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VECTOR ECOLOGY

Report of a WHO Scientific Group

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WHO SCIENTIFIC GROUP ON VECTOR ECOLOGY

Geneva, 6-10 December 1971

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VECTOR ECOLOGY

Report of a WHO Scientific Group

A WHO Scientific Group on Vector Ecology met in Geneva from 6 to 10 December 1971. The meeting was opened by Dr L. Bernard, Assistant Director-General, who welcomed the participants on behalf of the Director-General.

1. INTRODUCTION

The control of vector-borne diseases has become possible on a large and decisive scale owing to the remarkable effectiveness of the synthetic organochlorine, organophosphorus, and carbamate insecticides applied against the arthropod vectors. These insecticides have given excellent results during the past 30 years. Recently, the use of chemicals has encountered two complications — namely, the development of resistance by the vectors and the disturbing accumulation of these chemicals in the environment. Thus it has become necessary to develop alternative methods of control — genetic, biological, and environmental. This revision of strategy requires a knowledge of the basic mechanisms that govern the abundance of vectors. The importance of vector ecology in all control programmes against vector-borne disease is thus clearly demonstrated.

The Scientific Group on Mosquito Ecology convened by WHO 5 years ago strongly emphasized the need for obtaining quantitative assessments of the numbers of vectors per unit area or per unit of human population. A large amount of quantitative field work has been carried out since — notably by the WHO Inter-regional Research Units — utilizing a great variety of such assessments.

The present Scientific Group on Vector Ecology therefore devoted its attention to reviewing and assessing the quantitative data that had been gathered primarily on mosquitos but also on other arthropod vectors. From this assessment, the Group was able to outline a framework that would accommodate the data and show their relevance to vector-borne diseases as well as to the planning and development of control strategies.

Three general methods of collecting ecological data on vectors are recognized — namely: (a) surveys, (b) intensive ecological studies, and

(c) surveillance techniques. Surveys were characterized as measurements, at a given time and place, of the distribution and/or prevalence of a vector; however, such measurements may change rapidly and, by their nature, do not provide sufficiently detailed information for most planning purposes. Intensive ecological studies aim to reveal in detail one or more of the quantitative relationships in the vector-pathogen-host system; such detailed studies should suggest approaches for the manipulation of the vector population and allow the identification of the sensitive indices that may be standardized for use in surveillance. Surveillance is a continuous system of periodic assessments of various indices and allows the risk of infection to be monitored. Whatever methods of collecting ecological data are designed and used, it is important that, at the outset, the objectives of the study should be clearly defined and the subsequent utilization of the data planned.

2. INTENSIVE ECOLOGICAL STUDIES

2.1 The systems framework

The dynamics of a vector population and its interaction with the pathogen and vertebrate host is a complex system with many variables. The recent use of computer systems analysis and simulation techniques (Macdonald et al., 1968; Cuellar, 1969; Mills, 1969; Conway, 1970; McDonald & Rai, 1970;¹ Moor & Steffens, 1970; Curtis & Hill, 1971; Patten, 1971; Conway & Murdie, 1972) has considerable potential in elucidating complex systems of this nature.

The construction of systems models is valuable in:

- (a) ensuring a logical analysis of the components and their interactions;
- (b) allowing the quantitative testing of biological assumptions; and
- (c) allowing the simulation of the system and the prediction of the effects of natural changes and man-made interventions in various parameters.

A vector-disease system, with an autochthonous vector population, may be considered to have four basic submodels:

- (1) the life-budget of the immature stages of the vector;
- (2) the infection of the vector;
- (3) the extrinsic cycle; and
- (4) the infection of the host.

¹ Unpublished document WHO/VBC/70.226.

Each of these submodels provides a value (output) that is utilized in the next submodel, whereas the final host submodel will enable the number of newly infected hosts to be computed. The relationship of these submodels is shown in Fig. 1, together with the input parameters. These will be discussed in detail later in the report. However, their features will be briefly reviewed here:

Environmental factors. These are natural and man-imposed variables that may influence most of the parameter values fed into the model (input parameters) and include the availability of breeding and resting places; the number of predators; the topography; climatic and vegetational features and seasonal changes in these; and the impact of man's direct interventions by environmental changes including pesticides and drugs. The role of these different factors could be modelled where appropriate.

Numbers of adult vectors. The absolute population of these and their sex ratio and survival rate are required for the construction of the life-budget of the vector, as discussed by a previous scientific group.¹

Fecundity and survival of the females. The data required should allow the construction of an age-specific fecundity table for the population and will be the product of fecundity studies and estimates of female survival.

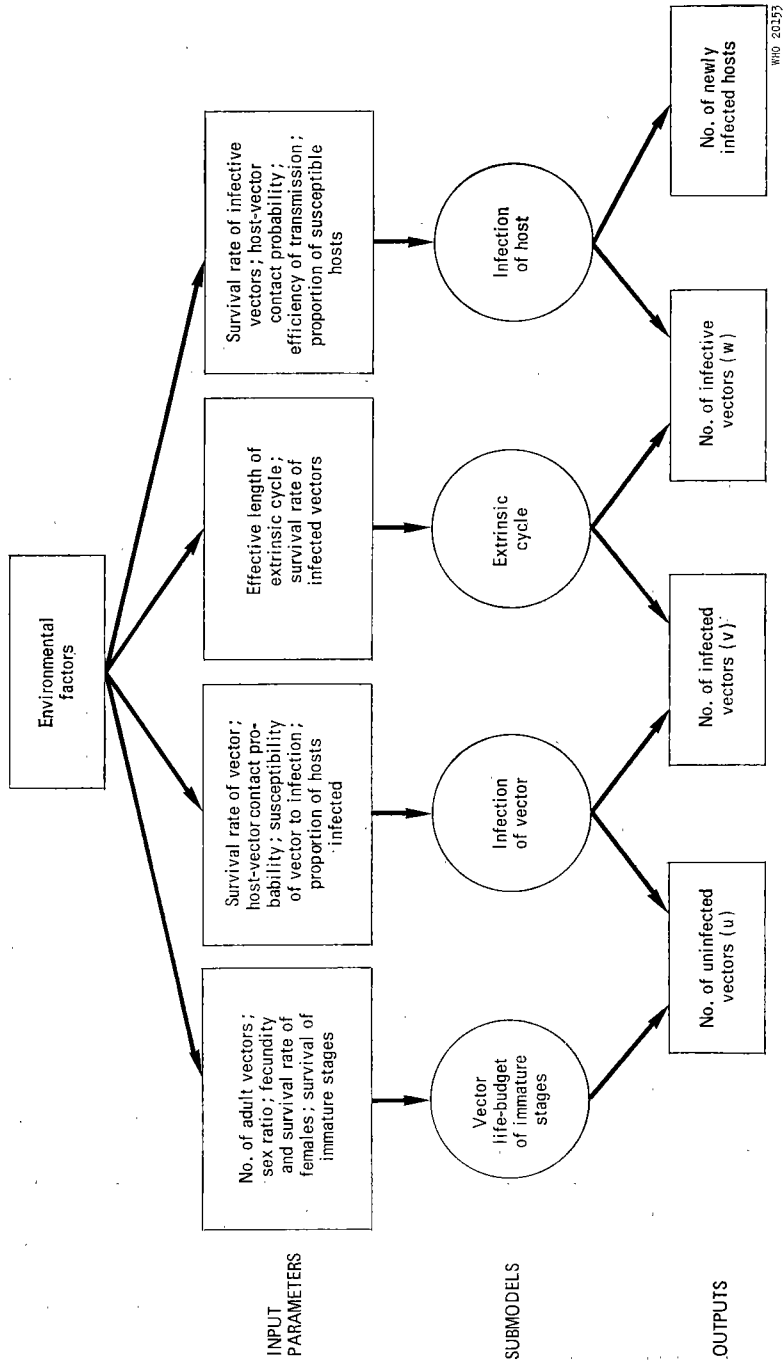
Survival rate of the immature stages. This parameter will be derived from absolute estimates of egg, larval, and pupal numbers in the field, together with, where possible, a direct assessment of mortality.

Survival rate of the vector. This parameter is required for uninfected (u), infected (v), and infective (w) vectors; with pathogens such as *Plasmodium* spp. the three may be similar, but other pathogens — e.g., *Wuchereria bancrofti* — are known to decrease longevity; for some arboviruses, emigrating adults will count as "deaths" for the population system considered. Thus, a further breakdown of the survival rate into its components would distinguish the level of migratory activity from true mortality.

Host-vector contact probability. This important parameter is taken to imply the probability that an individual vector will engage in the activity (usually feeding) that may allow the exchange of pathogen between host and vector. It is normally extremely difficult to assess, but the forage ratio (see p. 19) is an index of this parameter and could be used in its place. It is the aggregate of the abundance of the particular host species, the relation of this to the abundance of alternative hosts (if any), the activity times of host and vector, the microhabitats of host and

¹ *Wld Hlth Org. techn. Rep. Ser.*, 1967, No. 368.

FIG. 1. AN INFORMATION FLOW CHART FOR A VECTOR-DISEASE SYSTEM



vector, the vector's preference for different hosts, the physiological condition of the vector when it lands on the host, and the irritability of the host.

Susceptibility of vector to infection. This parameter is taken to measure the probability that a vector will be infected by the pathogen after feeding on an infectious host. This will depend basically on the genetic susceptibility of the vector population, although the amount of blood ingested — and hence the number of pathogens — may influence susceptibility.

Effective extrinsic cycle of the pathogen in the vector. The incubation period of the pathogen in the vector is often influenced by temperature. Where, as in mosquitos, there is a cycle of feeding (dependent on the gonotrophic cycle) of, say, 3 days, then the value of the parameter will have to be expressed in multiples of the length of this cycle to give an effective extrinsic cycle of, for example, 9, 12, or 15 days.

Efficiency of transmission. This parameter should express the probability of an infective vector's transmitting a pathogen to a susceptible host after they have made contact. It could be influenced, for example, by the degree of immunity and the administration of drugs to the host.

Changes in the host population with regard to disease status. The proportions infectious to the vector and susceptible to the disease need to be assessed. In the present context, reference will be limited to these two classes (Cvjetanović et al., 1971).

The model (Fig. 1) could be extended to include immigrant vectors arriving in the habitat from breeding sites elsewhere, whose infective condition would need to be assessed. The identification of immigrant vectors poses particular problems and the measurement of flight range is discussed on page 21.

The introduction into a model of values for a parameter is justified even if there is no method of estimating it in the field — e.g., the probability that a vector will feed upon a human being is a parameter that can be clearly defined, but cannot usually be accurately measured in the field. However, the simulation allows the effects of variations in this parameter over any specified range to be tested.

In determining what parts of any vector-disease system are to be modelled, attention should be paid to two, partly conflicting, requirements:

(a) The aggregation of parameters and the measurements of their resultant provide data that are statistically more reliable for simulation than the measurement of their components. For example, in a simulation study of host infection, if an adequate measure of infective vectors were available, then none of the parameters for the vector life-budget,

vector infection, and extrinsic cycle submodels would be required. Again, whereas the probability of host-vector contact is extremely difficult to estimate, the product of this and the population of vectors — i.e., the man-biting rate — over 24 hours can be measured.

(b) The analysis of the causes of variation in any output will require the measurement and modelling of the changes in its components. Therefore, from the ecological viewpoint, the model will be extended to include the maximum breakdown and measurement of parameters, so that eventually the key parameter for change can be identified and possibly manipulated. For instance, if the new cases of infection were found to fluctuate in relation to the numbers of infective vectors (w), rather than to changes in host susceptibility or efficiency of transmission, it would be desirable to determine which parameter, of the many shown in Fig. 1, had led to this change in the value of w . Further studies might show that this was due to changes in the number of adult vectors, indicating the desirability of life-budget analysis.

Intensive ecological studies are therefore of value in planning surveillance and disease control programmes, as well as having a long-term potential for planning the better management of the environment. It is hoped that, in countries with disease problems, studies of this type will be undertaken, perhaps as collaborative ventures involving scientific institutions, including university departments.

2.2 Significant ecological variables

2.2.1 *Vectorial capacity*

Vectorial capacity is the product of all the interacting factors that cause an arthropod vector to become infected with a given pathogen and to transmit it to its vertebrate host. At the present time, there is no suitable index that can quantify this generalized summation, although some attempts have been made. Nevertheless, it is an operational means of assessing the relative importance of a specific vector in connexion with a particular arthropod-borne disease.

Vectorial capacity involves two sets of considerations:

(a) The physiological or intrinsic factors that define the capacity of an arthropod species to become infective with a pathogen. These include genetic variation of the pathogen in relation to its virulence to the arthropod and to the vertebrate host; the vector's susceptibility to infection by the pathogen (including genetic components); the physiological factors within the vector that control the development of the pathogen; and the infectivity of the pathogen to susceptible hosts.

(b) The ecological expression of the physiological capacity through interactions with man and other vertebrate hosts. The most important factors are: population density and longevity; host preference and feeding patterns; and dispersal and flight range.

2.2.2 Population size and age structure

Population estimates are of two types: relative and absolute (Southwood, 1966).¹ Relative estimates express numbers in terms of some unit whose relation to total population is unclear, whereas absolute estimates are in terms of the numbers per unit of the habitat.

However, the former are usually easier to make and they provide:

(a) indices that may be used in certain parts of systems models (e.g., the man-biting rate);

(b) valuable checks of the order of magnitude of changes in absolute population estimates.

Evidence showing the correlation of relative and absolute population estimates is given in Tables 1 and 2, which are based on recent work by WHO teams. The types of indices that can be provided by relative methods of population measurement are of particular value in surveillance work and are discussed elsewhere (see p. 26).

There are 5 basic approaches to absolute estimates:

(1) the collection of the number of individuals found in sample units of the habitat — e.g., mosquito larvae per water jar when the total number of water jars is known, or adult *Heleidae* emerging per m² of marshland;

(2) the mark-and-recapture analysis, as used by Sheppard et al. (1969) for mosquitos in Wat Samphaya, Bangkok;

(3) removal trapping — i.e., the removal of a certain number of vectors per unit of effort. As the population is reduced by "removal", fewer individuals are caught per unit of effort. An extrapolation of the graph gives the total population — e.g., sequential dipping for aquatic larvae in irregular water holes (Wada, 1962a, 1962b);

(4) the nearest-neighbour technique: if the animals are randomly distributed, density may be determined from the mean distances between neighbours — a method that is of limited utility in vector work but has been used for snail populations (Keuls et al., 1963); and

(5) distortion of the population structure: the removal or addition of known numbers of animals, usually of one sex, thus causing the population structure to be distorted (Kelker, 1940).

¹ See also: *Wld Hlth Org. techn. Rep. Ser.*, 1967, No. 368.

TABLE 1. COMPARISON OF ABSOLUTE NUMBERS OF ADULTS WITH BITING INDEX : *AE. AEGYPTI*

	Adults per hectare		Landing-biting index	
	Males	Females	Males	Females
Wat Samphaya, Thailand				
August 1967	560	1 381 ^a	1.9	4.3 ^b
December 1967	500	1 225	1.0	2.4
Buguruni, Tanzania ^c				
September 1969	—	14 750	—	9.6
4 November 1969	—	8 112	—	5.3
24 November 1969	—	5 921	—	4.1

^a From Sheppard, P. M. et al. (1969) *J. Anim. Ecol.*, **38**, 661.

^b From Yasuno, M. & Tonn, R. J. (1970) *Bull. Wild Hlth Org.*, **43**, 319.

^c Lincoln Index values taken from Trpiš, M. (1971) Unpublished document WHO/VBC/71.291.

TABLE 2. COMPARISON OF ABSOLUTE NUMBERS OF LARVAE WITH LARVAL CONTAINER INDEX : *AE. AEGYPTI*

	Larvae per hectare	Container index
Bang Khen, Thailand ^a		
February 1969	3 161	38
Buguruni, Tanzania ^b		
May 1969	23 853	25
July 1969	14 611	17
August 1969	233	2
Msasani, Tanzania		
May 1969	4 058	49
August 1969	91	23

^a From the WHO *Aedes* Research Unit, Bangkok (unpublished monthly report, February 1969).

^b From Trpiš, M. (1970) Unpublished document WHO/VBC/70.227.

The following are the sampling methods employed to obtain absolute estimates in the case of the 4 developmental stages — eggs, larvae, pupae, and adults:

Eggs. Egg numbers are normally estimated by sampling units of the habitat. Estimates were made for the *Ae. aegypti* population in a limited area in Bangkok by providing simulated habitats (Southwood et al., 1972). Another attempt to estimate the absolute egg population of *Culex fatigans* has been made recently in villages near Delhi, making use of the unit-area samples of habitats (drains, ponds, and wells).

Larvae. As the larvae of many vectors are mobile, they may sometimes be extracted from samples by methods depending on larval behaviour, or by mechanical methods (Southwood, 1966). Direct counting of the total number of larvae in units or unit areas of habitats has also been employed to provide estimates. This latter method is practical for species such as *Ae. aegypti* (Southwood et al., 1972), *Ae. togoi*, and *Anopheles*

gambiae (Christie, 1954), all of which breed either in containers or in small ground pools. Likewise, anopheline mosquitos breeding in rice fields or pools have been estimated by unit-area sampling (Cambournac, 1939; Goodwin & Eyles, 1942; Service, 1970¹). The total population of larvae in a large pool can be collected from a habitat with the help of a pump (Christie, 1954), and the number of *An. quadrimaculatus* per unit of surface area has been estimated by a screen-dipper technique (Hess, 1941). Another approach — the removal method — has been utilized in estimating the larval populations of *C. pipiens* and *Ae. togoi* in irregular holes (Wada, 1962a, 1962b).

The mark-release-recapture method also has been used to estimate absolute larval populations. Mosquito larvae can be satisfactorily marked with radioisotopes (Welch, 1960; Garby et al., 1966) and with dyes. Certain dyes have been found particularly useful to mark the immature stages of certain species of phytophagous insects (Heron, 1968; Graham & Mangum, 1971), and recently Nile blue A has shown promise for marking larvae of *C. p. fatigans*. Genetic markers can also be used.

Pupae. Estimates of the numbers of pupae are very valuable. The mortality of immature stages can be derived from the numbers of eggs and of pupae. The above-mentioned methods of counting larvae may also be used to measure the population of pupae. Successful estimations have been made for *Ae. aegypti* in Bangkok (Southwood et al., 1972).

Adults. The assessment of the parameters relevant to the adult stage, at which the mosquitos are most frequently vectors, can be considered under two headings: the measurement of absolute population size and the age structure of the population. The survival rate — a parameter of considerable significance in epidemiological models — may be determined either from the emergence rate and successive population estimates or from an analysis of the age structure.

Population size. A knowledge of the numbers of adult mosquitos emerging from the pupal stage is always very useful in life-budget analysis, as each individual can be recorded on only one occasion. Emergence traps, many types of which have been devised (Bradley, 1926; Southwood, 1966), were used in the *Ae. aegypti* study in Bangkok.

The sampling of adult vectors on a unit-area basis will utilize many methods, depending on the vector and its habitat: extraction and "knock-down" as well as behavioural methods may be used. Mosquito populations are often estimated by room spray catches, but from 26% to 60% of the population may be missed in thatched rooms (Symes & Hadaway, 1947; Vincke, 1946). Many vectors feed in one habitat and rest in an-

¹ Service, M. W. (1970) Unpublished document WHO/VBC/247 — WHO/Mal/731.

other (see p. 22), adding further difficulties to an approach based on total collections from sample units of the habitat.

The major alternative method of determining numbers is based on the mark-release-recapture method.¹ The basic equation for the population estimate (\hat{P}_i) is:

$$\hat{P}_i = \frac{a_i n_i}{r_i}$$

where a_i = the number originally marked, n_i = the size of the second sample, and r_i = recaptures in the second sample. Thus, estimates based on this approach are very sensitive to errors in the number of recaptures. All experiments should be designed to achieve the highest possible recapture rate.

Adults. Despite the difficulties, mark-release-recapture experiments have now been applied to several species of mosquito with good results. The most ambitious experiment was made in a small area of Bangkok, where *Ae. aegypti* were marked and released several days a week for a year. Although the recapture rate over the whole period was only 4%, acceptable estimates of the total population could be calculated (Sheppard et al., 1969). In Dar es-Salaam the mark-release-recapture experiment with *Toxorhynchites brevialpis* attained a recovery rate of about 10%. An experiment with *Ae. aegypti* showed that this technique could measure the intervals between successive cycles of feeding (McClelland & Conway, 1971).

There are many different techniques for analysing data from mark-release-recapture experiments. These techniques differ particularly in the assumptions that they make regarding the survival of marked individuals. The method of analysis that the investigator intends to apply also determines whether an individual marking method or a group marking method is appropriate.

The advent of computers has revived the use of the original Fisher & Ford method, the iterative solution of which was formerly troublesome. This method still suffers from the disadvantage that it assumes a constant survival rate. Jolly's stochastic method (see Southwood, 1966), for which Davies (1971) has published a computer programme, allows the survival rate to vary throughout the duration of the experiment, but assumes that mortality is unrelated to the age of the marked animal. In many insect populations this is probably true: accidental death generally occurs before vitality is reduced by age. However, "mortality" in mark-and-recapture experiments is essentially the "loss rate" and includes migration as well as death: migration is a characteristic of newly-emerged insects (Johnson, 1969).

¹ *Wld Hlth Org. techn. Rep. Ser.*, 1967, No. 368.

Manly & Parr (1968) have developed a new approach in which the population estimates is independent of changes in life expectancy with age. In their method, total population (\hat{P}_1) is:

$$\hat{P}_1 = \frac{n_i}{p_i}$$

where n_i = the size of the total sample taken and p_i = the sampling intensity — i.e., the fraction of the population sampled. An estimate of p_i is obtained by comparing the number of marked animals caught in the sample n_i with the total number of marked animals known to be present because they were marked on an earlier occasion and caught on a later one. The method of Manly & Parr demands individual marking and a large number of animals caught three or more times.

Many different techniques have been used to mark adult insects (Southwood, 1966; Sheppard et al., 1969).¹ Recently the Research Unit on Genetic Control of Mosquitos in India, New Delhi,² has developed a method for self-marking of emerging mosquitos with fluorescent powders.

Using the population structure distortion method, the Research Unit in New Delhi has released a large and known number of male *C. p. fatigans* into the native mosquito population. The total population could be estimated from the distortion of the sex ratio. This method is particularly useful for populations where low recapture rates make estimates based on mark-release-recapture difficult.

Age structure. The survival rate may be determined from the age structure of the mosquito population when this has a stable age distribution. The assessment of age structure is often termed age-grading, and in many arthropods the changes in the female reproductive system following completion of one or more gonotrophic cycles allow estimates to be made of the physiological age of individual females. It is often possible to translate these estimates into calendar age. Most progress has been made with malaria vectors (Detinova, 1962). However, since the counting of individual follicular relics is very difficult in many species, a commonly applied alternative is to record whether the mosquito is parous or nulliparous, either by means of the condition of the ovarian tracheation or simply by observing whether follicular relics are present or absent. Whereas the accurate grading of individuals allows the age structure of the population to be defined, the simpler data provided by the parous proportion give only an index that can be used to compare populations separated in either space or time. However, if the intervals between feeding and the time of the first oviposition are known, it is possible to compute

¹ See also: *Wld Hlth Org. techn. Rep. Ser.*, 1967, No. 368.

² This is a joint undertaking of the Indian Council of Medical Research and WHO.

the daily survival rate in a stable population (Coz et al., 1961; Garrett-Jones & Grab, 1964). This rate is much more informative than the parous proportion and should be calculated wherever possible. The chief difficulty in such a study is that of collecting a representative sample of the population (Gillies, 1970).

There are other postmetamorphic structural changes that may be used for age-grading in adult insects (Southwood, 1966). The most general of these is the daily growth layers in the cuticle (Neville, 1963). Hitherto, a significant number of growth rings have been noted only in exopterygote insects, but Schlein & Gratz¹ have found them in the thoracic apodemes of several Diptera.

Age-grading has also been attempted in vector populations from the stage of development of the pathogen, and by measurements such as that of the delayed sporozoite rate in anopheline vectors (Draper & Davidson, 1953; Davidson, 1955; Laurence, 1963; Van Dijk, 1966).

Daily survival rates can also be computed from release-recapture data using, for example, either Fisher & Ford's deterministic model or Jolly's stochastic model. When the former method was used in a study of *Ae. aegypti* in Bangkok, the survival rate was found to range throughout the year between 0.7 and 0.9 (Sheppard et al., 1969). Near Rangoon, the survival rate for both sexes of *C. p. fatigans* was estimated to be 0.9 during the dry, cool season (Macdonald et al., 1968). Pioneer studies on the population structure of tsetse flies were made by Jackson (1940, 1944, 1948) using mark-release-recapture techniques.

2.2.3 *Life-budget analysis*

The causes of changes in the density of vectors may be recognized by life-budget (life-table) analysis. Such an understanding of the dynamics of vector populations is particularly pertinent in relation to alternative methods of control² and may indicate how environmental factors can be manipulated to reduce the level of the vector population. Life-budget analysis will also identify the mortality factors that are density-dependent and allow the net reproduction rate to be determined. The latter information is of basic importance for any genetic control technique. In some of the models for the technique of releasing sterile males a five-fold net reproduction rate has been assumed (Knipling, 1964). Under field conditions, the actual reproductive rate should be calculated over a period of time.

Absolute population estimates are essential for life-budget analysis. However, because with most census techniques the same individual may be counted more than once, census data must be converted before the

¹ Unpublished document WHO/VBC/71.293.

² *Off. Rec. Wld Hlth Org.*, 1970, No. 184, p. 68.

life-budget is constructed. Various techniques are available for insects with discrete generations (Southwood, 1966); methods have also been developed, in relation to studies on *Ae. aegypti*, by the WHO *Aedes* Research Unit in Bangkok (Southwood et al., 1972).

In 1967, a WHO scientific group drew attention to the lack of quantitative data on the population dynamics of vectors.¹ Since then, two studies have been completed. With *Ae. aegypti* in Bangkok (Sheppard et al., 1969; Southwood et al., 1972), 7 parameters were investigated: maximum potential natality, the number of eggs laid, the hatchability of the eggs, the number of immature vectors, the development rates of the immature stages, the size of the adult population, and its survival. The results showed that variations in the numbers of adults emerging were related more to variations in mortality than to those in natality, and that variations in total mortality from egg to pupa were due primarily to variations in the survival of larvae in their fourth instar and in the period between the egg and the second larval instar. The studies suggested a rise in adult numbers, resulting from the greatly increased survival of larvae and the enhanced survival of adults, before the season when the number of cases of dengue rises sharply. A study of *C. tarsalis* in California (Hagstrum, 1971) showed high larval mortalities between the third and fourth instars.

2.2.4 Larval habitats

Detailed ecological knowledge concerning the larval habitats of arthropod vectors is essential for an understanding of their production and control. This may involve the study of microhabitats and may require special techniques for studying the influence of environmental factors. In the case of mosquitos, this is relatively simple for stenotopic species, such as *Ae. aegypti*, which breed predominantly in man-made habitats. It is much more complex for eurytopic species, such as *An. quadrimaculatus*, *C. tritaeniorhynchus*, and *Ae. vexans*, which breed in a wide range of microhabitats within any one breeding area. In such cases it is desirable to develop ecological classifications of the habitats, including the plants with which larval production is associated. These ecological microhabitats may be ranked in quantitative categories with regard to their capacity for mosquito production (Hess & Hall, 1945). This information may then be used: (a) to map larval breeding areas that will require control measures; (b) for epidemiological evaluation in order to predict mosquito production that may result under natural circumstances or in man-made situations such as those associated with projects for the development of water resources (Hess et al., 1970); and (c) to select the most appropriate control measures. Detailed information

¹ *Wld Hlth Org. techn. Rep. Ser.*, 1967, No. 368.

on the larval microhabitats of some anopheline and culicine mosquitos has been gathered, but many species still require intensive ecological study.

2.2.5 *Mating behaviour*

Whereas the mating behaviour of vectors has been studied for a number of years, certain phases of the behaviour, relevant to genetic control, urgently require quantification. The age and frequency at which mating takes place can be established by a combination of field observation and laboratory experiments. The release of marked virgin female mosquitos of *Ae. aegypti* and *C. p. fatigans* and their subsequent recapture has provided information on the age at which mating takes place. Seasonal differences may be very important in relation to control. Studies on *C. p. fatigans* near Delhi showed, for example, that in the hot and wet seasons females usually mated when they were 54-72 hours old, whereas in the cool season their mating was delayed until they were 160 hours old.

2.2.6 *Host-vector contact*

A detailed knowledge of the patterns of contact between a vector and the vertebrate animal from which it takes a blood meal is essential for understanding the epidemiology of any vector-borne disease. It can also be an indication of the zooprophyllactic potential of domestic animals and other vertebrate hosts (Hess & Hayes, 1970).

The quantitative assessment of vector-host contacts at any given place and time makes it possible to predict epidemiologically dangerous situations and to take adequate measures of prevention and vector control.

The extent of contact between vector and host depends largely on the feeding habits of the vector and the availability and activity of hosts at the place and time of vector activity.

One important aspect of the feeding habits of vector species is their host preference — i.e., their preference for certain vertebrate species in the presence of alternative hosts. There are many different degrees of host preference between the extremes of the strict preference of lice for their appropriate hosts and the indiscriminate feeding of triatomines on a variety of hosts. Even within the same group of arthropods, host preferences can be quite different — e.g., *C. tarsalis* feeds on a wide variety of birds and mammals, *Culiseta inornata* feeds predominantly on mammals, and certain populations of *C. p. pipiens* feed almost exclusively on birds (Tempelis et al., 1967). Moreover, there can be marked differences in host preferences within the same species in the different geographical

areas in which they are found — e.g., *Ae. simpsoni* readily bites man in some parts of its range but not in others.

Host preferences can also be assessed by comparing the biting rates — considering the relative availability of alternative hosts — normally by capturing specimens that come into contact with the host for the purpose of taking a blood meal, or by using traps baited with various hosts (Dow et al., 1957). The rate at which infective vectors bite human beings is probably the single most critical index in transmission (Hess & Hayes, 1967). Another method is the determination of the sources of blood meals of vectors collected from natural habitats, usually by precipitin testing. Difficulties in the interpretation of this latter method arise from the problems of obtaining a representative sample of the mosquito population from its resting places, and also in identifying multiple feeds on the same host species.

The results obtained in such investigations can be interpreted as expressions of host preference only if the data on the relative availability of the hosts that are fed upon, and on the many other environmental factors discussed below, are taken into account. The kind and number of hosts available to the vectors at their feeding time must be known for calculating the actual host preference or forage ratio (Hess, Hayes & Tempelis, 1968). This is the ratio between the percentage of blood meals taken on a certain host and the percentage of this host in the total population of available hosts. A forage ratio of 1 indicates nonselective feeding; of less than 1, avoidance of the host; and greater than 1, actual host preference. An example of the application of this calculation is the study carried out on *C. p. fatigans* in Hawaii (Hess & Hayes, 1970). Precipitin tests in engorged specimens indicated that almost two-thirds of the feeds were on birds, thus suggesting that *C. p. fatigans* was ornithophilic; however, the calculation of forage ratios indicated an actual host preference for a mammal (dog), with a forage ratio of 7.

The availability of alternative hosts can have a marked influence on the human-blood index of a vector species. An index of anthropophily can be estimated from the human-blood index if data are also obtained on the relative availability of man and other hosts (forage index). Estimation of the forage ratio may also be used for a quantitative evaluation of the extent of indoor (endophagic) and outdoor (exophagic) feeding preferences.

It would be desirable to make greater use of indices of host selection such as the forage ratio for studying vectorial capacities and the zooprophyllactic potential of domestic animals and other vertebrate hosts. A direct measure of host preference may occasionally be obtained by means of formal choice experiments based on the olfactometer (Gouck, 1972) or other techniques of formal presentation of the alternative choices (Dow, Reeves & Bellamy, 1957).

Another important aspect of the feeding habits is the *biting cycle*. This is the interval between successive blood feeds of vectors. Estimation of the biting cycle will depend largely on observations under laboratory conditions, as direct observations in nature are often impossible. In the case of the Nematocera, the cycle may be estimated from the length of the gonotrophic cycle. The reciprocal of the vector's gonotrophic cycle in nature has been used as the expression of biting frequency (man-biting habits) for the estimation of the vectorial capacity of malaria vectors. However, it has been observed in the field for a number of vector populations that more than one blood meal may be taken during one gonotrophic cycle.

The frequency of the host-vector contact is much influenced by environmental factors, in particular temperature and humidity. Lower temperatures generally lead to decreased biting activity. Under adverse climatic conditions of cold or drought, the host-vector contact can be very much reduced or completely interrupted. On the other hand some mosquitos have a reduced host-vector contact on account of their autogeny — i.e., their ability to produce a first batch of eggs without a previous blood meal. Autogeny is a general pattern for urban *C. p. molestus*, and has been demonstrated in strains of many other species. This characteristic is mostly associated with stenogamy, which makes it easy to colonize some species that otherwise would be difficult to rear — e.g., *Ae. caspius*, *Ae. detritus*, and *C. modestus*. This association of characteristics is of interest for mass production for use in biological control.

Of further importance for the contact between host and vector are the time (diurnal, nocturnal) and place (indoors, outdoors) of the vector-biting activity in relation to the presence and assessibility of the hosts. These factors can vary much with the changing climatic conditions during the course of the year. Seasonal patterns of host-vector contact may be of great epidemiological significance. Large hosts, since they give off greater amounts of carbon dioxide, are generally more attractive to vectors. There are further inherent differences in the attractiveness of individuals within a host population.

Many of the biological parameters that contribute to the rate of host-vector contact (e.g., reproductive rate, movement patterns, longevity, and density) are themselves under the influence of environmental factors. This fact contributes significantly to the difficulty of obtaining satisfactory estimates of the host-vector contact rate.

For many non-flying arthropod vectors (e.g., fleas, ticks, and mites) there is a more intimate relationship between the vector and the host, vector density often being strongly dependent on that of the host species. Thus environmental factors that influence host movement patterns or densities have profound effects on the densities and infestation rates of the vector species and thereby on the contact rates observed.

2.2.7 *Vector susceptibility to infection*

A critical component in assessing the vectorial capacity of an arthropod is its susceptibility to infection by a given pathogen. Little attention has been devoted so far to the importance of genetic variations in the pathogen (in terms of its virulence) and in its vector (in terms of its suitability for the establishment, incubation, and development of the pathogen to the stage at which it can become infective to the next vertebrate host). In the case of Venezuelan equine encephalitis virus, endemic and epidemic strains are known; at the same time, different species and strains of mosquito are not equally capable of becoming infected with the pathogen and of transmitting it to susceptible hosts. For example, a genetic basis for susceptibility to infection with *Brugia* and *Wuchereria filariae* (Macdonald & Ramachandram, 1965) and to infection with *P. gallinaceum* (Kilama & Craig, 1969) has been demonstrated in *Ae. aegypti*.

Genetic variations that are expressed in the susceptibility of the insect to infection by the pathogen are translated into physiological factors regulating the pathogen's survival, multiplication, and development. Efforts to understand these genetic and physiological conditions need to be intensified if long-term integrated control operations are to be considered.

2.2.8 *Dispersal and flight range*

The dispersal of vectors from their breeding habitats is of considerable importance in the epidemiology of vector-borne diseases. It often determines the area in which a given vector will come into contact with man or other vertebrate hosts, as well as the extent of the contact. Some disperse predominantly by flying or running; others are passively distributed by the hosts upon which they rest or feed. Most studies on the dispersal of vectors have been concerned with Diptera, particularly mosquitos.

There are two basic types of arthropod dispersal: migratory and appetential (trivial). Information on flight dispersal patterns of mosquitos is usually obtained by marking immature or adult populations with dyes, fast-drying paints, or radioisotopes and then recapturing them at various distances from the release point. In the case of certain populations that have a single localized breeding source in a given region, the flight range has been deduced. Genetic markers, such as eye colour or abdominal and thoracic markings, are also used. A major problem is that collection by any one technique will give biased results not representative of the entire vector population. For this reason, some workers have used a combination of techniques, such as light-traps, bait traps, biting catches, carbon dioxide traps, and collections at the natural resting place.

Various indices of flight dispersal have been used. The maximum flight distance (MFD) is of little value because it is highly variable, difficult to determine, and of little epidemiological significance. A much more useful index is the distance at which various percentages of the population are recaptured, for example 50 % (FD₅₀) or 90 % (FD₉₀). Figures for the FD₅₀ and FD₉₀ have been obtained for *Ae. taeniorhynchus* in Florida (Provost, 1952) and Georgia (Bidlingmayer & Schoof, 1957). Errors will occur in the calculations of these indices if corrections are not made for the fact that the area of each concentric zone increases proportionately to the square of the distance from the centre. The flight distance indices also vary widely and must be determined separately for each situation. Such indices measure only the proportion of the population that has not lost visual contact with the ground — a proportion that has proved to be rather large in many insect species (Johnson, 1969) — and therefore they do not include insects that have risen to considerable heights.

The effective flight range is the distance from the larval habitat that the females of a given species travel in sufficient numbers to maintain the endemic or epidemic transmission of disease. It is difficult to quantify, being governed by the population density, the infection rate, the biting rate, and the distance of dispersal of the vector species. Such an index would be of value for determining the size of the area in which vector control would be required to protect a human population from the transmission of disease.

2.2.9 Resting places

A knowledge of the resting places of vectors is important in order to obtain population indices; to select appropriate chemical control measures; and to collect specimens for blood meal analysis, determination of infection rates, age-grading, and other population analyses. There are wide variations in the resting places of different kinds of vector, such as mosquitos, blackflies, sandflies, fleas, lice, and bugs. It is still very difficult to find the natural resting places of most exophilic vectors, such as *An. balabacensis* and *Simulium damnosum*.

The following data for *Glossina morsitans* provide a good example of the usefulness of knowledge of the resting place of vectors:

- (1) a large proportion (about 70 %) of tsetse flies resting during the day-time are fully or recently engorged;
- (2) during the day-time, engorged flies usually rest on tree trunks, as near to the ground as they possibly can;
- (3) tsetse flies that are not engorged show a diurnal change of preference for resting places: during the day they rest on tree trunks, at dusk

they rest on the upper surfaces of leaves, and at dawn they return to the tree trunks.

Since tsetse flies spend much of their time resting (digesting their meal or waiting for a host), identification of their preferred resting sites is important for enumerating the best places to apply insecticides. Such knowledge may also add another dimension to population studies of the various *Glossina* species, including those not strongly attracted to man.

Surveys of nocturnal resting places have been made by: (a) releasing tsetse flies marked with fluorescent stains and subsequently spotting them with ultraviolet light; or (b) releasing tsetse flies to which minute reflective glass beads have been attached with an adhesive and identifying them by torch-light.

2.2.10 *Hibernation and aestivation*

The study of hibernation and aestivation, as well as of the physiological changes in vectors during adverse climatic periods, forms an essential part of vector ecology. Techniques for collecting the dormant eggs of *Aedes* (*Ochlerotatus*) spp. have been refined, and genetic factors influencing the survival and hatching times of *Ae. aegypti* eggs have been demonstrated.

Most interest is attached to the adult stages and, although hibernation sites other than houses and caves are largely unknown, progress may be facilitated by constructing artificial shelters of vegetation as was done in France during studies of *C. modestus*. When plastic tents were erected over such artificial shelters, the rise in temperature and in the carbon dioxide concentration activated the hibernating females. Data on hibernation are greatly needed for most temperate zone vectors, such as *C. tritaeniorhynchus* in Korea.

Among the factors influencing hibernation, as well as reactivation in the springtime, is day-length, but other contributory factors should also be defined.

Some species, such as *C. pipiens*, take no blood meals either before or while they hibernate and, instead, feed only on sugars before hibernating. This enables them to build up a reserve of body-fat sufficient for winter survival, and their ovarian development is completely arrested until the spring. Others go into semihibernation with gonotropic dissociation, and continue to feed on blood throughout the winter at reduced levels. This can be sufficient to continue the transmission of diseases — e.g., of malaria in Europe by *An. labranchiae atroparvus*.

However, the nutritive requirements of most species, particularly those that hibernate in vegetation, are largely unknown and may vary from species to species. Whether or not a blood meal is taken is particularly important among potential vectors of viruses. A few viruses have been isolated from hibernating mosquitos — e.g., WEE virus from *C. tarsalis*

and Tahyna virus from *C. modestus* — but the role of hibernating mosquitos that might maintain a virus over the winter cannot be defined. JE virus has been shown experimentally to survive through winter conditions in *C. pipiens* in Japan, as has Tahyna virus in *Culiseta annulata* in Czechoslovakia.

Aestivation is less well documented than hibernation, but *An. gambiae* has recently been shown to survive for 9 months in a semidesert area of the Sudan (Omer & Cloudsley-Thompson, 1970). In the dry season in that area, which is also the winter, all possible larval habitats disappear for several months. Female *An. gambiae* were found to rest in houses, burrows, and cracks in the ground. The blood meals that they ingested at intervals of several weeks were smaller than usual, and they developed only one batch of eggs in the course of several months, ready to be laid at the beginning of the rainy season. There is a clear need for studies to establish the prevalence of such aestivating behaviour, in both *An. gambiae* and other species, in areas with extremes of climate.

2.2.11 *Daily and seasonal cycles*

When planning collection times and methods, the daily activity cycles of vectors must be taken into account. The variation in biting cycles among mosquito vector populations is well documented, and the primary requirement in bait catches is that they be related to sunset and sunrise times rather than fixed times, so that comparisons between localities or seasons are not rendered invalid. A second example of daily cycles is the significant variation within a 24-hour period in the choice of resting sites by vectors, and collections by hand or from artificial resting sites should be planned to take this possibility into account.

Daily cycles, in turn, may be influenced by seasonal changes. It has been found in France, for example, that *C. modestus* after leaving its hibernation sites in May bites only during the day-time. However, subsequent generations during the summer and early autumn bite mostly by night even when the night temperature is the same as in May.

The relevance of changing seasonal conditions — especially rainfall, temperature, and relative humidity — to vector populations is self-evident. All the parameters that determine the importance of a population are themselves directly or indirectly influenced by environmental changes. The following examples are given to illustrate such seasonal effects:

Development of immature stages. In life-table studies of *Ae. aegypti* in Bangkok, it has been shown that egg hatchability varies seasonally, the hatching rate being significantly lower during the cool season.

Larval development is clearly influenced by temperature. Near New Delhi, for example, the duration of the larval stage of *C. p. fatigans* averages 11 days in the hot season and 21 days in the cool season. In

temperate climates, the effect of temperature is more marked, and larval development may be completely arrested in winter. Other factors, which may themselves be seasonal, commonly influence the rate of larval growth — e.g., food supply. Life-table studies can help to identify all such factors.

Adult population size. Seasonal rainfall and temperature fluctuations influence the availability of larval habitats, and the duration of the immature stages, in turn, controls the size of adult populations. For example, the reduction in the numbers of adult *C. p. fatigans* during the wet season in Rangoon can be related to the flushing of many larval habitats by heavy rain. More commonly, however, rainfall increases the number of available habitats, and vectors such as *An. gambiae*, *C. tritaeniorhynchus*, *Ae. simpsoni* and, in parts of Africa, *Ae. aegypti*, show striking increases at the beginning of the wet season. On the other hand, where *Ae. aegypti* is essentially a domestic species — as in Thailand, Indonesia, and elsewhere in Asia — the daily production of adults may be relatively unaffected by rainfall.

Adult survival rates. Adult survival rates are closely dependent on temperature and relative humidity. During the cool months in Thailand and parts of India, both *Ae. aegypti* and *C. p. fatigans* show a lower rate than at other seasons. On the other hand, survival may be greatly increased during extremes of climate. For example, *An. gambiae* in the Sudan, probably species B, has been shown to aestivate through a 9-month season of extreme heat, and most *Culex* and *Anopheles* species in temperate and cold climates hibernate during the most severe winter months. An increase in temperature is the main factor determining the vector efficiency of *Xenopsylla cheopis* for the plague bacillus, whereas an increase in humidity is the main cause of an increase in the survival rate of flea larvae.

Host-vector contact. Several clear instances are now known of a seasonal shift, sometimes related to host availability, in the host choice of vector populations. During the summer months in California and Colorado, for example, *C. tarsalis* feeds increasingly on mammals as opposed to birds (Tempelis et al., 1965, 1967). A comparable shift has been reported from villages near Delhi in the case of *C. p. fatigans*, which during the summer months feeds more on man and less on cattle (Kaul & Wattal, 1968). Such seasonal changes, though difficult to measure, require further study.

Other seasonal changes in vector populations. Frequency of feeding is another parameter that may be influenced by seasonal changes, and the number of blood meals taken may show no direct relation to the stage of ovarian development. As a result, the reliability of age-grading methods based on changes in the reproductive organs may vary seasonally. Both the extrinsic incubation period of pathogens and the infection rates of

vector populations fluctuate in response to environmental changes, and it may also be that the intrinsic susceptibility of the vectors varies. Dispersal also has been shown to be dependent on the temperature: near Delhi, *C. p. fatigans* dispersed from a release point at a rate of about 4 metres per day in winter, and about 80 metres per day in summer.

In addition to variation as a result of environmental influences within years, there may also be variation between years. Therefore it may be concluded that, whenever possible, ecological studies on host-vector pathogen complexes should extend over a period of several years.

3. THE INTER-RELATIONSHIP OF ECOLOGY AND SURVEILLANCE

Fundamental ecological investigations conducted at study sites and routine surveillance applied on a national or international scale both contribute to the sum of our knowledge of disease vectors at a given time. Although it is desirable that the methods chosen for routine surveillance be based upon the information and experience gained in ecological investigations, it has often happened that valid routine surveillance methods have provided the basis for the development of ecological studies. Thus, ecology and surveillance must be considered together.

Surveillance methods are applied principally to the arthropod vectors, though in many instances the vertebrate reservoirs also have to be considered. In both cases, surveillance should cover the distribution of the disease organism as well as its incidence of infection. The essence of vector surveillance is: (a) to detect the presence or establish the absence of vectors; and (b) to quantify, albeit empirically, their density and/or man-vector contact. In view of the importance of chemical control, determination of the susceptibility levels of vectors and reservoirs to insecticides, acaricides, and rodenticides forms an integral part of surveillance.

3.1 Vertebrate reservoirs

In certain situations, the presence and/or density of a suitable reservoir is likely to determine whether a given disease will be present or not; in such cases it is essential to keep not only vectors but also reservoir populations under surveillance. Examples of such situations would be programmes for the surveillance of plague, zoonotic leishmaniasis, and Chagas' disease.

Although these recommendations refer to vector surveillance, the epidemiological risk of infection in the above-mentioned and other

zoonoses is determined by the presence of both the vector and the reservoir, as well as by their density. Therefore, as has been stated above, any surveillance programme must take both the vector and the reservoir into account.

3.2 National surveillance

Aims. The purposes of establishing national networks of vector surveillance are manifold. These networks are designed to (1) meet the local needs for estimates of vector population densities and distributions that will indicate the risks of disease; (2) provide the basis for an effective control programme; and (3) allow international co-ordination through WHO. Individual national surveys may be detailed far beyond the needs of the international programme and will depend on the needs and resources of individual countries. In national surveillance it is especially important that entomologists and epidemiologists work in close co-operation.

Priorities. In most cases, national governments will need to establish priorities in respect of the vectors for which minimum surveillance programmes can be developed in their countries. The decision on which geographical areas within the given country should be included in the continuous surveillance programmes will have to be based on epidemiological information showing where foci of the particular vector-borne disease occur. Prior epidemiological surveys may be needed when such information is lacking. This epidemiological information may also determine whether vector surveillance should be continuous or limited to a restrictive time span, and when it may be terminated.

Training. Adequately trained national personnel are indispensable for carrying out any routine surveillance programme, and it is essential that such a programme be administered and supervised by competent national scientific personnel. Although WHO can provide assistance in the training of personnel and in the launching of surveillance programmes, the programmes themselves must be maintained by national workers. If the techniques to be utilized in the surveillance programme are new to the country or to the personnel who are expected to carry them out, training in those techniques must be provided.

3.3 International surveillance

An international system of routine surveillance of vectors is an essential element in maintaining global awareness of the public health problems involved, and is particularly important in this age of international travel.¹

¹ *Vector control in international health*, unpublished document WHO/VBC/70.11.

Equally, awareness of the problems raised by vector-borne disease is of particular interest in developing countries with respect to planning projects for economic improvement. Surveillance of what were termed the quarantinable diseases has been undertaken on an international basis for many years.

The information required for international surveillance will not be as detailed as that used in many national disease surveillance programmes, but it must be sufficient to allow an appreciation of the probable epidemiological situation. Complicated methods of assessing vector incidence and density would generally not be suitable, since it is necessary that such methods be used universally in countries in different stages of development. Standard, uniform methods are needed in order to ensure that the data so obtained can be compared and analysed centrally for the whole international surveillance system. Data on the distribution and density of vectors, along with the results of tests of their insecticide susceptibility levels, would form a valuable addition to the international data pool.

Although assessment methods must be simple, the personnel involved in surveillance, who will be drawn from existing vector control programmes, will have to be specially trained. The means for carrying out surveillance, including adequate equipment and transport, must be provided. If the surveillance is to be of value, the collation and analysis or assessment of the data collected must be rapid.

3.4 Surveillance techniques

The many existing surveillance techniques present varying degrees of complexity. Once priorities have been established as indicated above, a surveillance technique fulfilling the following criteria must be selected: (1) it should be simple and reliable; (2) the parameters selected for measurement should be biologically and epidemiologically valid; and (3) since any surveillance technique is bound to be repetitive, the long-range cost in relation to the benefit of the information provided by the given techniques must be considered. The various techniques usable for body lice, *Anopheles* mosquitos and *Aedes* (*Stegomyia*) mosquitos have been described in WHO technical guides (WHO, 1971b, 1971c, 1971d) for several of the vector-borne diseases. The use of any of these techniques in surveillance will also provide the information required for the WHO international surveillance programme. Additional technical guides for the surveillance of vectors or potential vectors of other diseases should be made available. These techniques will be considered, group by group, in their ecological context. Methods suitable for the international surveillance of *Anopheles* mosquitos, *Ae. aegypti*, the flea vectors of plague, and the other principal groups of vectors are discussed below.

3.4.1 *Anopheline mosquitos*

The surveillance of *Anopheles* is important only in relation to its transmission of malaria, certain forms of filariasis, and certain virus infections. Malaria surveillance has become a well-established methodology because of the worldwide antimalaria programme and the attention devoted to the subject by the WHO Expert Committee on Malaria during a number of its meetings.¹ In its currently accepted connotation, malaria surveillance is "aimed at the discovery, investigation and elimination of continuing transmission, the prevention and cure of infections, and the final substantiation of claimed eradication" of the disease (WHO, 1963).

A system of surveillance of the major vectors of malaria is proposed as a means of assessing the potential malaria hazard in countries that have not yet embarked on national antimalaria operations. This system would be applicable also to areas where such operations are under way or have been completed. In the latter instances, surveillance would serve to indicate the entomological receptivity of the area to a re-establishment of the disease (WHO, 1971b).

A number of entomological parameters are currently measured in order to assess the transmission potential in malarious areas. No single parameter is sufficient for this purpose but each must be interpreted in conjunction with the other parameters for a particular vector and area, and in relation to the amount of the disease present.

Depending on what is known of a malaria situation and on the degree of control obtained, information may be required on points such as the ecology of the possible vectors; their reaction to control measures, including susceptibility to insecticides; the reasons for failures to interrupt transmission of the disease in areas where control measures have been taken; and the receptivity of the areas, in terms of the vector potential, where the disease now has little public health significance. In the last-mentioned instance, it should be remembered that both beneficial and adverse ecological changes may occur, the former permitting vigilance to be relaxed and the latter requiring its intensification.

The great variety in the behaviour of the various vectors of malaria and in the ecological conditions in which they occur does not permit the complete standardization of entomological methodology or the establishment of indices that could be completely comparable throughout the world. Therefore, although the appropriate surveillance technique should be used to define the malaria potential of a particular area, most of these techniques are unsuitable for establishing an international system of vector surveillance. It is therefore desirable to draw a distinction between

¹ *Wld Hlth Org. techn. Rep. Ser.*, 1957, No. 123; 1959, No. 162; 1961, No. 205; 1964, No. 272; 1968, No. 382; and 1971, No. 467.

the measurable parameters that are primarily of epidemiological importance and those of ecological significance (Garrett-Jones, 1970). Among the former are the two parameters that lend themselves best to some standardization and therefore can be useful for international systems of surveillance of malaria vectors. These are the man-vector contact index and the vector infection rate. If these two parameters are measured in a standard way, they may serve, along with measuring the reservoir of disease in an area, to provide an assessment of the malaria potential of the area. In foci of anopheline-transmitted filariasis, the same principles apply.

In view of the large differences in the biting habits of the various species of anopheline and in the habits of their hosts, the man-vector contact index can have valid epidemiological significance only if it is standardized as regards the actual man-vector contact that occurs in the area being investigated. In practical terms, this means that the numbers of baits and mosquito collectors should be fixed according to the number of persons who typically occupy a room or hut in the area, and the exact sites of collection, either indoors or outdoors, should be selected according to the biting habits of the vector species and the sleeping habits of the local population. This means that the actual baiting and collection techniques will differ from area to area but will be standardized in respect of the man-vector contact taking place in each area and therefore will provide comparable indices.

3.4.2 *Aedes aegypti*

Routine surveillance of this species — vector of yellow fever and other arbovirus diseases — in domestic and peridomestic situations has been conducted for half a century, and it has been mandatory for airports and seaports under the International Health Regulations (WHO, 1971a). The surveillance is based principally on a search for this vector's breeding places in and around houses or other premises. However, the degree of man-vector contact is best assessed by a "biting rate", which also indicates the density of the adult mosquito population.

More than 7 000 records of the distribution and density of *Ae. aegypti* and other *Stegomyia* have been stored in a computer for retrieval. These data have been shown on maps, using conversion factors to express the three empirically derived larval indices in terms of a common denominator which is a density figure chosen from the range of 1-9. For example, a density figure of 4 is generally equivalent to a "house index" of 18.28, a "container index" of 10.14, and/or a "Breteau index" of 20.34 (for an explanation of these indices, see below). Conversion factors relating adult to larval indices of abundance are under study. Ovitrap are valuable for detecting *Ae. aegypti* at low levels — e.g., the presence of survivors in a control or eradication campaign. However, it is not yet clear whether the results can be used quantitatively.

The biting rate is expressed in terms of the number of females collected on human bait per man-hour of exposure. The males, which sometime accompany the females, should be recorded separately but should be excluded from the computation of the biting rate. Assessments should be made at that time of the day or night when the mosquitos are most active.

The larval indices are obtained by examining every water-filled container in houses and their surroundings, including gardens and tree-holes. In small villages, every house can be examined, but in larger villages and small towns it is desirable to choose at least 50 houses representative of the ethnic, economic, and ecological conditions; in larger towns and cities, every quarter should be checked separately. From the scoring of houses as positive or negative for *Ae. aegypti* is derived the house index (percentage of houses examined that are positive¹); from the scoring of containers as positive or negative for *Ae. aegypti* are derived the container index (percentage of containers that are infested) and the Breteau index (number of positive containers per 100 houses). The Breteau index is the most informative of the three larval indices, although the house index is the most sensitive for detecting sparse surviving populations.

A rapid and simple method of making larval surveys consists in collecting one larva (at random) from each container. These single-larva surveys (Sheppard et al., 1969) measure the relative prevalence of different mosquito species in the containers. Where *Ae. aegypti* is predominant, the results may be used to derive the Breteau index for this species.

International routine surveillance for other *Stegomyia* mosquitos is in its first stages of development. For species such as *Ae. simpsoni*, *Ae. luteocephalus*, *Ae. albopictus*, and *Ae. polynesiensis*, the biting rate is the only method that is generally valid at present, and it has the advantage of revealing the differences in man-vector contact that may exist in different parts of their range. It is important to choose the time of day when their activity cycle is at its peak. A beginning has been made towards evolving methods for larval indices of species that develop in leaf-axils, tree-holes, or coconut shells, but these methods are not yet available for international surveillance.

3.4.3 Other mosquito species

The increasing abundance of *C. p. fatigans* in the cities of the tropics makes it necessary to consider methods for its surveillance, particularly since in many regions it is not only a nuisance but also a vector of Bancroft's filariasis. Thus it is important not only to assess this vector's biting rate, but also to ascertain whether it is infected with *W. bancrofti* and, if so,

¹ Described in the International Health Regulations (WHO, 1971a) as the "*Aedes aegypti* index".

the proportion that is infective. Relative estimates of adult populations have been made in terms of the average number per house caught by hand at their resting places over a fixed period — e.g., 15 minutes. A more complete assessment of house populations may be made by pyrethrum spray catches. It would be desirable to supplement these by assessments of the biting rate outdoors. Estimates of the larval population, based on the sampling of unit areas by means of dipping, or on the percentage of possible sources found positive, are now under study.

For *C. tarsalis* — the vector of western equine encephalitis — a thorough system of surveillance carried out in the USA by means of light-traps has allowed the accurate assessment of population levels in relation to their epidemiological danger and as a measure of the effectiveness of mosquito-control measures. For *C. tritaeniorhynchus* — an important vector of Japanese encephalitis — investigations in Korea and Taiwan have indicated that a sensitive method of assessing populations is the biting rate on domestic animals such as pigs. Good results have been obtained in Japan, Korea, and Taiwan by light-traps. Several other methods, such as larval estimation by dipping, have been developed locally but have not yet reached the stage of international standardization.

3.4.4 Fleas

It is mandatory under the International Health Regulations (WHO, 1971a) that regular examinations of rodents and their ectoparasites should be made in the ports and airports of any area suspected of being infected by rodent plague. A programme of periodic, long-term surveillance of plague vectors is indispensable in areas where natural foci exist and where there has been a history of outbreaks in man. Since the data gathered by such studies will be of the first importance in control operations, it is essential that the collection of surveillance data be related to three major activities: (a) ecological studies to elucidate the detailed natural history of flea vectors and their hosts; (b) epidemiological base-line studies of plague in wild rodents, commensal rodents, and human beings, and of the vectors involved; and (c) planning for the gathering of statistically valid data that can be used in systems analysis.

It should be noted that plague is characterized by delimited foci. In making general observations, trapping and hunting areas are selected on the basis of the amount of rodent activity in close proximity to human habitations and populations. Maps and general descriptions of the area are prepared, and specific trapping sites are designated. General observations will usually give the experienced operator a good idea of the types of mammal in the area, and this knowledge in turn will determine the kind of trapping or hunting to be done.

When frozen specimens are received in the laboratory, they are allowed to thaw and then carefully identified as to genus and species.

The ectoparasites are removed, and the fleas are identified, triturated, and streaked on blood agar plates. The residue is inoculated into susceptible laboratory animals.

Fleas received in the laboratory are identified and inoculated subcutaneously into test animals. Fleas of the same species from the same host and location are pooled. In all cases, care must be taken to keep records that will associate ectoparasites with their hosts.

The following indices are useful in the surveillance of fleas:

- (1) the total flea index (the average number of fleas of all species per rodent);
- (2) the specific index (the average number of fleas per species per host);
- (3) the burrow index (the average number of free-living fleas per species per rodent burrow);
- (4) the nest index (the average number of free-living fleas per species per rodent nest); and
- (5) the house index (the average number of *Pulex irritans*, or other human fleas, per house).

Improvements in the flea index have been made by: (a) computing the average number per infested rodent only; and (b) by counting only female fleas that (as in the case of *X. cheopis*) have been shown to be less variable than the males in their host association. More complete data are obtained by determining one or more of the above-mentioned indices and the percentage incidence of the various flea species, as well as the proportion of different host species infested by each flea species. Thus data on host-flea relationships can be obtained.

In comparatively recent years the idea of the "absolute flea index" has come into vogue. This is based on an examination of rodents, burrows, and nests, and the resultant data are applied to the formula

$$\text{AFI} = \frac{\text{RF} + \text{NF}}{\text{TR}}$$

where AFI is the absolute flea index; RF is the flea population on rodents; NF is the flea population in nests and burrows; and TR is the total rodent population. Such an absolute index will be difficult to obtain in most instances, but it should be a goal.

3.4.5 *Other vector species*

Sandflies of the genus *Phlebotomus* — vectors of leishmaniasis and sandfly fever — are in need of surveillance in view of their recrudescence in areas where indoor residual spraying with DDT has been discontinued.

A system employed in Iran is based on the numbers caught by hand in 15 minutes at representative stations in representative villages. The infestation of rodent burrows by *Phlebotomus* may be assessed quantitatively by means of sticky traps.

For blackflies of the genus *Simulium*, some of which are vectors of onchocerciasis, the most widely used index for surveillance is the biting rate. However, no attempt has been made yet to standardize the procedure internationally. The identification of blackfly populations is now realized to be very difficult, since at least 17 karyotypes are recognized in the *S. damnosum* complex.

For tsetse flies (*Glossina* spp.) — vectors of both human and animal trypanosomiasis — African interstate agencies have been trying for several decades to co-ordinate the efforts of research workers and operational personnel. Distribution maps delimiting the foci have already been evaluated. The densities of tsetse fly populations have been assessed by various methods such as catching by hand during "fly rounds", along transects, or at fixed stations, at regular intervals. Owing to the pronounced differences between species in their ecological characteristics, none of these methods is in general use. The level of transmission of human trypanosomiasis is usually estimated from epidemiological data, since the infection rate in tsetse flies is very low.

For the assessment of populations of the housefly *Musca domestica*, a method suitable for general application consists in counting the number of flies resting on a Scudder grill at a given instant. A method based on the same principle, which is used in Denmark, consists in the use of pigs as bait and counting the flies by means of camera snapshots. The density of a fly population may also be assessed by 24-hour exposures of sticky fly-papers. This method has the advantage of not being affected by the fluctuations of resting behaviour that occur during the daily cycle.

In the case of the body louse *Pediculus humanus* — vector of typhus and relapsing fever — surveillance activities are usually restricted to known foci of disease transmission and socioecological conditions favouring louse infestation. They consist in surveys to determine the prevalence of human lice by assessing the percentages of persons whose clothing and hair are infested. The increasing incidence of louse infestation in temperate climates is a matter of concern.

As a contribution to the surveillance of ixodid and argasid ticks, which are the vectors of many diseases of man and livestock, WHO, with the support of FAO, has begun a computer survey of the biology and distribution of ticks. At present this survey is mainly concerned with the relations of the various species of tick to various hosts, their habitats, and their geographical distribution.

With respect to the triatomine vectors of Chagas' disease, the basic step in surveillance also concerns the relations of the various species

to their habitat, and geographical location. It is important also to determine the rates of infection in the domestic, peridomestic, and sylvatic species, as well as their contact with human hosts and vertebrate reservoirs of Chagas' disease. A method of assessing the population densities of triatomines is needed, especially to support epidemiological and control studies now under way.

3.5 Evaluation and dissemination of information

Before beginning any national vector surveillance programme, arrangements must be made to provide for the analysis, evaluation, and dissemination of the data collected. It is also necessary to establish a mechanism for taking a decision expeditiously on the basis of data provided. This decision may call for additional surveillance, more intensive surveys, or the initiation of control operations, in a given vector.

In international as in national surveillance, once the data have been assessed and the results interpreted, these must be widely disseminated to public health authorities. This can be done through existing WHO machinery, such as the Weekly Epidemiological Record and periodic reports, the Regional Offices, and WHO Representatives. It is essential to sustain the interest of the co-operating groups that provide the data from the field, by ensuring that they are kept fully informed how their data have been utilized and interpreted.

In considering the surveillance indices proposed for the vectors reviewed above, it is important to recognize that there are considerable differences in the etiology of the individual diseases carried. Hence, the value of vector indices as a surveillance method must be considered, in each case, in relation to the epidemiology of the disease.

The results of routine surveillance, expressed in figures obtained by a standardized method, may be expected to warn health authorities when the activity or density of the vector, taken in conjunction with the epidemiological situation, is sufficiently high to indicate a danger of transmission of the disease. The concept of threshold densities has received much attention from malariologists over the years, but it is generally evident that these thresholds vary greatly with the species of anopheline and with the general ecological situation. Since approximate threshold figures have been derived in yellow fever epidemiology, and are useful with appropriate reservations, they are worth mentioning. Twenty years ago a house index (*Stegomyia* index) of 1% was chosen as the objective towards which control operations should be directed in order to achieve a wide margin of safety for towns and seaports in an endemic area,¹ the centres where the index exceeded that figure being considered as remaining

¹ *Wld Hlth Org. techn. Rep. Ser.*, 1950, No. 19.

in the danger zone.¹ Assessment of the yellow fever epidemic of 1965 in Senegal led to the conclusion that transmission is unlikely to occur where the Breteau Index is less than 5, whereas in places where this index exceeds 50, there is a high risk of *Ae. aegypti*-transmitted yellow fever (Chambon et al., 1971).

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¹ *Wld Hlth Org. techn. Rep. Ser.*, 1971, No. 479.

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