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Ecological Factors Limiting the Extension of Malaria in the Southwest Pacific—Their Bearing on Malaria Control or Eradication Programmes.

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1. Introduction.

Relatively little attention has been devoted to examining closely those *natural* factors that have impeded the geographical extension of malaria in such areas as the Southwest Pacific. While in some localities such as the Northern Territory of Australia malaria has regressed spontaneously (BLACK, 1950), in various islands in the eastern part of this region it appears to be more prevalent, for example on Rennell Island (LAIRD and LAIRD, 1959) and Sikaiana (BLACK, 1952). In the highlands of the main island of New Guinea too, malaria may be extending into new areas (PETERS et al., 1958). The recent programmes of residual insecticide spraying, sometimes combined with mass chemoprophylaxis or therapy have not fulfilled their earlier promise (PETERS, 1962). In this paper an attempt is made to examine the situation from the relatively neglected perspective of the natural, ecological factors that limit the spread of malaria, in the hope that new light may be shed on various aspects of which advantage may be taken.

2. The limits of distribution of malaria and its vectors in the Southwest Pacific.

The distribution of malaria is shown in figure 1. Within this area exist small localities, such as parts of the mountainous central region of the main island of New Guinea, from which malaria is absent although Anophelism without malaria occurs in places. The main malaria vectors are summarised in table 1.

Although as regards its behaviour, *A. punctulatus* is the most dangerous vector, *A. farauti* undoubtedly poses the most serious control problems in this region.

In view of the importance for modern control methods of even slight differences in breeding, resting and feeding habits it is essential to call attention again to the need for clarification of the differential systematics and bionomics of this vector complex.

It can be said in general that malaria is holoendemic (*sensu* METSELAAR and VAN THIEL, 1959) and stable (*sensu* MACDONALD, 1957) in most coastal and subcoastal areas of the New Guinea mainland where *A. punctulatus* is the dominant species such as Maprik in the Sepik District (PETERS and STANDFAST, 1960). In some areas where *A. farauti* may be the sole vector, it transmits malaria intensely and produces an unstable pattern varying from hypo- to

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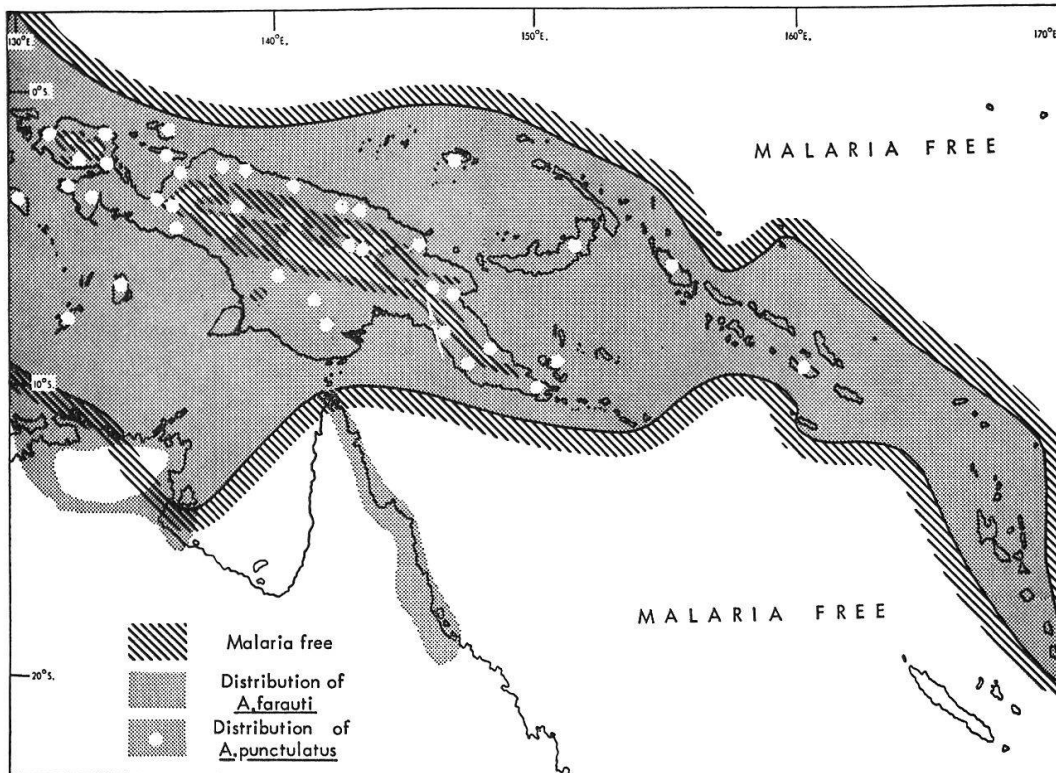


Fig. 1. Approximate distribution of malaria, *Anopheles farauti* and *A. punctulatus* in the Southwest Pacific. (Note that the distribution of *A. koliensis* closely follows that of *A. punctulatus*.)

holoendemicity. With increasing altitude inland the picture on the New Guinea mainland changes. In the mountainous area between 1500 and 2000 metres, *A. farauti*, aided in particularly favourable years by localised breeding of *A. punctulatus* or *A. koliensis*, produces severe epidemics (METSELAAR, 1959; PETERS and CHRISTIAN, 1960).

In Australia there may remain a few residual endemic malaria foci but Anophelism without malaria now exists in the area indicated in figure 1.

3. Main factors in the equation of malaria transmission.

The three factors in this cycle, the parasite, the mosquito and man have been correlated mathematically by MACDONALD (1957).

$$m = \frac{-r \log_e p}{a^2 b p^n} . *$$

* "r" and "b" refer to the duration of infection in the human host and his degree of premunity respectively. "a" and "p" are directly related to the vector, "a" representing its biting frequency on man and "p" its natural longevity. "n" is the duration of the extrinsic cycle of the malaria parasite in the vector and differs for the different species of *Plasmodium*, other conditions being equal.

"m" is the adult mosquito population density above which an increase in the quantum of malaria in a community can occur.

TABLE 1.
Malaria vectors of the Southwest Pacific.

Subgenus	Major vectors of widespread distribution	Proved minor vectors of limited distribution	Suspected but unproven vectors
<i>Anopheles</i> (<i>Anopheles</i>)		<i>bancroftii</i> Giles, 1902	<i>pseudobarbirostris</i> Ludlow, 1902
<i>Anopheles</i> (<i>Cellia</i>)	<i>farauti</i> Laveran, 1902 <i>punctulatus</i> Dönitz, 1901 <i>koliensis</i> Owen, 1945	<i>karwari</i> James, 1903 <i>amictus hilli</i> Lee & Woodhill, 1944	<i>subpictus</i> Grassi, 1899 <i>annulipes</i> Walker, 1856 <i>amictus amictus</i> Edwards, 1921 <i>longirostris</i> Brug, 1928 <i>meraukensis</i> Venhuis, 1932

Data on the various factors in this equation as they relate to Anopheline ecology and the intensity of malaria transmission *in the marginal areas* of its distribution are completely lacking except for part of the highlands of the Territory of Papua and New Guinea (PETERS and CHRISTIAN, 1960), where "m" varied between 11.2 in the dry and 0.67 in the rainy, epidemic season.

4. Vectorial capacity of the main vectors.

The vectorial capacity of the main vectors in a given area is governed by ecological conditions that may influence "a", "p" or "n".

a) *Natural longevity* ("p").

All three species of the *A. punctulatus* complex are long-lived and, from this point of view, potentially efficient vectors. *A. farauti* has an even greater longevity in the highlands, at least during the epidemic season, than in coastal or subcoastal areas.

The relative humidity undoubtedly plays a large role in the variations of longevity of the vectors and, in turn, is dependent upon the total rainfall. In the highlands more efficient drainage, a greater evaporation rate and the more seasonal character of the precipitation result in a distinct dry season when the macroclimate is unfavourable for Anopheline survival. It also seems likely that the increase in length of the gonotrophic cycle observed by SLOOFF (1961) in *A. koliensis* when oviposition sites were scarce takes place in *A. farauti* under similar circumstances.

Summing up, we may say that in the highlands, as a result of seasonal variations in longevity, an anti-Anopheline residual spraying campaign conducted in the dry season stands a better chance of success than in the rainy season. A 12% increase in the daily mortality of *A. farauti* would theoretically interrupt malaria transmission in the dry season but a 20% increase would be needed in the wetter months (PETERS and CHRISTIAN, 1960).

TABLE 2.
The longevity of Pacific malaria vectors.

Species	Locality	"p"	Author	Remarks
<i>A. punctulatus</i>	Nimboran Valley	0.79	Metselaar, 1957	
	Maprik	0.87	Peters & Standfast, 1960	
<i>A. farauti</i>	Minj	0.90 ± 0.2	Peters & Christian, 1960	0.92–0.88 depending on season
	Nimboran Valley	0.81	Metselaar	
	Maprik	? 0.87	Peters & Standfast	
	Merauke	0.68	Van den Assem, 1959	Insecticide spraying in progress
	Fergusson Island (D'Entrecasteaux)	0.85	Spencer & Spencer, 1960	
	Nissan Island	0.84	Spencer, 1961	
<i>A. koliensis</i>	Nimboran Valley	0.79	Metselaar	
	Hollandia	0.74–0.91	Van den Assem	
	Maprik	? 0.87	Peters & Standfast	
<i>A. bancroftii</i> sensu lata	Kimaan (Frederik Hendrik Island)	0.64	Van den Assem	Insecticide spraying in progress
	Merauke	0.69	Van den Assem	

b) *Anthropophilic habits* ("a").

A. farauti is readily deviated from man to non-human hosts. Nevertheless, when man is the most readily accessible host, the anthropophilic index is high. *A. punctulatus* is more inherently anthropophilic. An unusual feature of most of the Southwest Pacific islands, including New Guinea itself, is the relative scarcity of domestic animals living in close association with man. Curiously enough the level of endemicity of malaria is low in two of the most swampy areas of the New Guinea mainland although *A. farauti* is present at least in small numbers (VAN DIJK, 1958, Bangi-Ia area; PETERS, 1957, Fly River). In these areas the human population is very thinly spread whereas there is a relatively large wild fauna so that the ratio of availability of human to animal hosts is low.

It has been observed that *A. farauti* enters houses to feed at Minj less readily in the dry season. Since, in the cold evenings, the indigenous population

tends to retire indoors early, there is possibly a reduced man-mosquito contact which assists in reducing the amount of transmission during the dry months.

Important in relation to the natural limitation of transmission in the highlands is the fact that *A. annulipes*, which is the dominant species as judged by larval population densities, is very rarely taken indoors or in window traps and has never been recorded as biting man in New Guinea (PETERS and CHRISTIAN, 1963).

c) *Inherent receptivity to Plasmodia.*

Unfortunately, the species with the widest distribution, *A. farauti*, is both long-lived and a good host for *Plasmodia*. It may prove of considerable interest to study the inheritance of receptivity to malaria parasites in such a vector. WARD (1963) has recently investigated the receptivity of *Aedes aegypti* for *P. gallinaceum* and selectively bred a 98% resistant strain.

d) *Anopheline population dynamics ("n").*

The size of the adult vector population is the product of the chances of survival of the egg, larval instars and pupa. These in turn depend upon the following inter-related ecological conditions.

(i) Selection of oviposition sites.

All authors agree that *A. farauti* is the most adaptable vector as regards type of oviposition site and that it can develop in almost any type of surface water or water in natural or artificial containers when the necessity arises. Its ability to develop completely in brackish water has undoubtedly facilitated its extensive spread to the east over widely separated coralline-island chains. *A. koliensis* too can adopt many types of breeding sites except those containing significant quantities of sea water. In contrast the typical *A. punctulatus* breeding site, small transient puddles devoid of vegetation in clay-bearing soil, exposed to full sunlight, is almost obligatory for this species, a factor that accounts largely for its limited and patchy distribution and relative inability to extend its domain.

(ii) Availability of breeding sites.

It is quite clear that, particularly in their *marginal* areas of distribution, the natural limitation of available breeding sites for the various species has played a large part in creating these margins. The limitations are created by

Topography
Soil type
Total rainfall
Daily rainfall pattern.

Good natural drainage or highly porous subsoils (e.g. coralline) prevent the accumulation of suitable collections of surface water.

It should be remembered however that any unusual disturbance of the soil surface in an area, such as the clearing of jungle, road building or diverse wartime activities leads to the production of unlimited breeding sites for *A. punctulatus*, not to mention *A. farauti* and *A. koliensis*.

Of greater importance in limiting Anopheline breeding in view of their preferential breeding sites is the *daily rainfall pattern*. The significance of this was intimated by LAIRD (1946) whose observations, together with our own (PETERS and CHRISTIAN, 1963), fully support the suggestion of CHRISTIE (1959) that daily rainfall patterns determine the size of adult population densities of *A. punctulatus* as they do *A. gambiae* in Africa.

(iii) Larval competition.

The writer has observed that on certain atolls, such as Tasman Island, breeding sites are at such a premium that enormous numbers of *Culex annulirostris* occur in them and it seems most likely that cannibalism must take place. This may well play a role in limiting the breeding of *A. farauti* on those isolated coralline atolls where the two species coincide or where the latter is introduced from time to time. In the New Guinea highlands PETERS and CHRISTIAN (1963) have suggested that larval competition between *A. annulipes* and *A. farauti* must play an important part in keeping down the numbers of the latter. In the subcoastal area of Maprik they found that *Culicine* larval densities rose greatly when the competition pressure previously exerted by *A. punctulatus* was relieved as the adult Anophelines succumbed to residual house spraying.

(iv) Parasites and predators.

The relation between Anopheline larvae, their endo- and exoparasites and predators has been admirably documented by LAIRD (1947, 1956, 1959). As a result of his extensive investigations he recommended that the possibilities of biological control should be further investigated.

5. Geographical isolation.

As the flight range of *A. farauti* and *A. punctulatus* lies between $\frac{1}{2}$ and 1 mile (0.8–1.6 km), one is inclined to look to various methods of passive transport in order to explain the extensive distribution of *A. farauti* to the east.

That exotic species can be transported by human agency appears very likely, especially if the larval stages can withstand exposure to saline water (e.g. in canoes) or the adults are particularly hardy. BELKIN (1962) has summarised the methods by which transport across sea barriers may occur.

LAIRD (1956) emphasised that Buxton's Line at 170° E latitude merely marks the *present* eastern limit of the dispersal of *A. farauti* and that "it cannot be claimed that any general factor other than isolation is operating to prevent the extension of the range of *A. farauti* to those tropical islands east of Buxton's line where the requisite ecological conditions present themselves".

6. Relation to malaria control or eradication programmes.

From the above account it is obvious that, while various factors operate to circumscribe the distribution of malaria in the Southwest Pacific, such factors when varied may contribute to an extension of the disease, either quantitatively or geographically.

There is little doubt that much ground can still be gained by the judicious application of suitable insecticides and anti-malarial drugs in the combating of malaria in this region. Nevertheless the indications are that these alone may not suffice completely to interrupt malaria transmission. Various suggestions made above can be applied with little question. These are:

1. Quarantine measures to avoid artificial dispersal of vectors to new localities.
2. The provision of larger domestic animals (cattle, pigs) in special stables which are suitable for residual insecticide spraying.
3. Careful avoidance of the production of additional breeding sites.
4. Construction and maintenance of proper drainage and/or irrigation systems where practical.
5. The stabilising of migrant populations in suitable native-style housing.

Other lines of attack require careful prior scientific enquiry and include:

1. Ecological studies to clarify the importance of larval competition and its possible practical application.
2. Ecological investigations into the natural parasites and predators of all Anopheline stages and exploration of their potential value for *biological control* of Anopheline vectors.
3. Systematic studies designed to clarify behavioural differences and taxonomic status of closely related vectors.
4. Introduction on a trial basis of such predators as suitable species of "annual fish".

Of more general in addition to local interest would be:

1. Exploration of the morphological and genetic basis of vector susceptibility to *Plasmodial* infection.
2. The development of genetically selected insusceptible strains.
3. The selection of sterile mutant males for admixture with local populations of the same taxon.
4. Further ecological studies of malaria in the marginal areas of its distribution to seek so far undetermined limiting factors.

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