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The Assessment of Insecticidal Impact on the Malaria Mosquito's Vectorial Capacity, from Data on the Proportion of Parous Females

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In malaria eradication the residual insecticide exerts upon the mosquito's vectorial capacity a direct insecticidal impact, the order of which may be measured by observing the decrease in the proportion of parous females. The impact is expressed as the product of the degree of reduction of the expectation of infective life (termed the longevity factor of impact) and that of the expectation of life (the density factor). To compute the factors from the proportion parous it is necessary to know also the mean difference in age between the nulliparous and the youngest parous females in the sample, and the sporogonic period of the parasite.

Graphs are presented to enable the field worker, who has observed these parameters, to read off from his data the proportion surviving one day, the expectation of infective life and the expectation of life. Examples from the field are used to illustrate the manner of computing the direct insecticidal impact with the aid of the graphs. It is emphasized that this method can only measure the relative impact on vectorial capacity, and will not show whether the actual level of vectorial capacity is such that a malaria reproduction rate of <1 is indicated.

In the attack phase of malaria eradication, female mosquitos are killed by the insecticide and the female's expectation of life is thus shortened. In this way the existing female population, or density, is reduced, at the same time that the female's expectation of *infective* life is reduced to a much greater degree.

These combined effects may be said to represent the total insecticidal impact produced on the malaria mosquito's vectorial capacity. They constitute the direct object of the attack, and any good measurement of them will be valuable as an indication of whether the insecticide is likely to achieve its epidemiological objective, which is to bring all malaria transmission to an end. In this paper a means is suggested of measuring the insecticidal impact on the vector's capacity to transmit the disease.

The meaning of the term " vectorial capacity " in the present context is the following: the average number of inoculations with a specified parasite, originating from one case of malaria in unit time, that a vector population would distribute to man if all the vector females biting the case became infected. Vectorial capacity is thus a density-dependent attribute of the mosquito, unlike its " vector efficiency " as defined by the World Health Organization (1963). The relationship of vectorial capacity to the basic reproduction rate of malaria will be explained in the discussion (below).

The presence of insecticide in houses may also produce indirect effects which, not being strictly-speaking insecticidal in nature, do not enter into the measurement of insecticidal impact. Nevertheless they may exercise an important long-term influence on vectorial capacity, and three of them must be mentioned here. First, the mosquito may be irritated or repelled within the sprayed house or be deterred from entering it, and in this manner a reduction may be caused in the human blood index. Secondly, a similar reduction in the degree of association with man may be brought about by selection in favour of zoophily in the mosquito. And thirdly, the reduced female density due to kill may lead to a progressive reduction in output from the breeding places, so that

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the population will be further reduced in succeeding generations because this effect is superimposed on the direct impact. This will be referred to again in the discussion of the value of the index to be described here.

METHODS OF AGE-GRADING IN RELATION TO INSECTICIDAL IMPACT

No way is known of measuring directly the expectation of infective life of a mosquito population. The least indirect technique is that of Polovodova (1949), further developed by Detinova (1962): the parameter measured is the proportion of the dissected sample that has oviposited a given number of times, implying that the mosquito has attained at least the age when sporozoites would be expected to reach the salivary glands following infection at the first blood-meal. This proportion is expressed in Macdonald's (1957) notation as p^n (the probability of survival through n days) where p = the probability of survival through one day and n corresponds to the sporogonic period of a specified parasite.

From a known value of p^n the female's expectation of life may be computed, assuming the proportion of females surviving through one day to be the same for all age-groups. The product of p^n and the expectation of life would then express the expectation of infective life—that is to say, the average number of days of infective life per infected mosquito.

A serious drawback of this technique is the difficulty of the dissection itself, especially when applied to the smaller vector species (see Detinova & Gillies, 1964; Giglioli, 1963). Coupled with that difficulty is one of sampling: in any sprayed area the proportion of females reaching epidemiologically dangerous age should be small or very small; therefore the sample must be correspondingly large in order to include a statistically adequate number of specimens of dangerous age. It is not always feasible to collect a large enough sample from a limited area in the course of one month.

For routine work it is usual to rely on a simpler and quicker dissection, designed to determine the proportion of parous mosquitos in a selected sample. Where the rhythm of feeding is regular, this proportion may be considered as equivalent to p^2, p^3, etc. (Davidson, 1954, 1955). The relevant power of p depends on the difference, in days, between the mean age of the nulliparous specimens in the sample and that of the primiparous specimens in it. For practical purposes, this interval is often equated with the period of the gonotrophic cycle, or the oviposition interval, of the species,[1] which is justified provided there is no reason to suppose that the female's first batch of eggs takes longer to mature than the succeeding batches. As Davidson has emphasized, it is important that all the mosquitos included in the sample should be in approximately the same stage of ovarian development when collected. Thus, in a sample captured at rest when in stage III, the two youngest age-groups represented might be 3 and 5 days old; or in a sample of the same mosquito caught biting while in stages I and II, the mean ages of these groups might be 2 and 4 days. The proportion parous in either sample would represent p^2, the oviposition interval being two days.

It is supposed that in most *Anopheles* mosquitos the female normally takes a single blood-meal about the second day of adult life, develops and lays her eggs, and then seeks a fresh blood-meal to develop each succeeding batch of eggs. Excluding any period of seasonal diapause, a regular rhythm of blood-feeding and oviposition is believed to be maintained through life, the tempo depending principally on the species of mosquito and the mean temperature of the habitat. However, Gillies (1954) showed that in *Anopheles gambiae* on the East African coast two blood-meals are normally taken during the first gonotrophic cycle and the majority of females mate *after* the first feed. That means an irregular rhythm of feeding is likely to occur in some populations of *A. gambiae*, and that the nulliparous fraction of a biting sample will represent two age-groups instead of one. While such a condition has not been found so far in other vectors, it would be imprudent to conclude that it does not exist. To meet the rather complex possibilities raised by such irregularity, the daily survival rates computable for mosquitos having various irregular feeding-rhythms are given in an annex to the present paper.

In dissections for the proportion parous, not so large a sample is necessary, since this proportion is likely to be substantial even in a sprayed area. On the other hand the calculation of p^n, and still more

[1] In this context the concept of the oviposition interval, or mean number of days between ovipositions, is preferred to that of the gonotrophic cycle. The former may be a longer period owing to a delay, either in laying the eggs after maturation, or in seeking a blood-meal following oviposition (see Hamon et al., 1961; Hamon, 1963). The term " gonotrophic cycle " has also been used—e.g., by Gillies & Wilkes (1963)—to cover the whole interval from one blood-meal to the next, making it equivalent to the oviposition interval (see World Health Organization, 1963, p. 54).

that of the expectation of infective life, from an observed value corresponding to p^2 or p^3 involves the important assumption that the probability of survival through one day is uniform from the time of the first blood meal up to an advanced age. It would be unsound to estimate longevity from the proportion parous where there is reason to think that the value of p varies widely between different age-groups (see below, under " Discussion ").

Of several methods for determining the proportion parous the most widely used are those depending on measurement of the ampulla (Mer, 1932; Davidson, 1954, 1955) and on the coiling of the tracheoles of the ovaries (Detinova, 1945). Three methods of dissection, as well as alternative methods of sampling mosquito populations for this purpose, were compared by Hamon et al. (1961). They concluded that the changes in the ampulla are not a reliable guide to parity in the various species studied by them, while use of the coiling of the ovarian tracheoles is reliable only for mosquitos in stages I to late II of ovarian development. They preferred the latter method, applied only to samples caught biting man, kept chilled, and dissected within a few hours; the bulk of each species sampled was then in these stages, and the few specimens in later stages could be examined by another method or else be discarded. In the sprayed area adequate monthly samples were more easily collected while biting than at rest. Furthermore, it was found that some samples (notably of *A. funestus*) from artificial shelters in the unsprayed area contained an unduly high proportion of nullipars.

Any sampling of resting mosquitos is likely to include unfed nullipars. This may render it impossible to calculate the expectation of life of the infected mosquito, since these very young females probably have a higher daily mortality rate than the others and, in any case, their inclusion makes it harder to estimate the mean age-interval between the nulliparous and the primiparous fractions of the sample. Thus Brady (1963), who dissected spray-caught samples of *A. gambiae* and *A. funestus* in Ghana and demonstrated differences in the proportions parous according to the stages of blood-digestion and ovarian development, considered it more prudent not to calculate values of p from his data.

Care to avoid bias is also necessary, however, in collecting biting samples for age-grading dissection. The capture should continue through the whole period of biting-activity of the species, since different age-groups may tend to feed at different hours, as observed by Hamon and his co-workers at Bobo-Dioulasso.

As the killing of mosquitos reduces longevity and density, it is convenient, in assessing these effects quantitatively, to refer to the " longevity factor " and the " density factor " of insecticidal impact. The values of a known power of p, ascertained before and after spraying, can provide indices of both factors. It is clear that the longevity factor, of which the expectation of infective life is the index, depends on the sporogonic period and must be related to a specified parasite as well as to a particular species of mosquito: we may refer, for example, to " the longevity factor (*P. falciparum*) of impact on *A. gambiae* " at a given time and place. This is not true of the density factor, which relates to the mosquito alone.

DERIVATION OF THE LONGEVITY FACTOR OF INSECTICIDAL IMPACT FROM THE PROPORTION PAROUS

The longevity factor of impact may be deduced from information on the proportion parous, the oviposition interval and the sporogonic period. This task is essential for rendering the proportion parous into terms of epidemiological significance in relation to malaria transmission.

Table 1 is a conversion table, adapted from the first table in Macdonald (1957). It shows a series of values of p^3 and p^2 (expressions representing the proportion parous where only one blood-meal is taken before the first oviposition, and the oviposition interval is 3 days or 2 days, respectively), and corresponding values of the probability of survival through one day, the expectation of life, and the expectation of infective life. The last-mentioned index is tabulated for sporogonic periods of 9-14 days, covering most of the range considered normal for *P. vivax* and *P. falciparum* in warm climates (Macdonald, 1952).

For practical purposes, a table is less useful than a graph, which permits the interpolation of intermediate values. By making use of Fig. 1 the value of p can be read off from a known proportion of parous mosquitos where it has been established that the latter is equivalent to p^2, $p^{2\cdot5}$, p^3 or p^4. The inclusion of the second term is intended to cover seasons or conditions where the oviposition interval is believed to be two days in some specimens and three days in others.

TABLE 1

CONVERSION FROM VALUES OF VECTOR'S PROPORTION PAROUS (WHERE THIS CORRESPONDS TO p^3 OR p^2), TO ITS EXPECTATION OF INFECTIVE LIFE, FOR PARASITES EXHIBITING SPOROGONIC PERIODS OF 9-14 DAYS [a]

p^3	p^2	p	Expectation of life (days)	Expectation of infective life (days) where sporogonic period is:					
				9 days	10 days	11 days	12 days	13 days	14 days
0.857	0.903	0.95	19.5	12.3	11.7	11.1	10.5	10.0	9.51
0.729	0.810	0.90	9.49	3.68	3.31	2.98	2.68	2.41	2.17
0.614	0.723	0.85	6.15	1.42	1.21	1.03	0.875	0.744	0.630
0.512	0.640	0.80	4.48	0.601	0.481	0.385	0.308	0.246	0.197
0.422	0.563	0.75	3.48	0.261	0.16	0.147	0.110	0.083	0.0620
0.343	0.490	0.70	2.80	0.113	0.0791	0.0554	0.0388	0.0271	0.0190
0.275	0.423	0.65	2.32	0.0481	0.0312	0.0203	0.0132	0.00858	0.00558
0.216	0.360	0.60	1.96	0.0198	0.0119	0.00711	0.00427	0.00256	0.00154
0.166	0.303	0.55	1.67	0.00769	0.00423	0.00233	0.00128	0.000704	0.000387
0.125	0.250	0.50	1.44	0.00281	0.00141	0.000703	0.000352	0.000176	0.000088

[a] The figures in each line are calculated from the given value of p, representing probability of survival through one day. Expectation of life is expressed as $\frac{1}{-\log_e p}$ and expectation of *infective* life as $\frac{p^n}{-\log_e p}$, where n is the value (in days) of the sporogonic period.

Having thus determined the probability of survival through one day, the user may proceed in the same manner to obtain a reading of the expectation of infective life, by using Fig. 2. Six curves are shown, permitting application of the method for any sporogonic period of between 9 and 14 days that may have to be considered, according to the species of parasite and the mean temperature during the observations. The scale marked on the ordinate is logarithmic, and it is obvious from the steepness of the curves that quite a small change in the value of p will mean a much larger one in the expectation of infective life. For example, reduction in a vector's daily survival rate from 0.9 to 0.8 would entail a reduction from 2.68 days to 0.308 days in its expectation of infective life with a parasite having a sporogonic period of 12 days. The lower value is equivalent to survival through only one day of infective life by about one female mosquito in three.

The example cited indicates how the longevity factor of insecticidal impact is to be derived. The age-grading data required consist of observations on the proportion parous at various seasons before the application of insecticide and repeated observations at the corresponding seasons after its application. Alternatively, the observations can be made concurrently in the sprayed area and in a comparable unsprayed area with the same vector species. The longevity factor of impact is given as the ratio of the pre-spray to the post-spray values of the expectation of infective life, a ratio which would be 2.68:0.308, or 8.7:1, in the hypothetical example given above.

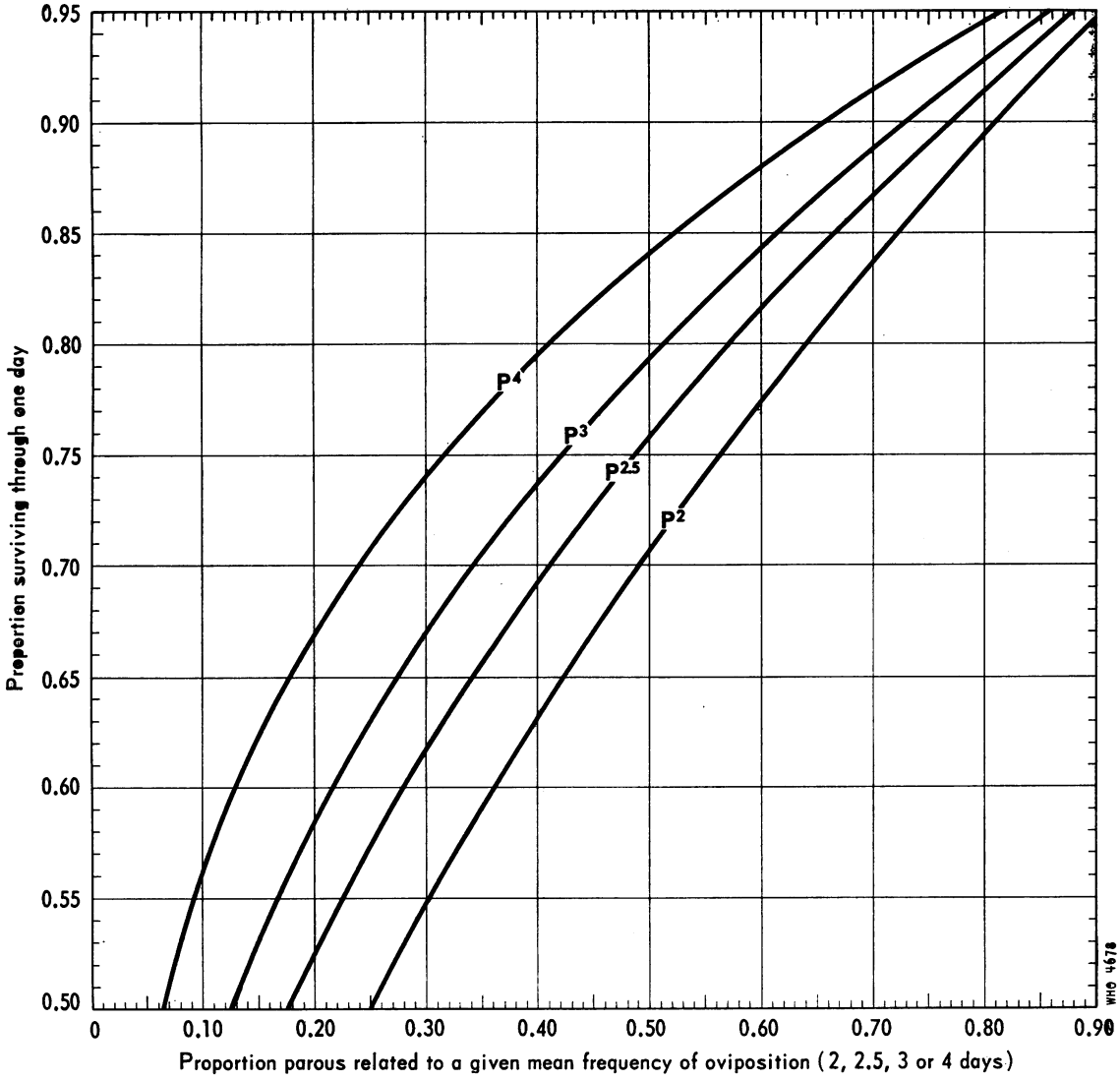
DERIVATION OF THE DENSITY FACTOR OF IMPACT

As has been pointed out by Macdonald (1957), the actual density of a mosquito population is one of the most difficult parameters to measure in the field; in fact it must usually remain an unknown quantity, except where it is certain that the great majority of all the female mosquitos is resting indoors and where a total collection of these can be made in a representative sample of indoor capture-stations.

It may seem unlikely at first that the proportion parous—essentially a measure of longevity—can also serve to tell us something about density. But although it is true that this measure can give us no clue to absolute density or to the density of mosquitos relative to that of man, *changes* in the proportion parous can readily yield a measure of *changes* in density that are due to the killing of

FIG. 1

CURVES FOR DERIVING THE PROPORTION SURVIVING THROUGH ONE DAY (p) FROM OBSERVED PROPORTIONS PAROUS REPRESENTING p^2, $p^{2.5}$, p^3 or p^4

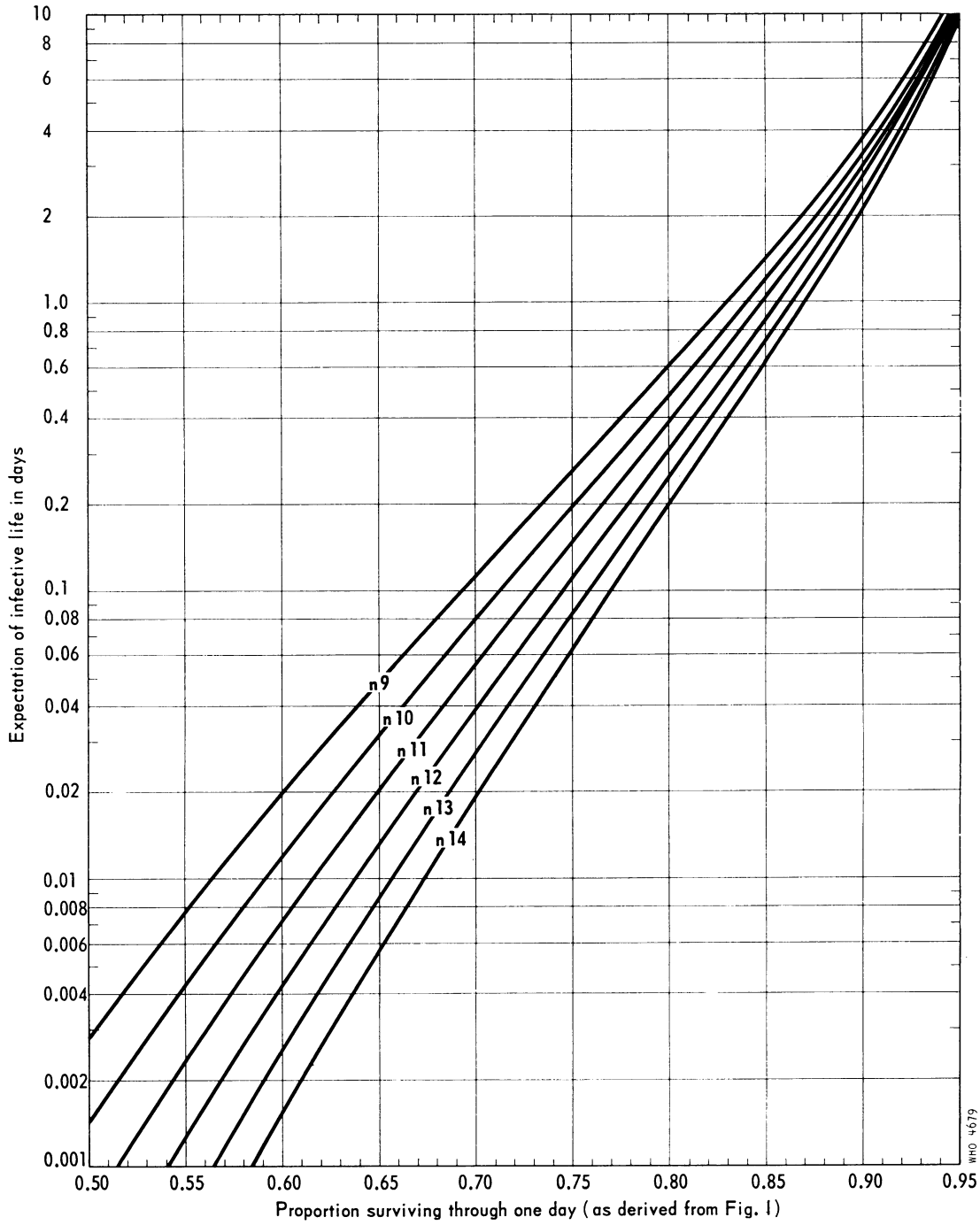


mosquitos by (and in the presence of) the insecticide. This is because, statistically speaking, the reduction in density produced by increased hazards of life in any given population is exactly proportional to the decrease in its expectation of life, expressed by the formula $\frac{1}{-\log_e p}$. In other words, a known change in the expectation of life due to the presence of insecticide will tell us how many times greater the density of the female mosquitos would be, at the given time and place, if all the sprayed surfaces were suddenly wiped clean of insecticide.

Thanks to the direct relationship between expectation of life and density, the reduction observed in the former following the application of insecticide may be used as an index of the density factor of insectici-

FIG. 2

CURVES FOR DERIVING THE EXPECTATION OF INFECTIVE LIFE OF THE VECTOR FROM KNOWN VALUES OF p, FOR SPOROGONIC PERIODS OF 9 TO 14 DAYS IN THE PARASITE



dal impact, just as the reduction in the expectation of *infective* life may serve to measure the longevity factor of that impact. The density factor is expressed as the ratio of the pre-spray to the post-spray value of the expectation of life, derived from the respective proportions parous. Curves to facilitate the derivation in a single step from proportions parous equivalent to p^2, $p^{2.5}$, p^3 and p^4 are given in Fig. 3, while the conversion from p to $\frac{1}{-\log_e p}$ is also shown in Table 1. To take again the hypothetical example already cited, where it was supposed that p was reduced from 0.9 to 0.8, it will be seen from Table 1 that this means a reduction from 9.49 to 4.48 days in the expectation of life—a ratio of 2.12:1 for the density factor.

ESTIMATION OF THE TOTAL INSECTICIDAL IMPACT IN A SPRAYED AREA

Having determined the sporogonic period of the parasite and the rhythm of feeding and oviposition of the vector mosquito, together with the proportions parous in biting samples in unsprayed and sprayed areas, the investigator can derive the factors of insecticidal impact in the manner indicated. The total insecticidal impact, likewise expressed as a ratio, is then easily computed by multiplying the two factors.

We would emphasize again that by " total insecticidal impact " is meant, in the present context, the insecticide's direct influence, by killing mosquitos or accelerating their death from other hazards, upon the capacity of a population to distribute infective bites from a unit source in unit time. This is likely to be the principal short-term effect of spraying upon the incidence of malaria. Any effects of a non-insecticidal nature, such as a change in the human blood index or a reduction in the output from the breeding places, whatever their strategic importance in stopping transmission by certain vectors, are not expected to be immediately and generally operative in all sprayed areas.

For a simple example of the computation of total insecticidal impact we may turn once more to the supposed instance of the daily survival rate of a vector of *P. falciparum* being reduced from 0.9 to 0.8. It was seen that:

(*a*) the longevity factor of impact was 8.70:1, and

(*b*) the density factor of impact was 2.12:1.

Therefore the total insecticidal impact in this instance would be (8.70 × 2.12):1, or 18.4:1. That is, the rate of distribution of infective bites per case per day, by a vector population subject to that degree of insecticidal control, would be 18.4 times less than in the absence of the control.

In algebraic terms, the total insecticidal impact is expressed by combining the formulae for the two factors of impact as follows: [1]

$$\frac{1}{-\log_e p} \times \frac{p^n}{-\log_e p} = \frac{p^n}{(-\log_e p)^2}$$

In our experience, there is no need to understand the meaning of these formulae, nor of expressions like "$-\log_e p$" when applying the method proposed in this paper to data obtained in the field. The user has merely to employ the appropriate graphs for reading off, from the observed proportions parous before and after spraying, the values of the expectation of life and the expectation of infective life. Having these four values, he may multiply the two parameters for each area (or each phase of the programme), thus obtaining two figures whose ratio represents the total insecticidal impact. If the estimation is regularly repeated in the attack phase its epidemiological usefulness is clear, since it should be possible to follow any weakening of the impact on the vector from month to month (within one round of spraying) and from year to year (as a result of selection pressure).

Before giving examples from field practice it may be helpful to see the full implications of the hypothetical example used in the foregoing pages. This will show at the same time (Table 2) how a given impact is necessarily greater on the mosquito's vectorial capacity for *P. falciparum* than for *P. vivax*, and greater still for *P. malariae*, owing to the different sporogonic periods of these parasites. The situation envisaged in Table 2 is one where the vector's oviposition interval is two days and where the sporogony of *P. vivax* takes 9 days, that of *P. falciparum* 12 days and that of *P. malariae* 20 days.

EXAMPLES OF INSECTICIDAL IMPACT, ESTIMATED FROM PUBLISHED DATA

Examples will be given from West Irian (Indonesia) and Upper Volta. In both, the values of the

[1] The authors are indebted to Professor G. Macdonald of the Ross Institute, London, for pointing out that the pre-spray: post-spray ratio may also be expressed as

$$\frac{p_1^n(-\log_e p_2)^2}{p_2^n(-\log_e p_1)^2}$$

where p_1 signifies the daily survival rate before spraying and p_2 the rate after spraying.

FIG. 3
CURVES FOR DERIVING THE EXPECTATION OF LIFE FROM OBSERVED PROPORTIONS PAROUS REPRESENTING p^2, $p^{2.5}$, p^3, OR p^4

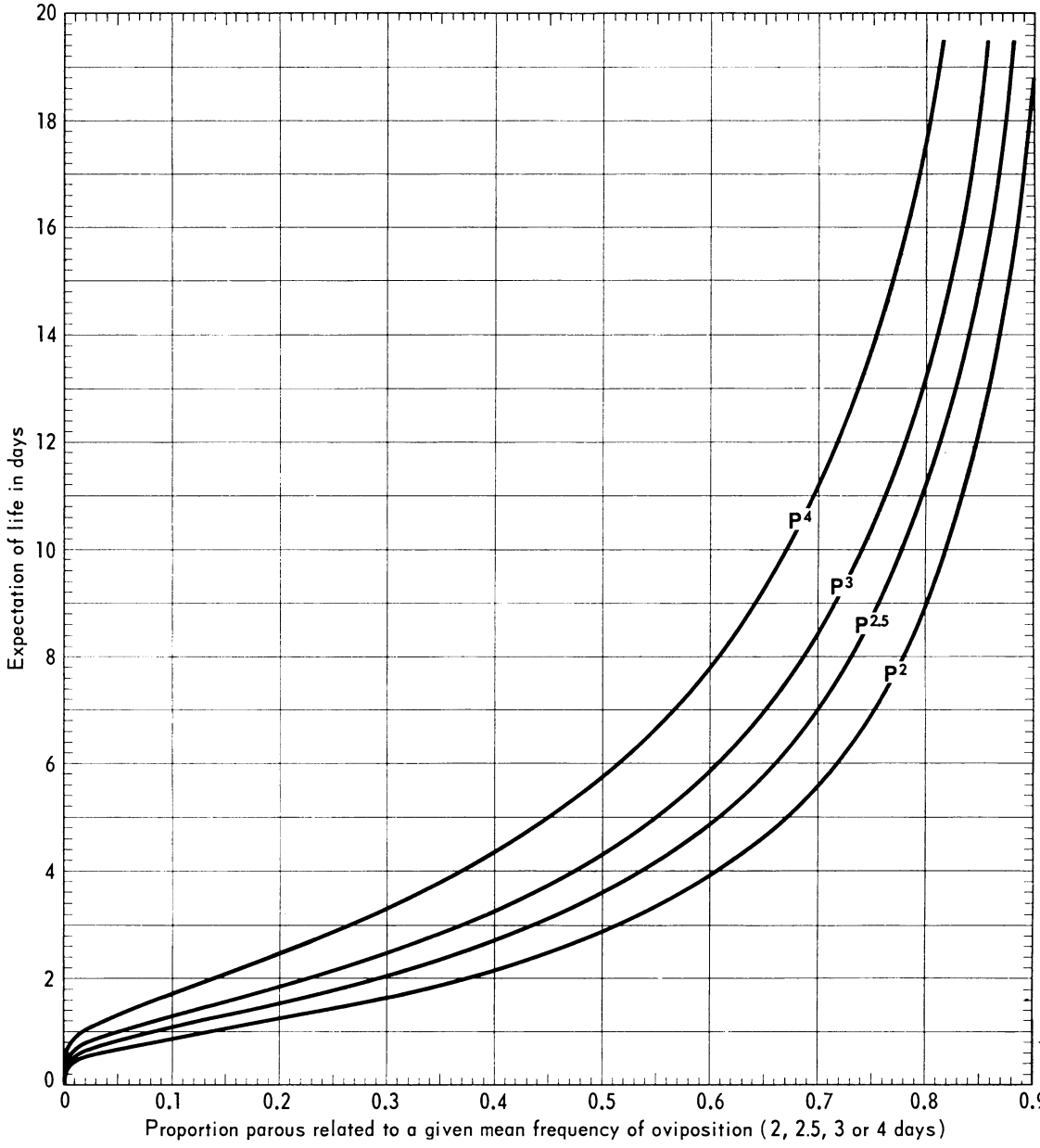


TABLE 2

INSECTICIDAL IMPACT ON A MOSQUITO'S VECTORIAL CAPACITY FOR THREE MALARIA PARASITES, SUPPOSING p IS REDUCED FROM 0.9 TO 0.8

Parameter	Pre-spraying value			Post-spray value		
Proportion parous	0.810			0.640		
Proportion surviving through one day	0.90			0.80		
Expectation of life (days) (EL)	9.49			4.48		
	P. v.	*P.f.*	*P.m.*	*P.v.*	*P.f.*	*P.m.*
Expectation of infective life (days) (EIL)	3.68	2.68	1.15	0.601	0.308	0.051
Product of factors (EL × EIL)	34.9	25.4	10.9	2.70	1.38	0.228
Ratio of products, pre-spray: post-spray	*P. vivax* 12.9 : 1		*P. falciparum* 18.4 : 1		*P. malariae* 47.8 : 1	

expectation of life and the expectation of infective life have been computed by the present writers by applying the graphs in this paper to the data recorded by the scientists in the field.

The proportions of parous mosquitos shown in Table 3 are those given by Slooff (1964) for Entrop (a village in the DDT-sprayed zone of Hollandia, West Irian) and for the unsprayed village of Arso, lying some 65 km into the interior. The table shows the impact of DDT on the capacities of two vectors to transmit *P. vivax*, with a sporogonic period of 10 days. The third vector of the group, *A. punctulatus*, was found to be too scarce in the sprayed village for measurement of the proportion parous. In this study, samples were collected biting man in the open and were dissected within 12 hours, using the technique of Detinova (1945). Owing to a delay between oviposition and feeding, Slooff considered the mean oviposition interval in all the vectors to be 2.5 days. The data are crude means, unrelated to the date of spraying. Here the assumption is made that the natural longevity of the respective vectors at

TABLE 3

THE FACTORS OF INSECTICIDAL IMPACT OF DDT ON TWO MALARIA VECTORS AT ENTROP, WEST IRIAN [a]

Species and locality	Proportion parous (and no. in sample)	Proportion surviving 1 day	Density factor		Longevity factor (*P. vivax*)		Total impact
			Expectation of life (days)	Ratio (A) : (B)	Expectation of infective life (days)	Ratio (A) : (B)	Product of ratios (A) : (B)
	$p^{2.5}$	p	$\frac{1}{-\log_e p}$		$\frac{p^{10}}{-\log_e p}$		
A. koliensis							
(A) Arso	0.675 (557)	0.855	6.4	1.5 : 1	1.31	3.4 : 1	5.1 : 1
(B) Entrop	0.553 (599)	0.788	4.18		0.385		
A. farauti							
(A) Arso	0.755 (98)	0.895	8.85	1.9 : 1	2.95	5.5 : 1	10.5 : 1
(B) Entrop	0.582 (1412)	0.806	4.6		0.535		
A. punctulatus							
(A) Arso	0.654 (572)	0.845	5.88	—	1.10	—	—

[a] From mean values of proportions parous given by Slooff (1964).

Entrop would have been the same as that observed at Arso.

It is clear from the calculations shown in the table that the over-all impact of the DDT on the vectorial capacity of these mosquitos to transmit *P. vivax*, and therefore on the " communicability " or " daily reproduction rate " of that disease, was relatively slight and could not be expected to lead to the interruption of transmission in an area of naturally high and perennial incidence. There are, however, two reservations to this conclusion: first, that *A. punctulatus*, which became rare at Entrop, might possibly have been the main vector before the attack with residual insecticide; and secondly, that a monthly break-down of the sampling might have revealed a much larger impact on the vectorial capacities of the other vectors in the first month or two following each DDT spray-round. It is the weakness of the average impact shown by Slooff's results that points to a prognosis of persisting *P. vivax* transmission (and probably of *P. falciparum* transmission also) under the form of attack ruling at the time of his field study.

Gruchet (1962) measured the proportion of parous *A. funestus* through 12 months in a dieldrin-sprayed district of Madagascar, using several sampling methods: capture on human baits indoors and out, capture by day in sprayed and in unsprayed houses, and capture in artificial outdoor shelters. He obtained statistically significant differences in the proportion parous, according to the method of sampling, and concluded that only the bait-captures and those in outdoor shelters far from the houses could be relied upon to give unbiassed samples with regard to age.

Bait-capture was also the sampling method preferred by Hamon (1963), who conducted intensive measurements of the proportions parous in all the man-biting anophelines of the Bobo-Dioulasso district (Upper Volta) over a period of 18 months, using Detinova's (1945) technique (supplemented by examination for the presence of follicular relics in a small proportion of each sample). The samples were collected biting man in the open in five unsprayed villages and in 11 villages and hamlets sprayed once a year (before the onset of the rains in May) with DDT at 2.2 g/m². Table 4 gives the crude mean values for only the four best-sampled species (as shown in Table 2 of the original account). The derivations of the longevity factor refer to the pre-

TABLE 4

THE FACTORS OF INSECTICIDAL IMPACT OF DDT ON FOUR MALARIA VECTORS AT BOBO-DIOULASSO, UPPER VOLTA [a]

Species and area	Proportion parous (and no. in sample)	Density factor		Longevity factor (*P. falciparum*)		Total impact
		Expectation of life (days)	Ratio (A) : (B)	Expectation of infective life (days)	Ratio (A) : (B)	Product of ratios (A) : (B)
	p^3	$\frac{1}{-\log_e p}$		$\frac{p^{12}}{-\log_e p}$		
A. gambiae						
(A) unsprayed	0.685 (1382)	8.0	2.2 : 1	1.8	12 : 1	26 : 1
(B) DDT-sprayed	0.446 (702)	3.7		0.15		
A. funestus						
(A) unsprayed	0.745 (2437)	10.2	2.2 : 1	3.05	8 : 1	18 : 1
(B) DDT-sprayed	0.527 (792)	4.7		0.37		
A. nili						
(A) unsprayed	0.590 (295)	5.8	1.6 : 1	0.70	5 : 1	8 : 1
(B) DDT-sprayed	0.444 (2325)	3.6		0.145		
A. coustani						
(A) unsprayed	0.702 (215)	8.5	1.8 : 1	2.05	6 : 1	10.8 : 1
(B) DDT-sprayed	0.522 (1896)	4.6		0.35		

[a] From mean values of proportions parous between June 1959 and December 1960, given by Hamon (1963).

TABLE 5
TOTAL INSECTICIDAL IMPACT OF DDT ON VECTORIAL CAPACITY (*P. FALCIPARUM*) OF *A. GAMBIAE* AND *A. FUNESTUS* AT BOBO-DIOULASSO IN CERTAIN MONTHS OF 1959/60 [a]

Month [b]		*A. gambiae*			*A. funestus*		
		Proportion parous	Product of factors	Total impact	Proportion parous	Product of factors	Total impact
June	A	0.65 (130)	8.95	27 : 1	0.81 (53)	81	—
	B	0.39 (76)	0.243		—	—	—
July	A	0.58 (299)	3.47	20 : 1	0.66 (126)	10.2	2.9 : 1
	B	0.37 (84)	0.177		0.58 (101)	3.47	
Aug.	A	0.74 (391)	29.5	29 : 1	0.52 (204)	1.56	2.0 : 1
	B	0.49 (109)	1.01		0.47 (107)	0.79	
Sept.	A	0.70 (213)	17.2	338 : 1	0.65 (259)	8.95	2.9 : 1
	B	0.30 (118)	0.051		0.57 (84)	3.08	
Oct.	A	0.77 (138)	45.2	—	0.71 (543)	19.5	60 : 1
	B	—	—		0.41 (113)	0.328	
Nov.	A	—	—	—	0.84 (618)	139	66 : 1
	B	—	—		0.54 (68)	2.10	
Dec.	A	0.60 (62)	4.55	1 : 1.7	0.81 (505)	81	20 : 1
	B	0.64 (138)	7.61		0.59 (147)	4.06	
Feb.	A	—	—	—	0.71 (62)	19.5	25 : 1
	B	—	—		0.47 (73)	0.79	
Mean values for 18 months (June 1959-Dec. 1960)							
	A	0.685	14.4	26 : 1	0.745	31.1	18 : 1
	B	0.446	0.56		0.527	1.74	

[a] From observations in Hamon (1963), Table 4.
[b] Line (A) refers to unsprayed, line (B) to DDT-sprayed villages. Numbers in samples are shown in brackets. No calculation made where sample contained fewer than 50 mosquitos.

valent parasite, *P. falciparum*, with a sporogonic period of 12 days. The equation of the proportion parous with p^3, rather than p^2, may cause surprise: it is based on the investigators' observation (Hamon et al., 1961) that " in nature the lapse of time between two successive ovipositions is certainly on an average considerably longer than the duration of the gonotrophic cycle "—a conclusion confirmed by Hamon (1963).

The data indicate over-all longevity factors (*P. falciparum*) of DDT impact of about 12:1 on *A. gambiae*, 8:1 on *A. funestus* [1], 5:1 on *A. nili* and 6:1 on *A. coustani*. But these calculations are of doubtful significance until subjected to a month-by-month break-down. That is done in Table 5 for the two principal vectors.

It would be beyond the scope of this paper to discuss the results revealed by this computation. It may be noted, however, that the DDT deposits were fairly new in June and oldest in February. The wettest months were July, August and September. The relative monthly prevalence of each species is reflected in the varying size of the samples dissected. The variations in monthly impact shown in Table 5 may be compared with the " relative reduction of the proportion parous ", given for these vectors in Table 21 of Hamon's (1963) original paper and discussed by him. It may be that some of the samples tabulated here (for instance, those of *A. gambiae* in September and December) were too small to give any reliable index of insecticidal impact. A possible

[1] As may be noted in Table 4, the natural mean proportion parous in *A. funestus* at Bobo-Dioulasso was 0.745. By an interesting coincidence, Gillies & Wilkes (1963), who dissected 14 000 *A. funestus* in an unsprayed area of Tanganyika, concluded that the proportion parous, representing p^3, varied between 0.73 and 0.76 according to season. They therefore estimated the value of p as about 0.90-0.91 in that species.

explanation for the small impact on *A. funestus* in the wettest months is the abundance of outdoor cover then available, as noted by Hamon, for resting mosquitos, combined with the high irritability of that species to DDT.

DISCUSSION

It is of some importance to state clearly the nature and purpose of the assessment of insecticidal impact and its limitations. Entomology has relied in the past upon partial indices (such as the density of resting mosquitos, larval density, densities in baited traps, mortalities in outlet-traps, or the proportion parous itself) as the best available indications of the impact of insecticide on the vector. Valuable as these can be, the epidemiological judgements to which they lead are essentially empirical, or at best qualitative, judgements.

Subject to unbiassed sampling of the females coming to bite when in stages I and II of ovarian development, the assessment now proposed will give a true measure of the degree of reduction of the mosquito's vectorial capacity, resulting from the shortening of its life in the presence of insecticide: the shortening of life due to kill by intoxication on the one hand, plus any additional shortening due to an increase in general hazards to its life in the sprayed area. Conversely, it will give a measure of the degree of recovery of vectorial capacity in the event of selection leading to insecticide resistance or avoidance, and resulting in increased longevity despite the continuing presence of the insecticide.

The assessment will *not* reflect any change in vectorial capacity occasioned by (*a*) a deviation of females from human to animal hosts in the sprayed area, or (*b*) a change in the output of females from the breeding places, or (*c*) any selected behavioural change not affecting longevity.

The assessment is one of relative impact, not absolute impact. It is expressed as a ratio (pre-spray: post-spray), and thus depends on the possibility of obtaining a pre-spray base-line datum—or alternatively, a base-line datum from a check area comparable to the sprayed area, obtained concurrently with the post-spray datum. This alternative is not available in countries under general insecticidal coverage, whether it be the house wall or the vegetation that is sprayed.

The basis of the longevity factor of insecticidal impact—namely, the expectation of infective life—is also used in computing absolute vectorial capacity and the daily and basic reproduction rates (Macdonald, 1957; Garrett-Jones, 1964). On the other hand, the density-factor of insecticidal impact, given by the expectation of life, is a purely relative measurement in this context, in that it reflects only the degree of automatic reduction of female density by kill, without telling us what the actual density was (relative to that of man, or to the locality) before or after spraying. The distinction is an important one. In fact it is one of the attractions of this assessment, that it enables us to evaluate the impact of spraying upon density while side-stepping the extremely awkward problems of measuring actual densities of the mosquito in the field.

The relationship of the density factor of impact to the man-biting rate [1] may be explained as follows. The former, as we have seen, reflects only the shortening of the mosquito's expectation of life in the sprayed area. The change in the man-biting rate, on the other hand, will reflect this shortening of life *and* any changes that may occur in the human blood index or in output from the breeding places, or both. Where the spraying of an area does not result in either of these last-mentioned changes, the reduction of the man-biting rate should logically proceed *pari passu* with that of the expectation of life, and a density factor of, say, 5:1 should be matched by a corresponding ratio of the pre-spray: post-spray man-biting rate. In these circumstances—and they may well be the normal ones in those areas where the vector is able to stabilize its mean density despite the insecticide—it should be useful to measure both indices and to check one against the other: the finding of corresponding fluctuations in expectation of life and man-biting rate will indicate that insecticidal kill is the only important factor operating to restrict the incidence of man-mosquito contact. If the man-biting rate appears to be reduced by much *less* than the expectation of life, there is probably some serious bias in the method of measuring one index or another. Alternatively, if the reduction in the man-biting rate is found to be significantly *greater* than the density factor of impact, this may indicate a deviation of mosquitos to animals (i.e., reduction of the human blood index) and/or a reduced output from the breeding places in the sprayed area. For example, in an area where selection for zoophily is

[1] The biting rate is defined in World Health Organization (1963) as the " average number of mosquito bites received by a host in unit time, specified according to host and mosquito species. The man-biting rate has been defined by Garrett-Jones (unpublished document WHO/Mal/450) as " the index of actual incidence of contact between man and mosquito ".

going on under pressure from insecticide one would expect the mosquito to exhibit a stable (or perhaps a rising) expectation of life, associated with a falling man-biting rate. Such a pattern would give grounds to suspect that selection of this type is operating.

Regarding the vector's expectation of infective life, it is sometimes objected that a mosquito may become infected at any age, so that its real average age of infectivity is greater than the value of n days representing the " epidemiologically dangerous age ". This is a fact, but reflection will show that it does not affect the calculations made in this paper. We are not concerned here with the age of the mosquitos as such, but with the future longevity of females *of mixed ages*, at the time of biting. They will have the *same* expectation of life, and of infective life, as would a sample of mosquitos all taking their first blood-meal—always on the assumption that the daily survival rate is substantially constant for all age-groups between the first blood-meal and, say, the tenth.

Epidemiologists in malaria eradication are interested in criteria of the absence of malaria transmission, and in criteria assuring them that the incidence of transmission is on the decline and will eventually cease if this trend can be maintained. It should be pointed out that the assessment of insecticidal impact meets neither of those requirements. As long as any vector females continue to bite people, there remains the theoretical possibility of a case of transmission occurring, since the vector always has a statistical expectation of infective life, however small it may be. A zero man-biting rate is the only entomological criterion of the *absence* of malaria transmission. The *trend* of transmission is, on the contrary, a mainly entomological matter (apart from the recovery rate, which is controlled by the detection and treatment of cases). It is a function, not of the relative reduction of vectorial capacity (indicated by the assessment now proposed) but of its absolute level, expressed as the product of the man-biting rate, the expectation of infective life, and the man-biting habit (Garrett-Jones, 1964).

The level of the mosquito's vectorial capacity at any place and time (or the sum of capacities of associated vectors) represents the daily reproduction rate of malaria—that is, the daily fraction of the basic reproduction rate. The daily reproduction rate is the same entity as the " communicability " of malaria (Moshkovski) [1], one of the two " epidemiological parameters " in his quantitative approach to the study of trends in malaria endemicity. He defines communicability as " the measure of the ' facility of transmission ' of the disease ", which, in malaria, " corresponds to the average number of infective bites inflicted on the population in a unit of time by mosquitos which have fed on one infected person belonging to this population ". The unit of time suggested by Garrett-Jones (1964) is one day, hence the term " daily reproduction rate ". The basic reproduction rate is equal to—

(*a*) $\frac{ma^2p^n}{r(-\log_e p)}$, provided all mosquitos with sporozoites are potentially infective (Macdonald, 1957); or

(*b*) $\frac{\text{daily reproduction rate}}{\text{recovery rate}}$ (Garrett-Jones, 1964); or

(*c*) $\frac{\text{communicability}}{\text{exhaustibility}}$ (Moshkovski).

From what has been said it follows that one can properly set a " critical level " of vectorial capacity (meaning that level below which the downward trend of transmission is assured). On the other hand, it would not be sound or helpful to suggest a similar " critical level " of insecticidal impact. The fact is that the degree of impact on the vector, required in order to secure success in a malaria eradication attack, differs in each endemic area: it depends on the natural intensity of transmission and, in the later stages, on the efficiency of case detection and surveillance. This limitation notwithstanding, the assessment of insecticidal impact in representative areas during the attack phase might help, by analogy from one area to another, in revealing where and when a satisfactory degree of vector control is, or is not, being maintained.

[1] Moshkovski, S.D., unpublished document WHO/Mal/436 (1964). This paper may be consulted for references to published works in Russian by the same author.

RÉSUMÉ

On définit la capacité vectrice d'une population de moustiques réceptifs à l'infection par le nombre moyen d'inoculations de sporozoïtes qu'elle pourrait en principe infliger à l'homme à partir d'une source unitaire (le cas infectant) dans l'unité de temps (par exemple un jour). La présence d'un insecticide à effet rémanent dans un endroit déterminé exerce, sur cette capacité vectrice, une action directe dont le présent travail donne une expression

mathématique nouvelle. Les auteurs analysent également les facteurs qui la composent et proposent, exemples à l'appui, de les calculer d'après la proportion des femelles pares parmi les individus capturés au moment du repas.

La destruction des femelles vectrices, au cours d'opérations d'éradication, réduit non seulement la proportion des moustiques qui survivront durant un cycle trophogonique et pendant un jour, mais aussi l'espérance de vie et l'espérance de vie infectante (avec un parasite déterminé). Ces différentes données constituent des paramètres qui sont en relation mathématique, et la mesure de l'un d'eux permet de calculer les autres. Avant et pendant une opération d'éradication, l'élément le plus facile à déterminer est la proportion de femelles pares, qui équivaut à la proportion d'individus survivant au cours de l'intervalle moyen entre l'âge des femelles nullipares et celui des plus jeunes femelles pares dans l'échantillon examiné. Cet intervalle devrait être recherché sur des moustiques capturés au moment du repas: on peut les disséquer et dénombrer les individus dont les ovaires sont aux stades I et II avec pelotons trachéolaires déroulés.

L'action directe de l'insecticide, exprimée sous la forme d'un rapport entre les observations faites avant et après application, résulte du produit de deux facteurs. Le premier, appelé facteur de densité, consiste en la diminution proportionnelle de l'espérance de vie: la densité des femelles (par rapport à un chiffre initial donné) varie en effet en fonction directe de l'espérance de vie et diminue en proportion. Le second, appelé facteur de longévité, est la diminution de la durée probable de vie infectante, c'est-à-dire le nombre moyen de jours de vie infectante par femelle infectée avec un parasite déterminé. Ce facteur est donc influencé par la durée du cycle sporogonique chez le parasite, cycle qui doit être connu si l'on veut calculer le facteur de longévité d'après la proportion de femelles pares.

Des graphiques permettent au chercheur de trouver ces deux facteurs dès qu'ont été déterminés *a*) la proportion de femelles pares d'un vecteur donné en présence et en l'absence d'insecticide dans des circonstances par ailleurs comparables; *b*) la puissance de " p " représentée par ces proportions; *c*) la durée (minimum) du cycle sporogonique de chaque parasite dont on entreprend l'éradication. La manière d'utiliser ces graphiques est illustrée par des exemples où il est fait état de données recueillies au cours d'enquêtes sur le terrain.

Par cette méthode, on peut calculer dans quelle mesure la capacité vectrice est affaiblie lorsque l'utilisation d'un insecticide a entraîné une réduction de la durée de vie du vecteur. C'est, semble-t-il, la première fois que certains des principes d'évaluation épidémiologique proposés par Macdonald (1957) peuvent recevoir une application pratique. Dans les projets-pilotes et les essais d'insecticides à grande échelle, il doit être désormais possible de suivre mois par mois et année par année les fluctuations de l'action directe exercée par un insecticide. Preuve en soit l'exemple de Bobo-Dioulasso, Haute-Volta.

Il faut souligner que cette méthode n'évalue l'action insecticide qu'en termes de comparaison et ne donne pas la valeur absolue de la capacité vectrice, qui ne peut être précisée sans l'appoint d'observations relatives à l'indice d'anthropophilie du vecteur et au taux de piqûres. Elle ne permet pas non plus de prendre en considération l'influence indirecte de certains phénomènes comme par exemple l'action de l'insecticide sur la production de femelles des gîtes larvaires.

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Annex

COMPUTATION OF THE DAILY SURVIVAL RATE IN A POPULATION OF MOSQUITOS WHERE THE FEEDING-RHYTHM IS IRREGULAR OR WHERE TWO BLOOD-MEALS ARE TAKEN BY THE NULLIPAR

It will be assumed for the purpose of this computation that all the mosquitos take their first blood-meal on the second day of adult life. Six alternative rhythms of feeding and first oviposition will be postulated, any of which might be found to rule in a natural mosquito population (e.g., of *A. gambiae*) at a given place and season. Five of the rhythms are irregular, but in each case the feeding-rhythm is assumed to become regular after the first oviposition, the time of which is indicated by the sign //. Against each rhythm is shown the algebraic expression of the proportion of parous mosquitos to be expected in a sample caught when biting, in terms of the daily survival rate (p). The computation applies only to a stable population in which the value of p is constant through life.

The value of p can be computed from the proportion parous in the biting sample, where the mosquito is known to exhibit one of the rhythms indicated opposite, by reading off the daily survival rate from the observed proportion parous in a biting-sample, using Table 6. If the proportion parous falls between two of the values tabulated, simple linear interpolation will provide an acceptable estimate of p for most purposes. Alternatively, in such cases the value of p may be read from Fig. 4, in which its correspondence to the proportion parous is plotted for these rhythms of feeding and oviposition.

Rhythm No.	*Supposed days of feeding and time of first oviposition (//)*	*Expression of proportion parous in terms of daily survival rate*
1	2, // 5, 7, 9, 11, ...	$\frac{p^3}{1-p^2+p^3}$
2	2, // 6, 9, 12, 15, ...	$\frac{p^4}{1-p^3+p^4}$
3	2, 4, // 6, 8, 10. ....[a]	p^4
4	2, 4, // 7, 9, 11, ...	$\frac{p^5}{1-p^4+p^5}$
5	2, 4, // 7, 10, 13, ...	$\frac{p^5}{1+p^2-p^3}$
6	2, 4, // 8, 11, 14, ...	$\frac{p^6}{1+p^2-p^3-p^5+p^6}$

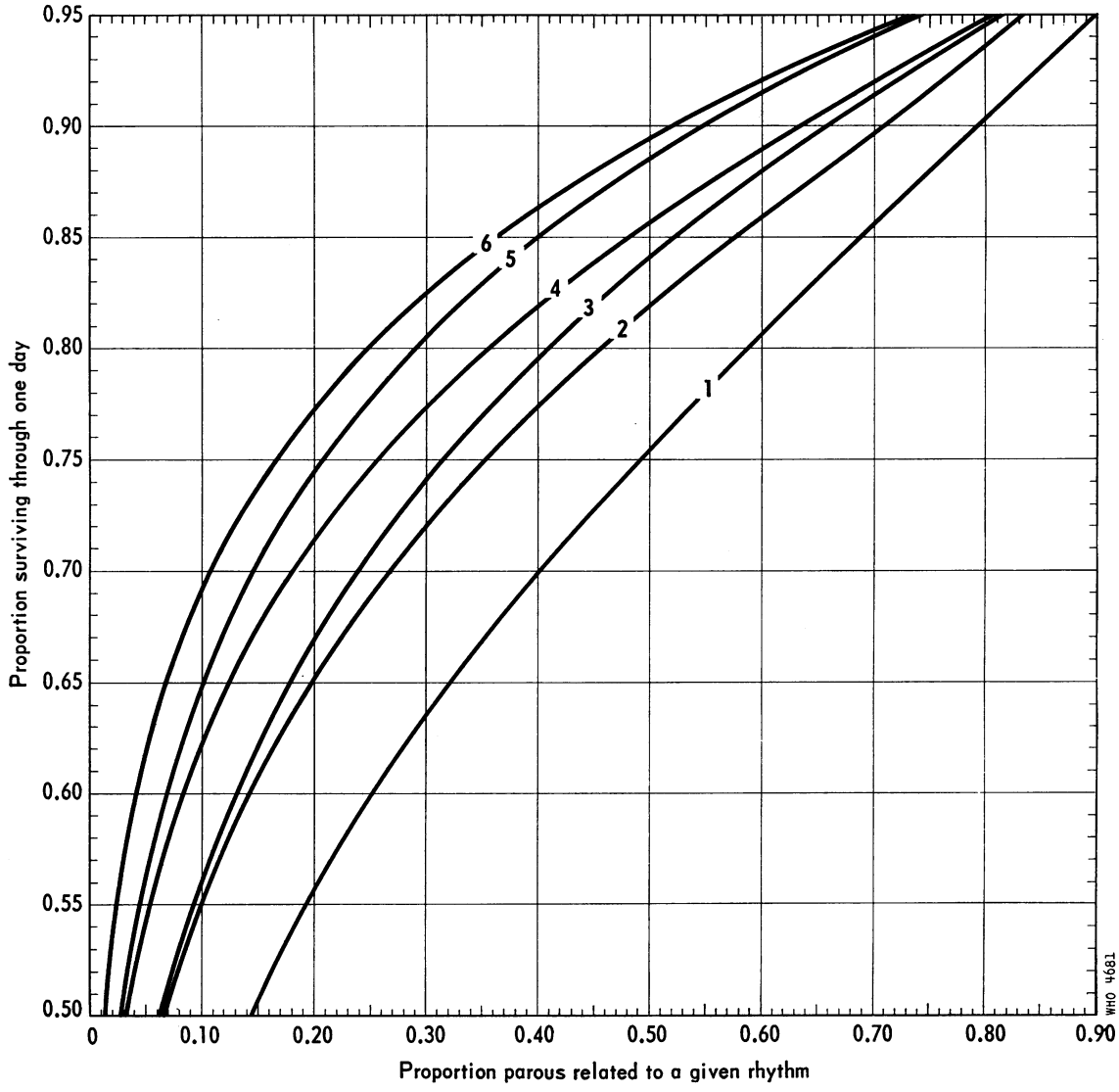
[a] It may be noted that rhythm No. 3 would give the same proportion parous in the biting sample (i.e., a proportion equivalent to p^4) as would a regular rhythm with an oviposition interval of four days, such as:
2, // 6, 10, 14, 18, ... or
3, // 7, 11, 15, 19, ...

TABLE 6
PROPORTIONS PAROUS AND CORRESPONDING DAILY SURVIVAL RATES, FOR SIX SPECIFIED RHYTHMS OF FEEDING AND OVIPOSITION DEFINED IN ANNEX

Observed proportions parous, related to rhythm no.:						Computable value of p
(1)	(2)	(3)	(4)	(5)	(6)	
0.898	0.833	0.815	0.807	0.740	0.730	0.95
0.793	0.708	0.656	0.632	0.546	0.520	0.90
0.689	0.575	0.522	0.482	0.400	0.362	0.85
0.587	0.457	0.410	0.357	0.291	0.247	0.80
0.491	0.353	0.316	0.257	0.208	0.165	0.75
0.402	0.268	0.240	0.181	0.146	0.108	0.70
0.323	0.198	0.179	0.124	0.101	0.0681	0.65
0.252	0.142	0.130	0.0821	0.0680	0.0420	0.60
0.192	0.0988	0.0915	0.0525	0.0442	0.0249	0.55
0.143	0.0666	0.0625	0.0323	0.0278	0.0141	0.50

FIG. 4

CURVES FOR DERIVING THE PROPORTION SURVIVING THROUGH ONE DAY (p) FROM OBSERVED PROPORTIONS PAROUS, RELATED TO VARIOUS IRREGULAR RHYTHMS OF FEEDING AND OVIPOSITION[a]



[a] Rhythms 1-6 defined in Annex.