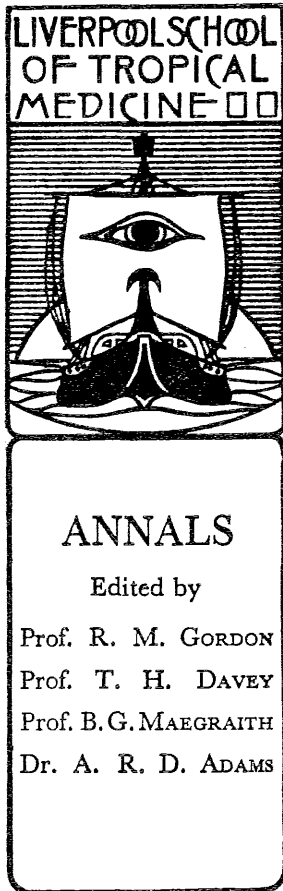


With the author's compliments



Notes on the Culicine Mosquitoes
of Singapore

III.—LARVAL BREEDING-PLACES

BY

D. H. COLLESS

REPRINTED FROM THE

ANNALS OF TROPICAL MEDICINE AND PARASITOLOGY

VOL. 51. No. 1. MARCH, 1957

ISSUED BY

THE LIVERPOOL SCHOOL OF TROPICAL MEDICINE

PATRON: HIS ROYAL HIGHNESS PRINCE PHILIP, DUKE OF EDINBURGH, K.G., K.T.

LIVERPOOL UNIVERSITY PRESS

NOTES ON THE CULICINE MOSQUITOES OF SINGAPORE

III.—LARVAL BREEDING-PLACES

BY
D. H. COLLESS

(From the Department of Parasitology, University of Malaya, Singapore)

(Received for publication December 17th, 1956)

Any consideration of mosquito breeding-places within a given area must begin with a scheme for their classification, as a means of summarizing an otherwise unwieldy mass of field observations. Such classification may at the same time serve several other distinct purposes. It may, for instance, be designed for the field worker, to enable him to predict with some reasonable degree of probability what species of mosquito are likely to be found in any given situation, and, with that end in view, it will make use of categories readily recognizable by the human eye. Alternatively, it may be designed for more fundamental purposes, to throw light on the factors which motivate the gravid mosquito when selecting a site for oviposition; in which case it will be based on such characters as are readily perceived by the mosquito. A third possible scheme might be designed to show the place of the mosquito in the general scheme of aquatic ecology. I am, however, here concerned only with the comparative biology of different mosquito species, and I therefore do not propose to consider any such broad outlines, despite their obvious value.

A remarkable feature of the first two of the above types of classification is the degree to which they correspond; for instance, a 'container' appears to be recognized with equal facility by *Homo sapiens* and by *Aedes albopictus*, although the qualities perceived must be radically different in each case. That being so, it seems that a useful all-purpose classification can be achieved by an initial break-down of the breeding-places into broad categories, which, although defined by complex groups of qualities, appear to be recognized as entities by both man and mosquito. Within such categories, dichotomies can be arranged according to simple chemical and physical properties.

Bates (1949) has discussed the various schemes presented by earlier workers such as Boyd (1930), Shannon (1931) and Hopkins (1936), who proposed as major divisions the distinction between rain-water and seepage, or between ground pools and containers, etc. He himself introduced division into permanent and transient habitats, and proposed a scheme with four major categories: (A) permanent or semi-permanent standing water, (B) running water, (C) transient ground pools, and (D) containers. More recently, Laird (1956) has produced a simplified and more logical scheme, based on 12 principal habitat types. His scheme, however, involves a primary division into fresh and saline habitats, which not only conflicts with Bates's proposals, but seems to be a rather trivial aspect of mosquito biology as such, since relatively few mosquito species occur in saline habitats, and most of those that do are closely related to species which occur in similar habitats but in fresh water. I propose therefore to relegate salinity to the level of a simple chemical dichotomy within the categories, otherwise following the broad categories proposed by Laird, with slight modifications in wording, as follows:

- A. Surface water.
 1. Lakes and ponds.
 2. Swamps and marshes.
 3. Transient pools.
 4. Obstructed streams.
 5. Flowing streams.
- B. Containers.
 6. Large simple containers.
 7. Small simple containers.
 8. Specialized containers.

Within these categories may be found subdivisions into fresh or saline, clean or polluted, sunlit or shaded, acid or alkaline, presence or absence of emergent vegetation, etc.; there may also be special plant associations.

In Singapore, these categories are by no means evenly represented, and certain of them, or certain subdivisions of them, are greatly affected by the activities of man. In particular, antimalarial measures directed against *Anopheles sundaicus* tend to make saline habitats rare or sterile, while those against *An. maculatus* have virtually eliminated the seepage* and are to a large extent responsible for the fact that almost all drainage channels are man-made, with greatly reduced potentialities for mosquito-breeding. On the other hand, the rural 'hyacinth-pond,' which is man-made, offers a widespread and useful niche for many species, while the accretion of empty tins, bottles, etc., particularly in semi-rural areas, supports an enormous population of *Ae. albopictus*. It may, in fact, be said with some justification that a considerable proportion of the culicine population of Singapore is directly supported by human activities.

A. SURFACE-WATER HABITATS

CATEGORY I. LAKES AND PONDS

There are in Singapore a number of lakes in the form of water-supply reservoirs, but they appear usually to support only a negligible mosquito population, owing to their lack of fringing vegetation. Category I therefore includes little beyond the widespread hyacinth-ponds and the rather rare permanent pools in the jungle.

(a) Hyacinth-Ponds

Hyacinth-ponds are rather large artificial ponds, about 20-30 square yards in area, in which are cultivated various plants used as pig-food. Water hyacinth (*Eichornia crassipes*) is the principal species grown, together with smaller amounts of water lettuce (*Pistia* sp.), with duckweeds and other small aquatic plants occurring as natural contaminants. The plants usually form a thick mat over much of the pond, but there is often a narrow more open strip around the margins. The ponds are a prominent feature of the economy of rural Singapore, and there are one or more in almost every back-yard. Many are found in the semi-rural areas also, wherever pig-raising is possible, and the total number for the whole island must be of the order of 5,000 or more.

Most hyacinth-ponds serve as cesspools, receiving regular or sporadic additions of human and animal excrement and other organic wastes, which serve as fertilizer for the plants. This practice of deliberate pollution, in conjunction with the periodic freshening

* In Malaysia as a whole, particularly from the point of view of anopheline biology, 'the seepage' might well rank as a major category.

of the water by heavy rains, means that conditions in a given pond may vary considerably in a short period from highly polluted to relatively clean. It should be noted that, although the hyacinth-pond is treated here as belonging to category 1, it is really a hybrid between categories 1 and 2, and may change from one to the other as the density of its vegetation changes: when vegetation is minimal, it is clearly a weedy pond, but when choked with hyacinth it is essentially a marsh of somewhat unusual depth.

Such variation enables a variety of species of mosquito to find their preferred niches in the same pond at various times and places, and there appears to be a definite succession of species accompanying gradual changes. No attempt has yet been made to follow these changes quantitatively, but, from field experience, the succession following pollution can be described in a broad and general fashion. At the stage of heavy pollution with faecal matter *Culex fatigans* may occur in large numbers, but in the absence of further pollution it soon disappears, and is replaced by species such as *C. fuscocephalus*, *C. gelidus* and *C. annulus*, followed closely by *C. tritaeniorhynchus* and *Ficalbia metallica*. Merging with these, at the other end of the scale, are the species which seem to choose cleaner waters, *C. pseudovishnui*, *C. perplexus*, *C. bitaeniorhynchus*, *F. minima* and *C. rubithoracis*. *F. minima* and *C. rubithoracis* appear to be restricted to very clean waters, while *C. bitaeniorhynchus* is always associated with the presence of filamentous green algae.

It is thus clear that there are factors other than pollution which affect the composition of the fauna of a given pond. Presumably there are important factors associated with type and density of vegetation, and there is a perplexing tendency, difficult to indicate quantitatively, for a given species suddenly to appear in almost all the pools in a given locality, whatever their condition. Moreover, it must not be forgotten that the presence of a given species is mainly an indication of the water conditions at the time when the eggs were laid. Larvae of most species seem to tolerate a wide range of conditions, and quite bewildering associations may hence be found if changes are sudden and irregular. Altogether, 23 species have been recorded from these ponds, with up to seven species (not including *Anopheles* and *Mansonia*) on a single occasion.

A fairly representative picture of breeding in hyacinth-ponds is given in Tables I-III, which show the combined results of weekly larval surveys of 17 such ponds made over a period of 12 months. The ponds were in three groups, of four, six and seven ponds respectively, in three widely separated areas, and all appeared to be fairly typical of hyacinth-ponds in general. Each pond was surveyed on each occasion by means of 20 dips with a ladle around its margin. One such survey of a single pond is referred to in the tables as a 'survey unit,' the final number of survey units performed totalling 752. No attempt was made in these surveys to collect *Mansonia* larvae.

By means of three different indices, Table I summarizes the prevalence of the 11 principal culicine species, and shows that considerable variation may occur from area to area. For instance, the ponds in area 2 were about twice as productive as those in area 3, largely because of the greater numbers of *C. gelidus*, *C. fuscocephalus*, *F. metallica* and *C. fatigans*. The presence of *C. fatigans* in the list suggests that the difference may to some extent have been due to more frequent pollution of the ponds in area 2—a supposition which is borne out by field observations. Also, for reasons unknown, *C. pseudovishnui* was far more common in area 3 than in area 1. Therefore, although it is proposed to treat the combined results as representative of this type of habitat, the existence of such local variations must be borne in mind.

Table I also shows that four species were comparatively rare, *C. bitaeniorhynchus*, *C. rubithoracis*, *C. perplexus* and *F. minima*, and that the commonest species was *C. tritaeniorhynchus*,* which predominated both in frequency of occurrence and in over-all abundance. There are two intermediate groups, one containing *C. pseudovishnui* and *C. gelidus*, and the other *C. fuscocephalus* and *C. annulus*, of which the first pair were distinctly more common than the second. Between these two intermediate groups comes *F. metallica*, which was found quite frequently but in rather small numbers. *C. gelidus*, which ranks fourth in frequency of occurrence, is noteworthy for its high larval concentrations, which bring it up to second place in over-all abundance. Similarly, *C. fatigans* is of rare occurrence, but shows the highest figure of all for individual concentrations of mature larvae.

TABLE I

Showing the results obtained in larval surveys of 17 hyacinth-ponds situated, in three groups of four, six and seven ponds respectively, in three widely separated areas of Singapore

Larvae collected	Ponds surveyed	<i>C. tritaeniorhynchus</i>	<i>C. pseudovishnui</i>	<i>C. annulus</i>	<i>C. perplexus</i>	<i>C. fuscocephalus</i>	<i>C. gelidus</i>	<i>F. metallica</i>	<i>F. minima</i>	<i>C. rubithoracis</i>	<i>C. fatigans</i>	<i>C. bitaeniorhynchus</i>
Occurrences, as percentage of total survey units*	Area 1	44	19	11	11	9	20	14	7	2	4	8
	„ 2	46	26	5	1	27	29	36	—	—	6	—
	„ 3	43	31	17	—	3	10	14	5	4	—	5
	Areas 1-3 combined	44	26	11	3	13	19	22	4	2	3	1
Average no. of mature larvae per occurrence	Area 1	6.0	2.5	5.5	2.4	4.3	7.0	2.2	1.7	7.8	5.3	2.4
	„ 2	4.3	3.1	4.5	1.0	4.7	11.4	3.7	—	—	19.0	—
	„ 3	4.6	4.8	5.8	1.0	1.7	3.9	1.9	2.7	3.9	1.0	3.5
	Areas 1-3 combined	4.9	3.8	5.5	2.2	4.4	8.9	3.0	2.1	4.6	14.0	2.9
Average no. of mature larvae per survey unit	Area 1	2.6	0.5	0.6	0.3	0.4	1.6	0.3	0.1	0.1	0.2	0.2
	„ 2	2.0	0.8	0.2	0.1	1.3	3.3	1.3	—	—	1.1	—
	„ 3	2.0	1.5	1.0	—	—	0.4	0.3	0.1	0.1	—	0.2
	Areas 1-3 combined	2.2	1.0	0.6	0.1	0.6	1.7	0.6	0.1	0.1	0.4	0.1

* A survey unit represents one survey of one pond.

Table II shows the first-order associations between the 11 species. The upper figure in each pair records the actual number of associations observed between the species shown at the head of the table and the species shown in column 1, while the lower figure expresses the number as a percentage of the total occurrences of the species named at the head of the table. The diagonal pairs, instead of expressing the association of a species with itself, i.e., 100 per cent., show the number and percentage of occasions when each species was found alone.

Table III is derived from Table II, and shows the 'index of association' between the 11 species, which expresses in a single figure the observed association between any two species.

* The Malaysian subspecies *C. tritaeniorhynchus summosus*.

TABLE II

Showing the first-order associations between larvae of the 11 principal culicine species found in hyacinth-ponds at Singapore. The upper figure in each pair records the number of associations observed between the species shown at the head of the table and the species shown in column 1; the lower figure expresses the number as a percentage of the total occurrences of the species named at the head of the table. The diagonal pairs show the number and percentage of occasions when each species was found alone

	<i>C. tritaeniorhynchus</i>	<i>C. pseudovishnui</i>	<i>C. annulus</i>	<i>C. perplexus</i>	<i>C. fuscocephalus</i>	<i>C. gelidus</i>	<i>F. metallica</i>	<i>F. minima</i>	<i>C. rubithoracis</i>	<i>C. fatigans</i>	<i>C. bitaeniorhynchus</i>
<i>C. tritaeniorhynchus</i> ...	72 22	111 56	47 55	13 52	63 65	97 66	54 33	11 39	10 63	12 52	10 32
<i>C. pseudovishnui</i> ...	111 33	29 15	27 31	14 56	13 13	21 14	81 50	8 29	12 75	3 13	10 32
<i>C. annulus</i> ...	47 14	27 14	22 26	5 20	11 11	11 8	6 4	0 0	2 13	1 4	2 6
<i>C. perplexus</i> ...	13 5	14 7	5 6	3 12	3 3	6 4	7 4	4 14	3 19	1 4	6 19
<i>C. fuscocephalus</i> ...	63 19	13 7	11 13	3 12	17 18	40 27	8 5	3 11	2 13	7 30	1 3
<i>C. gelidus</i> ...	97 29	21 11	11 13	6 20	40 41	33 23	28 17	2 7	3 19	9 39	2 6
<i>F. metallica</i> ...	54 22	81 41	6 7	7 28	8 8	28 19	26 16	17 61	7 44	3 13	7 23
<i>F. minima</i> ...	11 3	8 4	0 0	4 16	3 3	2 1	17 10	1 4	2 13	0 0	6 19
<i>C. rubithoracis</i> ...	10 3	12 6	2 2	3 12	2 3	3 2	7 4	2 7	0 0	0 0	2 6
<i>C. fatigans</i> ...	12 4	3 2	1 1	1 4	7 7	9 6	3 2	0 0	0 0	10 43	0 0
<i>C. bitaeniorhynchus</i> ...	10 3	10 5	2 2	6 24	1 1	2 1	7 4	6 21	2 13	0 0	9 29
Total no. of occurrences	333	199	86	25	97	146	163	28	16	23	31

The index is calculated thus: if A is the total number of occurrences of species A, B the total for species B, and N the number of occurrences of the two together, then the index = $\frac{100 \times N}{A+B-N}$; or, if p and q are the proportions (not percentages) of associated occurrences relative to total occurrences of each species respectively (Table II), the index = $\frac{100 \times pq}{p+q-pq}$.

The calculation of the index, and the concept which it expresses, are perhaps more clearly shown geometrically (fig. 1). The index is a useful one, since it combines in a single figure the pair of values shown in Table II (one under each species), varying from 0 per cent. for complete lack of association to 100 per cent. for invariable association.

TABLE III
(derived from Table II)

Showing the 'index of association' (see text and fig. 1) between larvae of the 11 principal culicine species found in hyacinth-ponds at Singapore, expressing in a single figure the observed association between any two species

	<i>C. tritaeniorhynchus</i>	<i>C. pseudovishnui</i>	<i>C. annulus</i>	<i>C. perplexus</i>	<i>C. fuscocephalus</i>	<i>C. gelidus</i>	<i>F. metallica</i>	<i>F. minima</i>	<i>C. rubithoracis</i>	<i>C. fatigans</i>	<i>C. bitaeniorhynchus</i>
<i>C. tritaeniorhynchus</i> ...	—	26	13	4	15	20	11	3	3	3	3
<i>C. pseudovishnui</i> ...	26	—	10	7	5	6	29	4	6	1	5
<i>C. annulus</i> ...	13	10	—	5	6	5	2	0	2	1	2
<i>C. perplexus</i> ...	4	7	5	—	3	4	4	8	8	2	12
<i>C. fuscocephalus</i> ...	15	5	6	3	—	20	3	2	2	6	1
<i>C. gelidus</i> ...	20	6	5	4	20	—	10	1	2	6	1
<i>F. metallica</i> ...	11	29	2	4	3	10	—	10	4	2	4
<i>F. minima</i> ...	3	4	0	8	2	1	10	—	5	0	11
<i>C. rubithoracis</i> ...	3	6	2	8	2	2	4	5	—	0	4
<i>C. fatigans</i> ...	3	1	1	2	6	6	2	0	0	—	0
<i>C. bitaeniorhynchus</i> ...	3	5	2	12	1	1	4	11	4	0	—

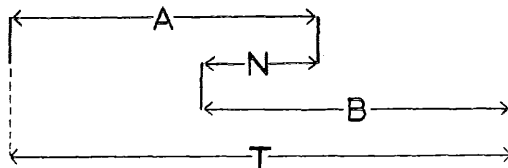


FIG. 1. Diagrammatic representation of the 'index of association.' Length A represents the total occurrences of species A, length B the total occurrences of species B, length N the number of associated occurrences, and length T the total of occurrences of each species alone plus associated occurrences.

$$\text{The index} = \frac{100 N}{T} = \frac{100 N}{A+B-N}$$

By selecting the higher values of the indices for each species in Table III, it is possible to express the major relationships diagrammatically (fig. 2). This diagram is particularly interesting, for it agrees closely with the subjective impressions formed by field experience, and appears to express, as one moves from top to bottom and left to right, the transition, noted above, from the heavily polluted pond, with its heavy breeding of *C. fatigans*, to the very clean waters which support *C. bitaeniorhynchus* and *C. rubithoracis*.

Little attention has yet been given to *Mansonia* spp., which were not included in the above surveys. Other surveys have shown *M. uniformis* and *M. indiana* to be abundant in many ponds, principally attached to the roots of the hyacinth plants. Certain peculiarities have been noticed, such as an apparent tendency for all the larvae present to belong to one species only, and their occasional absence for no apparent reason. The hyacinth-pond is presumably the major breeding-place of these two species in Singapore.

(b) *Miscellaneous Habitats*

Almost any sunlit permanent freshwater pond, containing some vegetation, will be found to support some part of the fauna described above for the hyacinth-pond, particularly the widespread species *C. tritaeniorhynchus*. Such ponds may occasionally contain brackish water (though antimalarial measures make this rare), and in such brackish sites *C. sitiens* and *C. annulus* have been taken, the latter at an unmeasured but low salinity.

A rare type of permanent pond occurs under deep shade. Only two of them are known: one is in secondary jungle and has consistently yielded larvae of *C. fraudator* only; the other is in a depression shielded by thick bushes and tall grass and fern, and has yielded, more or less regularly, *C. mimulus*, *C. fraudator*, *C. quadripalpis*, *C. spathifurca* and *C. hutchinsoni*. Both these pools contain clear fresh water.

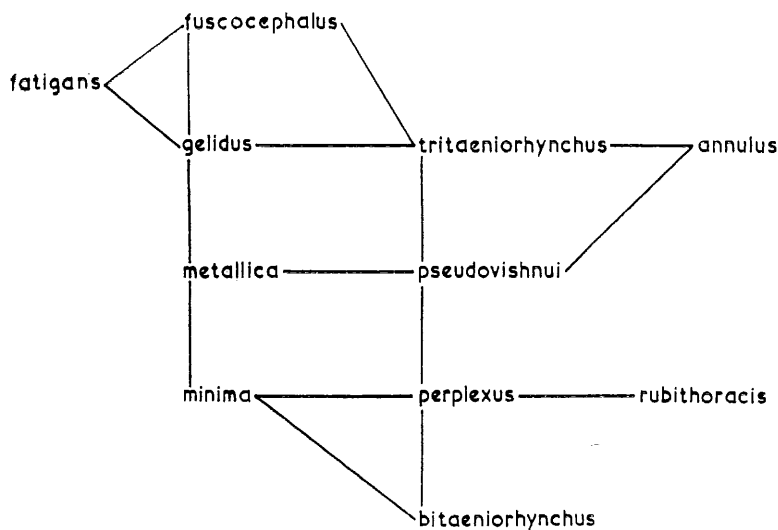


FIG. 2. Diagrammatic representation of the larval associations of the 11 principal culicine species found in hyacinth-ponds at Singapore. (Derived from Table III.)

CATEGORY 2. SWAMPS AND MARSHES

The topography of Singapore is such that freshwater swamps and marshes are uncommon, a situation further intensified by the extensive use of antimalarial and agricultural drainage; moreover, control measures against *An. sudaicus* make breeding in saltwater marsh uncommon. Habitats in this category have therefore not been investigated in any detail, but such surveys as have been made show that the open freshwater swamp or marsh is the native habitat of many of the hyacinth-pond species, with *C. tritaeniorhynchus* and other members of the *C. vishnui* group predominating. As already noted, there is an essential similarity between these habitats and those of the hyacinth-pond, in the relative permanency of the water and the great abundance of emergent vegetation.

In tidal marsh, *C. sitiens* is the typical species, although *C. tritaeniorhynchus* also has been taken at low salinities of up to 200 parts of chlorine per 100,000. At the edge of the mangrove, where vegetation is scarce and salinity high, *Ae. longirostris* may be found. This species is dominant in the mangrove swamp proper, both in sunshine and in shade, and is rather rigidly restricted to pools in the black mud which is typical of such sites. It occurs also in crab-holes, and has been found at salinities of up to 1,550 parts of chlorine per

100,000. *Ae. butleri* and a number of other rare species of *Aedes* and *Culex* are also known or suspected to breed in the mangrove swamp.

A further type of freshwater swamp, with a characteristic fauna, occurs under jungle shade. This type of habitat is rare in Singapore, but one case is known where inundated land occurs in secondary jungle, just above the tidal limits; there, heavy breeding of *C. fraudator* has been observed, with *C. cinctellus* and *Ae. butleri* as rarities. There is also evidence from elsewhere in Malaya suggesting that marsh along the jungle fringe may be a native breeding-place of *C. mimulus*.

CATEGORY 3. TRANSIENT POOLS

Transient pools, as defined by Laird (1956), are 'accumulations of water in relatively shallow hollows which do not intersect the water table.' They thus include most small casual pools and puddles, wheel-ruts, hoof-prints, small borrow-pits, etc., and are frequently without emergent or fringing vegetation. When open to the sun, such pools usually support a fauna of *Culex* spp.; if vegetation is present, *C. gelidus* and the ubiquitous *C. tritaeniorhynchus* may occur, but in the more usual type with no vegetation the typical species are *C. annulus* and *C. fuscocephalus*. This association of *C. annulus* and *C. fuscocephalus* with transient pools is so common as to be striking, and clearly differentiates the two species from the other members of the hyacinth-pond fauna. *C. nigropunctatus*, a rather less common species, also shows a tendency to breed in transient pools.

In most countries transient pools are the typical habitat of many species of *Aedes*, particularly of the subgenera *Aedimorphus*, *Ochlerotatus*, *Banksinella* and *Aedes*. Such species are uncommon in Singapore, but, when they do occur, they are nearly always found in this habitat, and almost every collection made of *Ae. lineatopennis*, *Ae. caecus*, *Ae. vexans* and *Ae. andamanensis* has come from a transient pool. These species select pools in rather open sites, but there appears to be quite a large group of rare jungle species, mainly of the subgenera *Aedes* and *Aedimorphus*, which breed in transient pools under jungle shade; the only four records known to me of larvae of *Ae. orbitae* in Malaya, for instance, all come from pools on jungle tracks.

The term 'transient' may also be applied to certain brackish pools of the tidal zone. These tend to merge with the brackish type of habitat in category 2, and support the same species, mainly *Ae. longirostris* and occasionally *Ae. butleri*.

CATEGORY 4. OBSTRUCTED STREAMS

In Singapore category 4 is almost entirely represented by obstructed, or otherwise stagnant, drains and ditches, for outside the catchment area almost all drainage channels have been constructed, or at least modified, by man. A typical breeding-place is produced by the obstruction of an earth drain with silt or vegetation, which often leaves only a slight, though perceptible, flow, which after heavy rains becomes strong enough to cause flushing. In open situations *C. tritaeniorhynchus* is again the dominant species, although *C. fatigans* may be common when, as often occurs, the water is polluted with sillage. *C. bitaeniorhynchus* is also common in the cleaner waters where conditions favour the growth of the green algae with which it is always associated. Concrete drains, through which the flow is often intermittent and frequently carries sillage water, tend to support *C. fatigans*. When neglected or unused, both types of drain may revert to a series of pools resembling those of category 3.

Table IV records the results obtained in surveys of 62 earth drains and 69 concrete drains round army camps on Blakang Mati Island. The dominance of *C. tritaeniorhynchus* in the earth drains, and of *C. fatigans* in the concrete drains, is most striking. Although these habitats rarely contain brackish water, they do occasionally support *C. sitiens* and *Ae. longirostris*.

TABLE IV

Showing the results obtained in larval surveys of 131 obstructed drains around army camps on Blakang Mati Island

Species	No. of occasions on which larvae were found in	
	Earth drains	Concrete drains
<i>C. tritaeniorhynchus</i>	44	9
<i>C. fatigans</i>	8	53
<i>C. fuscans</i>	7	7
<i>C. bitaeniorhynchus</i>	11	0
<i>C. gelidus</i>	2	0
<i>C. nigropunctatus</i>	2	2
<i>C. fuscocephalus</i>	0	5
<i>C. mimulus</i>	0	4
<i>C. sitiens</i>	0	2
<i>C. fraudator</i>	1	0
<i>Uranotaenia</i> sp.	0	1
<i>F. luzonensis</i>	1	0
<i>Ae. longirostris</i>	1	0
Total no. of drains surveyed	62	69

CATEGORY 5. FLOWING STREAMS

Category 5 merges imperceptibly with category 4, but I should place in it such habitats as occur along the grassy margins of streams and along the larger drains and ditches which have an obvious and regular current. Except for one very interesting site, I have not investigated this type of habitat in any detail. The exception was a terminal pool in a jungle stream which loses itself in marshy ground at the jungle margin. The pool might, with some justice, be placed in the previous category, but it has a distinct flow, though sufficiently gentle to allow the growth of a mass of bladderwort and green alga, and, although it is shaded, it is not deeply so. Eight species of mosquito have been found there during more than three years of surveys—*C. pseudosinensis* (regularly), *C. geminus* (once), *C. bitaeniorhynchus* (once), *Ae. butleri* (once), *An. umbrosus* (once), *An. aitkenii* (occasionally) and *An. breviostris* (regularly during the last year only). This pool is the only known breeding-place in Singapore of *C. pseudosinensis* and *C. geminus* and of the rare anopheline *An. breviostris*.

B. CONTAINER HABITATS

CATEGORY 6. LARGE SIMPLE CONTAINERS

Laird (1956) has pointed out that, although category 6 ('large simple containers') merges with the next ('small simple containers'), the size of a container is an important feature as regards its mosquito fauna. In the present work, I have classed as 'large' all containers of about the size of a kerosene tin or greater, i.e., with a volume measured in

gallons. Table V shows the survey results from 266 such containers on Blakang Mati Island. They are subdivided into two series: containers connected with the drainage-system, i.e., grease traps, septic tanks, 'catch-pits,' etc. (102), and discrete containers, such as tins, drums, canoes, etc. (164). Those in the first series were commonly polluted with sullage water, while those of the second series usually contained clean rain-water.

TABLE V
Showing the results obtained in larval surveys of 266 large simple containers on Blakang Mati Island

Species	No. of occasions on which larvae were found in	
	Containers connected with drainage	Discrete containers
<i>C. fatigans</i>	89	44
<i>Ae. albopictus</i>	8	88
<i>C. mimulus</i>	3	12
<i>C. tritaeniorhynchus</i>	3	9
<i>C. fuscans</i>	3	6
<i>T. speciosus</i>	0	10
<i>Ae. fumidus</i>	0	6
<i>Ae. aegypti</i>	0	3
<i>C. nigropunctatus</i>	1	1
<i>C. hutchinsoni</i>	1	2
<i>Ar. kuchingensis</i>	1	0
<i>C. fraudator</i>	2	1
<i>C. spathifurca</i>	0	1
<i>C. sitiens</i>	0	3
<i>C. annulus</i>	0	1
<i>C. fuscocephalus</i>	0	1
<i>C. propinquus</i>	0	1
<i>Ae. longirostris</i>	0	1
<i>U. nivipleura</i>	0	1
Total no. of containers surveyed ...	102	164

The dominant species in this habitat were *C. fatigans* and *Ae. albopictus*, with the former completely so where the water was polluted. This finding is in general agreement with results from other parts of the world, e.g., by Laird (1956) in the Pacific Islands. An important aspect in Singapore is the frequent presence of enormous numbers of *C. fatigans* in the large jars or tanks in which market gardeners store human or animal excrement for later use as fertilizer.

The predators *C. fuscans* and *Toxorhyncites speciosus* are common in large containers, although *C. fuscans* is more typically a breeder in ground pools, and *T. speciosus* in small containers, and always in clean water, as also are *Ae. fumidus* and *Uranotaenia nivipleura*. The presence in the list of *Ae. fumidus*, *C. sitiens* and *Ae. longirostris* is due to the occasional occurrence in the tidal zone of tins, canoes, etc., containing brackish water. The occasional records of ground-pool breeders, such as *C. tritaeniorhynchus*, came mostly from tins or drums, sometimes sunk into the earth and usually showing features in common with ground pools. An exception, however, is *C. mimulus*, which appears to breed quite successfully in fire-buckets, etc., and was in fact found more often in container habitats than in ground pools. This may reflect a degree of artificiality in this survey area, since elsewhere the normal habitat of the species seems to be marsh or transient pools along the jungle fringe.

CATEGORY 7. SMALL SIMPLE CONTAINERS

In contrast to the containers included in the previous category, the small simple containers have a volume of roughly one quart or less ; they include small tins, bottles, rubber-cups, coco-nut shells, bamboo stumps, tree-holes, etc. Table VI* shows the survey results from 374 such containers on Blakang Mati Island, subdivided into tree-holes (123) and miscellaneous containers (251).

The over-all total shows *Ae. albopictus* to be by far the most common species in these habitats, but the sub-totals reveal that in tree-holes it ranks equally with *Orthopodomyia maculipes*, the *Ae. niveus* group, and the predator *T. speciosus*. This finding reflects the ability of *Ae. albopictus* to leave the shelter of the jungle and to breed in peri-domestic situations, where tins, bottles, etc., abound. Something of the same ability is also shown by *T. speciosus*, but not by *O. maculipes*, the *Ae. niveus* group, or the less common *Heizmannia pilosa*, which rarely venture away from jungle shade. It should be noted that, although

TABLE VI
Showing the results obtained in larval surveys of 374 small simple containers on Blakang Mati Island

Species	No. of occasions on which larvae were found in	
	Tree-holes	Miscellaneous containers
<i>Ae. albopictus</i>	34	207
<i>O. maculipes</i>	33	2
<i>Ae. niveus</i> group	27	0
<i>T. speciosus</i>	29	16
<i>C. fatigans</i>	0	20
<i>H. pilosa</i>	11	2
<i>C. mimulus</i>	0	7
<i>Ae. fumidus</i>	2	6
<i>Armigeres</i> sp.	0	5
<i>Tripteroides</i> sp.	2	0
<i>C. hutchinsoni</i>	0	1
<i>C. fraudator</i>	0	1
<i>C. fuscatus</i>	0	2
<i>C. tritaeniorhynchus</i>	0	1
<i>U. nivipleura</i>	0	1
<i>C. sp. near fragilis</i>	0	1
Total no. of containers surveyed ...	123	251

Ae. albopictus does occur inside the jungle, its semi-domestic habits make it uncommon in tree-holes deep in the jungle, where species of the *Ae. niveus* group and others are more common.

Table VI also shows that *C. fatigans* breeds only to a very slight extent in small containers, but that *C. mimulus* breeds there as well as in the larger types of category 6. Also of interest is *Ae. fumidus* (under which name an occasional record of the related *Ae. amesii* may here be concealed). This species of the subgenus *Skusea* occupies a specialized niche, breeding in rot-holes in mangrove trees or other artificial containers in mangrove swamps. These artificial containers almost always contain brackish water, and salinities of up to

* This table does not include *Ae. aegypti*, which was rare in the area surveyed. Elsewhere in Singapore, principally in closely settled urban areas, *Ae. aegypti* is common in both large and small containers, always in close association with houses and their immediate surroundings.

1,650 parts of chlorine per 100,000 have been recorded in tree-holes, the salt being presumably derived from sea-spray. Laird (1956) has suggested that the habit of breeding in crab-holes found in certain other species of *Skusea* (and in *Geoskusea*) may be an extension of this habit of breeding in saline tree-holes. His suggestion seems possible, but the reverse would appear to be equally likely, i.e., that the saline tree-hole is an extension of the crab-hole habitat. In this connection, it may be noted that the not-too-distantly-related *Ae. longirostris* may also breed in crab-holes, which represent an extension of its normal habitat in saline pools in the mud of the mangrove swamp.

The two common species of *Armigeres*, *Ar. obturbans* and *Ar. kuchingensis*, were rarely taken in the surveys recorded in Table VI, but elsewhere in Singapore they have been found to be typical container-breeders, with a marked preference for foul waters. A newly opened coco-nut, or a newly cut bamboo stump, undergoes an initial period during which its organic contents ferment and putrefy and the contained water becomes very foul. It is during this stage that these two species of *Armigeres* often become the first colonists of the newly formed habitat, normally being replaced by *Ae. albopictus* when the water becomes clear. Both species may also be found in jars of human and animal excrement, and I have taken larvae of *Ar. obturbans* from a large shell on the sea-shore, breeding in the liquefied and putrescent remains of the former occupant. Generally they appear to be able to withstand a degree of pollution equalled only by *C. spathifurca*, which was recorded by Edwards (1926) from 'pots of pure urine.'

CATEGORY 8. SPECIALIZED CONTAINERS

Specialized container habitats, usually of plant origin, are a peculiarly interesting feature of tropical forests. So far, I have devoted very little time to them in Singapore, but certain observations have been made, as follows.

(a) *Pitcher-Plants*. 'Pitchers,' or 'monkey-cups,' are the modified leaf-tips of plants of the genus *Nepenthes*, which in their contained fluid support a very characteristic mosquito fauna. This fauna has been investigated in Singapore by Edwards and Given (1928), who record 16 species from pitchers, to which can now be added two more, *Ar. hybridus* and *Ar. conjungens*. Of these 18 species, some 10 or 11 appear to be entirely restricted to this habitat, as, for instance, the six species of *Culex*, subgenus *Lophoceratomyia*. I also have two records of *Ae. albopictus* from pitchers, but some doubt attaches to them, since the collections were made by untrained and unsupervised collectors. It should also be noted that, of all these nepenthicolous species, *Tripteroides aranoides* and *C. eminentia* are by far the commonest, particularly near the coast. On Blakang Mati Island, of 222 collections from pitchers, all but three contained *T. aranoides*, 33 contained *C. eminentia*, and other species were found in only six.

(b) *Wild Ginger Plants*. One or more species of the wild ginger plant (family Zingiberaceae), which is common in areas of secondary jungle, provide a peculiar breeding-place in the small amount of water (only some 10 c.cm.) which collects at the apex of its inflorescence. In certain areas these flowers almost always contain larvae of *Ar. hybridus* and *Ar. conjungens*, but no other. Although both species are sometimes found in pitchers, 'ginger flowers' appear to be their normal breeding-place in these areas.

(c) *Plant Axils*. Several searches in the leaf-axils of a large *Alocasia*-like aroid produced larvae of *Harpagomyia genurostris*, which were also found in the axils of nearby pineapple plants.

(d) *Fallen Leaves*. The fallen fronds of coco-nut and other palms not infrequently collect a little rain-water in their bases, and thus support larvae of such species as *Ae. albopictus* and *Ae. scutellaris*, but these habitats are better referred to category 7. A more specialized habitat is found in the dead fallen leaves of an unidentified jungle species of *Artocarpus*, which are frequently so curved as to hold a very small amount of rain-water, often only a few millimetres deep. No less than three species, all of different genera, have occupied this niche, *Zeugomyia gracilis* and *Ae. jugraensis*, first recorded by Leicester (1908), and *U. obscura*, first recorded by Edwards and Given (1928). Of these, *Z. gracilis* appears to be the most common in Singapore, and is reputed to be predacious, although I have not been able to confirm this in the laboratory. All three species appear to be entirely restricted to this habitat in the Singapore district, although in Sarawak I have taken *Z. gracilis* breeding in a shallow photographic tray inside a hut in the jungle.

This relatively simple habitat, with its restricted fauna, which includes a predator, would seem to offer an excellent field for ecological studies.

(e) *Crab-Holes*. Bates (1949) and Laird (1956) have both treated the crab-hole as a specialized saline derivative of the small container. Little attention has yet been given to this habitat in Singapore, but *Ae. longirostris* has been found in rather large and shallow crab-holes, which, however, differed but little from its normal habitat in mangrove-swamp pools. Thorough search may possibly reveal that other species, e.g., *Ae. curtipes*, occur in the more specialized crab-holes.

DISCUSSION

It is a well-established fact that all species of mosquito show at least some degree of discrimination when selecting a breeding-place, and that this choice is exerted by the ovipositing female. The evidence as regards the Anophelini has been discussed by Muirhead-Thomson (1951), who concludes that 'the association of a particular anopheline with a particular type of breeding place is mainly determined by the fact that egg laying by the female mosquito is almost completely confined to that habitat,' a conclusion which is clearly applicable to all mosquitoes. It is also clear that a basic factor determining the type of niche occupied by the larva must be its ability to compete with the various elements, organic and inorganic, which oppose it within the niches potentially available—that is to say, that the oviposition behaviour of the female will be determined to some extent by the requirements of larval biology. It has been pointed out (Colless, 1956) that, within the limits of genetic plasticity and in the absence of opposing or interfering factors, parallel adaptations will tend to accumulate in both adult and larval biology, to ensure (a) that eggs are normally laid in places suitable for larval development, and (b) that larval biology conforms to the requirements of life in the normal oviposition site.

As regards factors which may oppose or modify such tendencies, there is the fact that adult behaviour is the complex product of a host of selection pressures, of which the necessity to choose a suitable breeding-place is only one. Other requirements of adult life may force a compromise, and, for instance, it may well be that the tendency of *Ae. aegypti* in Malaya to breed mainly inside houses reflects to some extent the protection so gained by a mosquito which rarely ventures into the predator-ridden outside world.

It is difficult, however, to imagine that any selective advantage, as regards adult survival, is conferred by the habit, for instance, of breeding in rain-water only, and of ignoring an adjacent and otherwise identical site which contains an organic infusion.

Generally, it seems that the selection pressures which, through oviposition behaviour, determine the choice of breeding-place are concerned with the suitability of the habitat and act upon the larva. When one considers the relatively small number of mature larvae and pupae usually found in any given breeding-place, it seems that larval mortality must account for a large part of the wastage, from the 100 or so eggs usually laid, to the single gravid female necessary to perpetuate the species. Also relevant are such calculations as those of Davidson and Draper (1953), who estimate that during the gonotrophic cycle of *An. funestus* and *An. gambiae* mortality is of the order of only 15 per cent. From such considerations it seems probable that the pressures operating to adapt female oviposition behaviour to the requirements of larval biology are so strong as to override any opposing tendencies.

As regards the adaptation of larval biology to life in the chosen niche, this seems to be surprisingly broad, most larvae in fact appearing capable of full and free development in a much wider range of habitats than those in which they normally occur. As Muirhead-Thomson (1951) observes, 'the reactions of the female are evidently much more refined than those of the larva . . . and although we assume that in general the female selects the type of habitat which is most suitable for the larva, we are still far from certain that all of the places avoided by the female are really unsuitable for growth and development of the larvae.' This fact calls for some comment. In the first place, it must be noted that the advantages enjoyed by a larva in its usual breeding-place may not be detectable by the usual methods of investigation. Selective advantages of as little as 1 per cent. have been shown to produce quite efficient evolutionary pressures (Fisher, 1930), and from this point of view all habitats other than the usual one may, in the presence of interspecific competition, be considered unsuitable. Bates (1949) has discussed this point and has drawn attention to 'differences that would not be significant in the absence of competition.'

There is also the possibility that adaptation to a given type of habitat may become too specialized for the species to cope with fluctuations in the environment. For this reason, it will often be to a species' advantage to retain some ability to develop in a variety of habitats, as a safeguard against times when normal habitats become temporarily scarce. Assuming the necessary flexibility to be possible, such a tendency might well evolve as a normal feature of larval biology, and facultatively of oviposition behaviour. An interesting corollary of this point is that conditions of very stable environment, such as occur in tropical rain-forest, should enable much greater degrees of specialization to develop than, say, in temperate savannah, and should thus foster the subdivision of habitats amongst many species. This is presumably one of the factors responsible for the presence in tropical jungles of so many species of mosquito, many of them forming complexes of closely related forms which occupy very similar habitats.

As a final speculation, it is tempting to suggest that many mosquito species have developed a balanced system of adaptation, whereby the dangers of over-specialization in larval biology are overcome by vesting such specialization in the oviposition behaviour of the adult female, where, owing to the active nature of the mechanisms involved, it may remain at least partly facultative. Such a system would ensure that the larva retains the ability to develop in as wide a range of habitats as is necessary for the survival of the species, according to the requirements of the environment. It would also provide a highly sensitive mechanism for ensuring that, within that range, the species would normally develop in the type of habitat which provides conditions optimal for its survival.

SUMMARY

1. The breeding-places of culicine mosquitoes in Singapore are described, and are classified into eight major categories, derived from those of Laird (1956). The larval fauna typical of each category is described in detail, and an 'index of association' is presented and used to indicate successions within the hyacinth-pond habitat.

2. The evolution of adaptation to the larval habitat is discussed in general terms, particularly as regards the necessity for parallel adaptations in adult and larval biology.

ACKNOWLEDGEMENTS.—I am deeply indebted to my assistants, Mr. W. Chellapah, Enche' Rosnari bin H. Omar and Enche' Kasmin bin Jamah, who patiently performed much of the routine work on which this paper is based, and to the Deputy Assistant Director of Hygiene, Singapore Base District, for providing the stimulus and facilities for extensive surveys in military areas. The work was carried out as part requirement for the degree of Doctor of Philosophy in the University of Malaya.

REFERENCES

- BATES, M. (1949). The natural history of mosquitoes. N.Y.: Macmillan.
 BOYD, M. F. (1930). An introduction to malariology. Camb., Mass.: Harvard Univ. Press.
 COLLESS, D. H. (1956). The *Anopheles leucosphyrus* group. *Trans. R. ent. Soc. Lond.*, **108**, 37.
 DAVIDSON, G., and DRAPER, C. C. (1953). Field studies of some of the basic factors concerned in the transmission of malaria. *Trans. R. Soc. trop. Med. Hyg.*, **47**, 522.
 EDWARDS, F. W. (1926). Mosquito notes, VI. *Bull. ent. Res.*, **17**, 101.
 ——— and GIVEN, D. H. C. (1928). The early stages of some Singapore mosquitos. *Ibid.*, **18**, 337.
 FISHER, R. A. (1930). The genetical theory of natural selection. Oxford: Clarendon Press.
 HOPKINS, G. H. E. (1936). Mosquitoes of the Ethiopian region. 1: Larval bionomics of mosquitoes and taxonomy of culicine larvae. Lond.: Brit. Mus. (Nat. Hist.).
 LAIRD, M. (1956). Studies of mosquitoes and freshwater ecology in the South Pacific. *Bull. Roy. Soc. N.Z.*, no. 6.
 LEICESTER, G. F. (1908). The Culicidae of Malaya. *Stud. Inst. med. Res. F.M.S.*, **3** (3), 18.
 MUIRHEAD-THOMSON, R. C. (1951). Mosquito behaviour in relation to malaria transmission and control in the tropics. Lond.: Arnold.
 SHANNON, R. C. (1931). The environment and behavior of some Brazilian mosquitoes. *Proc. ent. Soc. Wash.*, **33**, 1.