually by a single technician.

In June 1971 I launched a programme of long-term before and after spraying entomological studies on San Cristobal Island. Preceding the long-term programme a vector distribution survey was made in nearly all the inhabited areas of San Cristobal. The results of this survey and others on the various islands of the BSIP have been reported elsewhere (Taylor, 1974). All three members of the *punctulatus* complex were found on

San Cristobal. *An.farauti* and *koliensis* were widely distributed but *punctulatus* was found only at a few localities.

The survey showed that all three species could be found at villages in the relatively close neighbourhood of the district headquarters at Kira Kira (the only place with an airfield and the base for local shipping operations). Five villages were originally chosen for the long-term study but poor catches at one of them limited the final work to four villages. Two of these are to the east of Kira Kira; Arohane is on the coast road 6 km away and Maniparegho is 4 km farther on and about 3·5 km inland in the Ravo River valley. The other two are to the west of Kira Kira; Baunasughu is coastal and less than 1 km distant and Manibwena is 6 km farther on and about 750 m inland.

After an initial five months of all-night catches Baunasughu and Manibwena were sprayed in October 1971 as part of the first round of routine DDT house spraying on San Cristobal. Arohane and Maniparegho remained unsprayed until October 1972. All-night catches were continued at all four villages until April 1973.

The houses in all four villages were of similar construction having a timber frame with sago palm-leaf thatching for the walls and roof. The houses at Maniparegho differed slightly in having walls of bamboo. Some houses were built on stilts and these usually had flooring of split betelnut palm.

The routine adopted for the all-night catches was to have twelve catching periods of 40 min duration alternating with 20 min rest periods. The first catching period commenced at 18.30 hours (the approximate time of local sunset) and the last catching period ended at 06.10 hours. Preliminary 24 h catches had shown no man-biting activity of anophelines during daylight hours.

The same team of a supervisor and three collectors did nearly all the collecting in the 21 months of work. During each night catch the collectors rotated their collecting places to lessen the effects of possible variations in their attractiveness as baits.

Climatically Kira Kira is fairly typical of the BSIP with annual mean maximum and minimum temperatures of around 29·6 and 22·3 °C respectively. The annual rainfall is around 4000 mm with no pronounced wet season. The wettest months are usually those at the beginning of the year when there are often periods of very heavy rainfall and sometimes cyclonic conditions. The daily patterns of rainfall can vary immensely between villages only a few miles apart.

Results of all-night catches of An.farauti

(i) *Biting cycles*

Summarised results of the all-night catches are shown in Table 1 and the biting cycles expressed graphically in figure 2. The outdoor and indoor before spray cycles are clearly dissimilar with more biting in the middle of the night in the indoor cycle. The indoor and outdoor after spray cycles are almost identical with 79% of the biting in the first quarter of the night and both show a change from their respective before spray cycles.

Calculation of χ^2 to test a null hypothesis that there is no significant difference between the cycles showed:

(a) a difference between the before spray indoor and outdoor cycles ($P < 0{\cdot}01$),
(b) a difference between the outdoor before and after spray cycles ($P < 0{\cdot}01$),
(c) a difference between the indoor before and after spray cycles ($P < 0{\cdot}01$), and
(d) no difference between the indoor and outdoor after spray cycles ($P > 0{\cdot}05$).

Table 1. Summarised results of *Anopheles farauti* biting cycle studies on San Cristobal, June 1971 to November 1972

	Before spraying			After spraying		
Time	% of outdoor catch	% of indoor catch	Ratio of nos. caught outdoor : indoor 1 : x	% of outdoor catch	% of indoor catch	Ratio of nos. caught outdoors : indoor 1 : x
1830–1910	16·9	11·0	0·71	45·5	47·0	0·52
1930–2010	15·6	13·7	0·95	20·2	19·1	0·47
2030–2110	13·2	12·0	0·99	13·5	12·7	0·47
2130–2210	11·2	12·4	1·21	9·4	9·4	0·50
2230–2310	9·8	9·9	1·09	5·6	5·5	0·49
2330–0010	8·1	13·7	1·84	1·7	2·1	0·64
0030–0110	5·8	5·5	1·04	1·8	0·6	0·17
0130–0210	5·3	6·5	1·34	0·3	0·6	1·00
0230–0310	5·2	4·9	1·02	0·6	0·3	0·25
0330–0410	3·6	4·7	1·42	0·8	1·2	0·85
0430–0510	3·3	3·6	1·18	0·5	0·3	0·33
0530–0610	1·8	2·1	1·26	0·0	1·2	—
Total caught	1767	2060		657	330	
No. of nights	56	60		37	37	

(ii) *Changes in feeding habits*

A marked change occurred in the ratio of indoor-biting to outdoor-biting. Table 1 also shows the before and after spray ratios for each of the collecting periods through the night. Before spray, except for the period 18.30–21.10, there is a greater proportion biting indoors reaching a peak of endophagy at 23.30–00.10. After spray, however, in all periods, except 02.30–03.10, there is a greater proportion biting outdoors. In 02.30–03.10 there are equal numbers in and out. The change to a dominance of exophagy after spraying is partly due to a deterrent effect of DDT (see later for evidence and discussion) but, if this was the only factor, one would not expect the changes that take place in the observed biting cycles.

Data collected by U.J.Mataika, at Koli on Guadalcanal, although not wholly comparable with the San Cristobal results, showed a change from dominant indoor-biting (2·31 indoors : 1 outdoors, October 1962 to April 1963) before spraying to dominant outdoor-biting (0·28 indoors : 1 outdoors, May to December 1963) after spraying. Collections made at Koli between January and December 1971, after eight years of sprav coverage, showed a ratio of 0·25 indoors : 1 outdoors.

(iii) *Population changes*

The apparent effect of the first spray round in October 1971 at Baunasughu and Manibwena was to decrease the numbers of *farauti* caught. Small catches persisted until July 1972 when numbers started to rise again and remained reasonably high thereafter.

At Arohane and Maniparegho there was a drop in numbers of *farauti* in the period December 1971 to February 1972 followed by a rise in March–April and another drop in May–June. A rise in July paralleled that at Baunasughu and Manibwena. However, the

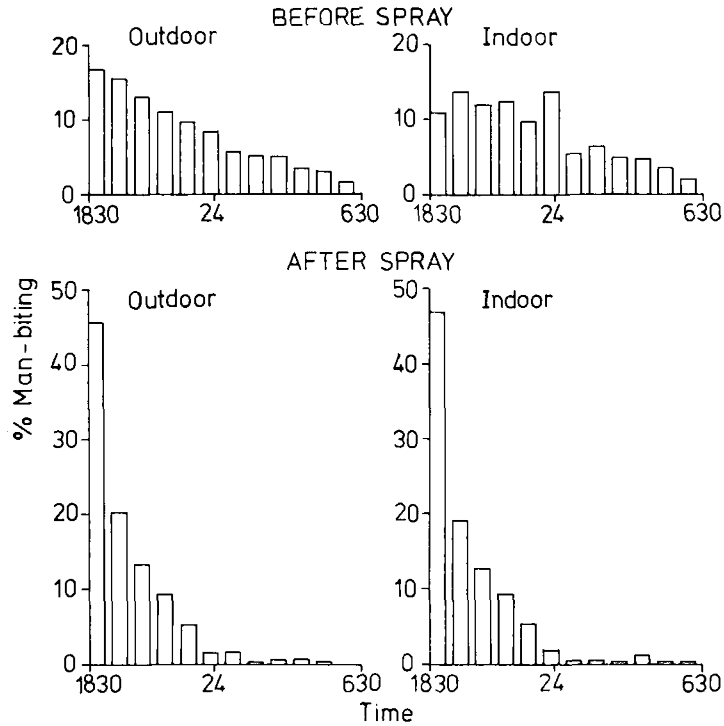

Fig. 2. Outdoor and indoor man-biting cycles of *An.farauti* before and after DDT residual spraying of houses.

first spray round at Arohane and Maniparegho caused only a slight reduction in *farauti* numbers.

A comparison of the periods of peak population at Arohane and Maniparegho indicates that a marked change to a predominance of outdoor-biting accompanied the rise in July 1972. The outdoor : indoor ratios were as follows:

(a) June–October 1971 (9 catches)—out 659 : in 780, i.e. 1 : 1·18.
(b) March–April 1972 (10 catches)—out 207 : in 303, i.e. 1 : 1·46.
(c) July–October 1972 (12 catches)—out 621 : in 509, i.e. 1 : 0·82.
(d) November 1972–March 1973 (11 catches)—out 2269 : in 1179, i.e. 1 : 0·52.

The biting cycles recorded indoors at Maniparegho also show a change to the early night peak activity characteristic of the after spray results at Baunasughu and Manibwena (fig. 3).

There is a clear implication that the *farauti* populations in the small unsprayed area were being replaced by the newly dominant populations from the surrounding sprayed area.

Results of An.koliensis *and* An.punctulatus *man-biting catches*

The technique used and the villages where the work was done were the same as for *An.farauti*. *An.koliensis* was collected at all four of the villages (484 in 56 outdoor catches

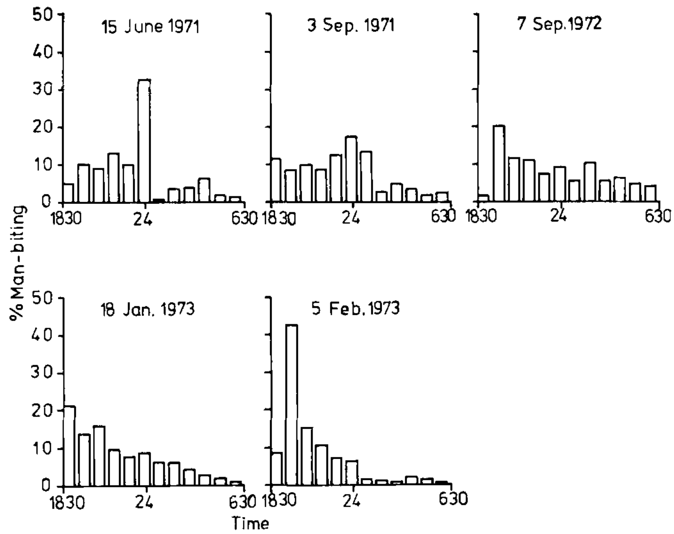

Fig. 3. Indoor man-biting cycles of *An.farauti* at Maniparegho. On 15th June, 1971, and 3rd September, 1971, before any DDT spraying; on 7th September, 1972, ten months after surrounding villages sprayed; on 18th January, 1973, and 5th February, 1973, after first spraying of Maniparegho on 11th October, 1972.

and 1097 in 60 indoor catches) with pronounced peaks in June to November 1971 and March to May 1972 at Arohane and Maniparegho (Manibwena and Baunasughu were sprayed in October 1971). *An.punctulatus* was never abundant and almost the only collections were at Maniparegho especially in April–May and August–October 1972. Altogether 51 *punctulatus* were caught in 18 outdoor catches and 109 were caught in 20 indoor catches. On two occasions a single specimen of *punctulatus* was taken at Manibwena (in June and August 1971). After spraying very few *koliensis* or *punctulatus* were collected. The biting cycles for both *koliensis* and *punctulatus* are shown graphically in figure 4.

The ratios of outdoor to indoor biting from the whole night totals were 1 : 2·13 for *koliensis* and 1 : 1·93 for *punctulatus*. At no period of the night did the ratio of *koliensis* indoors fall below 1·78 and it reached a maximum of about 3·25 around midnight. Too few *punctulatus* were collected to analyse their period by period ratios.

Both these species clearly feed later at night than *farauti* and have a strongly endophagic pattern of behaviour. The effect of DDT spraying is dramatic and leads to an almost complete disappearance of both species. However, the species were not eradicated as was shown when a resurgence of *punctulatus* occurred on Guadalcanal following a breakdown in spraying operations in 1972.

The deterrent effect of DDT

In early 1972 Dr H.A. van Seventer and I decided that the suspected tendency towards exophagy in *An.farauti* after spraying might be due to DDT deterring entry into the sprayed houses. To test this idea a single house in Arohane was sprayed on 12th April, 1972 with DDT in the usual manner. All-night catches were made at intervals for 162

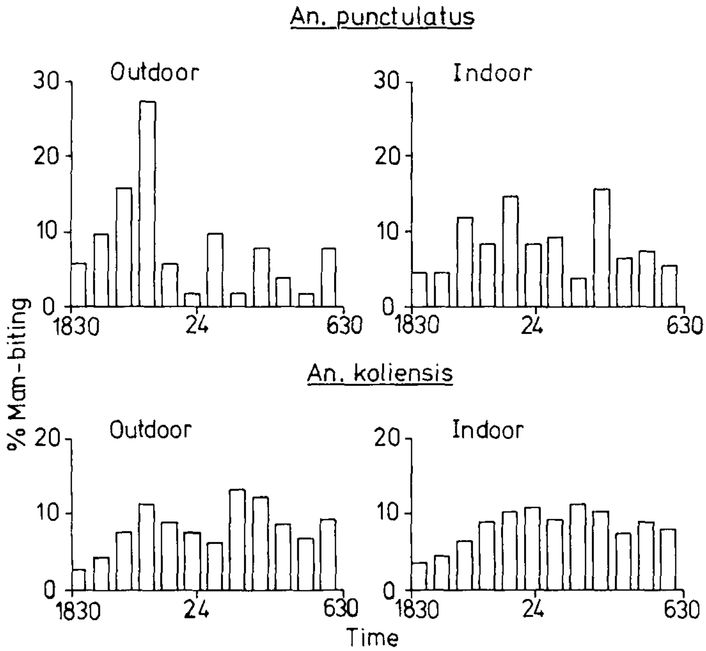

Fig. 4. Outdoor and indoor man-biting cycles of *An.punctulatus* and *An.koliensis* before DDT residual spraying.

Table 2. Results of single DDT sprayed house experiment at Arohane

Days after spraying	Nos. caught outdoors (O)	Nos. caught in unsprayed house (U)	Nos. caught in sprayed house (S)	% entering U (of O + U)	% entering S (of O + S)	% entering S (of U + S)
2	27	25	1	48·1	3·6	3·8
11	—	53	5	—	—	8·6
20	5	5	0	50·0	0·0	0·0*
36	11	14	4	56·0	26·7	22·2
64	4	3	1	42·9	20·0	25·0
80	25	22	5	46·8	16·7	18·5
93	18	15	4	45·5	18·2	21·5
108	—	81	21	—	—	20·6
134	39	14	11	26·4	22·0	44·0
143	46	15	14	24·6	23·3	48·3
162	36	32	33	47·1	47·8	50·8

* Not used in calculating correlation coefficient.

days. Catches were made in an unsprayed house and in the sprayed house on all occasions and on all but two occasions outdoor catches were also made.

Table 2 shows the numbers of *farauti* caught on each occasion. To examine the relationship between the passage of time and the percentage of *farauti* entering the sprayed house (of the total entering the sprayed and unsprayed houses) the correlation coefficient

(r) was calculated. The resultant $r = 0{\cdot}9755$ ($P = 0{\cdot}001\,\%$) indicates a deterrent effect of DDT decreasing with time.

During the experiment the overall ratio of indoor : outdoor biting dropped at the two unsprayed villages (Arohane and Maniparegho, see p. 281) and this could be thought to have influenced the results of this experiment. Figure 5 shows the percentages of *farauti* (a) entering the sprayed house, of the total entering the sprayed and unsprayed houses; (b) entering the unsprayed house, of the total collected in the unsprayed house and outdoors; and (c) entering the sprayed house, of the total collected in the sprayed house and outdoors. Whereas one might have expected (a) and (c) to be closely similar throughout, a marked drop in (b) caused a reduction in (c) on days 134 and 143. Moreover the result on day 134 indicates a considerable loss in deterrency of the DDT between days 108 and 134. If one of the major factors in the interruption of malaria transmission is the deterrent effect of DDT then, at least at Arohane, an interval of six months between rounds of DDT spraying is too long and four months would be preferable.

A weak point in this experiment is that the presence of a single sprayed house in an otherwise unsprayed village presents no special problems to the mosquito population which, if deterred from entering the sprayed house, can readily find available hosts in the unsprayed houses. Under conditions when the whole village is sprayed more entry and re-entry might occur. This was so at Arohane after the first spray cycle and was also seen in the other after spray results.

The deterrent effect of DDT has been observed before. De Zulueta and Cullen (1963) discussed results they had obtained of numbers of *An.gambiae* caught by window traps and floor captures. DDT sprayed at 2·0 g/m^2 on mud-wall and thatched roof houses in Uganda gave overall figures over seven months of only 30·5 % *gambiae* being

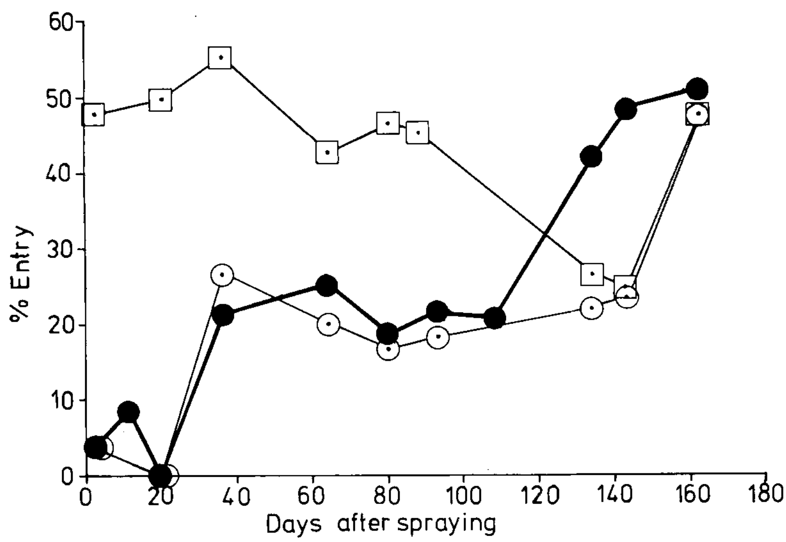

Fig. 5. Single DDT sprayed house experiment at Arohane. Percentage entry of *An.farauti* (a) into the sprayed house, of the total entering the sprayed house and an unsprayed house, ●——●; (b) into an unsprayed house, of the total collected in an unsprayed house and outdoors, ⊡——⊡; and (c) into the sprayed house, of the total in the sprayed house and outdoors, ⊙——⊙.

caught in the sprayed house. They concluded that this was not an irritant effect but Smith (1963) suggested the smaller number could also have resulted from the insecticides irritating the mosquitoes and inducing many to leave by the eaves. These contradictory conclusions could have been resolved if the technique used had not relied principally on exit traps and if simultaneous indoor and outdoor collections had been made.

Interpretation of the changes in the man-biting behaviour of An.farauti *following DDT spraying*

The changes in man-biting behaviour of *An.farauti* following DDT spraying occur in the degree of entry into houses and in the timing of the peak man-biting activity. These changes suggest that one of the primary effects of spraying houses with DDT is to eliminate a dominant endophagic fraction of the *farauti* population. This in time permits a significant and serious increase in an exophagic fraction of the *farauti* population and in turn this facilitates the resumption of malaria transmission.

The following considerations support this hypothesis:

(a) DDT has a deterrent effect and a direct result of spraying houses is an immediate reduction in the rate of entry by *farauti*. This alone, by preventing access to the primary source of bloodmeals, is enough to seriously reduce an endophagic fraction of the *farauti* population. The lethal effects of DDT on those mosquitoes which do enter the house and come into contact with the insecticide will reduce the population even further. The results from Baunasughu and Manibwena indicate that such a reduction did occur.

(b) If *farauti* was solely endophagic then the result of spraying would be a great reduction in the *farauti* population which, unless physiological resistance should develop, would remain low as long as DDT pressure was being exerted. There has been no evidence, however, of any development of physiological resistance to DDT in *farauti* anywhere in the Western Pacific. The effect of the first spraying round on *An.koliensis* and *punctulatus* was a great reduction in the population with no subsequent resurgence. The *farauti* population, however, recovered completely or even increased within nine months at Baunasughu and Manibwena. At Arohane and Maniparegho spraying had little or no effect on the overall *farauti* population but there appears to have been a change in the *farauti* population paralleling the resurgence in the surrounding sprayed areas.

(c) Because, in the absence of enough alternative hosts, *farauti* is anthropophilic, an endophagic fraction would tend to feed later at night (when the human prey is asleep and thus feeding is least hazardous) but an exophagic sector would have to feed primarily in the early hours of the night (when humans are still active outdoors but obviously alert, rendering the act of biting more unlikely). A reduction or elimination of an endophagic fraction would, therefore, lead to an apparent change in the observed biting cycles (fig. 2).

(d) The evidence for an after spraying dominance of an exophagic early-night active fraction of the *farauti* population is strong but whether or not this sector was present before spraying is more difficult to determine. Table 3 shows the number of *farauti* collected at all four villages between June and October 1971 (i.e. before any spraying operations); the before spray ratios of outdoor : indoor biting; the after spray ratios of outdoor : indoor biting (from Table 1); the

Table 3. Derivation of hypothetical after spray biting cycles

Time	Before spray (June to Oct. 1971) Ratio of out : in 1 : *x*	After spray* Ratio of out : in 1 : *x*	Ratio change Before spray less after spray	Hypothetical† After spray % biting Out	In
1830–1910	0·58	0·52	0·06	68·1	50·7
1930–2010	1·03	0·47	0·56	6·4	8·4
2030–2110	1·18	0·47	0·71	4·2	6·3
2130–2210	1·21	0·50	0·71	4·8	7·5
2230–2310	1·09	0·49	0·60	5·1	7·1
2330–0010	2·05	0·64	1·41	2·1	5·5
0030–0110	1·23	0·17	1·06	1·4	2·3
0130–0210	1·37	1·0	0·37	3·0	5·4
0230–0310	0·83	0·25	0·58	2·7	2·9
0330–0410	1·4	0·8	0·6	1·6	2·9
0430–0510	1·37	0·33	1·04	0·6	1·0
0530–0610	0·80	—	—	—	—

* At Baunasughu and Manibwena (from Table 1).

† Derived by multiplying the before spray figures by the reciprocals of the ratio changes and expressing the resultants as a percentage of the total for the night.

ratio changes (before spray minus after spray ratios); and the hypothetical after spray biting derived by multiplying the before spray figures by the reciprocal of the ratio changes and expressing the resultants as percentages of the whole-night totals. I have attempted to remove mathematically the contribution of the endophagic fraction to the before spray biting cycles and thus demonstrate the contribution of the exophagic fraction to the before spray cycle. Figure 6 shows the hypothetical after spray biting cycles in comparison with the actual after spray biting cycles (taken from fig. 2). The hypothetical and actual after spray cycles are reasonably similar although there is more late-night activity and a more marked concentration of activity in the first period of the hypothetical cycles. The reasons for these minor disparities are unknown but the most likely reason is that before spraying the endophagic and exophagic fractions would not have extremely rigid and closely defined biting cycles. If the onset of major activity in the exophagic fraction is at sunset, then the annual variations in the time of sunset would diffuse the peak of activity based on the mean of results obtained in nearly a year of collections. The endophagic fraction arriving late at night could be attracted to a collector sitting outside and thus the ratios of outdoor : indoor biting in the latter two-thirds of the night are not as extreme as might be expected. However, this 'mathematical removal of the endophagic fraction' gives useful further evidence in favour of the actual existence of a before spraying endophagic fraction.

DISCUSSION

In recent years there have been at least two review articles considering problems of mosquito behaviour in control or eradication situations. Mattingly (1962) in considering

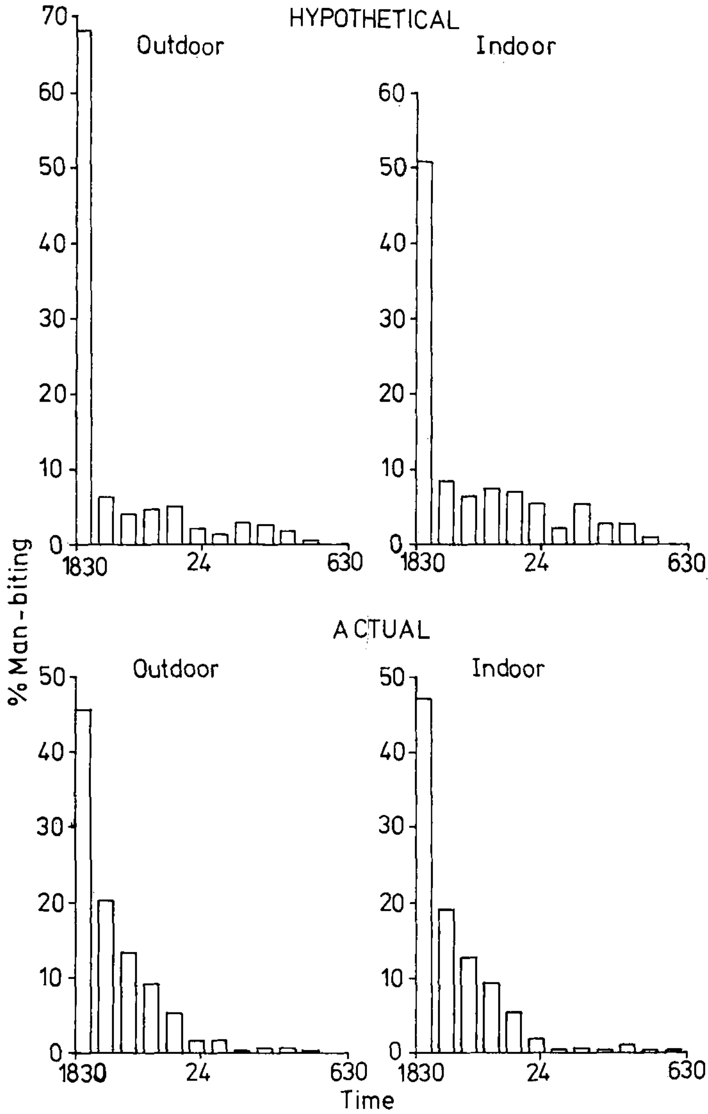

Fig. 6. Hypothetical and actual after spray man-biting cycles of *An.farauti.*

exophily as a problem covered four aspects and concluded "It seems likely that induced exophily will be most likely to occur, if at all, in parts of the range of a species where it is neither too closely man-associated nor is already, to a maximal extent, exophilic".

Hamon *et al.* (1970), discussing selected ecological and behaviouristic changes in vector populations, noted that, although, theoretically, insecticide pressure may induce ethological changes in vectors as it has selected insecticide-resistant populations, evidence is missing either because investigative methods are too inaccurate or too poorly used or because no such selection has occurred in the field.

Both reviews mentioned work on *Anopheles sundaicus* in southern Java where use of DDT failed to interrupt malaria transmission. This failure was attributed to selection of a strain of the vector having an increased tendency to insecticide avoidance. There was a decrease in numbers of *An.sundaicus* found resting on sprayed walls at night but larger numbers were taken at the same time on human bait.

Consideration of the continuing transmission of malaria in the BSIP and my results of *An.farauti* studies on San Cristobal in terms of Mattingly's (1962) discussion on exophily gives the following analysis:

1. There are no exophilic secondary vectors.
2. Irritability. No evidence was found for heightened activity following contact with DDT although such evidence was not positively sought.
3. Insecticide avoidance. There is clear and unequivocal evidence for a deterrent effect of DDT leading to an avoidance of entering DDT sprayed houses. This is not a total avoidance and is most marked during the latter two-thirds of the night. At Baunasughu and Manibwena there was no immediate increase in the exophilic fraction resulting from the expulsion of mosquitoes from houses. There was, however, a long-term absolute increase in the exophilic fraction and probably this was a result of the selective destruction of the endophilic fraction.
4. Deviation to alternative hosts. The BSIP is unusual in having a sparsity of alternative hosts; there are no wild primates or any abundant relatively large wild animals. Domestic animals are normally only pigs and dogs and these are always sparse relative to the human population.

It is worth drawing attention to the morphological and genetic relations within the *punctulatus* complex (Bryan 1973*a*, *b*, *c*, 1974). The morphological form previously regarded as a single species *farauti* throughout its range can be separated on genetic grounds into two distinct species termed *An.farauti* No. 1 and *An.farauti* No. 2. Specimens from Queensland, Australia, are *farauti* No. 2. The *farauti* No. 1 is the classical *farauti* described by Laveran from the New Hebrides (Bryan, pers. comm.) and this is found throughout the Melanesian arc from New Guinea through the Solomons to the New Hebrides. Specimens reared from eggs I obtained from San Cristobal females were found by Bryan to be of the 'Typical' *farauti*.

An.punctulatus and *koliensis* were confirmed as true species belying the earlier suspicions of *koliensis* being a hybrid.

A curious observation on the *farauti* from the Lunga area of Guadalcanal is that on two separate occasions eggs reared in the Ross Institute from Lunga females have given rise to adults which showed clear dieldrin resistance. These adults were, however, susceptible to DDT. The dieldrin history of the Lunga area is not clearly known. Certainly dieldrin has not been used in mosquito control of any type but the area is one of extensive coconut plantations and dieldrin may have been used on coconuts.

The complexity of Bryan's findings and the marked variation in behaviour reports of the *punctulatus* complex throughout its range in New Guinea and the Solomons has led me to ignore most research findings from outside the BSIP in considering my results and thus I have not made reference to the fairly extensive literature on the other areas. Peters (1965) presents a good summary of much of this other literature.

The continuing transmission of malaria has not been a problem throughout the BSIP. In many areas the parasite rates have dropped to a very low level and many of the cases detected have been either relapsing *P.vivax* cases or imported cases from elsewhere in the BSIP or from other countries. In general the coast line of the BSIP is quite rugged with no more than narrow coastal strips of land between the steeply folded mountains and the sea. The rivers and streams are extremely fast flowing and suitable breeding sites for *farauti* are few and far between. In these areas DDT pressure has pushed the already precarious balance of the mosquito's existence far enough to interrupt transmission. Removal of this DDT pressure can quickly permit a resurgence of *farauti* and a malaria epidemic could result. An example of this occurred on the south coast of Guadalcanal in 1972. Owing to operational problems the spraying supervisor decided to omit the August 1972 spray round. By the end of 1972 the malaria level, fortunately of *P.vivax*, was at its highest point for many years. The source of the epidemic was traced to two or perhaps three young children with residual *vivax* infections. These had relapsed, probably following inadequate drug treatment, and provided the gametocyte reservoir that accompanied a *farauti* resurgence from five to six months after the last spray round in February 1972. The problem was not simply one of the missed spray round but also one of inadequate treatment of the *vivax* malaria in small children.

In certain areas of the BSIP notably on north facing coasts there are moderate to extensive flat lands. These reach their maximum extent on Guadalcanal where coastal lagoons and blocked river mouths are common. Other such areas are found on north-west Choiseul and north-central San Cristobal. The Nggela Group is unique in being only moderately elevated and having shallow hills running into extensive mangrove swamps. It is these coastal swamps which provide the optimal breeding sites for *farauti* and in all these areas malaria transmission has continued despite regular six-monthly spray rounds with a good application of DDT. Even in these areas, however, the deterrent effect of DDT is enough to protect the human population from malaria provided they are in their houses after sunset. Traditionally, Solomon Islanders retire indoors at sunset but in more 'enlightened' areas this habit has broken down and, especially in the north coast areas of Guadalcanal, people are to be found out of doors well after sunset. Thus the mosquito has no need to enter houses and the apparent change to early-evening biting has led to malaria transmission continuing unabated despite malaria eradication operations of a high standard.

The work described in this paper was carried out while I was Government Entomologist, Medical Department, BSIP. My gratitude goes to my colleagues in the Malaria Eradication Programme especially the dedicated team of technicians, extremely ably led by Mr E.S.Horoto, which made the all-night catches on San Cristobal. My thanks also go to Dr Joan Bryan for her assistance, to Dr Mario Maffi for his encouragement and to Professor J.D.Gillett for his interest and advice.

GLOSSARY

(from *Terminology of malaria and of malaria eradication*, World Health Organisation, Geneva, 1963)

Anthropophilic. Showing a preference for feeding on man even when non-human hosts are available.

Bioassay. In applied entomology, the experimental testing of the biological effectiveness of an insecticide by deliberately exposing insects to it.

Biting cycle. Regular variations in the amount of blood-feeding activity exhibited by populations of mosquito species during each 24-h day-and-night period.
Endophagy. Tendency of mosquitoes to feed indoors.
Endophily. Tendency of mosquitoes to rest indoors, whether by day or night.
Exophagy. Tendency of mosquitoes to feed outdoors.
Exophily. Tendency of mosquitoes to rest outdoors, whether by day or night.

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Manuscript received 25th May, 1975