

Malaria Vectorial Capacity of a Population of *Anopheles gambiae*

An Exercise in Epidemiological Entomology

C. GARRETT-JONES¹ & G. R. SHIDRAWI²

*In order to assess the factors of malaria vectorial capacity and the daily reproduction rate, separate consideration is given to data from Kankiya, Northern Nigeria, concerning the incidence of vector-man contact (the man-biting rate), the vector's expectation of infective life, as reflected by the proportion of parous mosquitos under certain conditions, and the vector's man-biting habit, comprising the frequency of feeding and the human blood index. The main difficulty in the assessment of each of these factors was shown to be that of representative and adequate sampling, especially in a sprayed area. In order to compensate for deficiencies in the Kankiya data, especially with regard to the daily and cyclic survival-rates, the gonotrophic cycle and the effective sporogonic period, more complete published data on an *Anopheles gambiae* population in East Africa were examined, and extrapolations were made from these data in spite of the consequential risks involved.*

*The results of the analysis show that the spraying of an area with DDT reduced the malaria vectorial capacity of *Anopheles gambiae* sp. B (the main vector of *Plasmodium falciparum* in the area) by an over-all factor of about 23 times. Nevertheless the basic reproduction rate of the disease is estimated to have averaged slightly over 20 in the sprayed area during the 6 months of the main transmission season. This is consistent with an observed recovery in the parasite rate, which had been reduced to a very low level by regular mass drug administration through the preceding dry season.*

The analysis was a tentative exercise in "epidemiological entomology" and it is suggested that in the postgraduate teaching of tropical hygiene, the epidemiological approach to entomology should be preferred to the classical morphological-bionomical approach.

Epidemiological entomology involves the quantitative study of vector status, vector prevalence and population dynamics, the feeding preferences of vectors, their house-visiting habits, expectation of life, and so on. It also may need to embrace assessments of the vector's receptivity to infection and of its suitability as a vehicle for the incubation and multiplication of the disease organism. In this paper the following definition of epidemiological entomology is adopted:

"The sampling and study of vector populations in order to assess, according to the range of vector prevalence, longevity, biting-rhythm, host-selection, etc., the expected trends in the incidence of transfer of a pathogen

to a vertebrate host and back to the vector itself, whether before, during or after the operation of control measures."

The phrase "the trends in the incidence of transfer" is important. It is these that depend in the main on entomological factors. The actual incidence at any time and place is a function also of the size and condition of the reservoir of infection in the vertebrate host or hosts of the disease.

The subject is thus distinct from classical medical entomology, in which the main stress is laid on the systematics and general bionomics of medically important insects, and it is necessary to consider whether a shift in emphasis within the entomological curriculum of many postgraduate training programmes concerned with tropical medicine and hygiene would be advisable.

In this paper, in order to illustrate the methodological problems which arise in field practice, we shall

¹ Division of Malaria Eradication, World Health Organization, Geneva, Switzerland.

² WHO Field Research Project on Malaria, Kankiya, Northern Nigeria.

quote data from a WHO project in Northern Nigeria on the entomological parameters which determine the trend of malaria transmission, and consider the impact of anti-mosquito measures on them. As always in calculations of this nature, assumed values will have to be assigned to those factors that cannot (as yet) be measured or derived from observations in the field. Such assumptions will be mentioned where appropriate. It is desirable that the possible errors arising from them should tend to offset, not compound, one another.

THE VECTORIAL CAPACITY OF MALARIA VECTORS AND THE REPRODUCTION RATE OF MALARIA

Malariologists of the 1920s and 1930s developed indices which reflect the anopheline infective density and the malaria inoculation risk. These terms were defined by Christophers (1949). The anopheline infective density, or average number of sporozoite-positive *Anopheles* found at rest per house, was applied in West Africa and critically examined by Davey & Gordon (1933), and in East Africa by Wilson (1936). The index of inoculation risk was derived from the infective density by taking into account the mosquito's supposed biting-frequency and the average number of people per house. It may be noted that a similar "risk of infection index", but based on the incidence of infective mosquitos caught biting, has recently been proposed (de Meillon, Grab & Sebastian, 1967) for assessing the transmission of bancroftian filariasis by *Culex pipiens fatigans*. Previously Wharton (1962) had estimated the intensity of transmission of *Brugia malayi* by its *Mansonioides* vectors, in terms of a monthly index of the number of infective bites received by man and by goat, respectively.

In malaria epidemiology such a direct approach to the estimation of the inoculation rate was appropriate where (1) the endemicity of malaria was high, (2) the vectors were endophilic, and (3) vector control measures, if any, were directed against the aquatic stages. Since the development of residual insecticides and the systematic treatment of houses to end malaria transmission, those older methods of epidemiological study have fallen increasingly into disuse as they became inapplicable. In conditions of declining transmission it is hardly worth while, even where fair-sized samples can still be collected, to dissect mosquitos by the thousand on the off-chance of finding one sporozoite-positive specimen. The finding will anyway not give a good indication

of either vectorial capacity or vector efficiency (defined by the World Health Organization, 1963).

The need for a fresh quantitative approach to the interacting entomological variables that play a part in determining the malaria inoculation rate became evident in the years immediately following the widespread introduction of DDT. Boyd (1949a) pointed out that malariologists had largely ignored Ross's (1911) mathematical expression of the various factors involved in the perpetuation of a malaria situation; and in concluding his full review of the entomological factors (pp. 608-697) he wrote:

"It is to be regretted that even now quantitative values for Ross's factors are lacking. Observed data enable us to assign values to many of the factors on the human side of the equation, but not those pertaining to the vector."

Among other important contributions to such an approach were those of Beklemishev (1957a, 1957b), Davidson & Draper (1953), Davidson (1954, 1955), Detinova (1948, 1952, 1953), Macdonald (1952, 1955), Moshkovsky (1950), Moshkovsky & Rashina (1951), Polovodova (1949), Remennikova (1948), Shipitsina (1957), Swaroop (1949) and Trapido & Aitken (1953). Macdonald's (1957) textbook *The Epidemiology and Control of Malaria* was a landmark in that it brought together for consideration all the main quantitative factors, entomological, parasitological and immunological, which contribute to or limit malaria transmission. In the same year in the USSR the book [*Seasonal Phenomena in the Life of Malaria Mosquitos...*] (Beklemishev & Shipitsina, ed., 1957) was published. This was followed by a paper published in English (Beklemishev, Detinova & Polovodova, 1959), and later by the important monograph of Detinova (1962). The publications just mentioned represent the distinctive approach of Soviet science to epidemiological entomology, with its special emphasis on the phenology and the age-composition of vector populations.

In 1964 it was proposed that the product of the essential entomological readings might provide an epidemiological index of vectorial capacity. This was defined by Garrett-Jones (1964b). As pointed out by the WHO Expert Committee on Malaria (1966) this index is "the same as the reproduction rate considered on a daily basis". Where two or more vectors are transmitting the same disease, its daily reproduction rate is equal to the sum of their vectorial capacities. The use of the index of vectorial capacity, reflecting the expected quantum of new infections per infective case per day, offers the ad-

vantage of permitting assessment of the influence of entomological parameters on the malaria reproduction rate, apart from the parasitological and immunological variables that also influence it.

Measures to eradicate malaria by vector control are aimed at reducing the mosquito's vectorial capacity to levels at which there will be less than one inoculation of sporozoites per case of malaria, implying a basic reproduction rate of less than 1.0 (Macdonald, 1957). Under continuing control the number of infective cases will gradually decline until all the cases remaining can be found and treated before they give rise to any new infection. Only when no source of gametocytes remains is it safe to discontinue the vector-control measures, letting the mosquito's vectorial capacity regain its natural levels. We then have "anophelism without malaria", as seen in countries where these diseases have been eradicated. Here the index of vectorial capacity, if assessed, will show how receptive to transmission a given place may be, that is, what rate of inoculation may be expected to result from an imported case.

Short of the eradication of a vector it is not to be expected that the vectorial capacity of a sizeable population will ever be reduced to zero; that could only happen by its complete deviation from human to animal hosts. In most operations the vector's man-biting habit is disregarded while ways of reducing the other factors—the expectation of infective life and the man-biting rate—are sought. A way has been suggested of estimating the impact of house-spraying on these two factors by means of longitudinal observations on the proportion of parous females (Garrett-Jones & Grab, 1964), but, as will be seen, this is not as simple in practice as it may sound. Difficulties of representative sampling and of interpretation continue to pose serious obstacles to the operational assessment of each one of the factors of vectorial capacity. In view of these, coupled with the meagre training in epidemiological entomology available to malaria entomologists so far, it is perhaps not surprising that according to a recent analysis (G. Chauvet, unpublished report to WHO, 1968) very few successful attempts have been made to measure these factors in malaria eradication programmes.

ENTOMOLOGICAL OBSERVATIONS AT KANKIYA,
NORTHERN NIGERIA, IN 1967

For several years the World Health Organization has conducted a field research project at Kankiya, in the dry savanna zone of Northern Nigeria, where

Plasmodium falciparum malaria is holoendemic. In June 1967 spraying with DDT was carried out in an area with 50 000 population that had remained unsprayed for the previous 18 months. Entomological indices were measured by one of us (G.R.S.) throughout the year in this area and in an adjoining untreated control area. Good measurements of the density of *Anopheles gambiae* in the sprayed area were made, both by human-bait captures and by pyrethrum-spray captures in a few stations maintained unsprayed for that purpose.

Most of the malaria transmission during the year was caused by *A. gambiae* between June and October, species B being the only representative of that complex recognized in the area. This vector remained dominant through 9 months of 1967 (April–December), while *A. funestus* was found in much smaller numbers and was common only during the last 4 months. It will suffice to consider here the data relating to the vectorial capacity in *A. gambiae*, as observed in the unsprayed and in the DDT-sprayed areas.

The man-biting rate

The index of vectorial capacity is density-dependent and the parameter of density to be measured is the man-biting rate, or incidence of bites per inhabitant per day. It may be estimated directly from its indoor and outdoor components,¹ by means of captures through the night on human baits; or indirectly, from an index of the indoor-resting blood-fed females per inhabitant where (as at Kankiya) the vector is known to be predominantly endophagic and endophilic in behaviour. Both methods were employed at Kankiya in 1967. The resulting monthly indices for the unsprayed area are shown on a logarithmic scale in the accompanying figure, and it is clear that the two indices followed the same trend during 6 consecutive months but showed a discrepancy ranging from 3.0 : 1 to 4.2 : 1 in favour of the direct-capture method. This poses the question as to which index, if either, represents the true incidence of biting-contact. There is evidence from another part of West Africa (Odetoyinbo, 1969) that most hungry mosquitos, when not offered a sitting bait, are obliged to visit several houses before they can obtain a blood-meal. In that case the morning

¹ Garrett-Jones, C. (1964) *A method for measuring the man-biting rate* (unpublished document WHO/Mal/450). A limited number of copies of this document is available to persons officially or professionally interested on request to Distribution and Sales, World Health Organization, 1211 Geneva, Switzerland.

indoor-resting density of blood-fed females per sleeper may provide the better index of the man-biting rate in the check area. But this method is inapplicable in DDT-sprayed houses, where most of the resting females are either killed or driven out before morning, although the biting-rate may remain high.

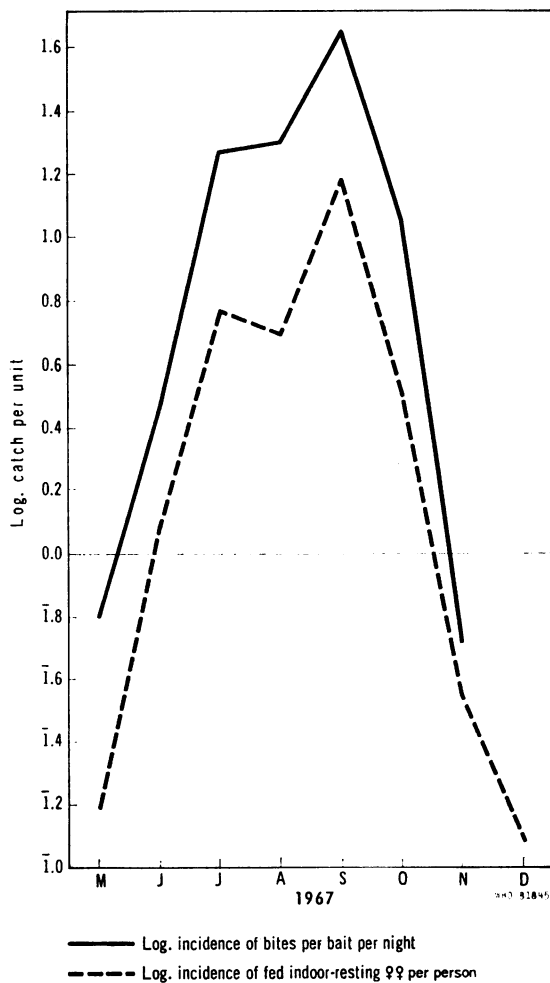
In the DDT-sprayed area at Kankiya the highest number per inhabitant of blood-fed females found resting in the sprayed huts was 0.16 (September); in huts kept unsprayed for checking purposes the number reached 3.1. At the same time the index of bites per bait per night rose to 15.9—so it is clear that no index of resting-density can tell us how many bites were actually being received per inhabitant; the direct-capture method, however, probably gave an exaggerated index. A correction factor must therefore be applied, to discount the "excess bites" believed to be recorded by this method. This factor has been set provisionally at 3 times, in view of the discrepancy apparent in the figure.¹ In Table 1 the corrected estimates of the monthly man-biting rates are shown for both areas. Despite the downward correction of the observed readings, the estimated incidence of vector-man contact in the presence of DDT reached moderately high levels in July, August and September.

The man-biting habit

The average frequency of biting on man by the individual mosquito is expected to vary less, in a given vector population, than the biting-density or the longevity. Nevertheless a good estimation is important because the vectorial capacity of a population varies as the square of its man-biting habit, since any mosquito must bite man at least twice in order to receive and transmit the disease. The value cannot be observed directly but must be derived from

¹ Further study of the data since the above was written leads us to believe that the man-biting rates as calculated here may be underestimated, for two reasons. (a) The baits probably did not catch all the mosquitoes feeding on them, as indicated by positive pyrethrum catches in the same huts the following morning. These reached peak levels of 16.5 and 0.39 per bait, in the check and the sprayed areas respectively. (b) Outlet-trap catches on normally occupied huts in the check area showed that a proportion of the feeding mosquitoes left the huts the same night. This proportion reached 38.7% in August-September 1967 (though it was much less—only 8.4%—in 1968, presumably for climatic reasons). These observations, which will be reported later, would require upward corrections to both the indices of vector-man contact shown in the figure. Any such corrections, however, would only partly offset the downward correction-factor adopted in the present calculations.

MONTHLY INDICES, FROM MAY TO DECEMBER, OF MEAN *ANOPHELES GAMBIAE* DENSITY IN UNSPRAYED LOCALITIES IN KANKIYA, NORTHERN NIGERIA, 1967



information on the frequency of biting and the proportion of bites taken on man (Macdonald, 1957). It is normal practice to express the biting frequency as the reciprocal of the vector's gonotrophic cycle in nature, since the number of bites actually taken per cycle is not observable. Nor is the measurement of the cycle itself an easy matter. Gillies & Wilkes (1965) showed by release and recapture experiments (see below) that all cycles after the first one were of 3 days in *A. gambiae* sp. A in Tanzania. This was supported by their finding of the first sporozoites (of *P. falciparum*) in females developing their fourth batch of eggs. An identical finding in *A. gambiae*

TABLE 1
ESTIMATED MAN-BITING RATES (MBR) OF *ANOPHELES GAMBIAE* SP.B IN 2 AREAS
OF KANKIYA, NORTHERN NIGERIA, 1967^a

Month ^b	Unsprayed area			DDT-sprayed area		
	Bait-nights worked	Observed biting-rate	Corrected ^c MBR	Bait-nights worked	Observed biting-rate	Corrected ^c MBR
May	20	0.50	0.17	12	0	0
June	18	2.56	0.85	18	0.17	0.06
				(first DDT application)		
June	18	3.50	1.2	18	0.78	0.26
July	35	18.4	6.1	36	4.78	1.6
August	33.5	19.9	6.6	36	5.53	1.8
September	36	43.7	14.8	36	15.9	5.3
October	18	20.5	6.8	18	3.67	1.2
				(second DDT application)		
Oct.-Nov.	36	2.94	0.98	36	0.17	0.06
Nov.-Dec.	24	0.58	0.16	18	0	0

^a Data supplied by one of us (G.R.S.), using the method of indoor and outdoor components of mosquito-man contact (Garrett-Jones (1964) *A method for measuring the man-biting rate*; unpublished document WHO/Mal/450).

^b In June and October the MBR was estimated before and after the DDT applications.

^c See text.

sp. B at Kankiya renders it highly probable that the gonotrophic cycle is 3 days in that population also. These indications are considered more significant in the present context than the evidence on which Muirhead-Thomson (1951) concluded that a 2-day gonotrophic cycle is of widespread occurrence in *A. gambiae*.

The proportion of bites taken on man, or human blood index, is assessed from precipitin tests performed on samples of blood-meals smeared on to filter-papers. The testing has been centralized and standardized for about 12 years under the auspices of WHO, and in this period some 120 000 anopheline blood-meals have been identified (Bruce-Chwatt, Garrett-Jones & Weitz, 1966). There are indications that the continued application of DDT or dieldrin in houses may affect the host-selection pattern of the mosquitos, reducing the human blood index (Garrett-Jones, 1964a). However, it is not clear whether such changes reflect a change in the endogenous host-preference of the species, or merely the action of the insecticide in killing or repelling females that would otherwise have been caught after feeding indoors.

The major problem in observing the human blood index is that of obtaining representative monthly samples of the blood-fed females. Even in unsprayed

areas it is not easy to collect adequate subsamples in the various daytime biotopes available to the mosquito. In DDT-sprayed areas, where the vector may be scarce and where many females may be driven to seek outdoor resting-places, the problem of sufficient and unbiased sampling is much aggravated.

The sampling for this parameter at Kankiya has been uneven and we must rely on findings from 1963-64. They indicated a human blood index of around 75% in the unsprayed area and 63% in DDT-sprayed localities. On a 3-day gonotrophic cycle this implies a man-biting habit of 0.25 and 0.21 respectively; that is, a female will feed on man once in 4 (or 5) days on an average.

THE EXPECTATION OF INFECTIVE LIFE

The malaria vector's expectation of infective life is defined as the mean number of days of life in the infective condition per mosquito receiving the infection (Garrett-Jones, 1964b). It is a function of the daily survival rate of the female mosquito and of the sporogonic period of the malaria parasite, parameters to which Macdonald (1952, 1957) assigns the symbols p and n . The mathematical expression

of the expectation of infective life in days is given by the formula:

$$\frac{p^n}{-\log_e p}$$

The period of sporogony differs according to the species of *Plasmodium* and varies with the mean temperature of the environment. Macdonald (1952), plotting the results of many experimental studies, showed that sporogonic periods of 8–9 days in *P. vivax* and 11–12 days in *P. falciparum* are normal at mean temperatures of 26°C–27.5°C.

An error of one day (say, 10%) in an estimate of the sporogonic period (n) would entail only a minor degree of error in the estimated infective life per mosquito; but a proportionate error in estimating the value of p will have more drastic consequences, as may be seen from Fig. 2 in Garrett-Jones & Grab (1964). Thus, where $n = 11$ and p is estimated at 0.70, the computed index of infective life will be 0.0554 day; but if the real value of p were 0.75 the true index would be 0.147 day, or about 2.8 times higher than the estimate. The importance of an accurate estimation of p is therefore evident. By the same token, even a modest reduction caused in a vector's daily survival rate by insecticidal attack may reduce its vectorial capacity very substantially. On the other hand the statistical difficulty of obtaining an accurate evaluation of p is illustrated by a table (Table 7) in a paper by de Meillon, Grab & Sebastian (1967). If the proportion parous is observed in a sample of 400 dissected mosquitos and found to be 0.40, the 95% confidence limits of the observation are 0.35–0.45. Supposing that the parous proportion represents p^3 , the value of p derived from this sample may be anything from 0.705 to 0.765. Larger samples would have to be dissected for greater accuracy.

It is still a matter of great difficulty to determine the rate of survival in a population of mosquitos in nature. The work of Russell & Rao (1942), who observed the survival of *A. culicifacies* in a large cage enclosing natural features, was critically evaluated by Macdonald (1952). The most comprehensive studies of age-composition made so far on *Anopheles* are those on *A. maculipennis messeae* in the USSR (Detinova, 1962, 1968). But by "age structure" she means "specifically the age composition of females, i.e. the occurrence of individuals of various physiological ages in the population" (Detinova, 1968). This analysis of age-groups, however, does not always reveal the survival rate from one physiological age-group to another; and

secondly, knowledge of the physiological survival rate is of little use unless it can be confidently related to calendar age. For epidemiological purposes, what we need to know is the mean probability that a mosquito, infected at any age, will survive through the operative sporogonic period of the parasite, plus the interval required before she will again bite a human being.

This assessment is not yet possible in *A. maculipennis* or other vectors in cool latitudes, where the mosquito completes only a few generations in the breeding season and spends much of the year in adult diapause. So much is clear on studying, for example, the detailed analysis of age-structure given in one of Detinova's tables (1962, p. 109). The fluctuations of age-structure in *A. maculipennis messeae* in Moscow, grouped into 5-day periods from 25 April to 30 September 1952, indicate that the species completed 3 gonoactive generations during that season, the approximate dates of maximal adult emergence being 25–30 April, 11–15 June and 16–20 July. A fourth generation, which emerged about 11–15 September, went into hibernation with the exception of a few gonoactive individuals. The 4 generations overlapped, since at the emergence of each generation the samples included some survivors from the preceding one: thus, on 11–15 June the surviving old mosquitos had, on dissection, most commonly laid 6–7 batches of eggs, on 16–20 July they had laid 4 batches and on 11–15 September 4–6 batches. These data could possibly indicate the length of the gonotrophic cycle but give no clue to the probability of survival through any given period. On the contrary, the big fluctuations in output, combined with the mixture of generations in each 5-day sample, effectively mask the natural mortality per gonotrophic cycle. Nor can the proportion of parous mosquitos, which swung from 100% to 37.1% between late May and mid-June and back to 96.3% in early July, afford any guide to the survival rate.

It is different under tropical conditions where the life-cycle of the mosquito is completed more rapidly and where, several weeks after the onset of the main breeding season, the fluctuations in the output of adults may become relatively small and rapid, eliminating the large "waves" due to the arrival of each new generation. So long as the conditions for intense breeding persist we may expect that the relative decline of numbers in successive age-groups, found in a random sample, carefully age-graded, will fairly reflect the rate of mortality from one age-group to the next.

The age-grading of *Anopheles* by Polovodova's (1949) technique, which was developed and is widely applied in the USSR, has been successfully applied to the main tropical malaria vectors in only one part of Africa as yet (although particularly careful work on *A. melas* was performed by Giglioli, 1965a, 1965b). From the published data of Gillies & Wilkes (1965) it is possible to discern the age-structure of a population of *A. gambiae*, to relate physiological age to calendar age, and to correlate the observed proportion of parous mosquitos with the average rate of survival through a known period of days. Since these authors' observations stand alone, they must serve for the time being as the only basis for interpreting data on the longevity of *A. gambiae s. l.* obtained elsewhere.

The life expectation of A. gambiae at Muheza, Tanzania

Throughout 1963, Gillies & Wilkes (1965) sampled the house-resting mosquitos at Muheza (*A. gambiae* sp. A and *A. funestus*) by pyrethrum-spray capture at fortnightly intervals. The occasional unfed mosquitos were discarded and the others classified as fed or gravid. Age-grading by Polovodova's technique was performed on the day of capture or the following day. Nulliparous specimens whose ovaries had not developed beyond Christophers' Stage mid-II were classed as pre-gravid.

Concurrently the mosquitos' calendar age was studied in relation to their physiological age, by means of the release and recapture of marked females. This showed that the parous females required on an average almost exactly 3 days to complete each gonotrophic cycle. The mean difference of age between nullipars and primipars was rather longer, about 3.3 days.

The results of dissections at Muheza, as set out in Table 2, provide independent indices of the proportion parous and of the "mean cyclic survival" under natural conditions; that is to say, the average rate of survival in the younger parous mosquitos from one gonotrophic cycle to the next. Since the latter index represents p^3 , the ratio between the logarithms of the two indices is equal to one-third of that power of p to which the proportion parous corresponds. This ratio is shown in the last column of the table. Thus, in December 1963 (line 1), the observed proportion parous is found to be equivalent to $p^{3 \times 1.33}$ or $p^{3.99}$, and so on.

In the table a ratio is shown for each month, and it is derived from one reading of the proportion

parous and 3 readings of the survival rate between successive cycles (1-par-4-par). But it is possible to avoid the necessity of interpreting our parous proportions differently for every month of observation, thanks to the limited variance in the monthly ratios from December to March and from May to August. The mean ratios for these seasons are given at the foot of the table. Each mean value is now derived from 3 replicate readings of the proportion parous and 9 of the cyclic survival rate. The results for January, April and July (indices in parentheses in Table 2) have been disregarded in these calculations because the half-monthly percentage changes observed in the *A. gambiae* resting densities (column 2) were excessive in those months, and such changes of density distort the proportion parous and invalidate it for use as an index of longevity. Only the results for months when the average density was high and relatively stable (changing by less than 25% within the month) are accepted for our present purpose.

In the period December-March when seasonal conditions were favourable to the survival of the nulliparous mosquitos, the mean ratio, log proportion parous : log p^3 , was 1.21. This implies that the proportion parous observed at that season corresponded to the proportion surviving through slightly more than 3.6 days. In the cooler season, represented by May, June and August, the mean ratio of the logarithms was 1.43, so at that time the proportion parous corresponded to the rate of survival through about 4.3 days. In the light of these values we may suppose that the observed proportion of parous *A. gambiae* at Kankiya, Northern Nigeria, was approximately equivalent to $p^{3.5}$ in the main breeding season, since the climatic conditions during the rains favour the survival of nulliparous *A. gambiae* in that district.

In Table 3 the probability of survival through 1 day (p) in young parous females is calculated from the unique data of Gillies & Wilkes (1965) on the East African populations of *A. gambiae* and *A. funestus* studied by them. In the case of *A. gambiae* sp. A at Muheza both the seasonal breakdown and a 9-months mean index are shown (the samples dissected being too small from September to November). Good monthly samples of *A. gambiae s.l.* (spp. A and B) were taken at Gonja during 12 months, and of *A. funestus* at Muheza during 14 months. In each case the mean cyclic survival is calculated in the same manner; but no seasonal breakdown is attempted for these other populations since we do not have data on the within-month trends in their densities. As

TABLE 2
MONTHLY RATIOS OF PROPORTION PAROUS TO CYCLIC SURVIVAL RATE IN 1-PAR TO 4-PAR
ANOPHELES GAMBIAE SP. A AT MUHEZA, TANZANIA, 1963^a

Month	Half-monthly change in mean resting-density (% + or % -)	No. dissected	Numbers according to physiological age (and proportion surviving cycle)							Mean cyclic survival (p ^b)	Proportion parous (PP)	Ratio log. PP: log. p ^b
			Pre-gravid	0-par	1-par	2-par	3-par	4-par	>4-par			
Dec. ^b	-19	378	53	105	73	60 0.822	40 0.667	20 0.500	27	0.663	0.581	1.33
Jan.	+107	452	69	112	114	65 0.570	31 0.477	33 1.06	28	0.702	(0.600)	(1.44)
Feb.	-1	284	39	49	69	47 0.682	29 0.618	20 0.690	31	0.663	0.690	0.91
March	-20	334	62	60	74	52 0.703	32 0.615	24 0.750	30	0.689	0.634	1.22
April	+48	425	115	99	92	53 0.576	29 0.548	18 0.621	19	0.582	(0.496)	(1.29)
May	-23	500	98	137	115	73 0.635	39 0.535	16 0.410	22	0.527	0.530	0.99
June	-22	472	117	97	83	58 0.699	46 0.794	31 0.674	40	0.722	0.546	1.79
July	-87	324	52	87	73	51 0.699	28 0.550	16 0.572	17	0.574	(0.571)	(1.00)
August	0	112	16	26	25	20 0.80	10 0.50	6 0.60	9	0.633	0.425	1.86
Sept.	-78	24	7	4	2	4 —	2 —	2 —	3	—	—	—
Oct.	-83	21	4	7	4	4 —	1 —	0 —	1	—	—	—
Nov.	+50	85	23	28	15	10 —	4 —	2 —	3	—	—	—
Totals		3411	655	811	739	497	291	188	230			
Means of values for 9 months						0.687	0.589	0.653		0.639	0.567	1.29
Mean monthly indices for two seasons— December, February, March May, June, August										0.672 0.617	0.618 0.500	1.21 1.43

^a From the number of captures reported by Gillies & Wilkes (1965).

^b December results are placed at the top because of their similarity to those of February and March—see text.

TABLE 3
DAILY SURVIVAL-RATES COMPUTED FOR YOUNG PAROUS ANOPHELINES RESTING IN HOUSES
IN TANZANIA ^a

Species	District	Months	Aggregate sample determined	Computed values of p , ^b by age-group				Power of p equivalent to mean proportion parous
				1-2-par	2-3-par	3-4-par	unweighted mean value	
<i>A. gambiae</i> A	Muheza	Feb., March, Dec./1963	996	0.906	0.858	0.865	0.876	3.63
		May, June, Aug./1963	1084	0.894	0.845	0.825	0.851	4.29
		Jan.-Aug., Dec./1963	3281	0.882	0.839	0.869	0.861	3.87
<i>A. gambiae</i> s.l.	Gonja	Dec./1962, Feb.-Sept./1963, Jan./1964	3163	0.873	0.779	—	0.826	3.27
<i>A. funestus</i>	Muheza	Nov./1962-Dec./1963	3993	0.920	0.850	0.876	0.894	4.26

^a From data of Gillies & Wilkes (1965).

^b Unweighted means of monthly values.

regards monthly variance in the mean cyclic survival rates, this index ranged from 0.709 (August) to 0.448 (February) in *A. gambiae* s.l. at Gonja, and from 0.819 (April) to 0.621 (November) in *A. funestus* at Muheza. The latter species, as Table 3 shows, appeared to be, in general, longer-lived than *A. gambiae* sp. A at Muheza, while this population was longer-lived than that of *A. gambiae* s.l. at Gonja.

In considering the correspondence between p and the observed proportions of parous mosquitos, it must be borne in mind that this is affected by the particular method of sampling, which in this instance was by the collection of blood-fed and gravid females resting indoors by day. A different sampling method would be likely to give a different proportion of parous mosquitos, as pointed out by the investigators.

Another quantity to be considered is the effective interval from the infection of the mosquito to the first potentially infective bite it will give in the event of survival. The Muheza and the Kankiya areas are each holoendemic for *P. falciparum* malaria. A long series of dissections by Gillies & Wilkes (*op. cit.*) showed that *A. gambiae* at Muheza could not normally become infective until it was mid-way through the fourth gonotrophic cycle: dissection of 232 blood-fed 3-par females demonstrated only 1 positive for sporozoites, whereas in gravid 3-pars there were 12 positive in 85 dissections. These mosquitos, presumably infected with *P. falciparum* at their first blood-meal, could have given their first infective bite only after laying their fourth batch of eggs (except in the

few cases where the gravid mosquito might seek a blood-meal). Following infection, the females might take subsequent feeds after 2, 4, 7, 10 and 13 days, or alternatively after 3, 6, 9, 12 and 15 days. The first infective bite, i.e., the one following the fourth oviposition, would thus occur either 13 or 12 days after the mosquito became infected. Consequently, the normal interval from infection of the vector to infection of man would be at least 12 days, even if sporozoites were able to reach the salivary glands 24 h or 36 h earlier. It is thus considered that the probability of survival through 12 days (p^{12}) is the index that should be used in calculating the expectation of infective life of a vector of *P. falciparum* in the rainy season at Muheza, and likewise at Kankiya.

The infective life of A. gambiae at Kankiya, Northern Nigeria

The results of age-grouping dissections at Kankiya, where the only measurement of the longevity of *A. gambiae* was the proportion parous month by month in biting samples, are shown in Table 4. As the proportion parous can reflect the rate of survival only when the output of adult mosquitos is relatively stable, the monthly fluctuations in resting density and biting density are included to show when peak densities were observed (July and September). We have not accepted the reading for August, when there was evidently a fresh burst of *A. gambiae* output, nor the one for October when the proportion parous reflected the progressive ageing of the population as the output of adults declined.

TABLE 4
RELATION BETWEEN THE PROPORTION OF PAROUS *ANOPHELES GAMBIAE* SP. B IN MAN-BITING CATCHES IN 2 AREAS AND THE MAN-BITING DENSITY AND THE INDOOR-RESTING DENSITY IN THE COMPARISON AREA IN KANKIYA, NORTHERN NIGERIA: ALSO THE ESTIMATED MEAN EXPECTATION OF INFECTIVE LIFE WITH *PLASMODIUM FALCIPARUM*

Month	Comparison area			DDT area
	Observed indoor-resting density ^a (blood-fed/sleeper)	Observed biting-density (bites/bait/night)	Proportion parous ^b	Proportion parous ^b
May	0.151	0.50	0.63 (73) ^c	—
June	1.02	2.98	0.87 (39)	0.86 (51) ^c
July	5.75	18.4	0.85 (399)	0.58 (120)
August	4.82	19.9	0.56 (414)	0.48 (141)
September	13.1	43.6	0.75 (875)	0.54 (409)
October	3.13	11.1	0.92 (283)	0.68 (62)
November	0.356	0.52	0.84 (144) ^c	— ^d
December	0.122	—	0.62 (72) ^c	—
<i>Estimated indices</i>				
$p^{3.5}$ (average for July + September)			0.80	0.56
p			0.938	0.848
p^{12}			0.464	0.136
$\frac{1}{-\log_e p}$			15.4 days	5.9 days
Expectation of infective life $\left(\frac{p^{12}}{-\log_e p}\right)$			7.14 days	0.803 days

^a The logarithms of these monthly mean indices are plotted in the figure.

^b Figures in parentheses show the numbers dissected.

^c Dissections of indoor-resting samples as the man-biting samples obtained were insufficient.

From these data it is permissible to make no more than a single rough estimate of the expectation of infective life for each area. In the unsprayed area the July and September indices, treated as replicates, indicate an average value of $p^{3.5} = 0.80$ in the rainy season. In the DDT-sprayed area the average for these two months was $p^{3.5} = 0.56$.¹ The estimated daily survival rates are therefore $p = 0.938$ and

0.848 respectively. Assigning to *P. falciparum* an effective sporogony of 12 days, the index of infective life was 7.14 days in the unsprayed area and 0.803 day in the DDT area.

From the indices of longevity calculated in Table 4, it is possible to assess the average impact of the DDT on *A. gambiae*, despite the fact that the pre-spraying density of the vector differed in the two areas. Applying the method of Garrett-Jones & Grab (1964), in which the longevity- and density-factors of impact are both derived from the reduction produced in the proportion parous, the mean longevity factor at Kankiya is estimated as 7.14 : 0.803 or 8.9 : 1; similarly, the density factor is 15.4 : 5.9 or 2.6 : 1. Thus the total impact of the DDT on the vectorial capacity, which is expressed as the product of these estimates, was of the order of 23 : 1. Any further (or lesser)

¹ Comparable data on the parous rates of *A. gambiae* in unsprayed and DDT-sprayed areas are given by Hamon (1963) for the Bobo-Dioulasso district, Upper Volta. The month of peak density was August, when the proportion parous in biting-samples was 0.74 (391 dissected) in the unsprayed area against 0.49 (109) in the DDT-sprayed area. These results accord with the inferred impact of DDT on the longevity of *A. gambiae* at Kankiya, where each index was slightly higher than the corresponding one at Bobo-Dioulasso. The latter locality is known to support a mixed population of *A. gambiae* sp. A and sp. B in the rainy season.

divergence of the vectorial capacity between the two areas would be attributable to natural causes, not to the insecticide.

THE VECTORIAL CAPACITY, THE BASIC REPRODUCTION RATE AND THE STABILITY INDEX AT KANKIYA

The incidence of malaria inoculations, per case per day, is influenced by all the parameters discussed, and is dependent on their product expressed by the following formula (Macdonald, 1957; Garrett-Jones, 1964a):

$$\frac{ma^2 p^n}{-\log_e p}$$

The mean vectorial capacities of *A. gambiae* in both areas at Kankiya are computed in Table 5, where the average vector density readings for two periods are distinguished: a peak period (July–September) and an off-peak period (late June, October, November and early December). It happens that each period is about equal to the supposed mean aggregate duration of infectivity of untreated *P. falciparum* infections in non-immune persons, i.e., 80 days (Macdonald, 1957).

On this supposition, the basic reproduction rates in the sprayed and the unsprayed areas, estimated from the entomological data, are shown in the same table.¹ This rate reached a mean level of almost 1300 inoculations per case in the unsprayed area during the 3 months of peak vector prevalence, which is similar to the level postulated by Macdonald (1957) in introducing his chapter on the “*Quantitative aspects of transmission*”. In the 3 off-peak months of the season the basic reproduction rate was down to 240. In the DDT-sprayed area the estimated basic reproduction rates of *P. falciparum* were 39.1 in the peak months, and 3.54 in the off-peak months of the season. Thus the average level during the 6-month main transmission season was 21.3 in the presence of DDT, as against a rate of 6.0 anticipated by Macdonald, Cuellar & Foll (1968), who applied a mathematical model on the basis of earlier findings in the same field project. Macdonald et al. supposed that the insecticide would reduce the vectors’ daily survival rate to 0.80, whereas, as we have seen, it was reduced by DDT only to about 0.85 in the case of *A. gambiae*. It is interesting to note that the anticipated reproduction rate of 6.0 was later corrected upwards to 17.04 (Foll, 1968), a level not far

TABLE 5
COMPUTATIONS OF THE VECTORIAL CAPACITY OF *ANOPHELES GAMBIAE* AND OF THE BASIC REPRODUCTION RATE OF *PLASMODIUM FALCIPARUM* IN KANKIYA, NORTHERN NIGERIA, 1967^a

Index	Unsprayed control area	DDT-sprayed area
Mean man-biting rate (<i>ma</i>)		
Peak-density period ^b	9.1	2.9
Off-peak period ^c	1.7	0.263
Man-biting habit	0.25	0.21
Infective life ($\frac{p^{12}}{-\log_e p}$)	7.14	0.803
Vectorial capacity ($\frac{ma^2 p^{12}}{-\log_e p}$)		
Peak period ^b	16.2	0.489
Off-peak period ^c	3.0	0.0444
Estimated <i>P. falciparum</i> reproduction rate (from <i>A. gambiae</i> only)		
Peak period ^b	1295	39.1
Off-peak period ^c	240	3.54

^a These basic reproduction rate values are derived on the assumption that a non-immune, untreated case of *P. falciparum* is infective to the vector for a total of 80 days (Macdonald, 1957). However, in the DDT-sprayed area at Kankiya, where carefully planned curative mass drug-administration took place every 2 months during 1967, and reached on average 80% of the people, the mean duration of gametocytaemia was certainly reduced. Moreover, various unknown variables come into operation at this point, e.g., the proportion of sporozoite-positive salivary injections that may be non-infective for any reason, and the proportion of inoculated persons already infected, having regard to the probability of differential biting-rates on different groups and individuals of the community.

^b July–September.

^c Late-June, October, November and early-December.

different from the one inferred from the latest entomological data.

On the other hand, the malaria stability index in the sprayed area was lower than forecast, because the man-biting habit of *A. gambiae*, about 0.21, was less than half the value assumed by Macdonald, Cuellar & Foll (1968). The stability index, expressed as

$$\frac{a}{-\log_e p}$$

represents the average number of bites taken on man by one mosquito in its whole lifetime (Macdonald, 1957). The calculated levels shown in Tables 4 and 5, above, indicate an index of 3.88 in the unsprayed and 1.24 in the sprayed area (that is,

¹ But see footnote *a* to Table 5.

in the rainy season). The lower of these levels is nevertheless high enough to give an expectation of increasing parasite rates (starting from any low level at the beginning of the season); and actual observations showed that, from July to September 1967, the parasite rate in the central part of the sprayed area underwent a rather rapid increase in spite of the continuing mass drug administrations (Najera, unpublished report to WHO). The actual levels of parasite rates were accurately forecast by computer runs (Foll, personal communication).

The infective gametocyte rate

The symbol x was designated by Macdonald (1952) to represent "the proportion of bites on man which are infective to the mosquito". This important parameter he called the infective gametocyte rate. But in a later work (Macdonald, 1957—see Appendix I, page iii) he redefined x as "the proportion of people affected (that is, showing parasitaemia)"—quite a different concept. In both the references cited he proposed the formula

$$s = \frac{p^n ax}{ax - \log_e p}$$

as a way of estimating the infective gametocyte rate where the values of s , p and n are known. Further, in the 1952 paper, an example is given of the application of this formula to data from Madras, India, where the infective gametocyte rate of *P. falciparum* ($n = 9$ days) to *A. culicifacies* was calculated as 13.0%.

Macdonald's formula may be turned round to give the following expression for x (the infective gametocyte rate):

$$x = \frac{s(-\log_e p)}{a(p^n - s)}$$

The results of applying either formula to the 1967 data from Kankiya are shown (for 2 consecutive periods) in Table 6. However, the tabulated values of x are of doubtful credibility and do not appear to represent the real situation in the 2 areas. It is unlikely that an infective gametocyte rate of only 0.94% should have ruled in the untreated check area in August–September, and particularly so alongside a rate of 3.3% in the adjoining area which received regular 2-monthly control by drug administration and was, moreover, also sprayed with DDT. Such a large discrepancy suggests a need for further investigations, where longitudinal records of patent

TABLE 6
OBSERVED SPOROZOITE RATES IN *ANOPHELES GAMBIAE* AND THE INFERRED PROPORTION OF THE BITES ON MAN WHICH WERE INFECTIVE TO THE VECTOR, IN KANKIYA, NORTHERN NIGERIA, 1967

Months	Unsprayed area		DDT-sprayed area	
	Sporozoite rate ^a	x^b	Sporozoite rate ^a	x^b
Aug.–Sept.	1.6 % (252)	0.0094	0.54 % (740)	0.033
Oct.–Nov.	5.9 % (545)	0.038	(1.5 %) (131)	(0.1)

^a The numbers dissected are shown in parentheses.

^b The symbol x represents the proportion of bites on man which were infective to the mosquito (Macdonald, 1952). The values represent an application of his formula $s = \frac{p^n ax}{ax - \log_e p}$, it being assumed that the values of a , p and n remained as shown in Tables 4 and 5.

gametocytaemias would have an important part to play.

It has been suggested by Gramiccia (unpublished report to WHO) that the known high mobility of the Kankiya population (30% per annum) may easily account for the rapid increase observed in the parasite rate, since there was ample time for transmission between each drug administration. In these conditions it is likely that the increase in the infectivity of the people began before the first DDT application could be made in mid-June. Indeed, such an increase as occurred in the rainy season would presuppose a substantial infective gametocyte rate in the people constituting the source of the sporozoite rate attained, despite reduced longevity, by *A. gambiae* in August–September. It seems clear, therefore, that the treated area became both vulnerable and receptive to transmission in the wet season, notwithstanding the combined measures of attack being aimed at its interruption.

CONCLUSIONS

(1) House-spraying with DDT in June and October 1967, in an area of Kankiya District, Northern Nigeria, substantially reduced the man-biting rate and the expectation of life of *A. gambiae* species B, the principal vector of malaria. A slight reduction in the vector's man-biting habit was also apparent.

(2) It appears that direct-biting captures on collector-baits, with indoor and outdoor components, may give an exaggerated index of the man-biting

rate under the local conditions. A downward correction-factor should therefore be applied to the observed catches in the sprayed and the unsprayed areas.

(3) A reduction in the proportion of parous *A. gambiae* caught biting was observed in each of the 4 months following the first spraying. However, this observation could only be used (for estimating average longevity through the rainy season) in those months (July and September) in which vector density was high and relatively stable. On these indices it is estimated that the DDT reduced the expectation of infective life of *A. gambiae* from about 7.1 days to 0.8 day, supposing that the mean interval from infection of the vector with *P. falciparum* to its first infective bite was 12 days. This is equivalent to a longevity-factor of impact of 8.9 : 1. Since the density-factor of impact is assessed as 2.6 : 1 the over-all impact of the DDT is estimated to have been of the order of 23 : 1, but this still left *A. gambiae* with a vectorial capacity of nearly 0.5 in the months July to September.

(4) The average basic reproduction rate of *P. falciparum* in the unsprayed control area in 1967 is assessed at 1295 during the 3 months of intense transmission (i.e., those months with very high *A. gambiae* densities), and at 240 during the other 3 months of the wet season. For the DDT-sprayed area the corresponding assessments are 39.1 and 3.54. The mean of these values, 21.3, is close to a forecast reproduction rate of 17.04, derived from an amended mathe-

matical model of anticipated trends at Kankiya. Actual parasite rates were observed to increase rather rapidly from the very low level brought about by regular mass drug-administration through the preceding dry season. This was to be expected, given the presence of a vector population with a capacity of the order indicated. A probable contributory factor was the influx of people from untreated areas, and the recovery of the parasite rate illustrated the inherent high stability of the disease as shown by the entomological index of stability, which remained at 1.24 even in the presence of the DDT.

(5) The present study is considered as an exercise in epidemiological entomology, and it is suggested that the epidemiological approach to entomology should be given priority in postgraduate training for tropical medicine and hygiene, and should be recognized as a subject distinct from classical medical entomology with its emphasis on the comparative morphology and general bionomics of vectors.

(6) The study of the data from Kankiya shows that the difficulties of representative sampling and correct interpretation are still major obstacles to the assessment of each of the factors that contribute to the vectorial capacity of a mosquito population, responsible for transmitting one disease or another. Continuing efforts are needed to refine and diversify the available sampling methods, in order to increase the possibility of obtaining good indices of vector longevity, density and feeding-habit under the variety of conditions found in nature or created by man.

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RÉSUMÉ

APTITUDE D'UNE POPULATION D'*ANOPHELES GAMBIAE* À TRANSMETTRE LE PALUDISME : EXEMPLE D'APPLICATION DE L'ENTOMOLOGIE ÉPIDÉMIOLOGIQUE

L'entomologie épidémiologique peut se définir comme suit: « Echantillonnage et étude des populations de vecteurs visant à établir, d'après la prévalence du vecteur, sa longévité, son rythme d'agressivité, ses préférences trophiques, etc., une évaluation quantitative des tendances prévues ou possibles dans l'incidence du transfert d'un germe pathogène à l'hôte vertébré, et de son retour au vecteur, que ce soit avant, pendant ou après l'exécution d'une campagne de lutte. »

Les auteurs examinent les applications antérieures de divers indices entomologiques à l'étude épidémiologique du paludisme. En 1964 a été établi un indice de capacité vectorielle applicable à n'importe quel vecteur de *Plasmodium* en un lieu et à un moment déterminés. La capacité vectorielle du moustique (ou la somme des capacités des vecteurs associés) est l'équivalent de l'indice de propagation du paludisme calculé sur une base quotidienne.

La capacité vectorielle d'un anophèle réceptif à l'infection peut être exprimée par une formule mathématique qui représente le produit de plusieurs facteurs: le taux d'agressivité pour l'homme, l'espérance de vie infectante du vecteur et l'indice d'anthropophilie. Certains de ces facteurs peuvent varier considérablement selon les conditions locales et sont sujets à de rapides fluctuations. Toute mesure de lutte contre les vecteurs doit tendre à réduire un ou plusieurs de ces facteurs dans une mesure suffisante pour ramener la capacité vectorielle globale au-dessous d'un seuil critique, ce qui entraînera une régression dans la transmission du paludisme. Même s'il n'est pas possible d'atteindre toujours et partout cet objectif, un résultat d'ensemble satisfaisant pourra néanmoins être obtenu si l'on parvient à diminuer l'importance de ces facteurs de façon quasi permanente dans la plupart des zones critiques. L'indice quotidien de propagation doit être maintenu à un niveau suffisamment bas jusqu'à ce que tous les cas restants (ou importés) puissent être rapidement dépistés et rendus non infectants pour le vecteur.

L'évaluation des facteurs influant sur la capacité vectorielle, en présence ou en l'absence de mesures de lutte, constitue le rôle essentiel de l'entomologiste dans les campagnes antipaludiques. Les applications d'insecticides à action rémanente ont pour but de réduire en premier lieu l'espérance de vie infectante des moustiques, et en deuxième lieu leur taux d'agressivité pour l'homme. Les mesures antilarvaires et les moyens de lutte génétique, qui ne font que restreindre la production d'insectes adultes, sont, par définition, d'une efficacité moins grande, sauf lorsque l'éradication du vecteur peut être envisagée.

Les difficultés techniques et administratives de l'évaluation entomologique dans la plupart des pays impaludés n'ont permis de réaliser jusqu'ici que des progrès irréguliers et limités. Le plus difficile est d'obtenir tous les

mois des échantillons non biaisés de taille suffisante, en particulier si des pulvérisations sont en cours dans la zone considérée. Il faut pour cela disposer d'un personnel entomologique assez nombreux, savoir le déployer et le diriger judicieusement, choisir les techniques à bon escient et interpréter correctement les résultats.

La capacité vectorielle moyenne d'*Anopheles gambiae* à l'égard de *Plasmodium falciparum* dans un district du Nigéria du Nord a été calculée pour deux périodes différentes de la saison de transmission de 1967. Les auteurs exposent ces calculs et établissent une comparaison entre les indices observés dans une zone traitée au DDT et ceux d'une région voisine non traitée. Sont également présentées des estimations des indices de propagation de base par région et selon la période de l'année. Les données ont été recueillies par une équipe OMS de recherche sur le terrain mais on s'est référé à une analyse complète par classes d'âge des populations d'*A. gambiae* d'Afrique orientale pour interpréter les observations sur les proportions de femelles pares et déterminer la fréquence des repas de sang.

Il apparaît que le DDT a permis de réduire la capacité vectorielle d'*A. gambiae* d'un facteur voisin de 23. Néanmoins, l'indice de propagation de base est demeuré très supérieur au seuil critique (1,0). L'insecticide n'a donc pas été un moyen de lutte épidémiologiquement efficace contre le vecteur principalement responsable d'une transmission très active, bien qu'il ait permis de réduire considérablement le taux d'agressivité et la longévité du moustique.

L'indice moyen de propagation pour six mois de l'année 1967, qui s'établit à 21,3 selon les estimations entomologiques faites dans les zones traitées au DDT, concorde avec une autre estimation obtenue au moyen de modèles mathématiques basés à partir des mouvements observés de l'indice plasmodique brut.

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